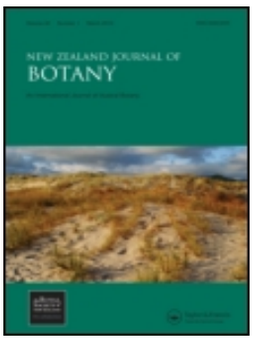

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Soil seed banks of secondary vegetation on the Port Hills and Banks Peninsula, Canterbury, New Zealand, and their role in succession

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Keywords soil seed banks; persistent buried seed; transient seed; *Cytisus scoparius*; *Ulex europaeus*; pasture; scrub; bracken; secondary forest; succession; initial floristics

Abstract Soil seed banks at 21 sites covered with poor quality pasture, bracken fernland, scrubland of broom or gorse, and various forest types, were examined by germinating seed in soil samples. At most sites the composition of upper and lower soil layers was similar. Persistent, deeply buried seed banks of *Cytisus scoparius*, *Ulex europaeus*, and more rarely *Sophora microphylla*, were discovered at seven sites, four of which lacked that particular species in the above-ground vegetation, and are thus considered to be of a former vegetation type. Forest sites tended to have more seeds and more species represented in the soil seed bank. Although an average of only 35% of the species in the seed bank were represented above ground at the sampling point, this rose to 60% within 5 m, and 72% within 10 m of that point. Those species further away were mostly widespread pasture weeds, even within forest sites, and are interpreted as being recently dispersed and transient. Large quantities of *Juncus* spp. in some sites are believed to be transported by water movement through the soil. Some species, including certain site dominants, were poorly or never represented in the soil seed bank. It is considered that the seed bank has an important role in establishing the initial floristic composition following disturbance. However, differential seedling survival, resprouting, and competition probably help in maintaining the pre-disturbance vegetation at non-forest sites. Where forest is disturbed, especially by burning, there is the potential for a completely different vegetation to develop from the seed bank.

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INTRODUCTION

Studies on soil seed banks are valuable for understanding aspects of vegetation dynamics. Early studies, including those of Darwin (see Porter 1986), concerned longevity of seeds stored in the soil (Brenchley 1918). Although records of extremely long-lived seeds are still of interest (e.g., Odum 1978) the ecological role of such seeds in vegetation dynamics is minor. Most recent work has concentrated on the soil seed bank in relation to the past, present, and future vegetation (Moore & Wein 1977; Rabinowitz 1981; Pratt et al. 1984; Williams 1984). This is of relevance to questions concerning the role of seed in determining initial floristic composition following disturbance, and the migration of seed into vegetation undergoing change (Hill & Stevens 1981; Swaine & Hall 1983; Hopkins & Graham 1984; Graham & Hutchings 1988). For instance, many studies have demonstrated that seeds of secondary species persist beneath stable vegetation (Cheke et al. 1979; Enright 1985; Granstrom 1988), and initiate succession following disturbance. Large scale migration from an adjacent source was, however, suggested by Strickler & Edgerton (1976) and Archibold (1979). The fate of the seed rain, especially in relation to seed predation has also been of interest (Mittelbach & Gross 1984; Wellington & Noble 1985).

The Port Hills and Banks Peninsula, Canterbury, contain diverse secondary scrub communities, mostly induced by fire (Williams 1983). Repeated firing has been used to maintain pasture on unploughable hill slopes where stock are too few to control scrub by grazing. Communities include native secondary forest dominated by mahoe (*Melicytus ramiflorus*)* or kanuka (*Kunzea ericoides*), adventive species including broom (*Cytisus scoparius*) and gorse (*Ulex*

europaeus), and bracken (*Pteridium esculentum*). The changing pattern of New Zealand's agricultural production and recognition of conservation values of native communities have, in recent times, created an interest in understanding the fate of these communities if they are either left alone or actively managed. This has resulted in recent publications on the ecology of various species (e.g., Williams 1981; Yin et al. 1984; Lee et al. 1986, Williams & Buxton 1986). This study was undertaken to examine the soil seed banks of various secondary communities to better understand their role in potential vegetation change, as advocated by Timmins & Williams (1987). The history of the vegetation, geology, climate, and soils of the Port Hills, much of it also applicable to Banks Peninsula, has been described by Williams (1983).

METHODS

Twenty-one sites were chosen for study which represented the four main vegetation types: grassland (3 sites), bracken fernland (6), adventive scrubland (3), and forest (9). All but seven were on the western Port Hills, the exceptions being four forest sites on Banks Peninsula, and three sites on the eastern Port Hills (Fig. 1). Characteristics of the sites are summarised in Table 1.

Soil samples were collected in either February 1984 or February 1985. As pilot studies indicated that changes in soil seed bank composition usually take place at about 2.5 cm depth, samples were, therefore, a surface layer including litter, of 2.5 cm depth, and a lower layer of a further 10 cm. The surface layer was collected from a 0.5 × 0.5 m square, and the subsurface layer from a 0.1 × 0.1 m subsquare located at the centre of the large square.

At each site, circular nested quadrats were set up at 1 m intervals up to 10 m radius to record species distance from the soil sample point. First occurrence of either rooted or overhanging plants within each was recorded.

Soil samples were spread in plastic seed trays above a layer of sand on newspaper. These trays were placed in larger metal trays containing water which was kept at below the soil surface level. All trays were placed in a glasshouse. Seedlings were counted as they emerged and removed as identified. White fly was controlled with insecticide. Only a small number of seedlings died, but most were identified. A control tray of only sand produced a few seedlings, mostly *Poa annua*. Small numbers of the native orchid *Microtis unifolia* appeared in both the control and other trays on one occasion. Although included in the results, an external origin is suspected. The experiment was spread over two seasons. Trays were left for 6–12 months, that is until germination had stopped for at least a month.

Similarities between soil seed banks were examined for both upper and lower soil layers by classification using the divisive technique of Two-way Indicator Species Analysis (Hill et al. 1975).

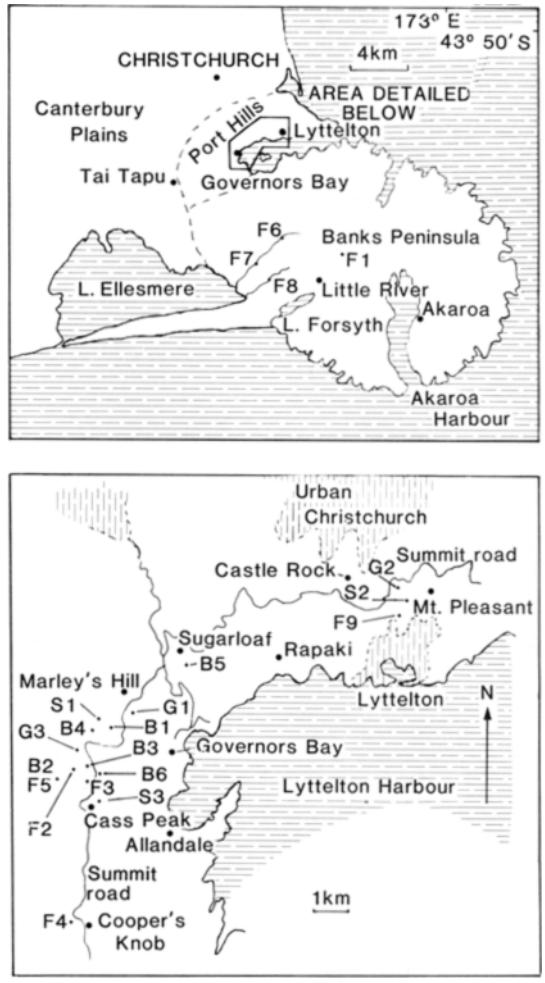

Fig. 1 Locations of the sample sites. G1–3, grassland sites; B1-6, bracken fernland; S1–3, scrubland; F1–9, forest.

*Authors of binomials used in the text can be found in the various volumes of Flora of New Zealand (see Connor & Edgar 1987; Webb et al. 1988 for references to earlier volumes and changes), except for grasses (see Hubbard 1984; Connor & Edgar 1987, unless otherwise given in the text), and ferns (see Brownsey et al. 1985).

SITE DESCRIPTIONS

Vegetation descriptions and comment on adjacent communities are made below.

Grassland sites

These all occur in poor quality pasture typical of upper slopes in the study area. Site G1 is dominated by *Anthoxanthum odoratum, Holcus lanatus, Agrostis capillaris*, and *Trifolium dubium*. A small stand of *Pteridium esculentum* is nearby. Site G2 is dense grassland of the native tussock *Poa cita*, with *Holcus lanatus, Agrostis capillaris, Dactylis glomerata, Anthoxanthum odoratum*, and *Trifolium repens* as common intertussock species. Shrubs of *Cytisus scoparius, Muehlenbeckia complexa*, and *Hymenanthera alpina* occur nearby. Site G3 is pasture dominated by *Agrostis capillaris, Anthoxanthum odoratum, Cynosurus cristatus, Dactylis glomerata*, and *Trifolium repens*. Forest immediately downslope has a 4 m canopy of *Melicytus ramiflorus, Fuchsia excorticata, Myrsine australis, Aristotelia serrata*, and *Pittosporum tenuifolium*, with *Coprosma robusta* and *C. propinqua* common around the margin.

Bracken sites

A variety of sites dominated by *Pteridium esculentum* were chosen. Site B1 is tall, dense *Pteridium* in a seepage channel with small amounts of *Agrostis stolonifera, Anthoxanthum odoratum*, and *Holcus lanatus*. Site B2 is 4 m on the *Pteridium* side of a *Pteridium/Kunzea ericoides* boundary. The *Pteridium* is tall and dense and has few associated species. The adjacent forest (site F5) is dominated by tall *Kunzea ericoides*, with *Melicytus ramiflorus, Coprosma* spp., *Fuchsia excorticata*, and the occasional tall *Sophora microphylla*. Site B3 is in a forest gap of approximately 4 m × 3 m and is occupied by *Pteridium* with a few pasture species (*Hypochaeris radicata, Anthoxanthum odoratum, Rytidosperma gracile*). The forest is dominated by *Kunzea ericoides* and *Melicytus ramiflorus* with much *Coprosma propinqua* around the edge of the gap. Site B4 is extensive, tall (1.6 m) *Pteridium*, over 40 m from any of the stand margins. Associated species are sparse, but some may have been overlooked as movement through the stand was greatly restricted. Site B5 is tall, open *Pteridium* adjacent to and downslope of *Fuchsia excorticata/ Melicytus ramiflorus* forest with some *Pittosporum tenuifolium* and *P. eugenioides*. Tree seedlings and pasture species are present in the *Pteridium*. Site B6 is open, short (0.2 m) *Pteridium* with pasture species such as *Anthoxanthum odoratum, Stipa variabilis* D.K. Hughes, *Agrostis capillaris, Lolium perenne*, and *Trifolium dubium*.

Table 1 Environmental features of the sites. G, grassland sites; B, bracken fernland; S, scrubland; F, forest.

Site	Altitude (m)	Aspect	Slope	Soil moisture
G1	425	WNW	Gentle	Dry
G2	435	E	Moderate	Dry
G3	400	SW	Moderate	Dry
B1	380	NW	Gentle	Wet
B2	275	NNE	Moderate	Dry
B3	400	WNW	Gentle	Dry
B4	370	NE	Gentle	Dry
B5	350	SE	Steep	Wet
B6	455	W	Gentle	Dry
S1	305	NE	Moderate	Dry
S2	275	S	Steep	Moist
S3	460	NE	Steep	Moist
F1	60	ENE	Moderate	Dry
F2	335	NW	Moderate	Dry
F3	430	WNW	Gentle	Dry
F4	460		Flat	Dry
F5	275	NNE	Moderate	Dry
F6	80		Flat	Wet
F7	15		Flat	Wet
F8	25		Flat	Moist
F9	170	SSE	Moderate	Dry

Scrub sites

Site S1 is a stand of tall, mature *Cytisus scoparius*, with two saplings of *Sambucus nigra* and etiolated plants of pasture species. There are also seedlings of forest species, especially *Coprosma propinqua*, which is found as isolated shrubs nearby. Site S2 is a very open, young *Cytisus* stand that has established within four years in dry pasture of *Holcus lanatus, Agrostis capillaris, Anthoxanthum odoratum, Dichelachne crinita*, and *Elymus rectisetus*. Site S3 has scattered *Ulex* up to 2 m tall, with *Pteridium* between. An adjacent rocky seepage upslope contains pasture species, specially *Rytidosperma gracile* and *Lolium perenne*, and some remnant native shrubs (*Melicytus ramiflorus, Coprosma propinqua, C. crassifolia*).

Forest sites

Site F1 is 5 m tall *Kunzea* forest surrounded by pasture and grazed beneath. Other forest species (e.g., *Melicytus, Coprosma* spp., *Parsonsia heterophylla*) occur in a 5 m wide band between the *Kunzea* and a road downslope. Site F2 is over-mature *Kunzea*, the crowns of which were dying back, with abundant *Melicytus, Fuchsia*, and *Myrsine australis* beneath, and a considerable distance from

any forest margin. Sub-canopy species include *Coprosma* spp. and *Urtica ferox*, but the herb layer has only *Hydrocotyle heteromeria* and seedlings of *Parsonsia heterophylla*. Site F3 is in planted forest of the coastal Wellington form of *Olearia paniculata*. Little grows beneath the canopy, but the site is within 20 m of both *Kunzea/Melicytus* forest and pasture. Site F4 is *Melicytus/Fuchsia* forest with scattered emergent *Podocarpus hallii* and only a little *Kunzea*. The understorey is diverse and dense, including *Coprosma* spp., *Melicope simplex*, *Pennantia corymbosa*, and *Lophomyrtus obcordata*. but there is little in the herb layer. Site F5 is associated with site B2, being 4 m on the forest side of a *Pteridium/Kunzea* boundary. The forest is dominated by tall *Kunzea*, with *Melicytus*, *Coprosma* spp., and *Fuchsia*, and with the occasional tall *Sophora microphylla*. The sub-canopy layer is diverse, and *Microlaena avenacea* dominates the herb layer. Site F6 is adjacent to a stream in mixed *Melicytus/Kunzea* forest with *Agrostis capillaris* pasture nearby. The vegetation of the area is a mosaic of forest remnants, scrub, *Pteridium*, and poor quality pasture: the result of unsuccessful attempts at clearing. Although highly modified and in an area popular with visitors, site F7 is in one of the few forests that has not been clear-felled since European arrival. Between the emergent trees of *Podocarpus totara* and occasional *Dacrycarpus dacrydioides* is a canopy of *Melicytus*, *Pittosporum* spp., *Plagianthus regius*, *Alectryon excelsus*, *Griselinia littoralis*, and many other species. *Muehlenbeckia australis* is a common climber. The forest strata are all diverse, the site being on fertile, moist, alluvial soils. Site F8 is also an unlogged forest remnant with an emergent layer of *Dacrycarpus dacrydioides* and *Prumnopitys taxifolia* above a canopy of *Alectryon excelsus*, *Melicytus*, *Sophora microphylla*, *Plagianthus regius*, and *Griselinia littoralis* on an alluvial valley floor. There is a diverse and dense subcanopy, but the herb layer is poor, probably because of grazing by stock. There are other tree species on adjacent slopes, including *Podocarpus totara*, *Fuchsia*, and some *Kunzea*. Site F9 is tall lowland/coastal forest of *Sophora microphylla* and *Plagianthus regius* as emergents above a small tree canopy of *Myoporum laetum* and scattered *Fuchsia*, *Melicytus*, and *Myrsine australis*. Sub-canopy species include *Coprosma* spp., *Melicope simplex*, *Pennantia corymbosa*, and *Teucridium parvifolium*. *Urtica ferox* is an occasional small

Table 2 Summary of soil seed bank characteristics of the sites. Site abbreviations given in Table 1.

Site	Seeds m^{-2}	Number of species represented	Percentage of seeds in upper layer	Abundant deeply buried species
G1	450	12	44	
G2	400	14	50	
G3	695	19	46	
B1	3789	11	20	*Juncus*
B2	2154	14	14	*Ulex*
B3	1556	19	16	*Ulex*
B4	74	6	32	
B5	1142	21	43	
B6	737	13	56	
S1	1580	15	30	*Cytisus*
S2	447	10	38	
S3	1173	14	30	*Ulex*
F1	507	7	46	
F2	1554	14	13	*Cytisus*
F3	5	3	100	
F4	1207	17	61	
F5	1950	18	31	*Ulex*
F6	1854	25	70	
F7	1128	26	56	
F8	1058	20	48	
F9	811	15	29	*Sophora*

shrub, but there is little in the ground layer as the site is grazed by sheep. Climbers, especially *Muehlenbeckia australis* and *Rubus squarrosus* are abundant.

RESULTS

The soil seed banks of sites on the Port Hills and Banks Peninsula showed a considerable range of seed and species densities (Table 2). Most noticeable was the presence in eight sites of deeply buried seed banks representing only four species.

Grassland sites

In general, the soil seed bank of grassland sites was very similar to the vegetation already present. Of the main species of the existing flora at site G1, only *Agrostis capillaris* and *Rytidosperma gracile* were not represented in the seed bank, and there were no seeds of species more than 3 m away (Table 3). Apart from some *Anthoxanthum odoratum* there were few deeply buried seeds. The dominant *Poa cita* at site G2 was also under-represented in the soil seed bank, especially when compared to the plentiful seed of the associated species. None of the three shrub species nearby was represented in the seed bank. The grassland species in the soil seed bank at site G3 closely matched those already present. Of the adjacent forest species, only four (*Melicytus ramiflorus, Fuchsia excorticata, Aristotelia serrata, Coprosma robusta*), all within 6 m of the sample point, were represented in the soil seed bank.

Bracken sites

The bracken dominated sites had some of the largest seed numbers per square metre, the result of large, deeply buried seed banks at half the sites (Table 4). Otherwise, the seed banks were dominated by associated species present at the sites.

Of the three species associated with bracken at site B1, *Agrostis stolonifera* and *Anthoxanthum odoratum* were well represented in the soil seed bank. Although some of the *Agrostis* may have grown from stolon fragments, this does not explain the large numbers in the lower layer. The large numbers of *Juncus effusus* seeds in both layers represented a species not found close to the site, but which was abundant in the same seepage channel as the site, but 200 m uphill.

Despite there being no sign of *Ulex europaeus* for some considerable distance from site B2, there was a large, deeply buried seed bank of this species, some 6500 m^{-2}. There were, however, few *Ulex* seeds in the upper layer. The species of the adjacent forest, especially *Kunzea ericoides, Fuchsia excorticata* and the forest margin species *Coprosma robusta*, were in the seed bank, as were the species associated with the *Pteridium* (*Holcus lanatus, Anthoxanthum odoratum, Dactylis glomerata*). At

Table 3 Seed banks and distance from sample site of the grassland sites. The first two numbers separated by a colon are the numbers of seeds per sample in the upper and lower layers, respectively. A dash indicates no seeds. The third number, following the slash is the nearest distance (m) to the sample site that the species first occurs. A dash indicates that it is not within 10 m.

Species	Site G1	G2	G3
Agrostis capillaris	–:–/1	4:–/1	5:–/1
A. stolonifera	2:–/1	1:–/2	–:–/1
Aira caryophyllea	–:–/6		
Anthoxanthum odoratum	17:4/1	7:1/1	19:2/1
Aristotelia serrata			2:–/3
Cardamine sp.			1:–/–
Cerastium fontanum	5:–/1	1:–/2	4:1/1
Cirsium vulgare	1:–/3		4:1/1
Coprosma propinqua			–:–/10
C. robusta			1:–/6
Crepis capillaris	1:1/1	2:2/1	5:1/1
Cynosurus cristatus		3:–/1	4:1/1
Cytisus scoparius		–:–/5	2:–/4
Dactylis glomerata	–:–/3	8:1/1	10:2/1
Dichelachne crinita	–:–/4	–:–/4	
Digitalis purpurea		3:–/2	
Elymus rectisetus	–:–/6	–:–/1	
Fuchsia excorticata			4:1/4
Holcus lanatus	11:1/1	10:2/1	
Hymenanthera alpina		–:–/8	
Hypochaeris radicata	1:–/2	–:–/2	4:–/1
Juncus articulatus		1:–/–	
J. effusus	1:1/6		3:5/3
Lolium perenne		2:–/1	1:–/2
Melicytus ramiflorus			6:–/3
Microlaena avenacea			–:–/10
Muehlenbeckia complexa		–:–/7	
Mycelis muralis			–:–/8
Myrsine australis			–:–/5
Olearia paniculata			–:–/10
Pittosporum tenuifolium			–:–/7
Poa annua	4:1/2		
P. cita		2:–/1	
P. pratensis	–:–/7		
Pteridium esculentum	/9		/8
Rytidosperma gracile	–:–/1		–:–/2
Sambucus nigra			–:–/9
Stellaria media			1:–/–
Stipa variabilis	2:–/1		
Trifolium dubium	3:2/1	–:–/2	–:–/1
T. repens	1:–/1	5:1/1	3:1/1
Vicia sativa		1:1/1	1:–/1

Table 4 Seed banks and distance from sample sites of the bracken sites. See caption to Table 3 for details.

Species	Site B1	B2	B3	B4	B5	B6
Agrostis capillaris					2:–/6	5:1/1
A. stolonifera	30:28/1				14:2/1	
Anthoxanthum odoratum	24:3/1	11:2/1	8:–/1	–:–/3	4:1/2	36:4/1
Aristotelia serrata			–:–/4			
Centella uniflora						–:–/5
Cerastium fontanum			1:–/–			
Cirsium vulgare	2:1/–			–:1/6		
Coprosma linariifolia		–:–/10				
C. propinqua		1:–/8	5:1/2		–:–/2	
C. rhamnoides		–:–/6	–:–/3		–:–/4	
C. robusta		11:–/5	1:–/2			
C. rotundifolia		–:–/8			–:–/5	
Cordyline australis					4:1/4	
Crepis capillaris	–:–/4	2:–/1		1:–/–	1:–/2	3:–/1
Cynosurus cristatus					8:1/1	
Cytisus scoparius	1:–/9				7:4/2	–:–/9
Dactylis glomerata	–:–/2	4:1/1	1:–/–	1:1/4	2:1/2	1:–/3
Dichelachne crinita			–:–/1			–:–/4
Digitalis purpurea	1:–/7		2:–/–		2:–/3	
Elymus rectisetus						2:–/2
Fuchsia excorticata		7:2/7			23:8/1	
Holcus lanatus	4:1/1	6:–/1	3:–/–		8:–/1	1:–/4
Hydrocotyle heteromeria		–:–/8	–:–/6			
Hypochaeris radicata			–:–/1	1:–/–		–:–/2
Juncus articulatus					1:–/–	
J. effusus	115:88/–					
J. gregiflorus					–:–/10	
Kunzea ericoides		15:3/4	17:2/3			
Lolium perenne	–:–/4	–:–/3				4:1/1
Melicope simplex			–:–/10		2:–/7	
Melicytus ramiflorus		4:–/5	11:4/4		16:2/2	
Microlaena avenacea		–:–/9				
Microtis unifolia			1:–/2			
Muehlenbeckia complexa						–:–/10
Mycelis muralis			2:–/1		–:–/4	
Myrsine australis			–:–/8			
Oxalis exilis	1:–/7					1:–/3
Parsonsia heterophylla			–:–/8		–:–/8	
Pennantia corymbosa			–:–/7		–:–/8	
Phormium tenax					–:–/5	
Pittosporum eugenioides					1:–/4	
P. tenuifolium			1:–/5		3:–/5	
Poa annua	6:–/4		1:–/–		1:–/–	
P. cita						–:–/6
P. imbecilla		–:–/10				
Polystichum vestitum					/4	
Pseudopanax colensoi		–:–/7				
Pteridium esculentum	/1	/1	/1	/1	/1	/1
Ribes sanguineum		1:–/–				
Rubus fruticosus		1:–/–			3:–/7	–:–/5
Rytidosperma gracile			–:–/1	1:–/–		4:–/1
Sambucus nigra		–:–/8				
Senecio minimus	1:–/3		1:–/–			
Solanum nigrum	–:–/6		1:–/–			
Sonchus oleraceus		–:–/4				
Sophora microphylla		–:–/7				
Stipa variabilis				–:–/8		9:1/1
Trifolium dubium			2:–/1			11:1/1
T. repens	–:–/3					6:2/1
Ulex europaeus		4:65/–	2:44/–		1:–/–	
Urtica ferox		1:–/6			9:1/2	
Verbascum thapsus			1:–/–			
Vicia sativa	6:–/2	8:1/1	3:1/–	2:–/1	11:5/1	20:3/1

site B3 there was also a deeply buried seed bank of *Ulex europaeus*, with little in the upper layer. The surface layer seed consisted of adjacent forest species and a number of herbaceous weeds, many of which were not present on the site. At site B4, there was very little seed, mostly of species adjacent or of species with wind dispersed seed (e.g., *Crepis capillaris, Hypochaeris radicata*).

Table 5 Seed banks and distance from sample sites of the scrub sites.See caption to Table 3 for details.

Species	Site S1	S2	S3
Agrostis capillaris		7:3/1	
A. stolonifera	11:1/1		
Aira caryophyllea		1:–/2	
Anthoxanthum odoratum	18:4/1	6:1/1	2:–/3
Cerastium fontanum		–:–/4	
Cirsium vulgare	–:–/7		
Coprosma crassifolia		–:–/7	–:–/6
C. propinqua	–:–/5		–:–/6
C. robusta	–:–/9		
Crepis capillaris		1:4/1	–:–/4
Cynosurus cristatus	7:2/1	–:–/5	
Cytisus scoparius	39:28/1	7:–/1	
Dactylis glomerata	3:–/3		8:2/1
Dichelachne crinita		1:–/2	–:–/5
Digitalis purpurea	16:3/1	4:1/1	4:4/1
Elymus rectisetus		–:–/4	
Fuchsia excorticata			4:–/–
Holcus lanatus	5:–/1	14:2/1	9:4/1
Hydrocotyle heteromeria	–:–/3		
Hypochaeris radicata	–:–/3	–:–/1	2:–/2
Juncus articulatus	1:–/–		
J. effusus	8:5/–		2:–/–
Leycesteria formosa	1:–/–		
Lolium perenne	2:–/1		17:4/1
Melicytus ramiflorus	–:–/8		3:–/6
Microtis unifolia		1:–/–	
Muehlenbeckia australis	–:–/10		
Poa annua			2:–/–
P. cita		–:–/8	
Polystichum vestitum		/10	/1
Pteridium esculentum	/4		/1
Rubus fruticosus	–:–/7		
Rumex crispus	1:–/2		
Sambucus nigra	2:–/3		1:–/–
Sedum acre			–:–/8
Solanum laciniatum	1:–/–		
S. nigrum	5:1/2		
Stellaria media	–:–/5		
Stipa variabilis		–:–/6	–:–/6
Taraxacum officinale			–:–/8
Trifolium dubium	–:–/5	2:–/1	1:–/3
T. repens	–:–/1	–:–/5	
Ulex europaeus			31:19/1
Urtica ferox		–:–/5	
Vicia sativa			–:–/3
Wahlenbergia albomargina			1:–/5

The large number of species in the seed bank at site B5 reflected the diversity of vegetation surrounding the site with elements of both forest and grassland well represented. There was however a paucity of forest understorey species in the seed bank, (e.g., *Coprosma*). At site B6 the seed bank reflected the on-site vegetation. Most seeds were in the upper soil layer, with *Anthoxanthum odoratum* and *Vicia sativa* the most common.

Scrub sites

The scrub site seed banks consisted of both the dominant scrub species found in both soil layers, and various herbaceous pasture plants, most of which were present at the site (Table 5). At site S1, many of the species not represented in the seed bank were present only as seedlings (e.g., *Coprosma propinqua, Melicytus ramiflorus*), while others growing beneath the *Cytisus scoparius* canopy were etiolated and probably not producing seed (e.g., *Trifolium repens*). *Cytisus* was represented by seeds in both the surface and buried layers. The two *Sambucus nigra* seeds must have come from elsewhere, as the plants on the site were immature. The *Agrostis stolonifera* may have been from stolon fragments.

Cytisus scoparius had contributed little to the seed bank in its short time at site S2, but as the plants age, they can be expected to contribute more seed. Otherwise, the rather depauperate seed bank reflected the present pasture vegetation. *Ulex europaeus* seeds were plentiful in both layers at site S3. Of the nearby woody species only *Melicytus ramiflorus* was found in the seed bank, but there were four seeds of *Fuchsia excorticata* and one of *Sambucus nigra*, two species found more than 15 m away.

Forest sites

The forest sites displayed a great deal of variability and included some with deeply buried seed banks (Table 6). At certain sites the soil seed bank highly resembled the site vegetation, while at others there was little similarity or none at all.

The *Agrostis stolonifera* at site F1 was probably mostly from stolon fragments. The seed bank was therefore almost entirely *Kunzea ericoides* and is very depauperate, like the site itself. Only a few pasture (e.g., *Lolium perenne, Anthoxanthum odoratum*) and forest (e.g., *Melicytus ramiflorus*) species contributed to the site. At site F2, there was a large number of seeds of *Cytisus scoparius*, all in the lower layer, but this species was absent from the sample site and surrounding area. Even though the site was some considerable distance from the nearest

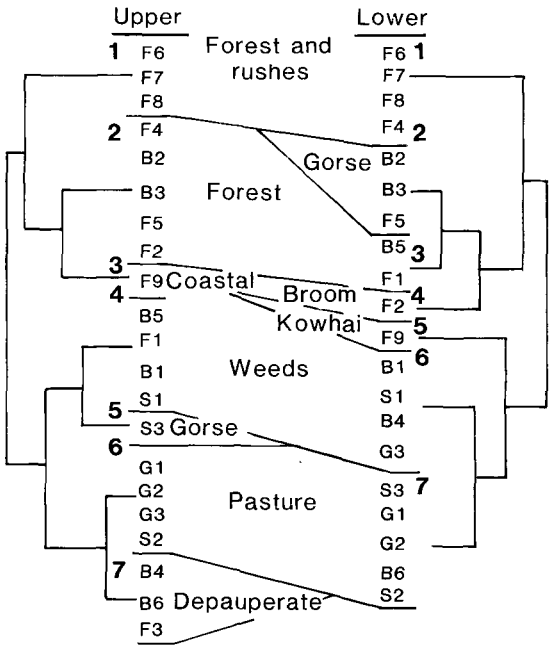

Fig. 2 Soil seed bank classification dendrograms and their ecological interpretation.

source of weed species of open areas, some of these were present (e.g., *Holcus lanatus, Vicia sativa*). Also present as seeds only were some woody weeds with fleshy fruits (e.g., *Crataegus monogyna, Ribes sanguineum*).

Despite the proximity of other vegetation types, there was little seed at site F3. Furthermore, the species at or adjacent to the site were not represented at all, thus the seed bank had nothing in common with the surrounding vegetation. At site F4 there were many seeds of the dominants *Melicytus ramiflorus* and *Fuchsia excorticata* and also of *Aristotelia serrata*, an important species in a large light gap near the sample site. There were small numbers of seeds of weed species of open areas, even though the nearest open areas are over 10 m away.

The dominant forest species at site F5 are well represented in the seed bank, and there is, like the adjacent site B2, a buried seed bank of *Ulex europaeus*, although the number of *Ulex* seeds is only about half that at B2 (Table 4). *Hydrocotyle heteromeria* has almost certainly come from stolon fragments. Only a small number of weed seeds from the adjacent *Pteridium* stand have dispersed into the forest. At site F6, the large number of seeds of *Juncus* spp. probably originated upstream and was deposited by flood waters sweeping over the site. This may apply to some of the other weeds as well (e.g., *Solanum nigrum*). The *Hydrocotyle heteromeria* was almost certainly from stolon fragments. The large number of species represented reflects the diversity of adjacent vegetation types.

A number of herbaceous weedy species from adjacent open areas were found in the seed bank at site F7, and of these *Digitalis purpurea* had high numbers. There was a large number of species represented, with relatively plentiful amounts of the dominants *Melicytus ramiflorus, Griselinia littoralis, Coprosma robusta, Alectryon excelsus*, and *Muehlenbeckia australis*. At site F8, seed numbers were not large, but there was a wide variety of species. Seeds of *Juncus* spp. probably arrived at the site during times of flooding of the small stream nearby. Other weeds were only a minor component, *Digitalis purpurea* being the most common. At site F9, seeds of *Sophora microphylla* were plentiful in the lower layer, and there was a smaller quantity in the surface layer. Many of the smaller forest trees were not represented in the seed bank, but there was a small number of seeds of weeds of the adjacent pasture, more than 10 m away.

Classification

The Two-way Indicator Species Analysis (TWINSPAN) classifications for both upper and lower soil layers are summarised in Fig. 2. The physiognomic groupings of sites by the existing site dominants was only partly reflected in the seed bank classification. The upper and lower layer classifications are rather similar. Four well-defined groups of seed banks are common to both, being two of forest species, with and without rushes, and two of herbaceous species, with either weeds or pasture species. Within the upper layer classification, finer division separates other seed banks dominated by coastal forest species, or gorse, or those which were depauperate. The lower layer classification divisions separate out the accumulated seed banks of either gorse, broom, or kowhai.

DISCUSSION

The soil seed banks examined here are made up of three parts: seed that can be attributed to the species on the sample site or immediately adjacent, seed that originates some distance away, and buried persistent seed. The latter may be related to either of the first two by origin.

Table 6 Seed banks and distance from sample sites of the forest sites. See caption to Table 3 for details.

Species	Site F1	F2	F3	F4	F5	F6	F7	F8	F9
Acaena sp.						3:–/5			
Acer pseudoplatanus							–:–/10		
Agrostis stolonifera	28:7/1							–:–/4	
Alectryon excelsus							7:–/1	9:1/1	
Anthoxanthum odoratum	7:–/7				–:–/8	–:–/8			2:–/–
Aristotelia serrata				33:1/1			2:–/8		
Asplenium bulbiferum							/1		
Astelia fragrans				–:–/2					
Blechnum fluviatile								/2	
Bromus diandrus									1:–/–
Cardamine sp.						2:–/5	2:–:–		
Carex sp.						2:–/–		–:–/4	
Centella uniflora	–:–/10								
Cerastium fontanum									2:–/–
C. holosteoides						1:–/9	1:–/–		
Cirsium arvense				1:–/–			2:–/–		
C. vulgare				2:–/–					1:1/–
Clematis vitalba							1:–/5		
Coprosma areolata					–:–/3	–:–/7	–:–/2	–:–/7	–:–/3
C. crassifolia	–:–/10			–:–/1					
C. linariifolia	–:–/9					–:–/1			–:–/9
C. propinqua		–:–/6	–:–/4	–:–/4	3:–/1	5:–/3	9:–/6	9:1/1	8:2/1
C. rhamnoides				–:–/1	–:–/1	1:–/1		2:–/1	
C. robusta	–:–/9	4:–/2		1:–/6	16:2/1	8:–/1	23:5/1		
C. rotundifolia		–:–/3					–:–/8	–:–/2	
C. virescens							–:–/9	–:–/2	
Crataegus monogyna		1:–/–		5:–/3			1:–/–		
Crepis capillaris					2:–/6		3:–/–		
Cynosurus cristatus	–:–/8								
Cytisus scoparius		–:49/–				2:–/–			
Dacrycarpus dacrydioides							–:–/9	5:–/1	
Dactylis glomerata	1:–/5				–:–/5				2:–/9
Digitalis purpurea	–:–/8					11:–/7	13:–/5	7:1/5	14:3/1
Elaeocarpus hookerianus								4:–/5	
Epilobium sp.		1:–/–		3:1/2					
Festuca arundinacea						–:–/6			
Fuchsia excorticata		10:3/1		74:11/1	27:5/1	18:2/2	11:4/4	11:2/7	2:–/5
Griselinia littoralis							9:1/3	4:–/4	
Holcus lanatus		1:–/–	1:–/–		–:–/7	–:–/7	1:–/–	–:–4	
Hydrocotyle heteromeria		1:–/2			38:2/1	40:4/1			
Hypochaeris radicata			1:–/–			2:–/10		1:1/–	
Juncus articulatus						44:16/–		19:2/4	
J. bufonius						27:5/8			
J. effusus				3:–/–	1:–/–	84:27/–	7:–/–	15:5/–	
J. gregiflorus						9:1/–			
Kunzea ericoides	17:4/1	19:–/1		1:–/8	36:7/1	9:3/1		1:–/–	
Leycesteria formosa		2:–/–		1:–/–	1:–/–	4:–/8			
Lolium perenne	2:–/8				–:–/5				3:–/–
Lophomyrtus obcordata				–:–/8					–:–/2
Melicope simplex				–:–/4		–:–/1	–:–/1	–:–/1	–:–/1
Melicytus ramiflorus	1:–/6	9:–/1		46:5/1	10:2/1	26:2/1	35:9/1	28:9/1	–:–/9
Microlaena avenacea				–:–/2	–:–/1		–:–/1	–:–/1	
Mimulus moschatus								2:–/4	
Muehlenbeckia australis							7:–/2		–:–/6
Mycelis muralis					–:–/4		3:–/6		

(*continued*)

Table 6 (*continued*)

Species	Site F1	F2	F3	F4	F5	F6	F7	F8	F9
Myoporum laetum									2:–/1
Myrsine australis		–:–/1	–:–/7		1:–3		2:–/4		1:–/3
M. divaricata				–:–/8					–:–/6
Neomyrtus pedunculata								1:–/3	
Olearia paniculata			–:–/1						
Paratrophis microphylla					–:–/5				
Parsonsia heterophylla	–:–/7	–:–/1		–:–/8	–:–/4		3:1/1	–:–/8	
Pennantia corymbosa				–:–/7					–:–/1
Phymatosorus diversifolius					/6				
Pittosporum eugenioides			–:–/9	–:–/10			–:–/1		
P. tenuifolium		–:–/10		–:–/5		–:–/2	4:–/3		
Plagianthus regius							–:–/5		9:1/1
Poa annua								1:–/–	
P. imbecilla					–:–2				–:–/1
P. pratensis	–:–/7				2:–/–	–:–/9			
Podocarpus hallii				–:–/5	1:–/9				
P. totara							3:–/4	1:–/10	
Polystichum richardii									/3
P. vestitum					/9		/1	/1	
Prumnopitys taxifolia								3:–/4	
Pseudognaphalium luteoalbum					1:–/–				
Pseudopanax colensoi					2:–/4	–:–/4			
Pteridium esculentum					/4	/8			
Ribes sanguineum		1:–/–		5:–/9					
Rubus fruticosus					1:–/9	4:–/8			
R. squarrosus		–:–/8							–:–/1
Rumex obtusifolius						1:–/10	1:–/–		
Sagina procumbens							1:–/–		
Sambucus nigra				2:1/6	1:–/4				1:–/10
Senecio biserratus				1:–/–					
S. jacobaea	2:–/4								
Solanum laciniatum						5:–/10	2:–/–		
S. nigrum				3:–/–		14:2/–	4:–/–	2:–/4	
Sophora microphylla					2:–/1			2:–/3	7:15/1
S. tetraptera (planted)				–:–/10					
Stellaria media		–:2/–							
Taraxacum officinale		1:–/–							
Teucridium parvifolium								–:–/4	
Ulex europaeus				1:–/5	1:35/–	1:–/–			4:1/3
Urtica ferox		–:–/8			5:1/2				
Vicia sativa		1:–/–	3:–/–		1:–/9				
Vinca major						–:–/7			

Buried persistent seed featured at seven sites, but included only *Ulex europaeus*, *Cytisus scoparius*, and *Sophora microphylla*. The large numbers of buried seeds of *Juncus* spp. were interpreted as having originated outside the site and are discussed later. At three of the sites, the species which contributed the buried seed was present in the vegetation as well, and seed of that species also occurred in the surface layer. Two of the three scrub sites fell into this category, but at the third site the *Cytisus scoparius* was young, and had contributed to only the surface layer. The only non-scrub species to contribute buried seed was *Sophora microphylla*, and then only at the site where it was a major component. The remaining four sites, two in bracken and two in forest, did not have the species of the persistent deeply buried seed bank growing at the site. As it is difficult to envisage such considerable numbers of large, heavy, non-fleshy seed being brought to the sites recently, it must be concluded that they represent former vegetation on the sites themselves.

The seeds of the species of the persistent, deeply buried seed banks all have thick, hard seed coats. Both *Ulex europaeus* and *Cytisus scoparius* are species that establish well from seed following fires. The seed survives the fire, and germination is probably promoted by fire. Such species are therefore prime candidates for long term survival as part of the seed bank.

There are two opposing views regarding the origins of seed in the soil seed bank. Livingston & Allessio (1968), Odum (1978), Thompson & Grime (1979), and many others have considered that most seed not contributed by the species presently on sample sites must originate from previous vegetation at the site. The view that species in the seed bank that are absent from the site vegetation are transient and dispersed to the site is less often expressed (Strickler & Edgerton 1976; Keeley 1977; Archibold 1979; Granstrom 1982). In this study, most of the seeds of species not at the site were interpreted as being dispersed to the site. The distribution of species with soil depth differs greatly between those considered part of the permanent seed bank (*Ulex europaeus*, *Cytisus scoparius*), and the others. In some studies, this kind of distribution is not detectable as there has been no separation of soil layers (e.g., Olmsted & Curtis 1947; Wesson & Wareing 1967; Thompson & Grime 1979). In this study, the persistent seed banks were deeply buried, extremely high in seed density, and were, unless the contributing species was still present at the site, absent from the upper layers. The other transient weedy species that contributed only small numbers of seed to the surface layers were clearly different. In the few cases where there were more seeds deeply buried than in the surface layer (e.g., *Stellaria media* at site F2, *Crepis capillaris* at site S2), the numbers were small and probably not ecologically significant.

Also important in this regard is the question of how distant contributing species were from the site. Table 7 shows that on average only 35% of the number of species in the seed bank grew on the site. This number would be greater, however, if weighted by seed number and site abundance. Within a distance of 5 m, the percentage increased to 60%, and by 10 m to 72%. This left an average of 28% not represented

Table 7 Percentage of the number of species found within the seed bank that are found at the site, and within 5 m and 10 m, as well as the percentage absent within 10 m.

	Percentage of species in the seed bank			
Site	At site	Within 5 m	Within 10 m	Not found
G1	67	92	100	0
G2	71	93	93	7
G3	53	84	89	11
B1	27	55	82	18
B2	36	57	79	21
B3	16	47	47	53
B4	17	33	50	50
B5	24	71	86	14
B6	69	100	100	0
S1	47	73	73	27
S2	70	90	90	10
S3	36	64	71	29
F1	29	57	100	0
F2	21	36	36	64
F3	0	0	0	100
F4	18	35	59	41
F5	39	61	78	22
F6	20	36	72	28
F7	15	46	58	42
F8	25	70	80	20
F9	33	53	67	33
Mean	35	60	72	28

Table 8 Percentage of species at the site and within 5 m and 10 m, not contributing to the seed bank.

	Percentage not contributing		
Site	At site	Within 5 m	Within 10 m
G1	20	27	37
G2	9	28	35
G3	17	20	37
B1	0	40	36
B2	0	20	50
B3	50	36	53
B4	0	33	40
B5	0	25	31
B6	0	24	35
S1	13	35	50
S2	13	40	50
S3	0	25	44
F1	0	0	53
F2	40	38	58
F3	100	100	100
F4	40	57	58
F5	22	45	44
F6	29	31	36
F7	43	29	38
F8	29	36	39
F9	44	43	50
Mean	22	35	46

near the site at all. As with other studies, comparing the on-site species with the seed bank results in a poor association between the two (Chippendale & Milton 1934; Pratt et al. 1984; Schneider & Sharitz 1986). Most studies, however, fail to define what is meant by "on-site" and even fewer take into account the possibility of short-distance dispersal. Morin & Payette (1988) and Enright & Cameron (1988) found that many of the buried seed species not at the site were at least close by. Certainly, there is no proof that seeds had originated from these nearby plants, nor indeed that those with plants growing above originated from them, but the data presented here do indicate that this is the simplest interpretation. The observation that so many of the missing on-site species were found but a short distance away, is very strong evidence for an origin from those plants.

If these dispersed seeds in the upper layers were transient, then there must be both continual addition and loss (Keeley 1977), including predation (Kjellson 1985; Wellington & Noble 1985), germination followed by unsuccessful establishment, and loss of viability with time (Schafer & Chilcote 1970; Weiss 1984). At some study sites unsuccessful establishment following germination has been observed in bracken stands adjacent to forest, where seedlings of forest species have been seen to survive during winter, but die the following summer. It is also probable that many light-demanding species fail to establish under a forest canopy.

A number of species at the sites did not contribute to the seed bank (Table 8). This number was low in the grassland, bracken, and scrub sites, but tended to be much greater in the forest vegetation. The percentages generally increased with distance from the site, but at 10 m, the differences between vegetation types were not apparent. Some of these absences could be attributed to the presence of only immature plants recently established at the site (e.g., *Parsonsia heterophylla*). Others may have been of short-lived seeds missed at the sampling time. Table 9 shows that within forest at least some species consistently contribute to the seed bank (e.g., *Kunzea ericoides*, *Melicytus ramiflorus*), even when some distance away (e.g., *Fuchsia excorticata*). Others contribute well when on the site, but not at increasing distance (e.g., *Coprosma propinqua*). Some, however, never contributed, the best example being *Melicope simplex* although it did germinate at site B5 in bracken. Seed of this species was collected from plants at site F8,

Table 9 Representation of common forest species at site and within 5 m and 10 m of the site in the seed banks of the forest sites. The + indicates the number of occurrences of the species in the seed banks, the – indicates the number of times it is absent. Seed from species greater than 10 m away is listed in the final column. The species are ordered by decreasing frequency.

Species	Occurrence within						
	0–1 m		0–5 m		0–10 m		> 10 m
	+	–	+	–	+	–	
Coprosma propinqua	3		4	2	5	3	
Melicytus ramiflorus	6		6		7	1	
Fuchsia excorticata	3		6		7		
Coprosma robusta	3		4		5	1	
Kunzea ericoides	4		4		5		1
Parsonsia heterophylla	1	1	1	2	1	5	
Coprosma areolata				3		5	
Melicope simplex		4		5		5	
Myrsine australis		1	3	1	3	2	
Urtica ferox			3		3	1	1
Pittosporum tenuifolium			1	2	1	3	
Leycesteria formosa					1		3
Coprosma rhamnoides	2	2	2	2	2	2	
Coprosma linariifolia		1		1		3	
Pittosporum eugenioides		1		1		3	
Coprosma rotundifolia				2		3	
Sambucus nigra			1		3		
Sophora microphylla	2		3		3		
Crataegus monogyna			1		1		2

but did not germinate in the laboratory. Three species with fleshy fruits attractive to birds, *Sambucus nigra*, (Williams 1983), *Leycesteria formosa*, and *Crataegus monogyna* dispersed to the sites from at least 10 m distant.

Site F3 in the planted *Olearia paniculata* had a particularly depauperate seed bank with none of the seed bank species being found within 10 m. The vegetation was almost a monoculture, and seedlings of any species were rare. The trees of *Olearia paniculata* flower, but it is not known whether they fruit or set good seed. Seedlings have never been observed at the site in 5 yrs. The hard, leathery leaves form a thick, dry litter layer which may inhibit establishment.

Large numbers of *Juncus* seeds, especially *J. effusus*, were in both soil layers at two sites, while at others there are smaller amounts, yet no rushes occurred at or near the sites. *Juncus* was an important constituent of wet seepage areas upstream of both the major sites, and it seems that their seeds were washed down by moving water. A similar soil distribution pattern for various *Juncus* species was described by Williams (1984), and for *J. effusus* by McGraw (1987).

One of the areas of interest regarding seed banks is the role they play in succession. Some authors suggest that the poor match between the seed bank and above ground vegetation results in a different vegetation establishing after disturbance (Brown & Oosterhuis 1981; Williams 1984; Morgan & Neuenschwander 1988), whereas others have expressed it as a potential alteration of the initial floristic composition (Swaine & Hall 1983; Hopkins & Graham 1984). From the non-forest sites, there was no indication from this or other studies that late-successional species persist for long periods to re-establish forest from the seed bank. This means that the seed bank plays no role in preserving such species through disturbances. Within the forest sites, however, ruderal and early-successional species were well represented, and can establish early stages of succession.

In this study area, it is expected that there will be both germination from the seed bank and resprouting following a disturbance. New Zealand's only known serotinous species, *Leptospermum scoparium* (Burrell 1965; Grant 1967) is absent from the study area but common in other parts of New Zealand. In grassland, bracken, and gorse communities many of the species will re-sprout, and in gorse and broom communities, the hard seeds of these species should survive and germinate to re-establish vegetation similar to that already present. Within forest, much will depend on survival of seed. Fire, the most used land-clearing practice in New Zealand, probably eliminates many seeds if the litter layer is burnt. Such a technique favours weedy species that are dispersed to the area, or agricultural species sown on to the site. With less destructive disturbance, an initial floristic composition of both weeds and forest species will be established, and unless conditions are unfavourable for growth of forest seedlings, they should compete successfully against the weeds and establish new forest vegetation. This process is frequently observed in forest gaps. However, many forest understorey species are poorly represented in the seed bank, and may be adversely affected by even slight disturbances. Those sites with deeply buried seed banks of gorse and broom may re-establish that former vegetation on a site, especially if the damage is particularly destructive. Forest species would then have to re-invade the site and compete against already established plants.

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