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Effect of *Coriaria arborea* on seed banks during primary succession on Mt Tarawera, New Zealand

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Abstract An experiment was conducted over two years to investigate the effect of *Coriaria arborea*, a native nitrogen-fixing shrub, on soil seed banks at sites representing a post-volcanic successional sequence on Mt Tarawera, New Zealand. The sites ranged from bare volcanic ash and lapilli substrate, through low-growing pre-*Coriaria* vegetation, to dense stands of *Coriaria* scrub. Soils (to a depth of 50 mm) under recently established *Coriaria* and older stands had more seedlings (1096 and 1585 seedlings 0.4 m^{-2}, respectively) and species (37 and 45 species 0.4 m^{-2}, respectively) emerge than where there was no *Coriaria* (243–320 seedlings 0.4 m^{-2}, 14–25 species 0.4 m^{-2}) and were the only soils with *Coriaria* seedlings. In total, 3488 seedlings representing 63 taxa were recorded. Seeds were still germinating after 24 months but rates declined markedly in the second year. For example, *Coriaria* reached a germination peak at 8 weeks but continued to germinate sporadically over the 2-year period. Tree species present in young forest within 0.5 km of the sites were absent. Establishment of *Coriaria* greatly accelerated an underlying trend of gradually increasing abundance and diversity of seeds in the soil with vegetation age. Adventive, wind-dispersed, and annual species were over-represented in the seed banks compared with the regional evergreen forest-dominated flora. These proportions are expected to decline as succession to forest gradually occurs.

Keywords *Coriaria arborea*; Mt Tarawera; nitrogen fixation; seed bank; volcanic primary succession

INTRODUCTION

Primary succession on Mt Tarawera in the North Island of New Zealand (Fig. 1) was initiated by a violent eruption in 1886. Virtually all the vegetation on the mountain top was destroyed and buried under several metres of mainly basaltic ash and lapilli (scoria). The eruption was the most significant in New Zealand since European settlement, and accounts of the vegetation before the eruption (Kirk 1872) and at intervals afterwards (Smith 1886; Aston 1915; Turner 1928; Burke 1964; Dickinson 1980; Timmins 1983; Clarkson & Clarkson 1983, 1995) enable post-volcanic successional changes to be determined.

The first plants recorded on the ash and lapilli surface near the summit were scattered solitary herbs (*Raoulia* spp.) and grasses (*Rytidosperma* spp.), with mosses in damp sites (Aston 1915). Within 60 years after the eruption, Turner (1928) noted sporadic stunted heath shrubs of *Dracophyllum subulatum* and *Gaultheria* spp., as well as herbaceous mats that were stabilising the loose ash and lapilli, facilitating establishment of other pioneer plants. At lower altitudes scattered clumps of *Coriaria arborea* were present, forming plant associations that included early successional forest shrub and tree species.

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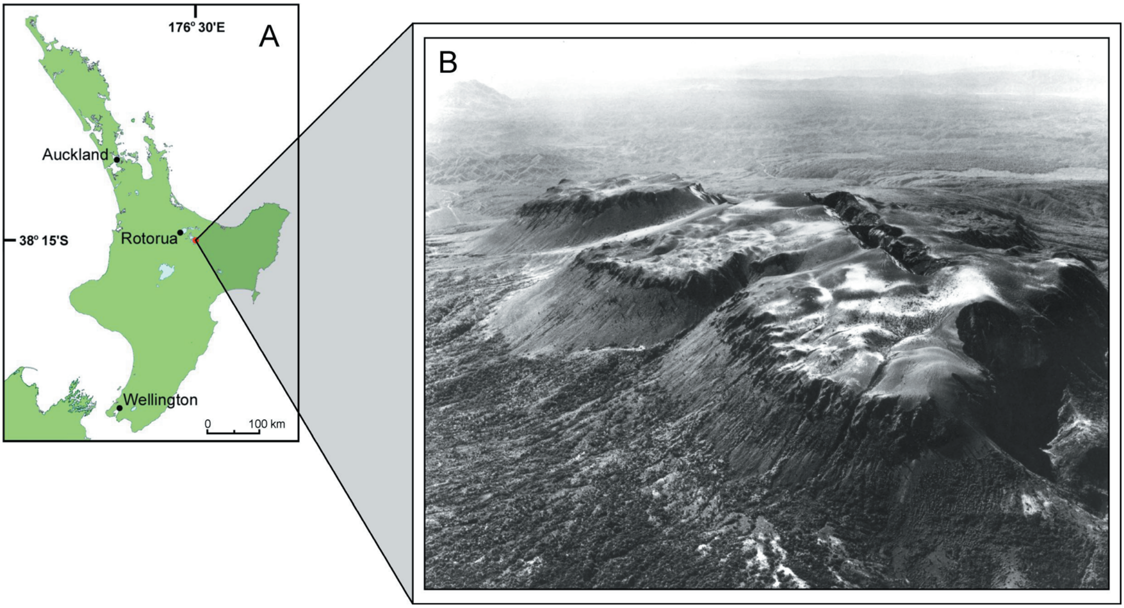

Fig. 1 North Island of New Zealand (**A**) and view looking north-east (**B**) to the dome tops of Mt Tarawera (photo D. L. Homer). The dome scarps rise 500 m above the surrounding plain.

The mountain summit, at 1111 m a.s.l., is about 50 m below the regional tree limit (Leathwick et al. 1988), yet, 110 years after the eruption, the high domes above 940 m remain largely bare, with only a sparse cover of mosses, lichens, and herbaceous and heath-like shrubby plants. Previous work suggests that establishment of *Coriaria arborea*, a native actinorhizal nitrogen-fixing shrub, is a precursor to forest establishment on Mt Tarawera (Clarkson & Clarkson 1983, 1995). *Coriaria*, here near its upper altitudinal limit, is a summer-green tall shrub, and produces racemes of abundant bird-dispersed fruits. The succession to young forest has occurred on the lower slopes and dome sides of Mt Tarawera, but *Coriaria* is still in the process of spreading onto and over the high domes. Once established, *Coriaria* dominates rapidly, forming dense thickets that provide suitable microhabitats for establishment of *Griselinia littoralis* and *Weinmannia racemosa*, dominant trees of the secondary forest nearby.

This investigation was part of a wider study focusing on the role of *Coriaria* in facilitating primary succession to forest on Mt Tarawera (Walker et al. unpubl. data). Specifically, the aim was to investigate the effect of *Coriaria* on seed banks in dome-top soils along a putative successional sequence from bare ash and lapilli substrate, to herbaceous mats, to heath shrubs, and finally to *Coriaria* thickets.

METHODS

Ten replicate samples of soils from each of five sites, selected as representing a successional sequence, were collected in late October 1998. Normally, the gradual invasion of plants from the lower slopes up onto the upper parts of the mountain gives rise to progressively younger stands of vegetation with increasing elevation. However, the early successional vegetation is now restricted to the plateau-like dome tops. We chose our five sites at the same elevation (950 ± 5 m a.s.l) on Kanakana Dome to represent major successional stages previously described by Clarkson & Clarkson (1995). All sites were within 1 km^2, with <10° slope and a south-east aspect. They were similar distances (c. 500 m) from the present tree line on the edges of the dome top to standardise effects of propagule dispersal from existing forest. The sites were "Open": no vegetation, approximating the initial

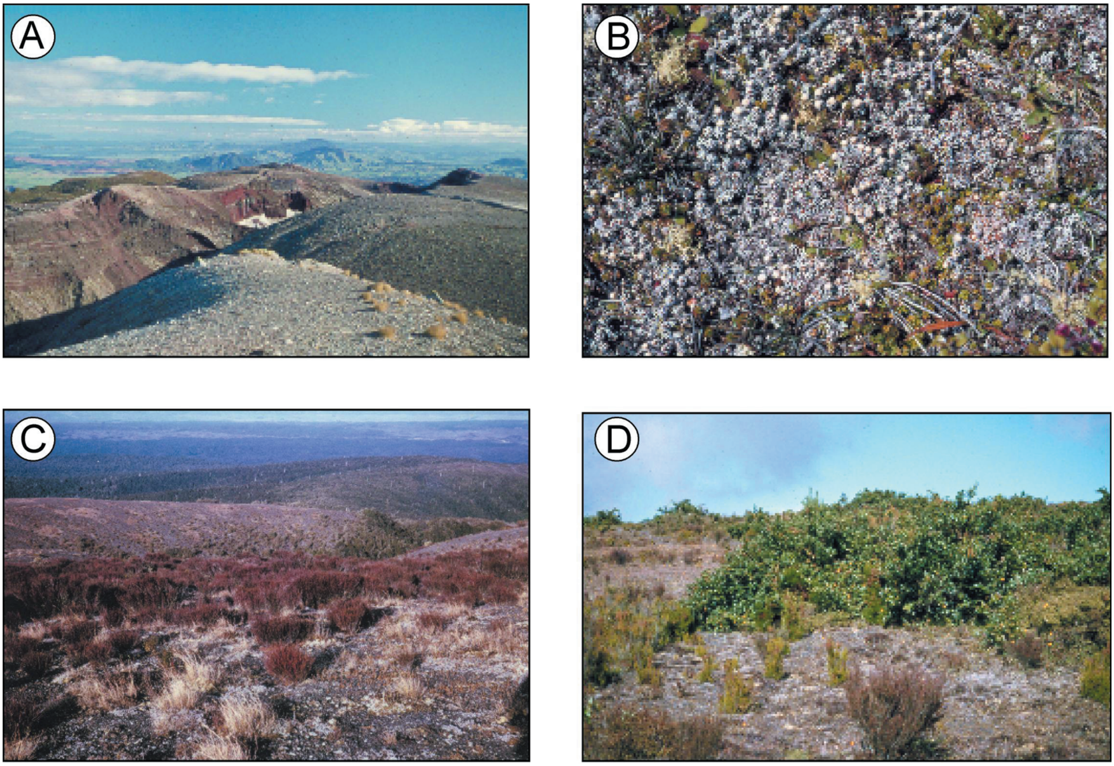

Fig. 2 Successional stages on Mt Tarawera. **A**, Open stage (grasses in foreground are 0.2 m tall); **B**, Herb stage (plant height averages 0.03–0.05 m); **C**, Shrub stage (shrub height = 0.5 m); **D**, New *Coriaria* (height = 1 m); **E**, Old *Coriaria* (height up to 2 m). Estimated ages of the vegetation (time from eruption to appearance of characteristic vegetation) are 0, 50, 80, 95, and 110 years, respectively.

condition following the eruption; "Herb": scattered herbaceous mats; "Shrub": dominated by *Dracophyllum subulatum* overtopping *Racomitrium lanuginosum* moss; "New *Coriaria*": scattered, newly invaded *Coriaria*; and "Old *Coriaria*": established stands of *Coriaria* (Fig. 2; Walker et al. unpubl. data).

At each sampling site any plants and litter were removed and the underlying soils collected from a quadrat of 250 mm by 160 mm (area = 40 000 mm^2) to a depth of 50 mm (volume = 2 litres per sample). Each soil sample was spread in a shallow tray to 20 mm soil depth, placed in a glasshouse, and watered daily. The glasshouse, located in Hamilton at 40 a.s.l., has a regime of 40% ambient light and warm temperatures (20–25°C) with a narrow yearly range (11–30°C for the 2-year period). Compared with the drought- and frost-prone top of Mt Tarawera (at Waiotapu Forest climatological station, 10 km south-west and 381 m a.s.l., mean

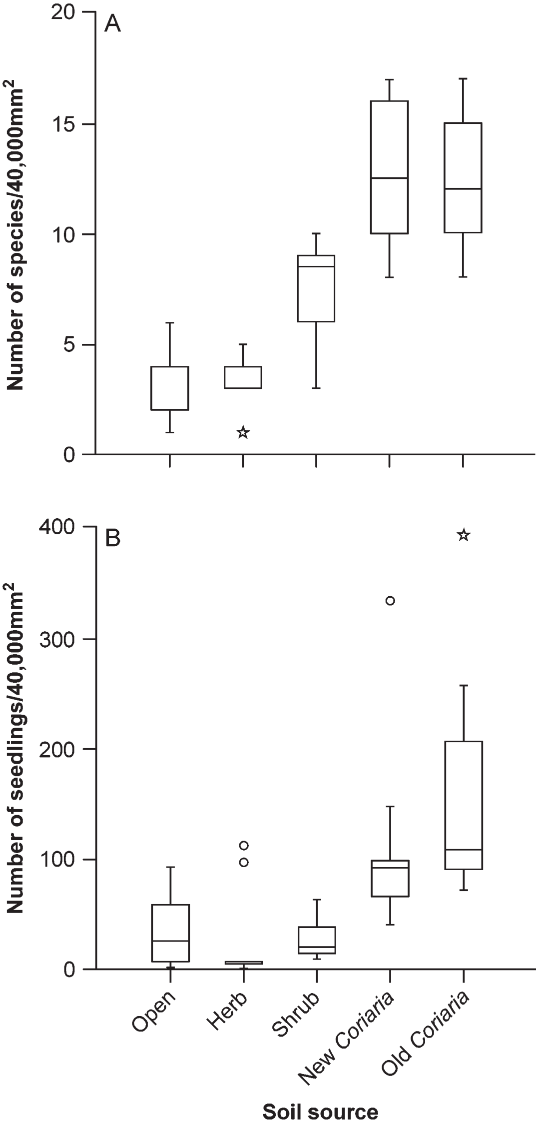

Fig. 3 Box plots showing medians, upper and lower quartiles, outside values (circles), and far outside values (stars) of **A**, species numbers and **B**, seedling numbers per 40 000 mm^2 for soils representing the successional sequence.

temperature is 11.1°C and yearly range is –6.9° to 33.3°C; New Zealand Meteorological Service 1973), these conditions would be conducive to rapid seed germination. A control for possible local contamination was provided by a concurrent seed-bank experiment in the same glasshouse. This revealed only one contaminant, an adventive herb, *Conyza albida*, which was removed from our analyses.

Seedlings were identified, recorded, and then removed once a month for the first year and then every 3 months for the second year until February 2001 (duration = 119 weeks). Any unidentified seedlings were removed and replanted in pots for later identification. All mosses and lichens and vegetative regrowth of rhizomatous herbs were also removed. One-way ANOVA followed by Tukey multiple comparison tests (SYSTAT version 7.0; Wilkinson 1997) was used to compare numbers of species and seedlings in seed banks from the different soil types.

RESULTS

Total numbers of seedlings ranged from 243 (Herb) to 1585 (Old *Coriaria*), and of species from 14 (Open) to 45 (Old *Coriaria*) (Appendix 1). New *Coriaria* and Old *Coriaria* soils had significantly greater numbers of species ($P < 0.001$) and seedlings ($P < 0.001$) than the other three soils (Fig. 3; Appendix 1). *Coriaria* seedlings were present only in New *Coriaria* and Old *Coriaria* soils where they represented 15 and 7%, respectively, of all seedlings that emerged. Although more *Coriaria* seedlings emerged from New *Coriaria* than Old *Coriaria* soils, the differences were not statistically significant.

Adventive species accounted for 40% of all species and 52% of all seedlings that emerged during the experiment. Patterns were similar to total trends (above), with New *Coriaria* and Old *Coriaria* soils having significantly ($P < 0.001$) more adventive species and seedlings than the other three soils.

Germination from the seed bank soils continued during the entire 119 weeks, but rates declined markedly during the second year (Fig. 4). However, the most common species germinated over distinct time periods with marked germination peaks (Fig. 5). *Holcus lanatus*, an adventive grass, had its germination peak at 3 weeks, followed by *Coriaria* (81% of which germinated by 8 weeks). Subsequent dominants included sporophytes of the native fern *Paesia scaberula* (most abundant at 14 weeks), the adventive herb *Sagina procumbens* (26 and 119 weeks), and the native composite herb *Pseudognaphalium luteo-album* (42 weeks). Seedlings of the native shrub *Dracophyllum subulatum* first emerged from the shrub stage soils

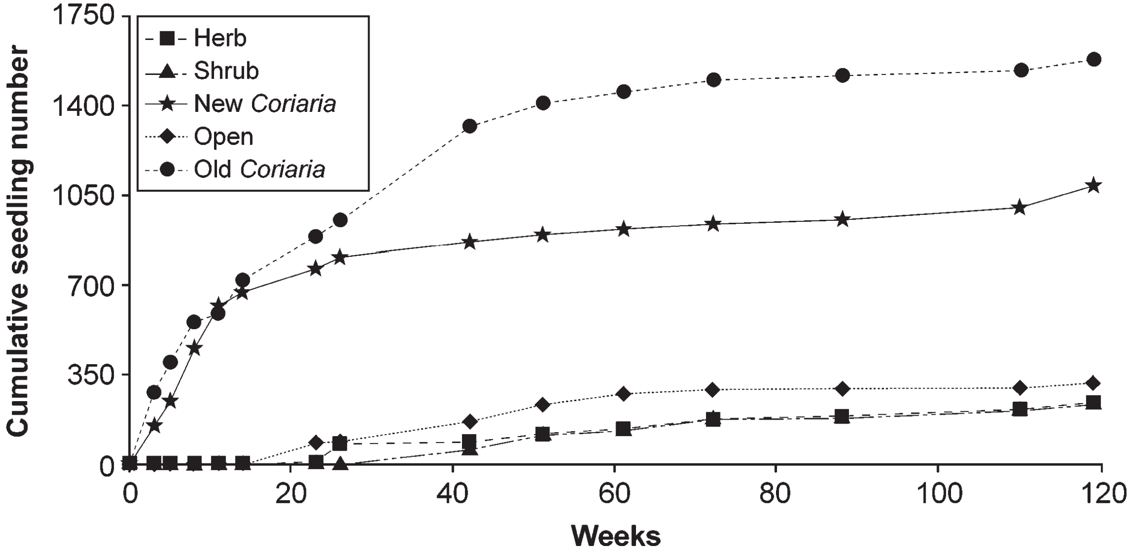

Fig. 4 Cumulative seed germination patterns over 2 years for soils from the five sites representing different successional stages.

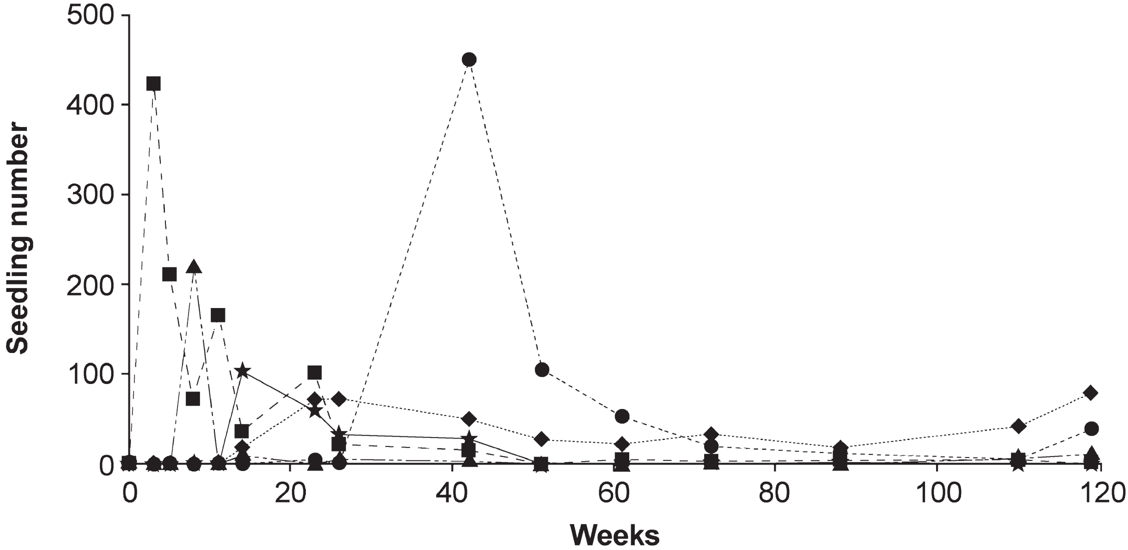

Fig. 5 Seed germination patterns (number germinated since last count) of the five most common species: *Holcus lanatus* (squares), *Coriaria arborea* (triangles), *Paesia scaberula* (stars), *Sagina procumbens* (diamonds), *Pseudognaphalium luteo-album* (circles).

at 72 weeks. Although most *Coriaria* seeds germinated within 8 weeks, seedlings were present in virtually all samples from this time, indicating that some seeds could remain viable for 2 years or more*.

The only native tree species to emerge during the experiment was a single seedling of *Metrosideros excelsa*, a tree of lower altitude lakeshore forests that established within 27 years of the eruption (Aston 1915). Seedlings of tree species common near the dome edge, such as *Griselinia littoralis*, *Weinmannia racemosa*, and *Podocarpus hallii*, were absent.

DISCUSSION

The results indicated that establishment of *Coriaria* greatly accelerated an underlying trend of gradually increasing seed abundance and species richness in the soil with vegetation age. This may be due partly to soil amelioration (Old *Coriaria* stages had significantly higher organic carbon, total nitrogen, available phosphorus, cation exchange capacity, calcium, potassium, and magnesium levels than other stages (Walker et al. unpubl. data) and greater water-holding capacity. The taller, denser vegetation would trap wind-dispersed seed, as well as provide perches and food to attract birds and associated bird-dispersed seeds. "Biological legacy", surviving seeds, roots, plants, and animals, considered to be a major determinant of successional rates and patterns elsewhere (e.g., Franklin et al. 1985; del Moral & Bliss 1993; Tsuyuzaki 1994), was not relevant in this study. This is because the dome tops of Mt Tarawera, with volcanic deposits up to 60 m thick (Burke 1964), are undergoing true primary succession, which, in initial stages, is dependent solely on immigration (Grandin & Rydin 1998).

All species in the soil seed bank, except *Metrosideros excelsa*, were already present above 900 m a.s.l. on the mountain (Clarkson & Clarkson 1983, 1995). *M. excelsa* has abundant, light, wind-dispersed seeds that could have blown up from populations growing around the shores of Lake Tarawera, at 300 m a.s.l., 5 km to the west. However, the seedlings are frost intolerant (Sakai & Wardle 1978) and presumably do not survive the harsh, frost-prone climate of the dome tops.

The absence of *Griselinia littoralis* and *Weinmannia racemosa* from the seed bank is noteworthy as these species dominate young forest on the dome sides, having replaced former *Coriaria* scrub. Pickett & McDonnell (1989) noted that seeds of late successional species are often under-represented until a site becomes very old. The sites sampled on Mt Tarawera were about 500 m from the advancing forest front but young shrub-sized *G. littoralis* individuals also occurred sporadically within the study area, in older *Coriaria* associations. As these have only recently established, and are mostly not reproductively mature, their large bird-dispersed seeds have not yet been incorporated into the seed bank. *W. racemosa* seeds are wind dispersed (Wardle 1966), but establishing plants are preferentially browsed by introduced animals, e.g., possums, rabbits, and deer, and the species is now rare on the dome tops (Clarkson & Clarkson 1995). *Podocarpus hallii* seeds are bird-dispersed, but only a single sapling has been recorded on the dome tops to date (Clarkson & Clarkson 1995). *P. hallii* is widespread in the surviving and partially damaged forest on the lower slopes of the mountain (Burke 1974).

Several early successional native species (e.g., *Luzula* spp., *Deyeuxia avenoides*, *Pseudognaphalium luteo-album*, *Raoulia glabra*, *Epilobium minutiflorum*) occurred in the seed banks of later successional *Coriaria* sites (see Appendix 1). These species are either still present at or near the sampling sites, or their seeds were incorporated into the seed bank under an earlier vegetation cover and have persisted. Grandin & Rydin (1998) showed in a true successional series (as opposed to a chronosequence) that 100 years of primary succession was not long enough for exhaustion of early species in the seed bank. Different ecological attributes, including seed longevity, weight, size, shape, and successional status also affect seed persistence in the soil (Thompson et al. 1993; Grime et al. 1995; Grandin & Rydin 1998; Moles et al. 2000). About one third (32%) of the 63 species recorded emerged only in the first 12 months and therefore could be considered as a temporary seed bank. Of these, 55% belonged to the family Asteraceae and 55% were adventive.

The ratio of native to adventive species in the seed bank was 38:25. This contrasts with the ratios of native and adventive species recorded in vegetation surveys of the dome tops in 1979 (73:27), 1992 (74:26), and 1995 (73:27) (Clarkson & Clarkson 1995). Although those surveys were of

*An occasional *Coriaria* seedling was still emerging after 3 years.

extant flora rather than seed banks, they provide some interesting comparisons with the current study. In addition, Grandin & Rydin (1998) showed relatively high similarities between species in the seed bank of the upper soil layers and those in the present vegetation (which decreased with increasing soil depth). The higher proportion of adventive species in the Mt Tarawera seed bank may be partly due to confining the study area to the ash and lapilli substrate, whereas previous studies encompassed all habitats, e.g., rhyolitic rock, craters, and small wetlands, dominated by native species.

Tourist traffic to the dome tops is increasing, thus potentially introducing new, mainly adventive species from beyond the immediate neighbourhood. Seedlings of adventive species accounted for 52% of total (= 3488) seedlings that emerged, despite fewer adventive species rather than native being recorded. Dominance of adventive seedlings in the seed bank is probably due also to the increased human activity on the mountain. Many of these species are opportunists, and their abundance should decline with reduction of open habitats on the mountain as the succession proceeds.

Of the species recorded, 68% were wind-dispersed, 11% animal-dispersed, and 21% dispersed by other means. Wind was the dominant dispersal mechanism for species of early post-volcanic succession on Mount St Helens, USA (Dale 1989; del Moral 1999), Mt Usu, Japan (Tsuyuzaki 1995), and Krakatau (Rakata), Indonesia (Whittaker et al. 1992). As succession proceeds on Mt Tarawera, the proportion of wind-dispersed species should decline as the species composition becomes increasingly similar to that of the regional flora, in which larger seeds dispersed by bird or other mechanisms are more important.

Annuals accounted for 19% of total species (native:adventive ratio = 5:14) that emerged, despite seed bank populations elsewhere being composed primarily of annuals (Whittaker 1975; Tsuyuzaki 1994). This low proportion is not unexpected given the inherent paucity of annuals in the New Zealand flora (6% of the flowering plants (Allan 1937)) and in the extant surviving vegetation, which is dominated by evergreen native forest. The proportion of annuals in the New Zealand naturalised flora is 30% and these annuals are well adapted to rapidly occupy continuously disturbed habitats (Webb et al. 1988). However, in the absence of future disturbance, the number and abundance of annuals on Mt Tarawera is expected to decline as native forest spreads over the dome tops.

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APPENDIX 1 Seedlings that emerged during 119 weeks in the glasshouse seed bank experiment in five soil types. Ten soil collections per soil type were combined, except to calculate mean (± SE) number of species and seedlings. Species followed by an asterisk are adventive to New Zealand. Mean numbers of seedlings and species followed by the same letter are not significantly different ($P > 0.05$). Nomenclature follows Parsons et al. (1998), Edgar & Connor (2000), and Brownsey & Smith-Dodsworth (2000).

	Soil Type					
Life form/family/species	Open	Herb	Shrub	New *Coriaria*	Old *Coriaria*	Total
FERNS						
Adiantaceae						
Adiantum cunninghamii	0	0	18	2	3	23
Blechnaceae						
Blechnum novae-zelandiae	1	3	16	16	48	84
Blechnum penna-marina	0	0	0	0	3	3
Blechnum vulcanicum	0	0	4	2	1	7
Doodia media	0	0	0	0	1	1
Dennstaedtiaceae						
Hypolepis distans	0	0	0	0	1	1
Dicksoniaceae						
Dicksonia squarrosa	0	0	0	4	20	24
Ophioglossaceae						
Ophioglossum coriaceum	0	0	0	1	11	12
Pteridaceae						
Paesia scaberula	0	0	2	2	228	232
Pteris tremula	0	0	1	7	15	23
MONOCOTYLEDONOUS HERBS						
Cyperaceae						
Luzula decipiens	0	1	0	6	2	9
Luzula sp. (unnamed)	0	0	1	7	25	33
Morelotia affinis	0	0	0	0	1	1
Orchidaceae						
Thelymitra longifolia	0	0	0	2	0	2
Poaceae						
Cortaderia fulvida	0	0	1	1	0	2
Deyeuxia avenoides	0	0	52	11	4	67
Hierochloe redolens	0	2	2	0	0	4
*Holcus lanatus**	2	0	1	503	549	1055
Rytidosperma gracile	0	0	1	2	0	3
DICOTYLEDONOUS HERBS						
Asteraceae						
*Aster subulatus**	5	6	5	3	10	29
Celmisia gracilenta	0	0	5	0	0	5
*Cirsium arvense**	0	0	0	0	2	2
*Cirsium vulgare**	0	0	0	1	11	12
*Crepis capillaris**	4	1	0	24	2	31
*Gnaphalium coarctatum**	0	2	1	1	0	4
Gnaphalium delicatulum	0	0	1	0	0	1
Gnaphalium limosum	0	0	0	1	1	2
*Gnaphalium sphaericum**	0	0	0	0	1	1
*Hypochoeris radicata**	0	0	0	27	17	44
*Leontodon taraxacoides**	0	0	0	0	1	1
*Mycelis muralis**	0	0	0	0	1	1
Pseudognaphalium luteo-album	201	11	11	67	405	695
Raoulia glabra	3	1	0	11	0	15
*Senecio bipinnatisectus**	0	0	0	0	1	1
*Senecio jacobaea**	0	0	0	7	0	7
Senecio minimus	0	0	0	0	9	9

(*continued over page*)

APPENDIX 1 (*continued*)

Life form/family/species	Soil Type: Open	Herb	Shrub	New *Coriaria*	Old *Coriaria*	Total
*Sonchus oleraceus**	0	0	0	0	2	2
Vittadinia australis	0	1	13	0	0	14
Caryophyllaceae						
*Cerastium fontanum**	0	0	0	60	27	87
*Sagina procumbens**	93	203	53	105	1	455
Stellaria decipiens	0	0	0	1	0	1
Clusiaceae						
Hypericum japonicum	0	0	0	18	3	21
Fabaceae						
*Lotus pedunculatus**	0	0	0	3	2	5
*Trifolium dubium**	0	0	0	0	5	5
Gentianaceae						
*Centaurium erythraea**	1	1	1	10	0	13
Lamiaceae						
*Prunella vulgaris**	5	0	0	9	3	17
Onagraceae						
*Epilobium ciliatum**	0	0	0	3	6	9
Epilobium minutiflorum	1	1	0	0	1	3
Epilobium tenuipes	0	1	0	0	8	9
Polygonaceae						
*Rumex acetosella**	0	0	0	0	6	6
Ranunculaceae						
*Ranunculus repens**	0	0	0	2	9	11
Rosaceae						
Acaena anserinifolia	1	0	0	1	0	2
Rubiaceae						
*Galium aparine**	0	0	0	0	1	1
Nertera depressa	0	0	0	0	18	18
DICOTYLEDONOUS SHRUBS AND TREES						
Coriariaceae						
Coriaria arborea	0	0	0	169	104	273
Epacridaceae						
Dracophyllum subulatum	0	0	32	0	0	32
Ericaceae						
*Erica lusitanica**	0	4	0	1	9	14
Gaultheria paniculata	0	0	16	0	1	17
Myrtaceae						
Metrosideros excelsa	0	1	0	0	0	1
Oxalidaceae						
Oxalis exilis	1	1	1	3	0	6
Polygonaceae						
Muehlenbeckia axillaris	0	1	1	0	0	2
Salicaceae						
*Salix cinerea**	1	2	4	3	6	16
Scrophulariaceae						
Hebe stricta	1	0	1	0	0	2
Total number of seedlings	320	243	244	1096	1585	3488
Total number of species	14	18	25	37	45	63
Mean number of seedlings (per 40 000 mm^{-2})	32 ± 10 a	24 ± 13 a	24 ± 5a	110 ± 26 b	159 ± 33 b	
Mean number of species (per 40 000 mm^{-2})	3.4 ± 0.5 a	3.4 ± 0.4 a	7.5 ± 0.6 b	12.7 ± 1.1 c	12.3 ± 0.9 c	