The soil seed bank of a kauri (*Agathis australis*) forest remnant near Auckland, New Zealand

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Abstract   The "transient" and "persistent" components of the soil seed bank beneath a kauri forest remnant are described. The methodology employed separates recent seed rain (collected in trays over a two year period) from dormant viable seed with longevity >2 years (soil beneath trays). A total of 46 vascular plant species, and 908 individuals, were recorded from tray and sub-tray samples. Species composition of trays and sub-trays varies markedly. Trays are dominated by four woody, native species; *Kunzea ericoides, Coprosma arborea, Myrsine australis,* and *Carpodetus serratus*. Sub-tray samples show an accumulation of seeds from light-demanding weedy species, including many adventives such as *Solanum mauritianum, Phytolacca octandra,* and *Cirsium vulgare*. In addition, seeds of two woody, native species, *Cordyline australis* and *Geniostoma rupestre*, are abundant. Detrended correspondence analysis (DECORANA) shows clear differences between floristic composition of trays and sub-trays and, further, between on-site vegetation and components of the soil seed bank. These differences are explained in terms of seed longevity, seed accumulation rates, suitability of site conditions for growth of individual species, and the role of seed dispersal agents, especially birds.

INTRODUCTION

The importance of buried viable seed, the soil seed bank, as a contributor of both species and individuals to the early stages of plant succession is now recognised for a number of plant communities (e.g., Harper 1977, Whitmore 1983, Gibson & Brown 1985). Several early studies illustrate the existence of a large soil-stored seed bank of native pasture and heath species under modified pasture in Wales (Brenchley & Warington 1933, Chippendale & Milton 1934). Soil seed banks in temperate forests have been studied by Oosting & Humphreys (1940), Olmsted & Curtis (1947), Livingston & Allessio (1968), Kellman (1970a), Stricker & Edgerton (1976), and Moore & Wein (1977). Thompson (1978) reviews the findings of these temperate forest and pasture studies noting several trends:

1. Seeds of weedy, early successional species dominate the seed banks, even for forest sites >100 years old.
2. Species characteristic of the later stages of succession are poorly represented, and those of the forest dominants are often totally absent.
3. The seed bank flora is different to the growing vegetation of the site, dissimilarity increasing with successional time.

More recent studies have illustrated the existence of seed banks under tropical rainforest (Kellman 1970b, Cheke et al. 1979, Hall & Swaine 1980, Hopkins & Graham 1983, Putz 1983, Enright 1985a). Here, pioneer woody species (e.g., *Cecropia* in S America, *Trema* and *Pipturus* in SE Asia) often dominate the seed bank rather than the weedy herbs of temperate situations. Again, later successional trees tend to be poorly represented. This has usually been ascribed to the absence of dormancy in such species which are often characterised by large seed size and the ability to tolerate shading at the seedling stage (Whitmore 1983, Hopkins & Graham 1987). Large seeds are not easily incorporated into the soil profile and may suffer considerable predation losses shortly after falling from the parent tree (Thompson 1978).

Hopkins & Graham (1987) buried seed from 50 tropical woody species for up to 2 years. They found

that early successional species were characterised by enforced dormancy and retention of viability for at least this length of time. Primary forest species either germinated rapidly, even when buried, or lost viability within 6 weeks to 6 months.

Published studies on soil seed banks vary in their methodologies and this may influence both the results and possible interpretations of seed bank dynamics. Livingston & Allessio (1968) note that exclusion of the litter layer, and sieving of soil samples, may account partly for the poor representation of later successional species. Separation of soil samples into layers by depth has been common (Kellman 1970a, Cheke et al. 1979, Hopkins & Graham 1983, Enright 1985a), and gives some indication of likely longevity for different species. That is, deeply buried seeds are assumed to be older than seeds near the soil surface. However, mixing by soil fauna, and leaching of small seeds down the profile may confuse such interpretations. Based upon these depth-stratified studies, a fourth trend common to most seed banks is identifiable; that species diversity declines with increasing depth, while dominance by one or a few species increases.

There is little published information concerning seed banks for New Zealand forests. Herbert (1976) collected forest duff from several sites in Pureora and Tihoi State Forests (West Taupo). A total of about 20 000 seedlings and sporelings of 46 indigenous vascular plants arose, with densities ranging from 56 to 1070 individuals m^{-2}. Such findings refer almost solely to recent seed rain rather than the dormant seed bank, and provide little information either about seed longevities in the soil or the history of seed accumulation at a site. Ogden (1985) alludes to unpublished data on seed banks under, and near, kanuka (*Kunzea ericoides*) stands, noting that soil-stored seed densities vary markedly from year to year, and site to site, even within quite small areas. He describes seed banks for a number of North Island forest sites as falling within the range 150–3000 individuals m^{-2}. This large range encompasses densities found for forest seed banks in other parts of the world.

This paper examines the seed bank in a kauri (*Agathis australis*) forest remnant 15 ha in size and bounded on three sides by cleared farmland. The forest area is a scientific reserve owned by the University of Auckland and located near Huapai in the northern part of the Waitakere Ranges (36°46′S, grid reference NZMS 260 Q11 435885, Waitakere; 70–100 m a.s.l.). Average annual rainfall is approximately 1328 mm and shows a winter maximum. Temperatures are mild all year round, but are highest in February (monthly mean 19°C) and lowest in July (monthly mean 10.4°C). Soils are brown granular clays (Parau clay) derived from andesitic tuffs (Thomas & Ogden 1983).

Kauri forest is a temperate rainforest containing a mixture of broadleaved, evergreen angiosperm and gymnosperm species and showing considerable structural and floristic similarities to tropical and sub-tropical forests of New Guinea and eastern Australia (Webb 1976).

Aims of the present study are to:
1. describe, quantitatively, the viable seed bank;
2. separate recent seed rain from the longer lived, dormant component of the seed bank;
3. document invasion of adventive species into the kauri forest seed bank;
4. compare present vegetation at this site with species composition of the seed bank;
5. consider the likely importance of the seed bank in contributing individuals to the early stages of succession.

METHODS

Seven plastic seedling trays, each 0.125 m^2 in area, were filled to a depth of 5 cm with sterilised potting mix and placed in the field in September 1983. Trays were located in a variety of sites within the kauri forest, ranging from seral vegetation about 120 years old to mature kauri forest (Table 1). Trays were allowed to accumulate litter (including the seed rain) for a period of two years. They were collected from the field in September 1985 and placed in a glasshouse at the University of Auckland where the viable seed rain was estimated through germination. Soil beneath the trays (including litter) was excavated to a depth of 5 cm, care being taken to avoid sampling too close to the tray edges. In this way, a sample 0.1 m^2 in size was collected at each tray position. These samples had been denied seed rain additions for the two year period, and so contained viable seed only for species capable of enduring at least 2 years of enforced (or induced) dormancy, and are referred to as "sub-tray" samples. Lateral transport of seeds by soil fauna was not considered likely to seriously influence composition of sub-tray soil. Sub-tray samples were spread out over sterilised potting mix in plastic seedling trays and placed in the glasshouse, paired with the appropriate seed rain tray. Two "control" trays containing sterilised potting mix only, were also placed in the glasshouse.

Table 1 Age and type of vegetation at each tray position.

Tray number	Estimated vegetation age (yr)*	Dominant woody species
1	130	*Kunzea ericoides, Coprosma arborea, Myrsine australis, Vitex lucens* (remnant).
2	120	*Agathis australis, Kunzea ericoides, Phyllocladus trichomanoides.*
4	500	*Agathis australis, Vitex lucens, Rhopalostylis sapida.*
5	200	*Coprosma arborea, Myrsine australis, Ripogonum scandens, Rhopalostylis sapida.*
7	500	*Agathis australis, Dysoxylum spectabile, Vitex lucens, Rhopalostylis sapida.*
8	350	*Agathis australis, Phyllocladus trichomanoides, Podocarpus totara.*
9	250	*Agathis australis, Phyllocladus trichomanoides, Podocarpus totara.*

*Vegetation age was estimated using known, or assumed, size-age relationships for trees at each site (kauri age from Ogden 1983, nikau palm age from Enright 1985b).

All samples were kept continuously moist and in full sunlight. Germinants were counted weekly for the first 12 weeks and then fortnightly until further germination ceased and all individuals had been identified. After positive identification, individuals were discarded so that overcrowding of trays was avoided.

Detrended Correspondence Analysis (DECORANA), an ordination technique particularly suited to the analysis of heterogeneous data sets where non-linearity of species response is likely to be a problem, was used to determine the relationship between seed bank samples and existing vegetation (Hill & Gauch 1980). Two analyses were run:

1. DECORANA of woody species in trays, sub-trays, and canopy and understorey vegetation for 100m² plots surrounding the tray location, (29 species × 28 sites) (28 sites = 7 tray + 7 sub-tray + 7 canopy + 7 understorey).
2. DECORANA of all species in trays and sub-trays only (42 species × 14 sites).

Nomenclature of species follows Brownsey et al. (1985) for ferns, and Allan (1961), Moore & Edgar (1970), Healy & Edgar (1980), and Healy (1984) for gymnosperms and angiosperms. Nomenclature changes relating to native plants are reviewed by Edgar (1971) and Edgar & Connor (1978, 1983), many of which are followed. The remainder are referenced below: *Actinidia deliciosa*, Liang and Ferguson (1986); and *Kunzea ericoides*, Thompson (1983).

RESULTS

A total of 494 seedlings emerged from the seven trays, and 396 seedlings from sub-trays over a period of 20 weeks. When differences in the ground area sampled are taken into account, both trays and sub-trays show a similar sized pool of viable seeds: trays 565±446 m⁻², sub-trays 566±383 m⁻². Variation between samples was considerable and is reflected in a high standard deviation. The total of 1131 m⁻² is similar to estimates obtained for other New Zealand forest sites (Ogden 1985), and to estimates for many temperate and tropical forests elsewhere.

Only two individuals were growing in trays at the time of their collection from the forest; a nikau palm (*Rhopalostylis sapida*) seedling, and the climbing fern *Phymatosorus diversifolius*. Both are tolerant of shade.

The pattern of germination over time varies between tray and sub-tray samples (Fig. 1). Germination commences within the first week for trays, indicating that many seeds (and species) were already in the process of germinating, or could respond immediately to the changed environmental conditions experienced in the glasshouse. The rate of addition of new individuals to trays slows markedly after about 8 weeks and the number of new germinants is negligible after 14 weeks.

There is a clear lag of 1–2 weeks before germination of seed from sub-trays begins. This suggests that seeds were experiencing enforced, or induced, dormancy, and that several days in the changed environment of the glasshouse were required to break this dormancy. After the second week, the rate of germination for individuals from sub-trays is similar to that for individuals from trays.

There are a total of 46 vascular plant species in the combined tray and sub-tray samples, including four ferns. Of the 42 species of phanerogams, only one gymnosperm (*Dacrycarpus dacrydioides*) was
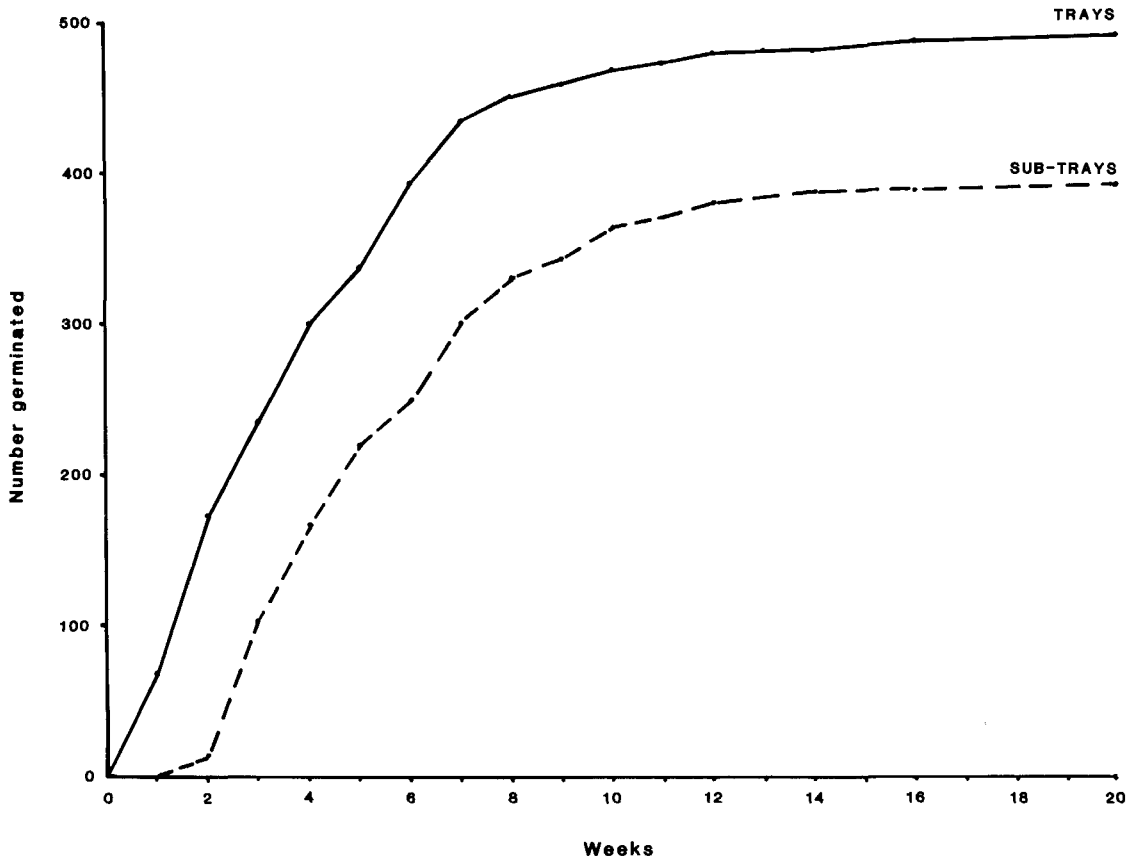
Fig. 1 Pattern of seed germination over time for all species in trays and sub-trays. Note: total soil area sampled was 0.875 m² for trays and 0.700 m² for sub-trays.

recorded. This is despite the existence of at least six species of gymnosperms in the immediate vicinity of tray locations. All four fern species are present in both trays and sub-trays. They are light-demanding species and were not recorded as existing plants within the 100 m² plots centred on tray position. It is possible that fern spores in sub-trays may have been leached through drainage holes in the trays.

Table 2 summarises the major quantitative features of the tray and sub-tray viable seed pools. Species richness is greatest in trays largely due to a higher number of woody native species. This woody species component also makes up a larger proportion of the total number of individuals than does the woody species component of the sub-tray seed pool. Although the number of adventive species is similar in both trays and sub-trays, sub-trays show a much greater accumulation of

individuals for this component. This suggests markedly different seed longevities for dominant components of the recent seed rain (i.e., seed in trays) *versus* the more abundant components of the dormant seedbank (i.e., seed in sub-trays).

A few woody species strongly dominate the viable seed pool in trays – *Kunzea ericoides, Coprosma arborea, Myrsine australis*, and *Carpodetus serratus* – accounting for nearly 77% of all individuals germinating in trays. Their patterns of germination over time vary somewhat. *C. arborea* and *M. australis* germinate within one week of placement in the glasshouse, while *K. ericoides* germination commences in the second week (Fig. 2). *C. serratus* germination is slow until weeks 5 and 6 when the rate of germination increases markedly. *C. arborea* and *M. australis* germination was abundant under parent trees in the field at the time of

Table 2 Major quantitative characteristics of the tray and sub-tray viable seed pools.

Seedbank variable	Trays	Subtrays	Total
No. of individuals m^{-2}	565	566	1131
No. of species	33(4)*	26(4)	42(4)
No. of species site^{-1}	11.3±4.7†	9.7±4.5	17.3±6.8
No. of woody native species (% of individuals)	17 (83.6)	11 (60.9)	19 (72.3)
No. of adventive species (% of individuals)	12 (10.6)	12 (36.4)	16 (23.5)

*Value in brackets is the number of fern species recorded and should be added to obtain total number of species.
†Standard deviation.

tray collection and it appears that germination of these species did not require increases in light intensity, temperature, or other trigger mechanisms. Seeds of *K. ericoides* and *C. serratus*, on the other hand, did not commence germination until after their removal from the shaded forest floor. No seedlings of these species were noted in the field either at the time of tray collection or subsequently.

Other species which germinated quickly, and whose presence was noted as current year seedling cohorts in the field, included *Knightia excelsa* and *Rhopalostylis sapida*.

Eight of a total of 17 woody, native species recorded in trays are absent from sub-trays (Table 3). This implies a seed longevity of <2 years for these species since sub-tray samples were denied seed rain for two years. Six non-woody species found in trays are also absent from sub-trays, but of these only one, *Uncinia uncinata*, is a normal component of kauri forest. The other five species are weedy plants with good dispersal abilities, and include *Typha orientalis*, seed of which must have originated more than 1 km from the field site.

The Australian rain forest tree *Acmena smithii* (lilly-pilly) was recorded both from a tray, and as seedlings in the field. No individuals >30 cm tall were noted and its ability to establish is not clear.

Four woody and five herbaceous species dominate the viable seed pool in sub-trays. All nine species are slow to germinate, reflecting the need for stimuli to break dormancy (Fig. 3). The woody native species *Geniostoma rupestre* and *Cordyline australis* are abundant in sub-trays, while having only low densities in trays. This implies a considerable period of accumulation for seed, and a longevity in the soil of perhaps 23–50 years (based on the accumulation rate in trays over two years, and

assuming no loss of viability). Such estimates are highly speculative, however, given that seed crops may vary markedly from year to year. *K. ericoides* is represented in sub-trays at about 20% of its density in trays. This suggests a marked loss of viability with time, but the survival of at least some viable seed for more than two years. Germination does not commence until week 3, whereas *K. ericoides* seed in trays germinates in week 2 suggesting more complete (or stronger) dormancy in the buried seed. *G. rupestre* shows the longest lag time (approx. seven weeks) between provision of stimulus and germination.

Weedy species are well represented in sub-trays. *Solanum americanum*, *S. mauritianum*, *Cirsium vulgare*, *Phytolacca octandra*, and *Hypochoeris radicata* are all common. Of these, only *S. americanum* is a native species (although not endemic, and is itself a widespread weed in the SW Pacific region). The greater density of these weed species in sub-trays, as opposed to trays, suggests accumulation of dormant, viable seed in the soil over a number of years. Minimum estimates for accumulation time (assuming no loss of viability) range from 12–30 years if we assume seed rain is constant at the rate measured over two years in trays. These estimates are well within the known range for longevity of such weedy species (Harrington 1972). Many other weedy herbaceous species are present in both trays and sub-trays at low density (see Table 3).

It is clear that soils under kauri forest at Huapai contain a mixture of local forest species, and an invasion of both native and adventive woody and herbaceous species which are not part of the normal forest flora. These invasive species are, predominantly, colonisers of disturbed sites. There is no clear difference in mode of dispersal between

Table 3 The number and identity of seedlings and fern sporelings germinated from tray and sub-tray samples over a 20 week period. Number of adventives, mode of dispersal, proximity of potential parent plants, season of fruiting, and known seed longevities are also given.

Species	Common name	No. germinated Trays	No. germinated Sub-trays	Probable mode of dispersal	Proximity of source (m)	Time of fruiting	Seed longevity (yr)†
Kunzea ericoides (A. Rich.) J. Thompson	kanuka	175	35	wind	0–62	autumn	
Coprosma arborea Kirk	mamangi	98	0	bird	0–20	autumn	
Pseudopanax crassifolius (Sol. ex A. Cunn.) Koch	lancewood	9	0	bird	5–20	autumn	
Rhopalostylis sapida Wendl. et Drude	nikau palm	3	0	bird	5–20	autumn–spring	
Myrsine australis (A. Rich.) Allan	mapou	57	2	bird	0–20	spring–autumn	
Coprosma lucida J.R. et G. Forst.	shining karamu	1	0	bird	30	autumn	
Carpodetus serratus J.R. et G. Forst.	putaputaweta	49	0	bird	? local	autumn	
Knightia excelsa R. Br.	rewarewa	3	0	wind	5–15	summer	
Dacrycarpus dacrydioides (A. Rich.) de Laub.	kahikatea	6	1	bird	>40	autumn	
Vitex lucens Kirk	puriri	2	1	bird	0–10	summer–autumn	
Olearia rani (A. Cunn.) Druce	heketara	4	2	wind	25	late summer	
Metrosideros perforata (J.R. et G. Forst.) A. Rich	aka	3	0	wind	0–10	autumn–winter	
Melicytus macrophyllus Hook. f.		1	0	bird	6	autumn	
Schefflera digitata J.R. et G. Forst.	pate	2	1	bird	? local	late summer–early autumn	
Freycinetia baueriana Endl.	kiekie	4	0	animal incl. bird	10–50	summer	
Cordyline australis (Forst. f.) Endl.	cabbage tree	4	86	bird	>25	late summer–early autumn	
Geniostoma rupestre A. Rich.	hangehange	12	111	bird	0–25	autumn	
Pittosporum tenuifolium Sol. ex Gaertn.	kohuhu	0	1	bird/drop	?	late summer	
Fuchsia excorticata (J.R. et G. Forst.) Linn. f.	kotukutuku	0	1	bird	?	spring–autumn	
Acmena smithii (Poir.) Men. et Perry	lilly-pilly	1	0	bird	?	winter	<1.25
Actinidia deliciosa (A. Chev.) C.F. Liang et A. R. Ferguson	kiwifruit	0	1	animal incl. bird	?	autumn–winter	
Uncinia uncinata (Linn. f.) Kuk	hooked sedge	5	0	animal	? local	summer	
Gnaphalium spicatum Lam.	purple cudweed	2	2	wind	>100	summer–winter	>18
Conyza albida Spreng.	fleabane	8	1	wind	>100	summer–autumn	>10
Lamium purpureum L.	red dead-nettle	1	1	wind	>100	spring–autumn	
Senecio bipinnatisectus Belcher	Australian fireweed	1	1	wind	>100	summer–autumn	>20
Typha orientalis Presl	raupo	2	0	wind	>1000	autumn	
Ludwigia palustris (L.) Ell.	water purslane	1	0	drop	>100	summer–autumn	
Juncus gregiflorus L. Johnson	leafless rush	1	0	animal/wind	>100	summer–autumn	60
Cortaderia selloana (Schult.) Asch. et Graeb.	pampas grass	1	0	wind	>100	late summer–early autumn	
Poa trivialis L.	rough-stalked meadow grass	1	0	animal/wind	>100	summer	39
Chenopodium album L.	fathen	0	1	animal	>100	all year	60
Juncus effusus L.	leafless rush	0	3	animal/wind	?	summer–autumn	60,75
J. planifolius R. Br.	grass-leaved rush	0	2	animal/wind	?	summer–autumn	60
Gahnia pauciflora Kirk		0	3	drop	0–10	all year	
Solanum americanum Mill.	small-flowered nightshade	15	79	bird	>100	all year	

Species	Common name			Dispersal	Longevity†	Flowering
*S. mauritianum Scop.	woolly nightshade	13	14	bird	>39	autumn–spring
*S. nigrum L.	black nightshade	3	1	bird	>25	all year
*Cirsium vulgare (Savi) Ten.	Scotch thistle	0	11	wind	>100	autumn
*Phytolacca octandra L.	inkweed	3	18	bird	>100	all year
*Hypochoeris radicata L.	catsear	2	10	wind	>100	all year
Gnaphalium gymnocephalum DC.	creeping cudweed	0	3	wind	>100	summer–autumn
Unidentified		1	4			
TOTALS		494	396			
Ferns:						
Paesia scaberula (A. Rich.) Kuhn	ring fern	3	6	wind	>100	late summer–early autumn
Histiopteris incisa (Thunb.) J. Smith	water fern	1	2	wind	>100	late summer–early autumn
Hypolepis ambigua (A. Rich.) Brownsey et Chinnock		2	1	wind	>100	late summer–early autumn
Pteridium esculentum (Forst. f.) Cockayne	bracken	1	2	wind	>100	late summer–early autumn

*Adventive species
†Seed longevities after Harrington (1972), Ashton & Frankenberg (1976), and Taylor (1980, 1981).

forest and invasive species types; both wind and birds being common agents of dispersal for their seeds (Table 3).

Collection of trays from the field in spring may preclude the existence of viable seed of some species in tray samples. Species fruiting in autumn, and characterised by short-lived seed, are most likely to be absent from tray samples. Kauri is an example of this; cones ripen and fall in March, April, and May, seeds remaining viable for only 6–8 weeks (Mirams 1957). Thus, by late July, no viable seed of this species will be available, even directly beneath parent trees. A number of other canopy tree species present close to tray locations follow this pattern including *Hedycarya arborea, Ripogonum scandens, Dysoxylum spectabile, Nestegis lanceolata, Phyllocladus trichomanoides, Podocarpus totara,* and *Dacrydium cupressinum. Prumnopitys ferruginea* also fruits in autumn, but seeds can take several years to ripen and germinate. Despite its presence in the field area, no seedlings of this species were recorded either from trays or sub-trays.

The absence of certain components of the likely seed rain at tray locations, due to short seed life, infrequent seed production, and season of seed dispersal, immediately reduces the similarity between species composition of the seed bank and existing vegetation surrounding trays. Nevertheless, one may expect some similarity between vegetation, seed rain, and seed bank floristics at any given site. Detrended correspondence analyses of two data sets are described. These analyses illustrate the relationships between each sample type.

Fig. 4 presents results of the DECORANA for woody species (29 species × 28 samples). Eigenvalues decline rapidly over the first three axes (0.723, 0.305, 0.135) indicating that axes 1 and 2 adequately summarise the major sources of variation in species composition present in the data. Sites are readily divided into four zones in ordination space, these zones representing each of the sample types (sub-tray, tray, canopy vegetation, understorey vegetation) (Fig. 4(a)). This implies that each sample type has a characteristic flora. Perhaps surprisingly, canopy composition is more similar to tray floristic composition than is understorey composition at the same site. Inspection of Fig. 4(b) suggests that existing seedlings include shade-tolerant, bird dispersed species (such as *Corynocarpus laevigatus* and *Acmena smithii*), which are not represented by mature individuals on site. The small area of trays relative to vegetation plots may preclude representation of such species in
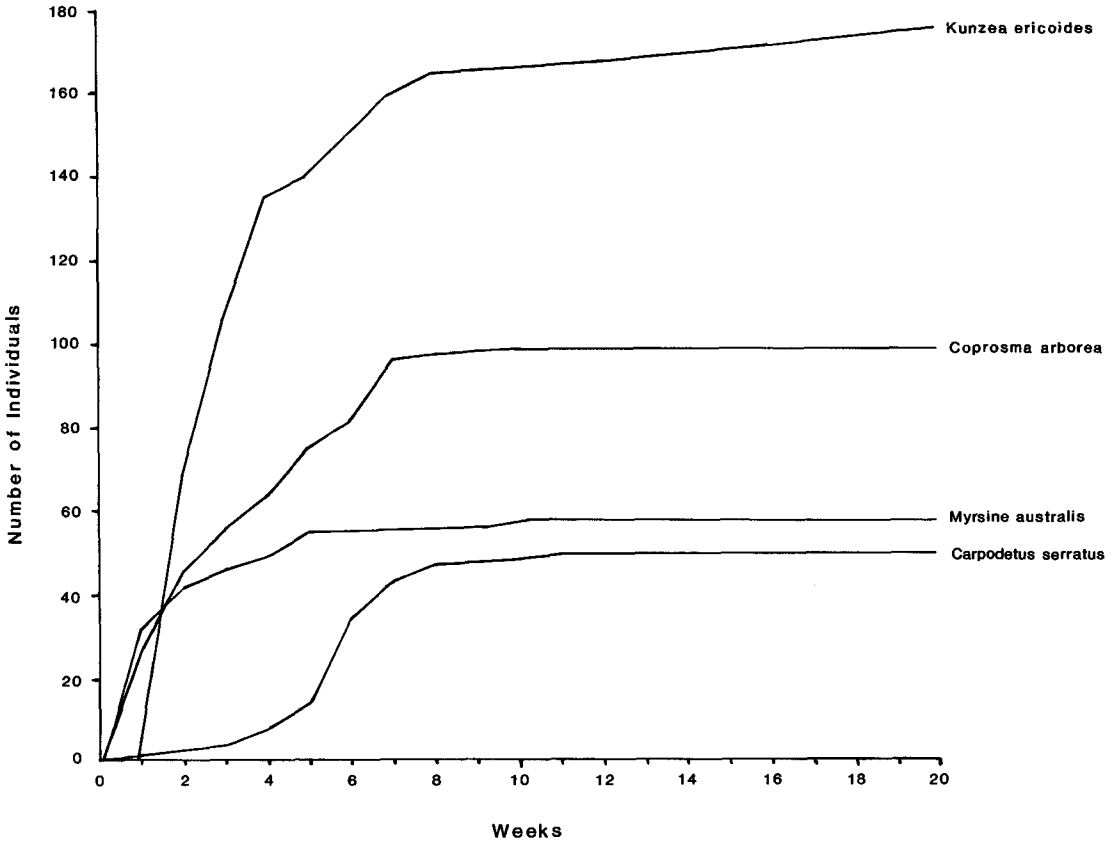
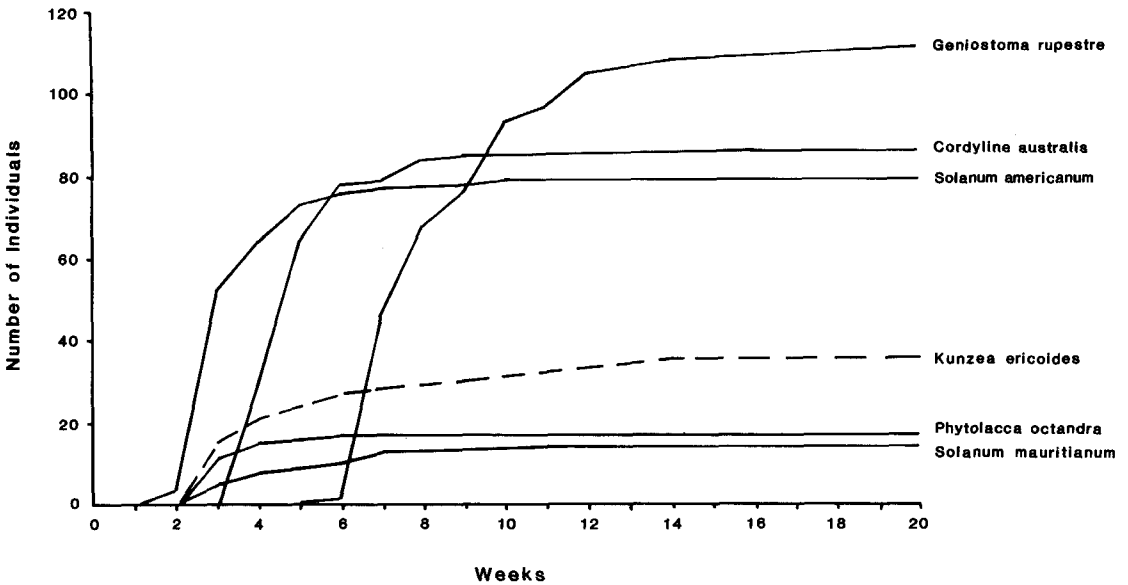**Fig. 2** Pattern of germination over time for dominant components of the soil seed bank in trays.

Fig. 3 Pattern of germination over time for dominant components of the soil seed bank in sub-trays.
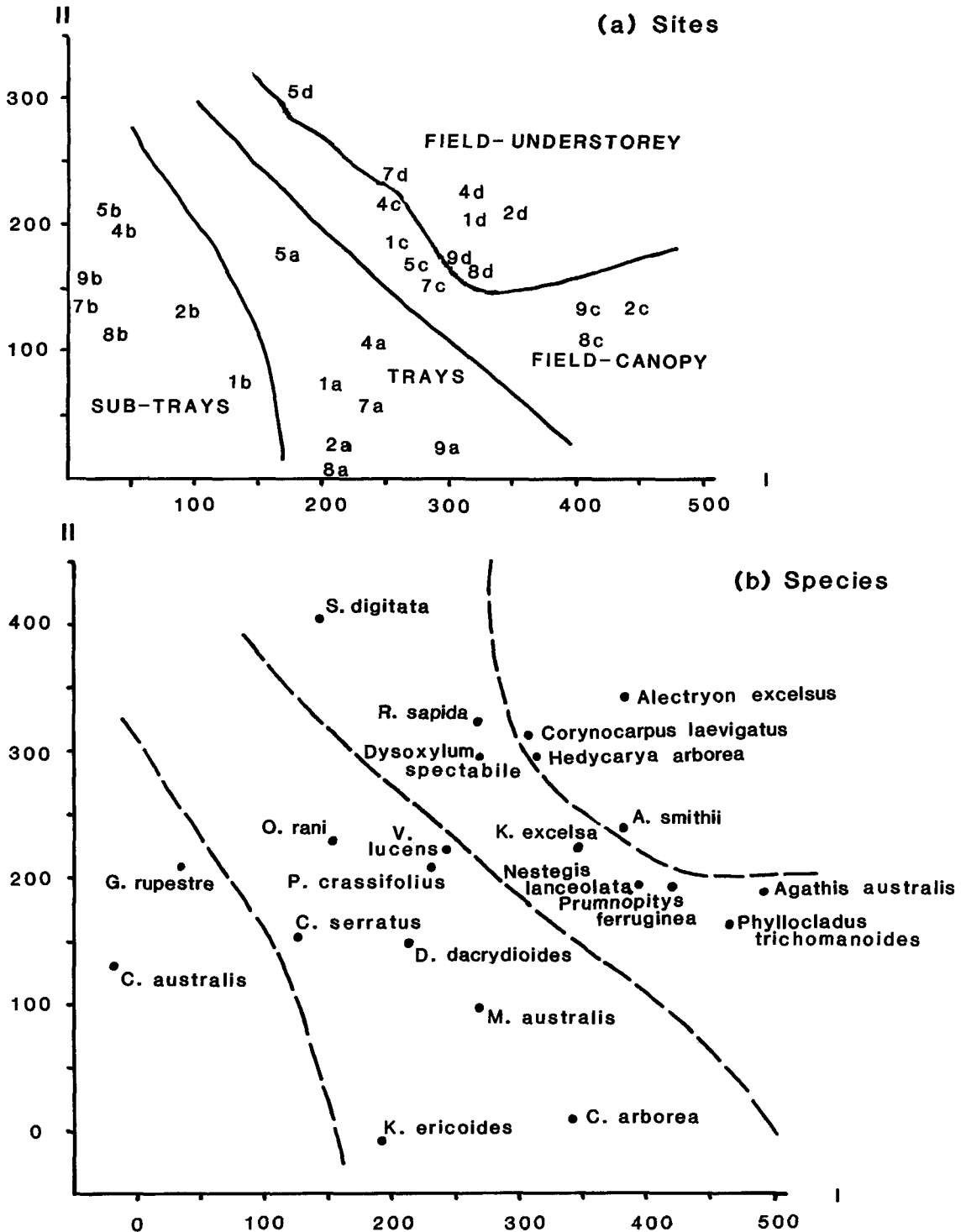
Fig. 4 Location of sites (a) and species (b) on DECORANA axes I and II for the 28 site × 29 species data matrix (woody species only). For expanded binomials see Table 3.

tray samples. Further, tray samples are dominated by shade-intolerant species (including *K. ericoides, Coprosma arborea*, and *Myrsine australis*). These species are unlikely to establish successfully under a well developed forest canopy, but may be present in the canopy as mature individuals. Sub-tray locations in ordination space are determined largely by the abundance of *Geniostoma rupestre* and *Cordyline australis*.

There is no relationship apparent between vegetation age, as estimated using the largest/oldest tree in the 100 m² plot, and either species richness, or similarity between on-site vegetation and the seed bank flora. Sample size is too small to examine these issues further.

While it seems inappropriate to include herbaceous weedy species in the above analysis, since none are likely to grow in the shaded forest understorey, inclusion of these species is justifiable when comparing the floristics of tray and sub-tray samples. DECORANA again divides trays from sub-trays on the first axis (Fig. 5(a)) (eigenvalues decline rapidly; 0.673, 0.228, 0.064). Species present in trays only (i.e., no evidence of seed longevity >2 years) have high loadings on Axis I, while species showing accumulation in the dormant seed bank (seed longevity probably much greater than 2 years) have low loadings (Fig. 5(b)).

DISCUSSION

A number of methodological problems became apparent during the course of this study. For example, seed rain and the seed bank are described in terms of germination and it must be remembered that some viable seed may not have germinated, while much non-viable seed may also be present in the soil samples. Further, collection of the trays in September precludes the presence of some species in the sample, that is, those species fruiting in summer–autumn and having a short seed life. Drainage holes in tray bases could have allowed seed of some species to leach through from tray to sub-tray, thus adding short-lived seed to the supposedly dormant seed bank. While this may have occurred for fern spores, it is not considered likely for any other species recorded here. Finally, although changes in the quality and intensity of light probably triggered germination of most viable, dormant seed in the samples, it is acknowledged that some seed may not have received the appropriate stimuli (King 1966, Vazques-Yanes & Orozco-Segovia 1982).

Five aims were outlined in the introduction, and these are discussed in turn below.

1. The viable seed bank has been described quantitatively. The number of seeds m⁻² is comparable with figures obtained for both tropical and temperate forest sites in a number of other studies (e.g., Kellman 1970a,b, Moore & Wein 1977, Hopkins & Graham 1983, Enright 1985a). However, it should be noted that variability of the estimate is high because of the small ground area sampled and the likely real spatial variation in seed bank characteristics. In the present study lowest seed densities in sub-trays were found in the wettest site (Site 5), and the site with the thickest layer of humus and fine roots (Site 8). This suggests that site conditions may influence seed survival; wet sites, and acid-organic sites, being less favourable than sites with good drainage and lower acidity. Ogden (1985) notes particularly low seed bank densities for sites from Waipoua forest which are similar to site 8 (above) in soil properties and vegetation cover (i.e., dominance of gymnosperm species such as *Phyllocladus trichomanoides* and *Podocarpus totara*).

The perching behaviour of fruit-eating birds may also lead to spatial heterogeneity in the seed bank (Cavers 1983). Bird-deposited seed of *R. sapida* (nikau palm) and *C. laevigatus* (karaka) is particularly abundant on the forest floor at Huapai beneath apparent perch sites (probably for the New Zealand pigeon – *Hemiphaga novaeseelandiae*). While these species have only limited seed longevities, other species may also be added to the seed bank in this way.

2. Tray and sub-tray samples are suggested to represent the seed rain and dormant seed bank respectively. However, while sub-trays are assumed only to contain viable seed of species capable of surviving >2 years in a dormant state, and thus give a clear picture of the "persistent" seed bank (*sensu* Thompson & Grime 1979), tray sample species composition provides a biased view of the seed rain (or "transient" seed bank; *sensu* Thompson & Grime 1979). Trays were left in the field for two years, and thus some accumulation of dormant seed was possible (e.g., *K. ericoides* and *S. americanum*). Furthermore, collection of trays in spring precludes the sampling of species dispersing short-lived seed at other times of the year.

Several woody species are abundant in the persistent seed bank (= sub-trays), including *G. rupestre, Cordyline australis*, and *K. ericoides*. Whereas dominance of seed banks by one or a few
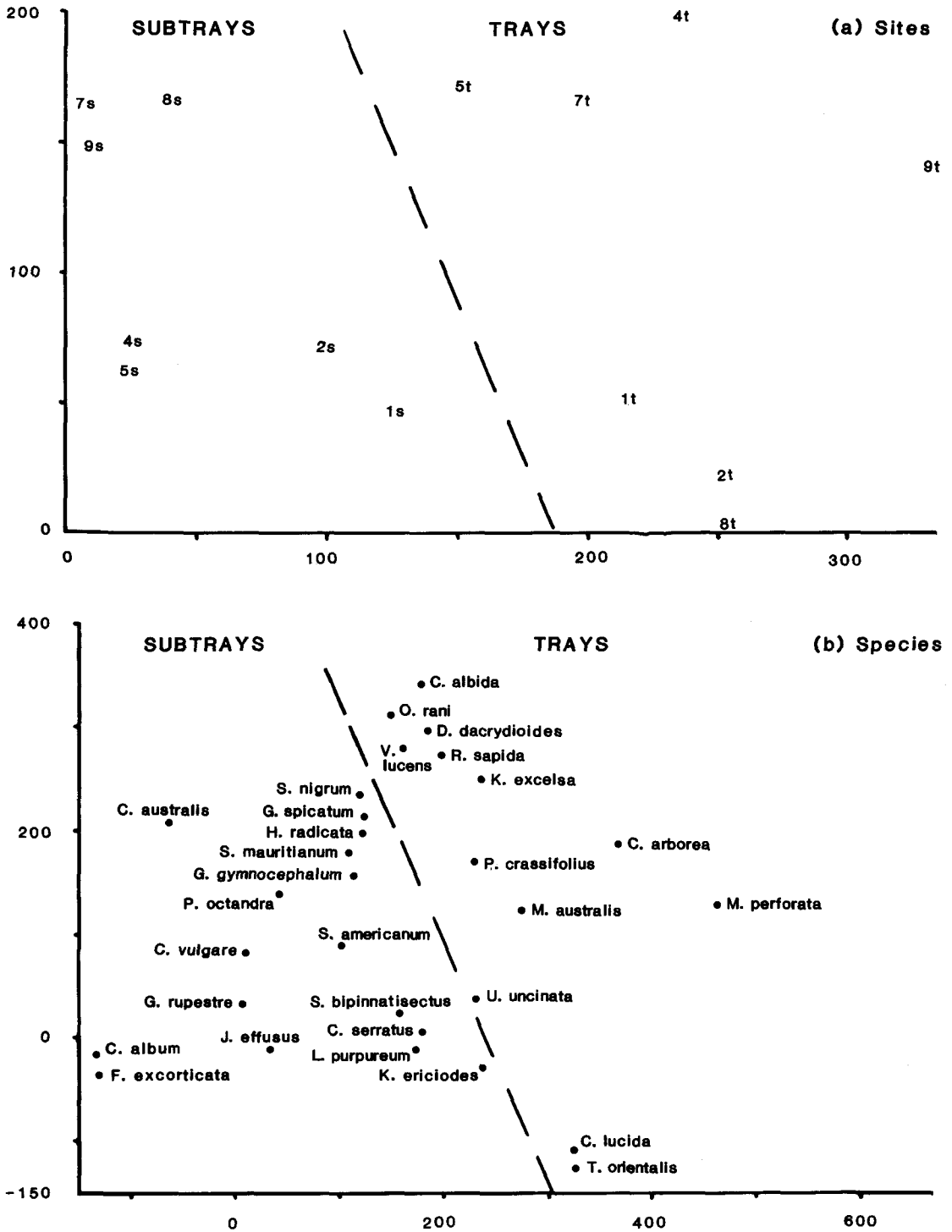
Fig. 5 Location of sites (a) and species (b) on DECORANA axes I and II for the 14 site × 42 species data matrix. For expanded binomials see Table 3. Note: only the 30 most abundant species are shown in (b).

early secondary woody species seems common for tropical forests (e.g., Cheke et al. 1979, Hopkins & Graham 1983, Putz 1983, Enright 1985a), Thompson (1978) notes the absence of woody species from most temperate forest seed banks, these being more commonly dominated by weedy herbs. However, Flaccus (1959), and Canham & Marks (1985), note large seed banks of pin cherry (*Prunus pensylvanica*) in North American hardwood forests, and Kellman (1970a) found *Alnus rubra* to dominate the seed bank under forest in coastal British Columbia. In neither case is it clear how long seed accumulation has been occurring, nor what the likely longevity of seed in the soil may be, although Marks (1974) suggests a longevity of at least several decades for *P. pensylvanica*. Hopkins & Graham (1987) have also illustrated that the seeds of many early and mid-successional species from tropical Australian forests can survive burial for at least two years.

3. Invasion of the forest soil seed bank at Huapai by adventive weedy species is evident. A number of common pasture and roadside weeds are present in the persistent seed bank. These include scotch thistle (*Cirsium vulgare*), inkweed (*Phytolacca octandra*), catsear (*Hypochoeris radicata*), and woolly nightshade (*Solanum mauritianum*). The native weed *S. americanum* (small-flowered nightshade) and weedy native ferns are also common. Seeds and spores of these species derive from adjacent farmland and road verges, and are dispersed into the forest by animals and wind (Taylor 1980, 1981). One such species, *Solanum mauritianum*, was recorded as an epiphyte in the canopies of two nikau palms. Another, *Acmena smithii*, is common as seedlings at Huapai, and in many forest patches in the Auckland region. This species develops a lignotuber over the first few years of growth and is then drought-tolerant (Ashton & Frankenberg 1976). However, no mature individuals are known to the authors for such forest areas and its ability to establish must be limited by factors which remain unknown at present.

The remnant nature of the present field site makes it particularly susceptible to invasion by seeds of adventive weedy species because of the closeness of potential source areas for these seeds. It seems likely that the importance of this invasive component will decline for more secluded forest sites as distance from forest edges increases. Piroznikow (1983) found that in the middle of Bailowieza National Park (the largest forest area in Europe), the soil seed bank was species-poor and contained no weedy species. Only late-successional forest species were present.

4. The similarity between on-site vegetation and species composition of the seed bank was shown to vary in a consistent manner. The persistent seed bank (= sub-tray samples) bears little relationship to on-site vegetation. The seed rain (= tray samples) is more similar to the canopy vegetation on site than to the understorey vegetation, and also shows some similarity to the seed bank flora (since part of the seed rain is destined to enter the persistent seed bank).

Thompson (1978), and others (e.g., Livingston & Allessio 1968) note that seed bank density declines with vegetation age, presumably due to the slow loss of viability of seeds from early successional species. In "old" sites (say >100 years) the continued presence of such species may depend upon the raining-in of immigrant seed. The importance of "inheritance" (addition of seed from parent plants formerly occupying the area e.g., at an earlier successional stage) in determining floristic composition of the seed bank is unclear. In the present study, the high densities of dormant seeds of *Cordyline australis* and *G. rupestre* could be due to the former presence of parent plants near the collection sites. However, whilst densities for both species are particularly high in one site, they are present at moderate density in nearly all sites sampled. The abundance of *G. rupestre* in the persistent seed bank is indicative of its adaptation to disturbed sites and, presumably, its need for canopy gaps for successful regeneration. Ogden (1985) specifically notes this species as a gap coloniser. However, it is common in the forest understorey, and, once established, appears able to survive shading for many years. The species is monoecious and has a sex ratio of 8♂:5♀ at the Huapai field site (Rattenbury pers. comm.). This could help to explain site to site variations in the seed bank for this species.

Ogden (1985) also describes *Carpodetus serratus* and *Fuchsia excorticata* as gap colonizers. One individual of *F. excorticata*, which is bird dispersed, was recorded for the persistent seed bank at Huapai. On the other hand, all *C. serratus* at Huapai were recorded from the transient seed bank component, suggesting efficient dispersal, but limited seed longevity.

5. The role of the seed bank in secondary successions in kauri forest assumes greater

significance as the number of adventive species (and individuals) increases. Of 25 species showing seed survival >2 years, 12 are adventive species. The number, and density, of such species is likely to be highest for forest areas close to disturbed or modified sites.

Many of the component species of kauri forest are able to resprout after being damaged by events such as tree falls and storms. Species at Huapai showing the ability to resprout include *Cordyline australis, Melicytus macrophyllus, G. rupestre, Coprosma lucida, Carpodetus serratus, Schefflera digitata, Hedycarya arborea, Vitex lucens, Olearia rani,* and others. These species range from having short-lived seeds (e.g., *M. macrophyllus*) to abundant seeds in the seed bank (e.g., *C. australis* and *G. rupestre*). Disturbances which do not expose the litter and soil to increased light intensity will not trigger germination of seeds from the seed bank. Tree falls often increase the depth of litter (tree fall debris) over much of the canopy-gap area created, and this precludes involvement in vegetation recovery by the seed bank. Rather, repair is effected mostly through recovery (resprouting) of existing individuals, and increased growth rate for undamaged seedlings. Only in small patches where the soil is exposed will seed bank individuals germinate. The pattern described here is clearly illustrated in a canopy-gap at Huapai caused by the tree-fall of a large kauri late in 1985. Where soil is exposed to increased light intensity, a number of the species recorded in sub-tray samples are found. These include *Cirsium vulgare, Phytolacca octandra, Solanum mauritianum, S. americanum, Hypochoeris radicata, Cordyline australis,* and *Geniostoma rupestre.* Other seedlings noted include *Haloragis erecta, Pseudopanax crassifolius, Coprosma arborea,* and *Dacrycarpus dacrydioides.* The last three of these represent seasonal seed rain, and highlight the fact that species composition following site disturbance (or destruction) will vary with the time of site creation as well as with the site's suitability for colonisation by components of the seed bank.

Site destruction (e.g., by fire) decreases the possibility of recovery from resprouts and necessitates the initiation of a succession from seed for most species. The fact that many of the species in kauri forest both produce abundant seed and resprout, may imply adaptation to both levels of site disturbance. Indeed, Ogden (1985) implies that fire must have been important in the development of large kauri forest stands. In these circumstances the seed bank may be a more important contributor to the succession, providing a ground cover, first of weedy herbaceous species, and later, of relatively short lived woody species including *K. ericoides, C. australis,* and *G. rupestre.* Even some slower-growing, late-successional species such as *Vitex lucens, D. dacrydioides,* and *P. ferruginea* may originate from the seed bank.

ACKNOWLEDGMENTS

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