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Gap regeneration and forest dynamics in a  
lowland podocarp-broadleaved forest  
remnant, Keeble's Bush, Manawatu.

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Massey University, Palmerston North.

“New Zealand’s protected natural areas are more than just museum pieces, a window into the past. They are a source of hope, because within these areas is an abundant source of seeds, the genetic material which could be used to recreate and restore each region’s distinctive forest heritage.”

The living forests of New Zealand - Cobb *et al.*, 1992.

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## Abstract

Gap phase regeneration and forest dynamics were investigated in a lowland podocarp-broadleaved forest remnant, Keeble's Bush, Manawatu, in order to assess its ecological integrity. To this end the seed rain (*i.e.*, viability and diversity of fresh seed input), seedling diversity and survival, and soil seed bank composition were all assessed.

A total of 40 different species were trapped in the seed rain, contributing a total of 2398 seeds/m<sup>2</sup>/yr. A high coefficient of variation for seed number and diversity was recorded between traps, illustrating the spatial heterogeneity of the seed rain. Strong seasonal patterns were recorded in the fruiting phenology of the species trapped. A lack of red-arilled viable seeds suggested that 1992 was not a mast year for rimu.

Most of the seeds likely originated from individuals less than 50 m from the seed traps, reflecting the paucity of native frugivores to disperse seeds further, particularly those less than 10 mm in size. Virtually all the adventive species trapped were herbaceous with most having wind dispersed seeds. All of them were local in origin; *i.e.*, already present within the gaps at the time of trapping.

The total number of seedlings, and the seedling densities in the two gap sites studied were very similar in both 1992 and 1993. Despite the flux of seedlings into and out of the populations at each site seedling numbers remained stable. Species diversity and number of species/m<sup>2</sup>, varied between gaps, with the species population in Gap Two species poor compared with that in Gap One (10 species were shared, with 9 exclusive to Gap One, and 3 present only in Gap Two). Seedling mortality in Gap One fitted the well documented phenomenon of huge mortality during the initial period of establishment and growth. Seedlings in Gap Two, however, showed equal probability of mortality in all height classes. Competition (both above and below ground), browsing by exotic herbivores, drought stress, and litter burial all likely contribute to seedling mortality. The results suggest that the seedling populations in gaps differ between those gaps within the forest interior (Gap One), and those at the forest margin (Gap Two).

Seedlings from 36 species emerged and were identified from the sampled soil seed bank, contributing a total of 821 seedlings. Herbs were the most important life-form in the soil seed bank, making up 77.5% of the total seedlings. Adventive species accounted for 16 of the 36 species, 14 of which were herbaceous. Seedlings of primary forest trees contributed only 1.2% of the seedlings, and emerged from only three of the eight sampling sites. Germination was rapid with the first seedlings emerging from the soil samples within seven days of the start of the experiment; over 86% of the seedlings emerged within the first month. Adventive species dominated the seedlings emerging for the first five weeks.

The number of species and individuals which germinated decreased with soil sample depth. The highest number of seedlings and species occurred in the top 2 cm of soil, with 80% of the seedlings within the top 4 cm. The soil seed banks of the gaps were more diverse, with greater numbers of species and seedlings, compared with sites beneath intact canopy. The results of the longevity experiment suggest tawa and titoki may maintain a short-term transient seed bank, if the seeds are buried rapidly. Kawakawa seeds appear to suffer high predation/decomposition and are likely to last for a shorter period in the soil. Radiata pine does not maintain a seed bank in the soil.

Management implications for Keeble's Bush were discussed, and directions for future research suggested.

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# Chapter 1

## 1.1 Introduction

Natural disturbances (*e.g.*, windstorms, landslides, drought, glacial advances, and volcanic eruptions; Ogden & Stewart, 1995) in biological communities create mosaics of patches, on different spatial and temporal scales (Pickett & White, 1985). The three main components of disturbance are intensity, size, and extent, all of which are inter-related. As size and intensity of disturbance increase, so do the opportunities for species change and the probabilities that species composition will be altered (Hopkins, 1990). Most often disturbances result in the creation of 'open space', *e.g.*, gaps in forests.

The ability of forests to regenerate following disturbance is crucial for their long term maintenance, with factors such as seed production, seed maturation, germination, seedling survival and establishment (refer Chapter 4), and availability of suitable germination substrates, all involved in the regenerative process (Fenner, 1985; Zasada *et al.*, 1992). However, the most basic requirement is the production of viable seeds (Fenner, 1985).

Vegetation regrowth patterns after disturbance are extremely diverse, according to the nature of the disturbance and the regenerative nature of the species concerned; the individual properties of the tree species which occur in any region are a major determinant of the patterns of sequential change (Burrows, 1990). The regeneration patterns of species that reproduce by means of seed are affected by the periodicity of seeding, the number of viable seeds produced, the numbers of seedlings which become established, the time taken for seedlings to reach reproductive age, the mortality through these stages, and the longevity of the adults (Burrows, 1990). Burrows (1990) provides a recent review on the evolution of theories and ideas relating to vegetation change and dynamics.

In many forests the gap phase is of vital significance as part of the 'forest growth cycle' (Whitmore, 1975). The 'gap phase' is the relatively brief period during which the gap is receptive to colonisation, from the time of its formation to the development of a seedling/sapling thicket (Smale & Kimberley, 1983). It is followed by the building and mature phases of the forest growth cycle (Watt, 1947). Studies of gap formation and closure provide

insight into future forest composition and structure, though most have concentrated on replacement of small scale gaps (*e.g.*, created by one or several tree falls) (Spies & Franklin, 1989).

Following disturbances, rainforests regenerate along a number of pathways: the seed bank (refer Chapter 5), the dormant soil seed bank, advanced regeneration, coppice and canopy ingrowth (*e.g.*, Brokaw, 1985; Garwood, 1989). Different regenerative pathways are favoured under different disturbance regimes and intensities (Russel-Smith & Lucas, 1994). For example, chronic tree falls create canopy gaps and constitute the main form of small-scale disturbance in rainforests (Alvarez-Buylla & Garcia-Barrios, 1991). In these canopy gaps regeneration of tree species occurs primarily through seedlings and advanced regeneration, with a relatively small contribution by the soil seed bank (Hopkins & Graham, 1984). Canopy gap dynamics are important in temperate forests too, with small canopy gaps resulting from the fall of one or a few trees common (*e.g.*, North American temperate deciduous forest, Runkle, 1985; New Zealand kauri forest, Enright *et al.*, 1993).

Potentially important gap properties which determine suitability for a species include size, shape, slope, aspect, soil texture, within-gap environmental heterogeneity, time of formation and length of persistence, influence of gap-creating species and interference with understorey plants (Fenner, 1985; Stewart *et al.*, 1991; de Freitas & Enright, 1995). The capability of a species to utilise a gap depends on its ability to disperse into it, and establish on an appropriate microsite, and compete with other individuals in a potentially changing environment; the gap canopy boundaries, and below- and above-ground competition change over the period from dispersal to seedling establishment, and sapling growth.

Gap size is of fundamental importance, as it influences the microclimate relating to seedling growth and so determines those species most likely to capture a gap of given size (de Freitas & Enright, 1995). The bigger the gap the greater the solar radiation at the forest floor, and the greater the changes in other facets of microclimate above- and below-ground from conditions beneath the closed canopy. Falling tree size is strongly correlated with the subsequent area of the gap created (Brokaw, 1982), so as tree size increases during secondary succession, larger gaps become more frequent.

### 1.1.1 Regeneration gaps and forest dynamics in New Zealand forests

“Early research into forest dynamics in New Zealand was strongly influenced by the imported idea of a gradual and orderly succession to a predetermined and stable climax community” (Ogden, 1985). These ideas are now considered inappropriate as a demographic framework for New Zealand forests because of the prevalence of disturbance; *e.g.*, storm damage (*e.g.*, snapping of trunks or over turning of whole trees can occur during violent storms associated with deep depressions (Wardle, 1991)), fires, vulcanism, earthquakes and avalanches (Ogden, 1985).

According to the scale and severity of natural disturbance in New Zealand forests, three main types of regeneration pattern can be discerned (Ogden & Stewart, 1995):

1. ‘Catastrophic regeneration’ which refers to the establishment of most of a population during a short term in large openings (canopy gaps) formed by infrequent, massive disturbances such as fire or windthrow. This is the typical regeneration pattern of shade-intolerant species.
2. ‘Gap-phase regeneration’ referring to regeneration in smaller gaps (<1000 m<sup>2</sup>), such as those resulting from the death of one to several trees. This type of regeneration results in smaller patch sizes (*e.g.*, Lusk & Ogden, 1992).
3. ‘Continuous regeneration’ resulting from the growth of shade-tolerant seedlings and saplings beneath forest canopies so that there is a continuous replacement of older, dying canopy trees.

The dynamics of podocarp-broadleaved forests, like that studied here, are complex (Lusk & Ogden, 1992). They typically experiences regular small-scale disturbances, *e.g.*, creating single or multiple tree-fall gaps, and therefore undergo gap-phase regeneration. Most tree deaths are the result of the combined effects of disease (*e.g.*, wood borer, fungal rot), attacks by grazers, physiological stress, and damage caused by weather (Burrows, 1990). The resulting regeneration within these gaps produces a mosaic of patches of different ages and

different species composition.

### 1.1.2 Exotic modifying influences

Response to disturbance of the canopy depends largely on the composition and condition of the understorey, especially its content of young plants of dominant species (Wardle, 1991). However, in most New Zealand forests the understorey has now been influenced by a suite of introduced browsers and predators (see below). The degree of forest damage caused by introduced herbivores is a reflection of many factors, but in particular, the concentration of the introduced animals, their length of occupation, and the availability of alternative food sources (*e.g.*, pasture species are available to animals occupying forest margins bordering agricultural land). Even with complete removal of introduced herbivores it is unlikely vegetation will quickly to a return to its original structure and composition. The composition of the understorey will have changed, and palatable tree and shrub species will have been selectively removed. Those species that have increased in abundance due to their unpalatability or increased vigour from increased light may continue to dominate for decades or centuries (Wardle, 1991).

The main browser of foliage in New Zealand forests today is the brushtail possum (*Trichosurus vulpecula*). These marsupials often completely and repeatedly defoliate their preferred species, to the point where whole stands are killed; *e.g.*, northern rata (*Metrosideros robusta*<sup>1</sup>), kamahi (*Weinmannia racemosa*), tree fuchsia (*Fuchsia excorticata*), and mistletoes (*e.g.*, *Elytranthe* spp.) (Wardle, 1991). They are virtually ubiquitous now, having successfully spread to most corners of New Zealand from their numerous release sites (from 1858 to the middle of this century; King, 1995). Other widespread exotic animals include deer (*e.g.*, *Cervus* spp.), feral goats (*Capra hircus*), pigs (*Sus scrofa*), and domestic stock (sheep [*Ovis aries*], goats and cattle [*Bos taurus*]) *etc.* Their influences on indigenous vegetation, both alone and in combination, have also been considerable, though their distributions are less

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<sup>1</sup> Nomenclature follows Allan (1961), Moore & Edgar (1970), and Connor & Edgar (1987) for native angiosperms and gymnosperms, and Webb *et al.* (1988) for adventives. Common and scientific names used in the text are listed in Appendix 1.

continuous than those of possums. A comprehensive account of their introduction histories, current distribution and ecology is given in King (1995).

Predators have also had an impact on vegetation composition in indigenous ecosystems, though the effects are less direct and harder to quantify. Mustelids (stoats [*Mustela erminea*] and weasels [*Mustela nivalis vulgaris*]) reduce native bird numbers and diversity, which may lead to reduced flower pollination, seed set and dispersal. Rats (*e.g.*, ship rats [*Rattus rattus*]) also predate native birds, and together with mice (*Mus musculus*), destroy seeds and fruit of a number of plant species (*e.g.*, mahoe [*Meliccytus ramiflorus*], pigeonwood [*Hedycarya arborea*], *Coprosma* spp. and supplejack [*Ripogonum scandens*]; Allen *et al.*, 1994).

### 1.1.3 Forest fragmentation

The fragmentation of continuous tracts of forests into smaller, spatially discrete, units is a worldwide phenomenon. In New Zealand extensive forest fragmentation has taken place over the past 150 years (Young & Mitchell, 1994), with present forest cover reduced to less than 23% of its original extent. An understanding of regeneration and forest dynamics within the resulting forest fragments then is of great importance; they are often the only remaining examples of previously widespread forest types (*e.g.*, kahikatea (*Dacrycarpus dacrydioides*) forest on alluvial terraces in the Waikato Region; Leathwick *et al.*, 1995), and provide refuges for local, rare and endangered species (or even common, widespread species that are now locally rare).

Direct and immediate results of forest fragmentation include an increase in the perimeter:area ratio, and a reduction in the number of species (both plant and animal) the forest is able to sustain. Along these 'artificial' forest margins, differences in both the microclimate and vegetation composition occur, these are termed 'edge effects' (Young & Mitchell, 1994). Margins experience increased wind velocity, drought stress, lower relative humidity, greater light levels (PAR) and greater temperature fluctuations than sites in the forest interior (Williams-Linera, 1990), and are therefore dominated by species (*e.g.*, mapou [*Myrsine australis*]) that can tolerate these conditions. The effects may be seasonal, with differences more extreme during the summer months, and may penetrate forest remnants for up to 50 m

( Young & Mitchell, 1994). Understorey exposure is increased, and large trees, no longer buffered by a surrounding continuous canopy, may experience greater canopy damage and even windthrow.

A number of characteristics are likely to govern the likelihood of long term sustainability of a forest remnant, including size, shape, distance to the nearest (indigenous) neighbour, concentration and diversity of introduced herbivores and predators, and presence of threatening adventive weeds (*e.g.*, old mans beard [*Clematis vitalba*] or wandering willy [*Tradescantia fluminensis*]). Large, compact forest remnants, close to large tracts of native forest, with low exotic animal numbers, are more likely to be vital and self sustaining; edge effect is minimised, possible seed sources are close by to maintain species diversity, bird diversity and density are likely to remain higher with species travelling between the two, and the selective removal of palatable species is less likely.

## 1.2 Aim of the study and thesis outline

### *Aim*

Three aspects of regeneration ecology were investigated in this study:

1. seed rain, *i.e.*, viability and diversity of fresh seed input,
2. seedling diversity and survival, and
3. soil seed bank composition,

focusing on the gap phase of the forest growth cycle (Watt, 1947), in order to assess the ecological integrity of the forest remnant studied (Keeble's Bush; Location map Fig. 2.1), in one of the most deforested Ecological Districts in New Zealand (Ravine, 1995).

### *Thesis outline*

This thesis is presented in four primary chapters. Chapter 2 provides a brief history of the pattern of vegetation modification that has occurred in the Manawatu Ecological District, following the arrival of humans. It introduces Keeble's Bush, the study area, and describes

each of the main study sites.

Chapter 3 examines the pattern of seed rain into the four gaps studied (G1, G2, BG1, BG2) and into the adjacent forest understorey. The diversity, temporal variation and viability of the seed rain are all assessed, along with the relative contributions of seeds from local and distant sources. Data is also presented on the proportion of adventive propagules.

In chapter 4 the diversity, density, and survival rates of the woody tree and shrub species within two gap sites (G1 and G2) is assessed. In addition, comparisons are made between the adult assemblages of the surrounding vegetation, and the current seedling populations. Survival rates and mortality factors are also investigated for seedlings of titoki (*Alectryon excelsus*), a dominant canopy tree in the study area.

Chapter 5 describes the species composition and density of viable seed in the soil seed bank, at different soil depths. Seed longevity of four species (kawakawa [*Macropiper excelsum*], mahoe, radiata pine [*Pinus radiata*], and titoki) following artificial burial is also determined.

The final chapter draws together results from the preceding chapters, providing an overview. Some management recommendations are made, and suggestions for further research.

# Chapter 2

## The study area.

### 2.1 Location and description

#### 2.1.1 The Manawatu

The vegetation of New Zealand has been influenced by humans since the earliest arrivals about 1000 years ago. Despite the simple technology and the handful of plants and animals they brought with them, early humans had far reaching effects on the New Zealand biota (Bishop, 1992). Large tracts of forest were destroyed by 'hunting fires', most notably those in the central North Island, and east of the Southern Alps in the South. Within 500 years many of our unique flightless birds were extinct, with many more rare or restricted in their ranges.

The original Maori population in the Manawatu was sparse in comparison with other New Zealand districts. Maori settlements were established mainly on the margins of the rivers (the Rangitikei, Manawatu and Oroua), where there was arable soil (Esler, 1978). The rivers served as the main inland means of communication. Consequently most of the forest remained intact except for a few small clearings, mostly natural, where pa and kainga were located (Esler, 1978). Europeans reached the Manawatu around 1840, with settlements established in the 1860's. Since that time the vegetation of the Manawatu district has undergone dramatic changes.

Virtually all the forest in the area had been logged or burnt for farming and urban development, by the early 1900's. The Manawatu's forests yielded millions of cubic metres of millable timber. Totara (*Podocarpus totara*), once present in huge stands, was highly sought after and so removed first. Rimu (*Dacrydium cupressinum*), matai (*Prumnopitys taxifolia*) and kahikatea were also sought after, much of the latter becoming butter boxes. The once extensive lowland forests were consequently reduced to small isolated fragments.

Unfortunately few records were made of the botanical composition of the original forests of the Manawatu. Esler (1978) provides the definitive account of what is known, offering several

reasons for the lack of botanical exploration in the district;

1. The coast offered no anchorage for large visiting ships,
2. Travel routes lay along the Manawatu River and the sandy coast, while the heavy forest and swamps were not easily penetrable, and
3. the region lacked prominent features such as lakes or outstanding mountain peaks to attract the special attention of plant hunters and explorers.

Those remnants which remain provide glimpses of the structure and composition of the original extensive lowland vegetation.

### 2.1.2 Keeble's Bush

Keeble's Bush where the present study was undertaken is one such remnant. Situated 2 km southwest of the Massey University campus (NZMS 260, Palmerston North, T24 863305) (Fig. 2.1), it is the finest remaining fragment of the mixed podocarp-broadleaved forest that was once widespread on lowland alluvial terraces in the Manawatu. The Bush covers an area of 14.3 ha on low-level terraces above and south of the flood plain of the Maungatungaroa Stream, a true left tributary of the Manawatu River. It is bounded on the north-western and southern sides by farm roads, and to the south-east and north-east by pasture. The vegetation of the bush has been described in Esler (1962).

The bush contains more vascular species than any of the other surviving remnants in the district, and in parts still retains the canopy and structure of the original forest. All five species of lowland podocarp are present, with rimu, matai and kahikatea the most abundant. There are also a number of plants which now occur naturally nowhere else in the district. Esler (1962) identified 35 native plant species that occurred in Keeble's Bush and only one other of the 10 remnants (greater than or equal to 15 ha) described, in the Manawatu. Of those 35 species, 18 were still present, ten were uncommon, one was no longer found, and six were not recorded by Druce & Greenwood (1979). Atkinson & Greenwood (1972) also indicate that Keeble's Bush is of particular value from a scientific point of view, as it lies in a rainfall of 1000 mm, near the climatic limit of rimu.

Fenced off by Mr C.T. Keeble, who purchased the block of land including the bush in 1894, the bush has been kept virtually free of domestic stock with minimal human interference for nearly a hundred years. Selective logging of some mature podocarps may have occurred in the 1930's (Don Ravine, *pers. comm.*). Following Mr Keeble's death in 1971, fencing did deteriorate and some stock trespass occurred, but the fence has been maintained since the early 1980's. Despite low levels of human interference, natural processes have modified or destroyed the canopy in a number of places, and the vegetation is in a state of flux. Much of the canopy modification can be attributed to wind-thrown trees, with increased exposure of the tree crowns, and influence of exotic animal species (see below).

Natural tree falls have created many gaps, many of which have been colonised by adventive species which are now part of the surrounding vegetation. A number of these are aggressive, and once established are extremely difficult to remove (Myers, 1987; Timmins & Williams, 1991). Blackberry (*Rubus fruticosus*) is one of the most persistent, filling some gaps with canes which remain and can resprout after spraying. Other aggressive and potentially harmful weeds present include wandering willy, old man's beard, Japanese honeysuckle (*Lonicera japonica*), and elderberry (*Sambucus nigra*).

The clearing of the land surrounding the bush and its conversion to pasture last century has, as mentioned, increased the exposure of the tree crowns. This has made the bush more vulnerable to strong winds, like those experienced in the 1936 gale (Esler, 1978) which blew down a number of emergent podocarps (Greenwood & Skipworth, 1972). The increased exposure also makes the canopy trees susceptible to drought, as illustrated by that of 1969-70 (Atkinson & Greenwood, 1972) which caused a number of tree deaths, particularly of rimu and tawa (*Beilschmiedia tawa*). To alleviate these problems Mr Keeble planted radiata pine, eucalypt (*Eucalyptus* spp.), macrocarpa (*Cupressus macrocarpa*) and wattle (*Racosperma* spp.) around the perimeter of the bush to provide shelter (Atkinson & Greenwood, 1972).

Introduced mammals are responsible for further degradation within the bush. There are many possums in the bush, and in the surrounding shelter belts, as evident from the amount of sign, and the number trapped. The exact impact of the possums on the bush is difficult to determine, but studies in the Orongorongo Valley suggest that they affect both the survival of

existing trees and regeneration (Brockie, 1992; Cowan, 1990; 1991). In addition to possums, rabbits (*Oryctolagus cuniculus*), hares (*Lepus europaeus occidentalis*), ship rats (Innes, 1977) and mice (Moore, 1977) also appear to be abundant.

### 2.1.3 Management of Keeble's Bush

Following the death of Mr C.T. Keeble in 1971 Keeble's Bush was left to be administered by a trust board (consisting of representatives from Massey University, the Manawatu District Council, and the Dept. of Conservation), who were charged with

“holding the area of land comprising approximately 30 acres of native bush at Fitzherbert West (together with access thereto from the Palmerston North-Shannon highway)...**to keep maintain and preserve the same and the indigenous forest and growth thereon in perpetuity as a specimen and example of primitive and undamaged Manawatu rainforest for study and observation** in accordance with the trust in the said will set forth and to that end....” .

The will was contested, preventing the trust board from being established until the late 1970's. Since that time the fences have been maintained, areas of rank grass at the margins of the Bush have been planted to encourage re-establishment of native vegetation, and most of the large radiata pines along the margin have been felled (April 1995). No formal management plan has been established; however, some planting, weed control, and sporadic animal control has been carried out over the last 25 years.

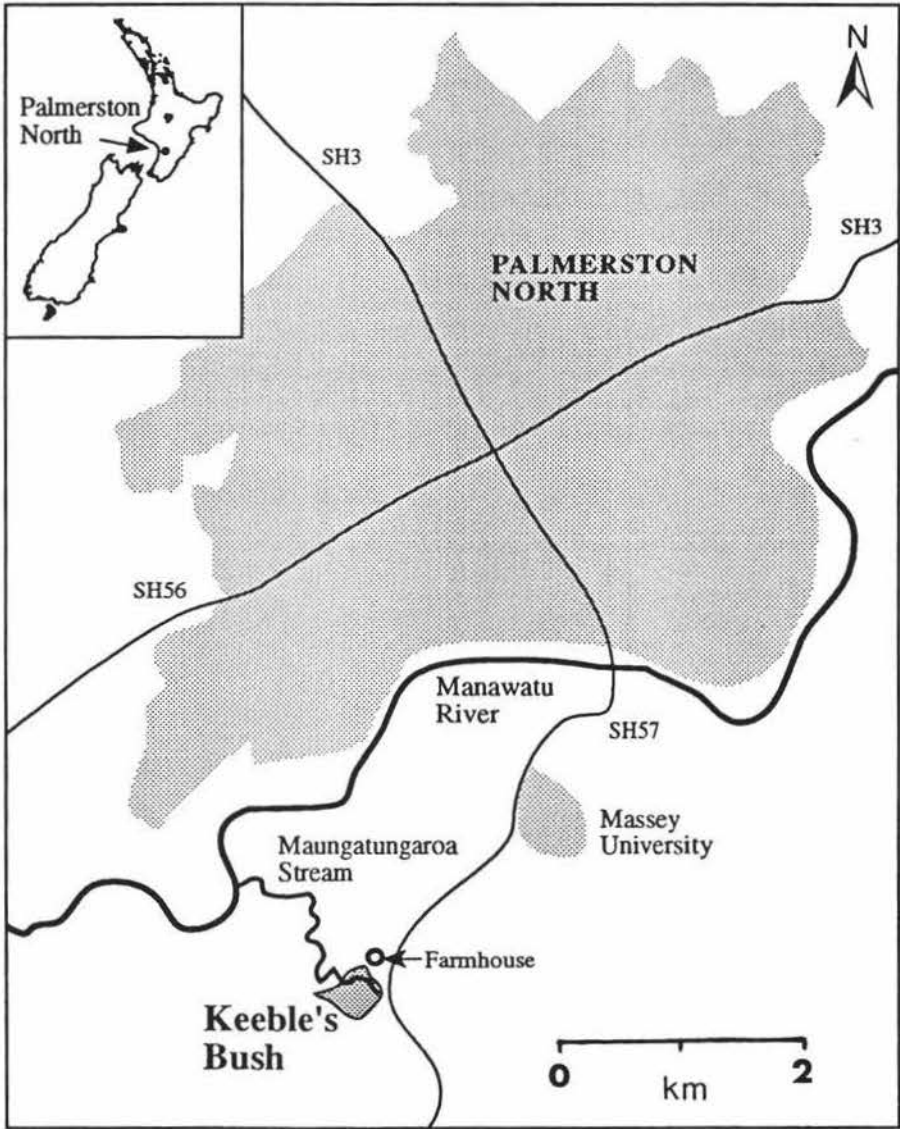


Fig. 2.1 Location of Keeble's Bush.

## 2.2 Climate

The climate of the Manawatu is characterised by warm summers, mild winters and reliable rainfall distributed evenly throughout the year. The prevailing winds are westerly to north-westerly, and occur 30-50% of the time. Gales are relatively frequent (Tomlinson, 1976), with high average daily wind runs throughout the Manawatu Plains Ecological District (Ravine, 1995).

Rainfall varies between 800-1200mm per annum (Ravine, 1995). The average numbers of rain days per annum range from 120 to 173 in different parts of the Manawatu district. There is large variation in total annual fall with lighter fall experienced in the coastal belt (Burgess, 1988). The rainfall is fairly evenly spread throughout the year, with March the driest month, and June the wettest month.

Mean monthly temperatures range from 8°C in July to 17.5°C in February, with 12.6°C the average annual temperature (Burgess, 1988). The highest temperatures are attained in central parts of the Manawatu Ecological District, with the average maxima of 28.5°C at Kairanga and 28.3°C at Palmerston North airport (Ravine, 1995).

The number of days with ground frost recorded at the D.S.I.R. station, opposite the University averages 64.3 per year. Frosts are most common from April to October. The greatest number of frosts occur in June, July and August; the numbers averaging 11.5, 14.7 and 12 respectively, and these include quite severe frosts (Burgess, 1988). Snow fall is rare beneath 610 m on the Tararua Ranges.

For five months of the year (summer and autumn) the water needs of the plants exceed rainfall. The reserves of moisture in the soil is normally sufficient to maintain plant growth during this period. On average, there are 10-15 days in both January and February when a wilting point deficit occurs (Burgess, 1988).

## 2.3 Soils

The soil which underlies Keeble's Bush has been mapped as Ohakea silt loam, a weakly leached, strongly gleyed yellow grey earth described as having poor natural drainage, weak clay differentiation and a moderate to strongly acid top soil with high phosphorous, calcium and potassium content and medium magnesium content (Cowie *et al.*, 1973; Abraham, 1981).

## 2.4 Description of study sites

The study sites were selected subjectively in an attempt to include gaps representative of those throughout the bush. The gaps chosen were at least 20 m<sup>2</sup> in extent, easily accessible, and discrete from each other (Fig. 2.2). No rigorous definition of a gap was applied to the sites chosen as such; they were areas without a continuous high canopy, with vegetation <1.5 m in height.

### 2.4.1 Gap One (G1)

Gap One is 23 m<sup>2</sup>, and likely formed as the result of a natural tree fall at an unknown time in the past. The original size has probably been reduced by lateral ingrowth of surrounding individuals (Figure 2.2; 2.3). The ground cover within the gap is dominated by *Hydrocotyle* spp. and *Carex* spp., *Haloragis erecta*, bracken (*Pteridium esculentum*), spear thistle (*Cirsium vulgare*), and foxglove (*Digitalis purpurea*). A large cabbage tree (*Cordyline australis*) grows in the centre of the gap. *Fuchsia perscandens* forms a delicate curtain along the eastern edge, with pohuehue (*Muehlenbeckia australis*) blanketing patches of the surrounding canopy. The surrounding forest canopy (12-20 m high) is predominantly mahoe and titoki, with several tawa trees, houhere (*Hoheria populnea* var. *sexstylosa*), rewarewa (*Knightia excelsa*), kaikomako (*Pennantia corymbosa*), and lemonwood (*Pittosporum eugenioides*). A single large emergent rimu is the only podocarp within 30 m of the gap. Kawakawa dominates the understorey with lower numbers of kaikomako, kanono (*Coprosma grandifolia*), rangiora (*Brachglottis repanda*), hangehange (*Geniostoma rupestre*), mapou, poataniwha (*Melicope simplex*) and small-leaved milktree (*Streblus heterophyllus*).

### 2.4.2 Gap Two (G2)

Gap Two lies close to the forest margin in the north-western corner, and covers approximately 21 m<sup>2</sup> (Figure 2.2; 2.4). A decomposing trunk and root ball at the eastern edge of the gap is all that remains of the titoki tree which originally created it, probably over 15 years ago. The fern *Phymatosorus scandens* is common over parts of the gap floor, as are the annual small-flowered (*Solanum americanum*) and black nightshade (*Solanum nigrum*) during the summer months.

The area surrounding the gap differs considerably in composition to the interior of the forest. Kawakawa, mahoe and titoki dominate both the understorey and low canopy. Also present in low numbers are the shrubs *Coprosma areolata*, small-leaved milktree, poataniwha, mapou, shrubby mahoe (*Melicytus micranthus*), and houhere. Three trees have been planted in the gap (one shrubby mahoe and two ribbonwood [*Plagianthus regius*]). Pohuehue forms dense aerial thickets over much of the surrounding subcanopy.

There are a number of larger emergent titoki trees, and several large podocarps (matai, kahikatea and totara) within 40 m of the gap. The large pine trees around the perimeter are visible from the gap, and their needles and spent male cones contribute to the litter <sup>2</sup>.

After creation the gap was invaded by elderberry. In 1986 a work party poisoned the 13 well established elderberry trees in the vicinity of the gap. They died, leaving standing skeletons of trunks and branches. Weed control in the gap was halted during the period of this study (August 1992-July 1994). As a consequence the roots of the three trees immediately around the gap resprouted, and a number of seedlings have established. Future control will be needed or they will again dominate the site.

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<sup>2</sup> The pines around the perimeter near Gap Two were felled and removed in April 1995.

### 2.4.3 Adjacent Forest (AF)

The Adjacent Forest site occurs beneath continuous canopy directly north-east of Gap Two (within the 30x30 m plot; Figure 2.4). The forest has a low canopy (9-15 m) of mahoe and titoki, with a patchy understorey mainly of kawakawa, mapou and young mahoe.

### 2.4.4 Blackberry Gap One

This gap was also initially formed by a natural treefall, and subsequently invaded by blackberry (Figure 2.2). A successful spraying campaign, run over a number of summers, has killed almost all the blackberry with only scattered dead canes and only small numbers of seedlings remaining. The gap is near the south-western edge of the bush, and has several large emergent titoki, tawa and matai trees around its perimeter. The surrounding shrub layer is diverse, and includes karamu (*Coprosma lucida*), kanono, mahoe, hangehange and rangiora. Many of these species are now represented within the gap as shrubs and seedlings. Additional trees have been planted to aid gap closure (koromiko [*Hebe stricta*], wineberry [*Aristotelia serrata*] and ngaio [*Myoporum laetum*]). They are fast growing and help to prevent weed regrowth

Recent observations (January 1995) suggest that natural regeneration is occurring rapidly within the gap. When this study was begun in late 1991 the vegetation within the gap was only 1-1.5 metres high, the tallest trees being those that had been planted. The vegetation now has an average height of 2 m over much of the gap, with numerous karamu, wineberry and mahoe saplings.

### 2.4.5 Blackberry Gap Two

This is the largest of the four gaps studied, and covers an area of ca. 50 m<sup>2</sup> (Figure 2.2). Its exact origin is unknown. Blackberry canes cover much of the gap, dead canes forming numerous tangled mounds. Over the summers of 1989-1992 the blackberry was sprayed in an attempt to encourage native seedling establishment. During the 1994-1995 growing season there have been dramatic changes in the vegetation of the gap. Most notable are the large

numbers of young cabbage trees which now carpet the once bare areas between the dead blackberry canes. Karamu, mahoe and wineberry saplings are now thriving, with many new seedlings established.

This gap has a high number of adventive species, in comparison with the other three gap sites, with black nightshade, Japanese honeysuckle, pennyroyal (*Mentha pulegium*), and numerous pasture species (e.g., yorkshire fog [*Holcus lanatus*] and Californian thistle [*Cirsium arvense*]). The edges of the gap are swathed in the native climbers pohuehue and New Zealand passion vine (*Passiflora tetrandra*).

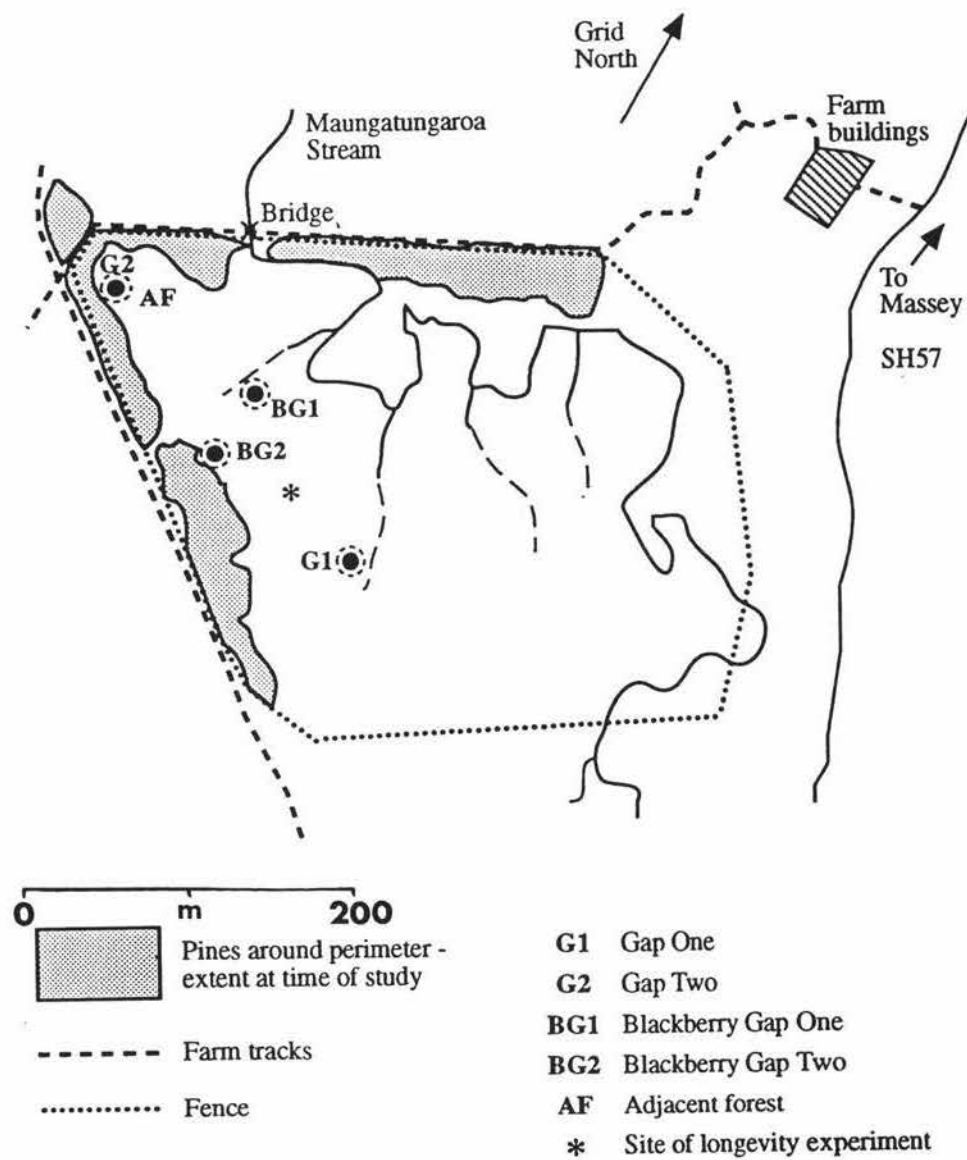
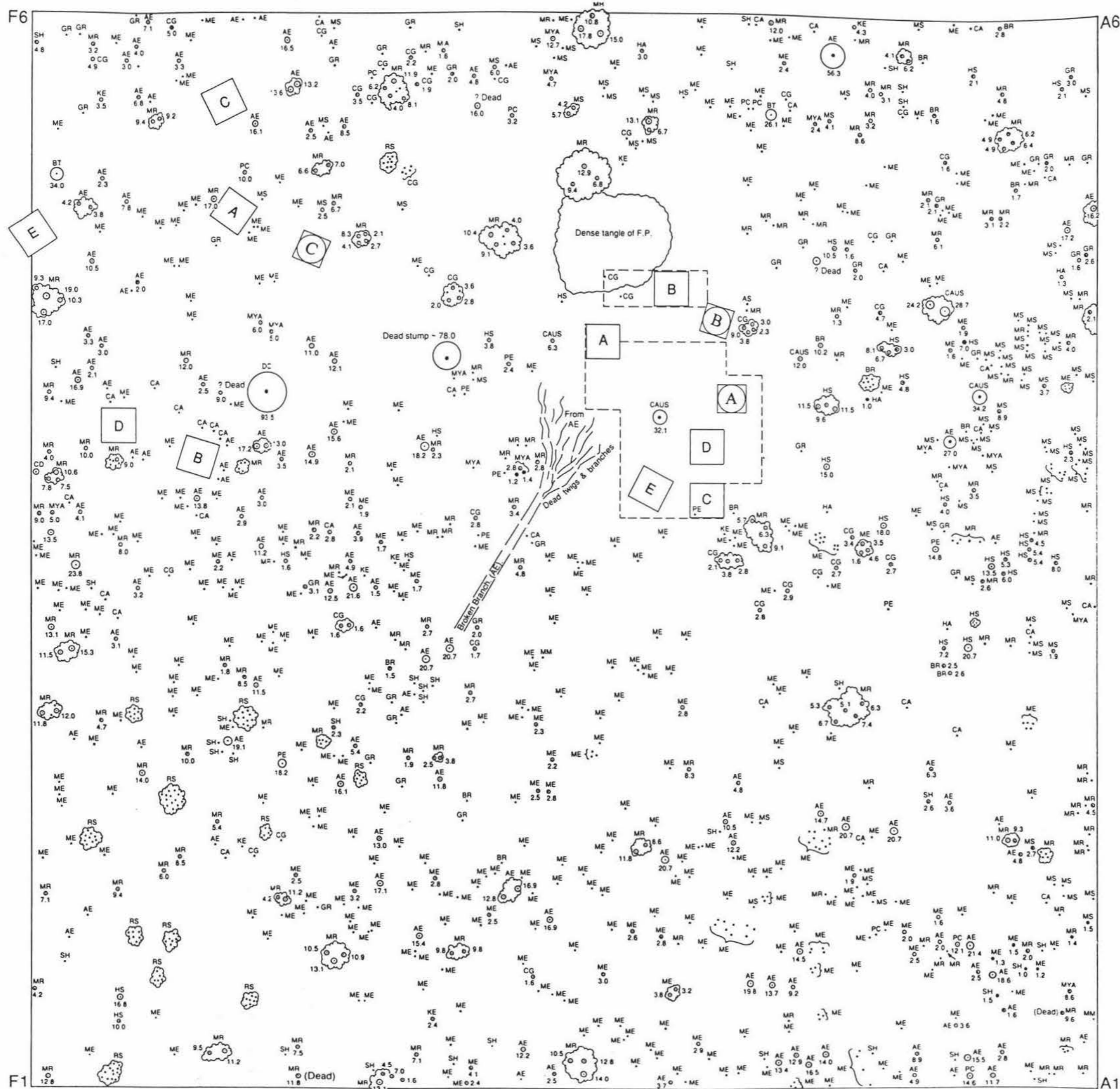


Fig. 2.2 Location of study sites within Keeble's Bush.

Fig. 2.3 Gap One - Map of the distribution of trees and shrubs >1.5 cm d.b.h. in a permanent 30x30 m plot around Gap One.



GAP ONE  
Species code

TREES

- AE *Alectryon excelsus*
- AS *Aristotelia serrata*
- BT *Beilschmiedia tawa*
- CAUS *Cordyline australis*
- DC *Dacrydium cupressinum*
- GR *Geniostoma rupestre*
- HA *Hedycarya arborea*
- HS *Hoheria populnea* var. *sexstylosa*
- KE *Knightia excelsa*
- MR *Meliccytus ramiflorus*
- MYA *Myrsine australis*
- PC *Pennantia corymbosa*
- PE *Pittosporum eugenoidies*
- SH *Streblus heterophyllus*

Tree fern

- CD *Cyathea dealbata*

Shrubs

- BR *Brachyglottis repanda*
- CA *Coprosma areolata*
- CG *C. grandifolia*
- ME *Macropiper excelsum*
- MM *Meliccytus micranthus*
- MS *Melicope simplex*

Lianes

- FP *Fuchsia perscandens*
- RS *Ripogonum scandens*

LEGEND

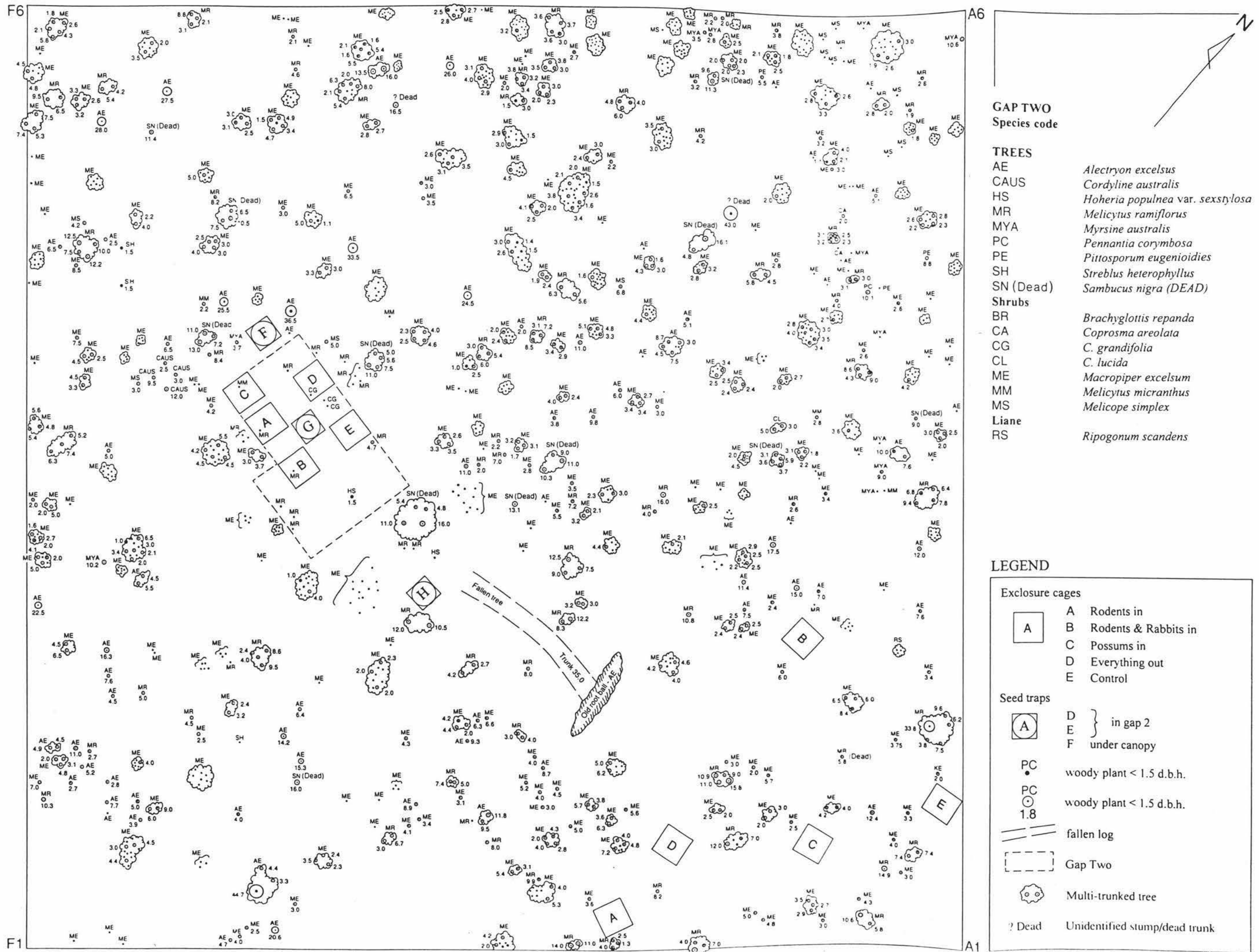
Enclosure cages

- A Rodents in
- B Rabbits and Rodents in
- C Possums in
- D Everything out
- E Control

Seed traps

- A } in gap 1
- B } in gap 1
- C } under canopy
- PC • woody plant < 1.5 d.b.h.
- PC ○ woody plant > 1.5 d.b.h.
- 1.8 fallen log
- Gap One
- Multi-trunked tree
- ? Dead Unidentified stump/dead trunk

Fig. 2.4 Gap two - Map of the distribution of trees and shrubs >1.5 cm d.b.h. in a permanent 30x30 m plot around Gap Two.



- GAP TWO**  
Species code
- TREES**  
 AE *Alectryon excelsus*  
 CAUS *Cordyline australis*  
 HS *Hoheria populnea* var. *sexstylosa*  
 MR *Melicytus ramiflorus*  
 MYA *Myrsine australis*  
 PC *Pennantia corymbosa*  
 PE *Pittosporum eugenioides*  
 SH *Sireblus heterophyllus*  
 SN (Dead) *Sambucus nigra* (DEAD)
- Shrubs**  
 BR *Brachyglottis repanda*  
 CA *Coprosma areolata*  
 CG *C. grandifolia*  
 CL *C. lucida*  
 ME *Macropiper excelsum*  
 MM *Melicytus micranthus*  
 MS *Melicope simplex*
- Liane**  
 RS *Ripogonum scandens*

- LEGEND**
- Exclosure cages**  
 A Rodents in  
 B Rodents & Rabbits in  
 C Possums in  
 D Everything out  
 E Control
- Seed traps**  
 A } in gap 2  
 E }  
 F under canopy
- PC • woody plant < 1.5 d.b.h.  
 PC ○ 1.8 woody plant < 1.5 d.b.h.
- fallen log
- Gap Two
- Multi-trunked tree
- ? Dead Unidentified stump/dead trunk

# Chapter 3

## Seed rain

### 3.1 Introduction

When an area is subject to disturbance, the composition and viability of the seed rain (current seed input) have an enormous influence on what species will regenerate and be represented in the subsequent vegetation. The composition of the seed rain reaching an area of ground is influenced by a number of factors including the proximity and number of seed-bearing parents contributing seeds, their fruiting period, the abundance of the crop, the dispersal modes of the species concerned, predatory attrition and stochastic events (Burrows, 1990). Further, the seed rain reaching a site is composed of seeds produced by surrounding vegetation (local or autochthonous seeds) and seeds produced by distant trees (immigrant or allochthonous seeds) (Martinez-Ramos & Soto-Castro, 1993).

The successful regeneration of a plant depends upon its seeds being dispersed to situations in which they can germinate and establish as seedlings (Fenner, 1985). Places where such conditions exist are called 'safe sites' (Harper, 1977), and each species has its own characteristic requirements in this respect, so that a safe site for one species may be unsafe for another (Fenner, 1985). Of the seeds that a plant produces, only a small proportion ever reach a 'safe site', and even fewer attain reproductive age themselves.

During the pre-dispersal phase there are four main causes of mortality of ovules and seeds. These are pollination failure, resource deficiency, predation, and developmental failure due to genetic defects (Fenner, 1985). All these factors may play a role in determining the amount of sound seed a plant produces. Those seeds which escape pre-dispersal predation contribute to the seed rain falling onto a site (Moore & Chapman, 1986). The fate of seeds once they are taken or released from parent plants continues to be a subject of intense research interest (Fleming & Estrada, 1986).

### 3.1.1 Dispersal agents

The transport of ripe fruit and seeds away from the parent plant commonly involves external agents such as wind, water, animals or birds. A comprehensive survey of dispersal mechanisms in a world context is given by Van der Pijl (1972). Each habitat type has plants which exhibit a wide range of dispersal mechanisms, though the proportion of species using the various agencies varies from one vegetation type to another (Fenner, 1985). The proportion of different mechanisms is directly related to the vegetational complexity, and successional stage of the community. Many studies have been carried out to determine the dispersal mechanisms and patterns of different species (*e.g.*, Michaux, 1989; Spence, 1990a). The numbers of seeds deposited and their distances from the parent plant can be plotted, creating dispersal curves, with different shaped curves resulting from different dispersal mechanisms.

Patterns of seed dispersal around plants with wind dispersed seeds are typically leptokurtic (sharp peaked and long tailed) (Fenner, 1985). The shape of the curve depends on a number of factors including the seed size and shape, the height of the parent plant, the speed of the wind and the density of the surrounding vegetation. Wind-borne seeds are characteristically tiny and produced in large numbers, with a large surface/volume ratio (Willson, 1983). They often have specialised structures such as wings, plumes, or hairs which aid in dispersal. In general early successional sites tend to have high numbers of plants whose seeds are wind dispersed. Northern temperate forests are also dominated by trees which are dispersed by wind (maple [*Acer campestre*], ash [*Fraxinus excelsior*], hornbeam [*Carpinus betulus*] and elm [*Ulmus glabrata*]) (Fenner, 1985). New Zealand forest species with wind dispersed seeds include beech (*Nothofagus* spp.), rewarewa, pukatea (*Laurelia novaezelandia*), houhere, rangiora, New Zealand jasmine (*Parsonsia heterophylla*) and *Clematis* spp. (Evans, 1987; Webb & Kelly, 1993). Perhaps the best known wind dispersed seeds are those of the daisy family (Asteraceae).

Water plays an important part in dispersal of seeds and fruit of some plants, especially those living in water or along the borders of streams or lakes, and shores of oceans (*e.g.*, mangroves [*Avicennia marina* var. *resinifera*]). Such seeds float either because they are resistant to

sinking (hairs or slime), lighter than water and unwettable, or because they produce structures that render them buoyant (air spaces, cork, oil) (Howe & Smallwood, 1982). They must be resistant to prolonged soaking and in some cases to extended immersion in salt water. The dispersal distance ranges from short-distance movement by rain-wash or sheet flooding over the ground or within-pond movements, to very long distance travel by river or ocean currents (Willson, 1983).

A wide variety of plants, ranging in size from forest floor herbs to giant canopy trees, rely on animals to disperse their seeds (Estrada & Fleming, 1986). Animal dispersal may be either external, with the seeds or fruit possessing barbs, bristles, hooks or viscous materials which act to attach them to fur, feathers, or hair (of passing animals) (Smith *et al.*, 1953); or internal, with the plant producing brightly coloured and/or fleshy fruits and seeds to entice the animals to consume them (Howe & Smallwood, 1982). Adaptions to cling to fur or feathers were important in primaeval New Zealand, judging by the number of low herbs with barbs and hooks (*e.g.*, *Acaena* spp. and *Uncinia* spp.) (Wardle, 1991). External dispersal may also be facilitated by hoarding animals and insects (primarily ants), which transport the seeds to terrestrial or arboreal burrows, or bury them in underground caches (Murray, 1986). The dispersal pattern produced by animals is likely to be very patchy (Willson, 1983).

The dispersal of seeds by frugivorous birds has been widely investigated (*e.g.*, Estrada & Fleming, 1986). Most plants whose seeds are dispersed predominantly by fruit-eating birds produce fruits in colourful displays: often reds, blues and black (van der Pijl, 1972). They are also usually rather small, with an upper limit of about 4-7 mm for an oval fruit (Snow, 1981). Frugivorous birds may either pick or squeeze the pulp free from the seed (in which case they are probably poor seed dispersers), or swallow the entire fruit and either regurgitate or defecate the seed (Willson, 1983). In most cases regurgitation of seeds occurs in a matter of minutes (Clout, 1985), whereas defaecation may take an hour or even several hours (Walsberg, 1975).

Willson (1993) found, in her review of existing information on dispersal modes, seed shadows and colonization patterns within a wide range of vegetation communities, that many plants appear to lack specialized morphology for dispersal, and achieve only short-distance dispersal.

### 3.1.2 Frugivory in New Zealand forests

About 70% of New Zealand tree species (250 species in 50 families) (as well as 40% of shrubs and 30% of vines) have fruit with fleshy pericarps or accessory tissues (Webb & Kelly, 1993; Burrows, 1994a) suited to vertebrate dispersal. They occur in all tiers of the forest from canopy to ground level (e.g., *Nertera* spp.), and from the coast almost to the limits of vegetation (e.g., *Coprosma perpusilla*) (Wardle, 1991). Of those the majority are probably adapted for bird dispersal (Clout & Hay, 1989; Holdaway, 1989; Burrows, 1994a).

With the fragmentation of New Zealand's forests, and the introduction of many predatory and herbivorous mammals, many forest dwelling birds have become extinct, rare or restricted in their distribution (Burrows, 1994d). Frugivorous species now extinct include moa (estimated 12 species), piopio (*Turnagra capensis*) and huia (*Heterolocha acutirostris*), all of which were probably important as seed dispersers. Of the 18 extant frugivorous species, only four remain relatively common (kereru [*Hemiphaga novaeseelandiae*], tui [*Prosthemadera novaeseelandiae*], bellbird [*Anthornis melanura*] and silvereye [*Zosterops lateralis*]). Three (little spotted kiwi [*Apteryx oweni*], saddleback [*Philesturnus carunculatus*], and stitchbird [*Notiomystis cincta*]) are restricted to off-shore islands, with the remainder restricted in their distribution or only minor frugivores (Clout & Hay, 1989).

Of those forest frugivores that are still relatively common, the kereru is the most specialized and important in terms of seed dispersal. This is especially true for those species whose seeds are >10 mm diameter that would once have also been dispersed by forest moas (Burrows, 1994a; Clout & Hay, 1989), such as karaka (*Corynocarpus laevigatus*), kohekohe (*Dysoxylum spectabile*), miro (*Prumnopitys furruginea*), taraire (*Beischmeidia taraire*) and tawa (McEwen, 1978; Bishop, 1992; Burrows, 1994a). Moas would have been unable to reach many of these seeds on the trees, but perhaps foraged for them on the ground. For these plants kereru are now virtually the sole disperser (Clout & Hay, 1989). The three other important native frugivores that are still relatively widely distributed (tui, bellbird and silvereye) have smaller gapes (9 mm, 6 mm and 5 mm respectively).

In addition to native birds, other native fauna has been implicated in seed dispersal. Most of

these too are now restricted in their distribution, as a result of human and introduced predator pressure. A number of species of New Zealand lizards have been found to consume a variety of fleshy fruits. Most of the fruits they are known to consume have sweet flesh, are small (<5 mm diameter), odourless and generally white or translucent (Whitaker, 1987). Many come from divaricating shrubs or tangled vines and it has been suggested that these plants may be adapted to seed dispersal by lizards (Whitaker, 1987). New Zealand's three species of bats (one long and two short tailed), now also greatly reduced in their distribution (one species of short tailed bat may already be extinct), are known to take fruits from a range of forest species (Daniel, 1976; Lord, 1991; Bishop, 1992; Ecroyd, 1993). The potential of birds and lizards as seed dispersers has not been determined.

### 3.1.3 Seed rain investigations overseas

The many studies carried out overseas in regard to seed rain, have been in tropical rain forests. Investigations have focused on the influence of seed rain in relation to gap regeneration (Denslow & Gomez Diaz, 1990; Martínez-Ramos & Soto-Castro, 1993) and forest dynamics (Young *et al.*, 1987), seed rain across habitat boundaries (Willson & Crome, 1989), and the role of different dispersing frugivores in seed dispersal (Guevara & Laborde, 1993).

Seed rain entering Northern Hemisphere temperate forests has also been investigated. Many studies have sought to quantify annual seed rain and analyse seed quality (*e.g.*, spruce forest, Beerling & Woodward, 1993), to analyse temporal and spatial aspects of the seed rain (*e.g.*, tropical rainforest in Northern Thailand; Cheke *et al.*, 1979; North Eastern American deciduous forest, Houle & Payette, 1991; high altitude northern Swedish old growth spruce forest, Hofgaard, 1993), and to assess spatial and seasonal seed dissemination patterns of bird dispersed deciduous tree species (*e.g.*, Japanese temperate deciduous forest, Masaki *et al.*, 1994). In most cases the studies have concentrated on the dominant tree species of the forests, rather than assessing the seed rain of the entire forest community.

### 3.1.4 Seed rain investigations in New Zealand

Most early seed rain investigations in New Zealand have also been concerned with dominant canopy trees, and those of high economic value. The studies have concentrated on single species (*i.e.*, rimu, totara, kauri [*Agathis australis*], and kahikatea), looking at their total seed crops and seasonal fluctuations (Hinds & Reid, 1957; James & Franklin, 1978; Ogden *et al.*, 1987).

The longest running multi-species seed rain investigations have been carried out in the Orongorongo Valley, Wellington. Seed trapping to assess annual crops of forest seeds, berries and fruits has continued since 1966 (Brockie 1992). A number of studies have also looked at seasonal fluctuations (*e.g.*, Leathwick, 1984), in regards to periodic heavy seeding (mast fruiting) (Ogden, 1985), which is exhibited by a number of New Zealand trees and long-lived herbs (Connor, 1966; Mark, 1965; Norton & Kelly, 1988; Allen & Platt, 1990; Spence, 1990a).

Recent work by Burrows (1994b) in the Port Hills, Canterbury, has assessed the year to year variation and the total seed rain composition of a lowland forest remnant, in the context of available frugivorous bird species and forest regeneration.

The following chapter examines the pattern of seed rain in four study areas in Keeble's Bush, Manawatu (Fig. 2.2; Location map of gap sites). Of particular interest was:

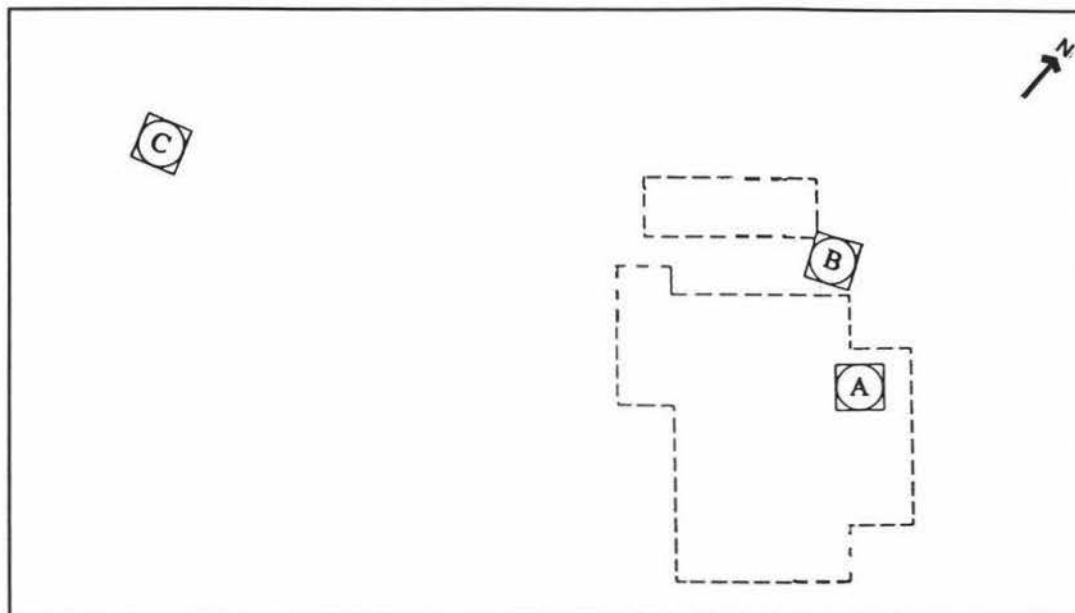
1. the diversity, temporal variation, and viability of the seed rain,
2. the relative contributions of seeds originating from local and distant sources in each of the sites, and
3. the proportion of adventive species.

All these aims were investigated in light of the now reduced native bird diversity and numbers within the forest remnant.

## 3.2 Methods

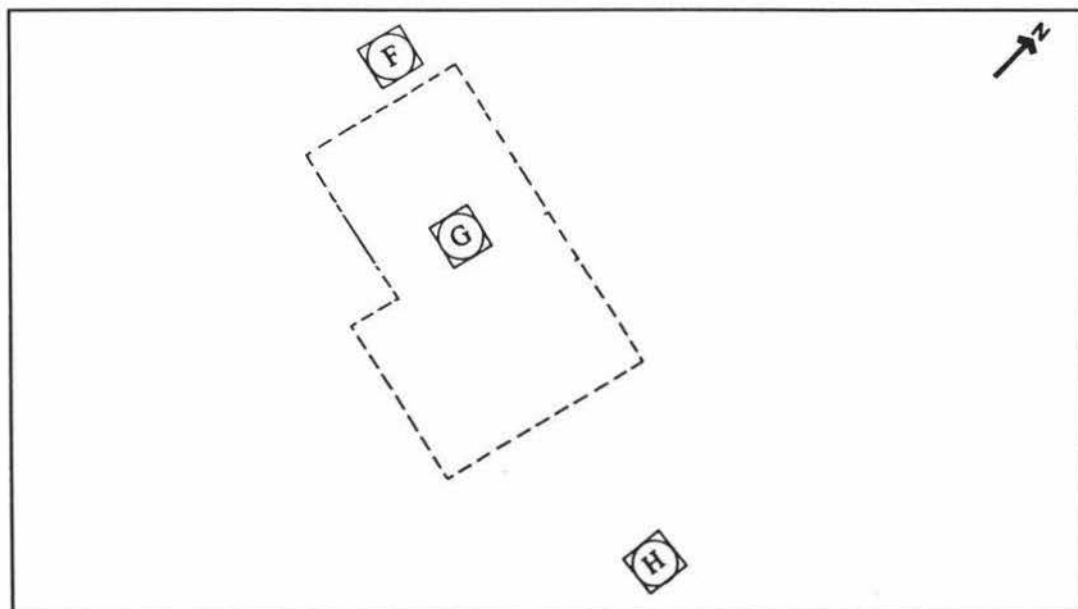
### 3.2.1 Study sites

a)



Gap One: G1A, G1B and G1C

b)



Gap Two: G2F, G2G and G2H

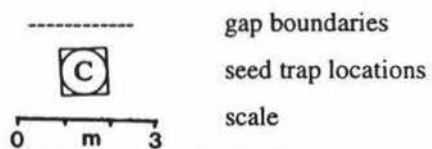
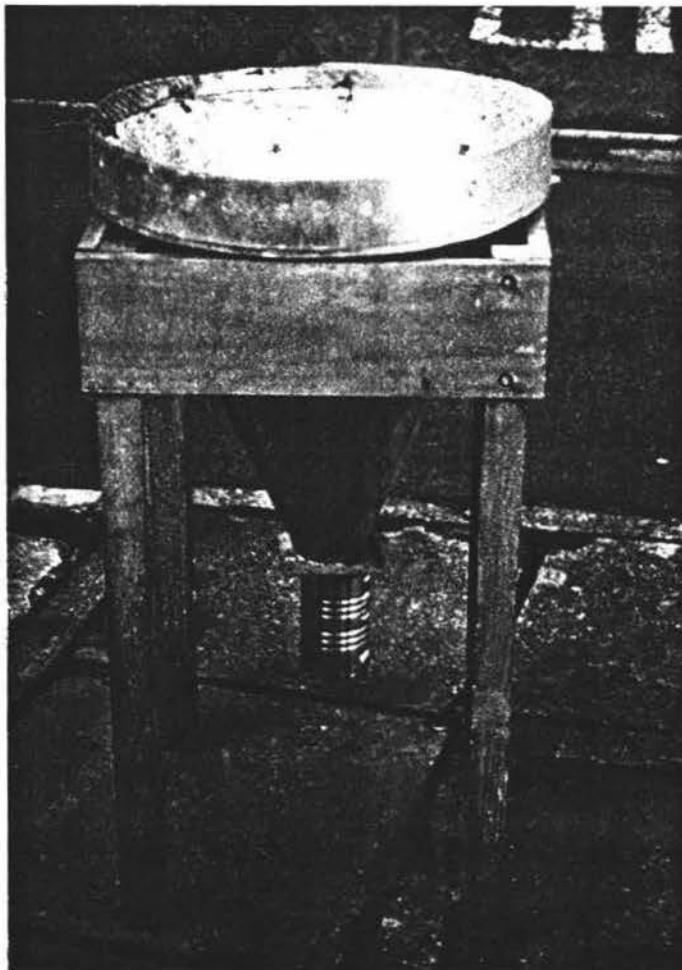


Fig. 3.1 a & b Positions of the seed traps in and around Gaps One and Two.

### 3.2.2 Seed trapping

Eight seed traps were set up in Keeble's bush on the 20th November 1992. Two traps were positioned randomly (but avoiding tagged seedlings [see Chapter 4.]) in both Gaps One (G1A and G1B) and Two (G2F and G2G) (Fig. 3.1 a&b). A disproportionate number of traps were placed in Gaps One and Two, where the majority of work for this thesis was carried out. A further trap was also placed under the canopy of the adjacent forest areas (G1C and G2H). The last two traps were located in Blackberry Gap One (BG1D) and Blackberry Gap Two (BG2E) (Fig. 2.2). The position of the trap in Blackberry Gap Two was influenced by the thick swards of dead blackberry canes covering much of it.

Each trap consisted of a metal funnel (0.5 m diameter mouth with a total catching area of 0.2 m<sup>2</sup>) with a possum and rodent proof lid (covered in 1 cm mesh), set into a collapsible wooden frame (made of tannalised pine) (Fig. 3.2). The catching tin hung below the funnel and was detachable. The base of the catching tin was removed and replaced with 0.5 mm plastic mesh secured with silicon sealant, to allow drainage and prevent water from collecting and causing the seeds to rot. The traps were left in position until the final collection in December 1993.



**Fig. 3.2** One of the seed traps used in this study.

### 3.2.3 Collection of trap contents and seed identification

Collections were made fortnightly (from the 6th of December 1992 until the 19th of December 1993), to lessen the possibility of seed predation during the time the seed was in the trap. The contents of each catching tin were removed and taken back to the laboratory for analysis. Any debris was removed from the trap lid at the time of collection, to prevent build up which may have impeded seed entry to the trap in the intervening weeks. Trapped seeds and fruits were sorted by hand under a 10-45x dissecting microscope, and both intact and damaged seeds were recorded. A seed was taken as intact if there were no signs of external damage, and if it was not shrivelled.

A number of seeds were identified immediately from a reference collection obtained from Proseed (Proseed, 1992), and from fruits collected from Keeble's Bush and the Massey University campus gardens. Blackberry seeds were collected from a variety of sources, including blackberry jam. Most of the remainder were identified after germination. The majority of seeds were identified to species, with a few being classified only to genus. A small proportion of seeds in all but one of the traps remained unidentified. Some of these were damaged or non-viable on collection and so could not be germinated and grown on. Others germinated readily but died when only small seedlings, making identification difficult or impossible.

The smaller intact seeds were placed on moist filter paper, sealed in petri dishes, and placed in an incubator set at 20°C. Each dish was checked weekly for any germination. Once germinated the seeds were planted out in the glasshouse in seed raising mix, to verify identification. All seeds that had not germinated by September 1994 were stained with tetrazolium and discarded. Many of the seeds had been in the incubator for well over six months. The viability of larger seeds was also established by staining with tetrazolium (Freeland, 1976).

### 3.2.4 Nearest seed source

The distribution of each of the woody trees and shrubs over 1 m in height and >1.5 cm d.b.h. (diameter at breast height) were recorded in 30x30 m plots, centred around both Gaps One and Two (Fig. 2.3; 2.4). The total basal area was determined for each woody species. The nearest source tree for each species of seed caught was measured, with that tree assumed to be the likely contributing individual. In the case of dioecious species, female trees were noted. Where the source individual was not within the 30x30 m plots (and was not apparent in the immediate vicinity), it was assumed to be a migrant seed.

### 3.2.5 Analysis

Statistical analysis is limited as much of the data in this chapter is by nature descriptive. Chi-square ( $\chi^2$ ) analyses were used to compare differences in species and seedling number from year to year. Differences were regarded as significant if  $P \leq 0.05$ . Critical values for all statistics were obtained from Zar (1984). Coefficients of variation were calculated to determine the heterogeneity of the seed rain.

### 3.3 Results

#### 3.3.1 Seeds counts

A total of 40 different types of seed (regarded here as different species) were caught in the eight seed traps during the sampling period (Dec 1992-Dec 1993), contributing to a total seed rain of 3764 seeds (viable and non-viable inclusive), or 2398 seeds/m<sup>2</sup>/yr. The numbers of seeds intercepted by each trap ranged from 26-1862 (mean=450±588.1). Of those 40 different types of seed, 25 (62.5%) were identified to species, four to genus (16%), two (5%) to family (Asteraceae), with nine (22.5%) remaining unidentified (refer Appendix 1.). Only six of the 40 species caught were represented by >100 seeds, with 30 species represented by <50 seeds. Over half of those 30 (21) were represented by <10 seeds. Trees species accounted for 45% of the identified species caught over the study period. Herbaceous, liane and shrub species contributed 25.8%, 16% and 12.9% respectively.

Table 3.1 summaries the distribution and abundance of seed rain of the nine most profuse species (represented by >50 seeds) in each of the traps. All nine are considered common within the bush (Druce & Greenwood, 1979). The high coefficient of variation between traps for all species illustrates the heterogeneity of the seed rain. None of the 40 species caught over the trapping period were represented in all traps.

Rimu contributed the largest number of seeds to the year's total seed rain, with 1612 seeds (42.8% of the total seeds trapped). Rimu also showed the most spatial heterogeneity, with a coefficient of variation of 265% (Table 3.1.). Pohuehue, with the second largest contribution, had 479 seeds. At 139% its coefficient of variation was the second lowest, as expected with its even distribution throughout the bush.

**Table 3.1** Species represented by >50 seeds in the trapped seed rain, Dec. 1992-Dec. 1993.

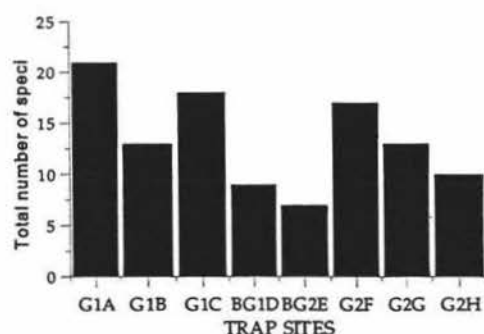
Species with >50 seeds trapped	G1A	G1B	G1C	BG1D	BG2E	G2F	G2G	G2H	Total	<sup>1</sup> c.o.v. (sd/x.100)
cabbage tree	356	5	103	0	6	5	1	3	490	208
houhere	65	51	0	17	3	0	0	1	137	152
lemonwood	9	2	60	0	0	2	3	3	79	206
kahikatea	24	3	22	0	0	5	2	0	56	143
kawakawa	5	0	3	0	0	227	62	2	299	206
pohuehue	5	2	37	0	0	110	165	33	352	139
rangiora	256	194	0	0	0	0	0	0	450	187
rimu	26	21	1564	0	0	1	0	0	1612	265
titoki	2	0	7	0	0	25	11	10	55	119

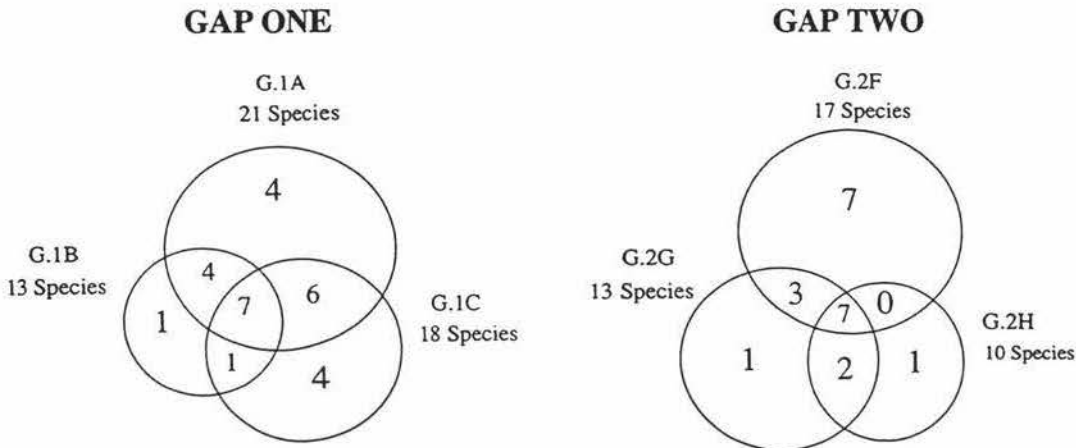
<sup>1</sup> coefficient of variation.

The unknown species contributed only 74 seeds (1.95%) to the total trapped seed rain. Of those 74 seeds, 70 were from five species (each seed distinctly different), with the remaining from four species (represented by single seeds).

### 3.3.2 Seed rain heterogeneity

The richness of species intercepted over the sampling period by each trap varied (Fig. 3.3), even when the seed traps were only a few metres apart. This is well illustrated by those traps in, and adjacent to Gaps One and Two (Fig. 3.4). The highest number of species, 21, was caught in trap C (Gap One), with the lowest number, seven, in trap D (Blackberry Gap Two).

**Fig. 3.3** Total number of species caught in each trap during the sampling period (Dec 1992-Dec 1993).



**Fig. 3.4** The number of species unique to, and shared between the three traps in Gap One (A, B, C), and in Gap Two (F, G, H) are illustrated. Both C and H were positioned under closed canopy outside the gaps. In both cases the traps shared seven species.

The total numbers of seeds caught by each trap also varied markedly (Table 3.3), from 1862, caught by trap G1C (under closed canopy adjacent to Gap One), to 26 caught by trap BG2E (located in the largest blackberry gap). The majority (86.6%) of the seed rain intercepted by trap C originated from one species, rimu (Table 3.1). This is because the trap lay directly beneath the canopy of a large emergent rimu tree.

**Table 3.2** Total number of seeds caught by each trap during the sampling period (Dec. 1992-Dec. 1993). The percentages of seeds identified and those which remained unknown are also shown.

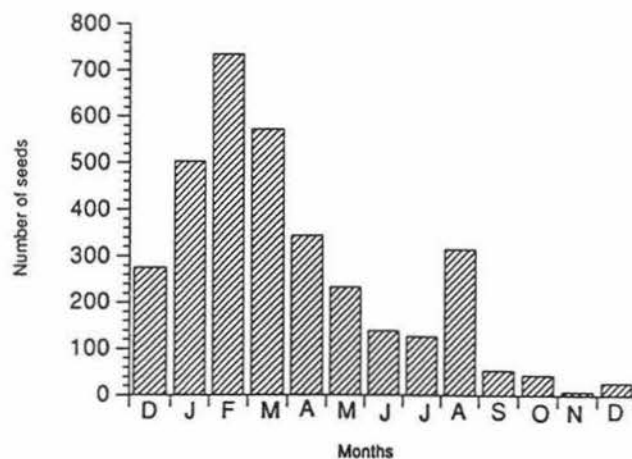
SITE	No. of identified seeds	% of seeds identified	No. of unknown seeds	% unknown seeds	TOTAL Seeds
G1A	763	95.6%	35	4.4%	798
G1B	287	93.8%	19	6.2%	306
G1C	1852	99.4%	10	0.54%	1862
BG1D	49	98%	1	2.0%	50
BG2E	25	96.2%	1	3.8%	26
G2F	390	98%	8	2.0%	398
G2G	257	100%	0	0.0%	257
G2H	57	100%	0	0.0%	57

Table 3.2 shows the small contribution made by the unknown seeds in relation to the total seed numbers for each trap.

### 3.3.3 Seed rain variability

The seed rain data indicates peaks of fruiting and the lengths of fruiting were distinct for each species, during the year of sampling. Most species fruited abundantly for 1-3 months of the year (Fig. 3.5). Fig. 3.5 shows the seasonal distribution of total seed numbers for the nine most abundant species in the seed rain. A long mid-summer to late-summer peak is illustrated, with a short peak in August. The August peak is predominately due to *rimu*, which contributed 249 (79%) of the 316 seeds. The timing and extent of these peaks probably vary from year to year, most notably in those species, like *rimu*, that display mast seeding.

Little can be said about the seasonality of those species represented by only a small number (<10 seeds) of seeds during the collection period, other than their presence or absence in a particular month.



**Fig. 3.5** The total number of seed which fell in each month, for the nine most abundant species (Table 3.1).

### 3.3.4 Seed viability

Only the viability of the seed rain of the nine most abundant species is discussed in detail, and only the traps where each species was most abundant have been considered here. This is because all species were more common in one site or another. In each case the site/traps being considered are stated.

A number of the intact seeds caught, when placed in the incubator (at 20°C) did not germinate. This may be because the seeds remained dormant, or appeared externally intact, while being damaged internally. This may have been especially true for the smaller seeds, which were difficult to examine internally. In addition a number of New Zealand's native forest species have recalcitrant seeds; *i.e.* they quickly lose viability when their moisture content drops below a certain high level (Fountain & Outred, 1991).

#### *rimu* (*Dacrydium cupressinum*) (G1A & G1C - Gap One)

Almost all (97%) the rimu seeds were collected from G1C. The trap lies 3.4 m away from a large emergent rimu tree, with some of the canopy overhanging the trap. Rimu litter was also the most common debris deposited in the catching jar.

The high number of damaged or non-viable persistent small brown seeds, and the low number of intact seeds with red 'arils' suggests that 1992 was not a mast seeding year for the mature rimu trees in Keeble's Bush. The majority of seed fell during January to March, with another, much smaller peak in August (Fig. 3.6a). Almost half (44%) of the rimu seeds which fell were damaged or inviable (small brown persistent seeds [Salmon, 1980]). Of those seeds that were viable, only three had fleshy red receptacles. Many of the damaged seeds were split halves, with the embryos removed, suggesting ship rat predation (Innes, 1977). Very few of the intact seeds germinated during the months of incubation (4.6%).

*cabbage tree (Cordyline australis)* (G1C - Gap One)

A number of cabbage trees are present in the canopy of the bush surrounding Gap One, with one large individual near the centre of the gap. Most of the cabbage tree seeds collected from Gap One were in trap G1A (79%), which lay close to the central tree. The bulk of seeds fell between January and March, with the majority shed in February (Fig. 3.6b). A few seeds fell at other times during the year but these are suggested to be seeds retained within old fruit on the tree. Some of the ripe seed did fall while still inside the white pulpy fruit. 24% of the cabbage tree seeds caught in the traps in Gap One were damaged. None of the intact seeds germinated in the incubator.

*rangiora (Brachyglottis repanda)* (G1A &G1B)

Rangiora seed was present only in two traps, G1A and G1B. The traps lay near several adult rangiora shrubs, which flowered and set seed profusely during 1992. Despite the large amount of seed set and caught, none of it germinated, with a large proportion of it shrivelled and non-viable (35%). The seeds were shed only during December and January (Fig. 3.6c). Although the seeds are wind dispersed none were deposited in trap G1C, only 10 m away. This may indicate that there is insufficient air movement in the understorey to disperse the seeds far.

*pohuehue (Muehlenbeckia australis)* (G2F & G2G - Gap Two)

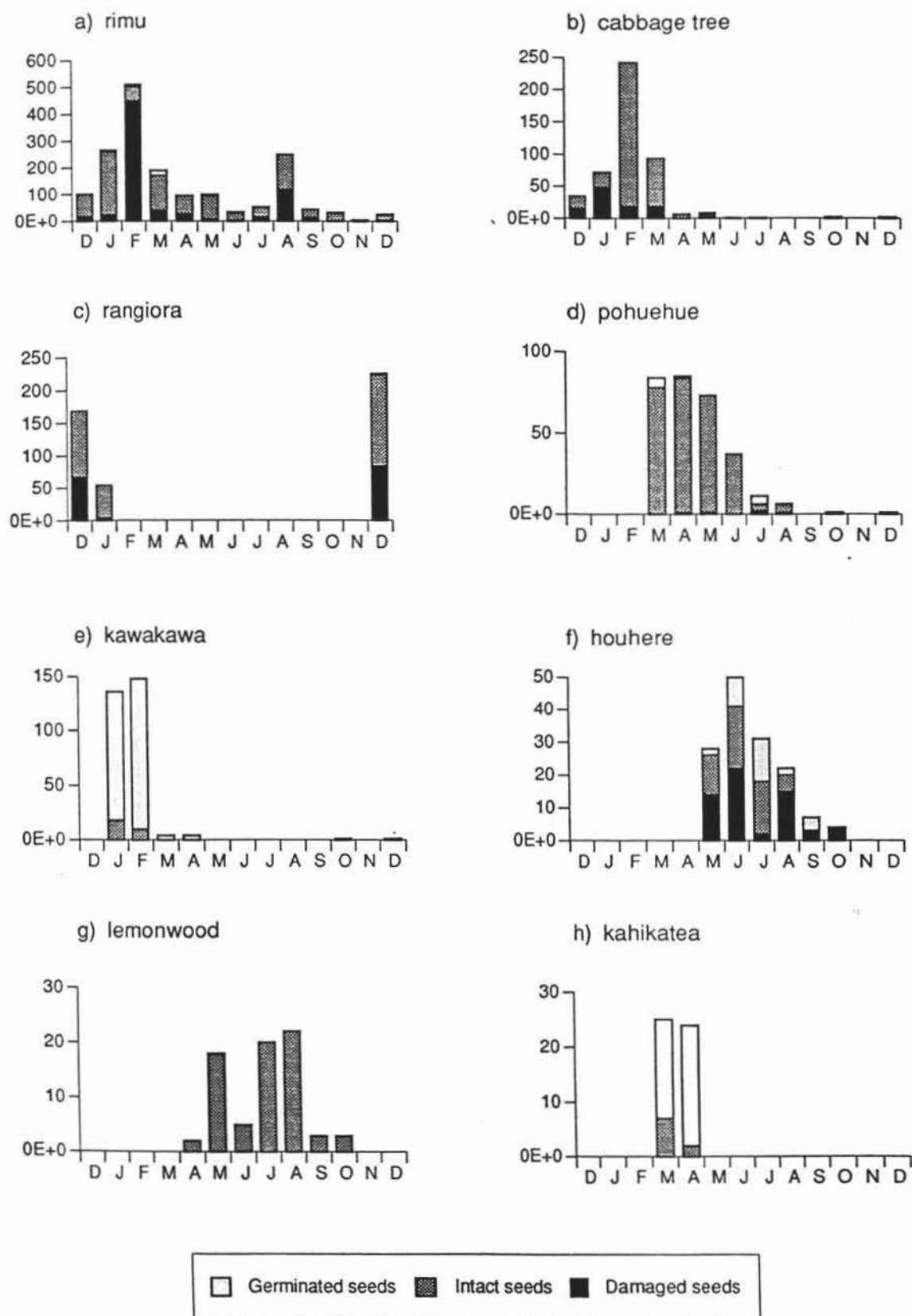
Pohuehue seed was present in traps G2F and G2G, from March to December, with the majority being caught from March to June (Fig. 3.6d). Very few of the seeds caught were damaged (1.7%). Despite the high proportion of intact seeds (98%), only 12 seeds germinated.

*kawakawa (Macropiper excelsum)* (G2F & G2G - Gap Two)

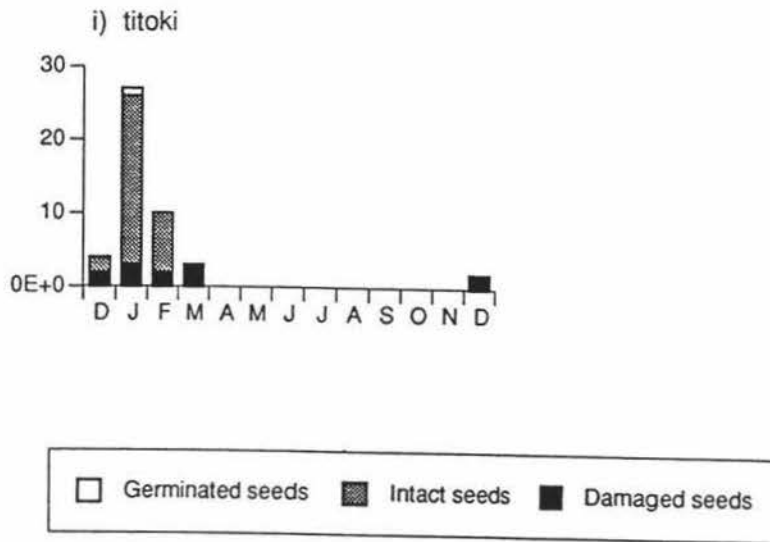
All kawakawa seeds caught in G2F and G2G were intact, and had a very high percentage germination (82.9%). Most of the seeds fell in January and February, with a very small number caught in March (4), April (4), October (1) and December (1) (Fig. 3.6e). Those seeds trapped in October and December were probably old seeds, intact but non-viable.

*houhere* (*Hoheria populnea* var. *sexstylosa*) (G1A & G1B - Gap One)

The wind dispersed seeds of houhere (*Hoheria populnea* var. *sexstylosa*) were caught between June and November (Fig. 3.6f). A large number of the damaged seeds collected had a small hole in their testas suggesting insect predation. The percentage germination of the seeds intercepted ranged from 0% in October to 57% in September.



**Fig. 3.6** *a, b, c, d, e, f, g, h, i* These graphs illustrate the proportions of germinated, intact, and damaged seed, and their temporal distributions of the eight most abundant species in the seed rain.



**Fig. 3.6 j** This graph illustrates the proportions of germinated, intact, and damaged titoki seed and its temporal distribution, in the seed rain.

***lemonwood* (*Pittosporum eugenioides*) (G1A, G1B & G1C - Gap One)**

The *Pittosporum* seeds intercepted by traps G1A, G1B and G1C were from lemonwood (*Pittosporum eugenioides*), one of the two *Pittosporum* species present in Keeble's Bush (Druce & Greenwood, 1979). All of the seeds trapped were intact, but none germinated in the incubator. The bulk of the lemonwood seeds caught in the traps fell in May, July and August (Fig 3.6g).

***kahikatea* (*Dacrycarpus dacrydioides*) (G2F & G2G - Gap Two)**

Kahikatea seeds were present in the seed rain for only a short period of the year, during February and March (Fig. 3.6h). All the seeds that fell were intact, with a very high percentage germination (81.6%). None of the seeds which fell into the traps retained their 'arils'.

***titoki* (*Alectryon excelsus*) (G2F, G2G & G2H - Gap Two)**

Ripe intact seeds were caught between December and February (Fig. 3.6i). Those seeds that fell in December 1993 were all immature. During this month a large number of juvenile titoki seeds were observed in litter beneath mature trees. Only one of the intact seeds caught

germinated, suggesting a stratification period may have been required. Most of the damaged seeds had been predated by a moth larvae (*Conopomorpha cyanocephala* [Sullivan *et al.*, 1995]), as indicated by a small circular entry hole in the capsule or seed wall.

### 3.3.5 Adventive invasion

Twenty four seeds from seven adventive species were caught in the seed rain (Table 3.3), including two tree (T), four herbaceous (H) and one grass (G) species. All the herbaceous adventive species intercepted were allochthonous, occurring in the surrounding weedy bush margin or farm paddocks. Silver birch (*Betula pendula*) and pine seeds appear to have dispersed the farthest; the nearest birch tree grows beside the farmhouse 200 m away, and pines surround the bush along two of the margins (at the time of this study).

**Table 3.3** Adventive species present in the seed rain: Dec. 1992-Dec. 1993.

SPECIES	Lifeform	G1C	BG1D	BG2E	G2F	G2G	G2H	TOTAL
*scotch thistle	H		13	1				14
*bitter cress	H			13				13
*pine	T	1	3	1		1	1	7
*dandelion	H					2	1	3
*birch	T		1		1			2
*tall willow-herb	H		2					2
*yorkshire fog	G					1		1
<b>TOTAL</b>		1	19	15	1	3	2	24

- \* Wind dispersal
- ° Explosive dispersal
- ° Gravity
- T tree
- H herb
- G grass

### 3.3.6 Nearest seed source

The location of the nearest seed source is based in the assumption that each seed trapped came from the nearest fruiting individual of its species (Martínez-Ramos & Soto-Castro, 1993). The bulk of the tree and shrub species in the seed rain came from local trees, *i.e.* those less than 70 m from the traps (Fig. 3.7 *a* & *b*). The average distances to the nearest seed sources are given in Table 3.4.

#### *Gap one* (G1A, G1B & G1C)

The two traps in (G1A & G1B) and one adjacent to (G1C) Gap one intercepted 16 woody tree and shrub species during the sampling period. Of those 16 species, 11 were recorded as mature (seed producing) individuals within the 30x30 m plots (Fig. 3.7*a*).

The five species not occurring within the plot include four native (kahikatea, totara, matai and pukatea), and one adventive tree species (radiata pine). Of those, kahikatea, totara and matai are all fairly common throughout the bush, with emergent trees of all three lying within 70 m of the traps. Pukatea occurs only on the lower terrace (>70 m away), and pine, the only adventive tree species caught, grows along the northern and eastern boundaries. The closest pine tree grows 400 m from trap G1C, which caught it.

Despite the fact that there were several large tawa trees within 15 m of all three traps, no tawa fruits were intercepted. Also recorded but not represented in the seed rain were poataniwha, small-leaved milktree and *Coprosma areolata*. Seeds of poataniwha and small-leaved milk tree may have been amongst the 59 unidentified seeds. Certainly no *Coprosma areolata* seeds were caught, as the only *Coprosma* seeds identified were those of kanono.

**Table 3.4** The mean ( $\bar{x}$ ) and range of distances from the seed traps to the nearest mature fruiting individual in the surrounding forest (30x30 m plot) are shown. The number of tree and shrub species present in the seed rain and in the 30x30 m plot are also given.

TRAP	No. of species in 30x30 m plot	$\bar{x}$ distance to nearest individual (m)	Range of distances (m)
G1A	11	5.76	2-12.75
G1B	6	8.51	1-12.5
G1C	9	4.68	1.3-10.55
G2F	5	5.11	1.15-17.7
G2G	5	5.79	1-17.9
G2H	5	7.76	1.15-19.5

*Gap two (G2F, G2G & G2H)*

Between them the three traps (two inside [G2F & G2G] and one under the adjacent canopy [G2H]) caught seeds of 10 tree and shrub species; 5 of those 10 were caught in all traps. Of those 10 species, 4 were not recorded in the 30x30 m plot, 2 native (totara and kahikatea) and 2 adventive (radiata pine and silverbirch). Both totara and kahikatea are represented by individuals less than 70 m from the Gap. Pine trees occur along the north and north-western boundary and are 20-200 m away. The nearest birch tree is approximately 500 m away, beside the farm house.

Four species were recorded within the plot but were not represented in the trapped seed rain (poataniwha, small-leaved milktree, shrubby mahoe, kaikomako). All four are predominantly understorey or sub-canopy species. These species may however be included in the 11 seeds not identified in traps G2F and G2G.

A weak, but not significant, correlation was found between the distance from the seed traps, and the nearest mature individual ( $p=0.2043$ ).

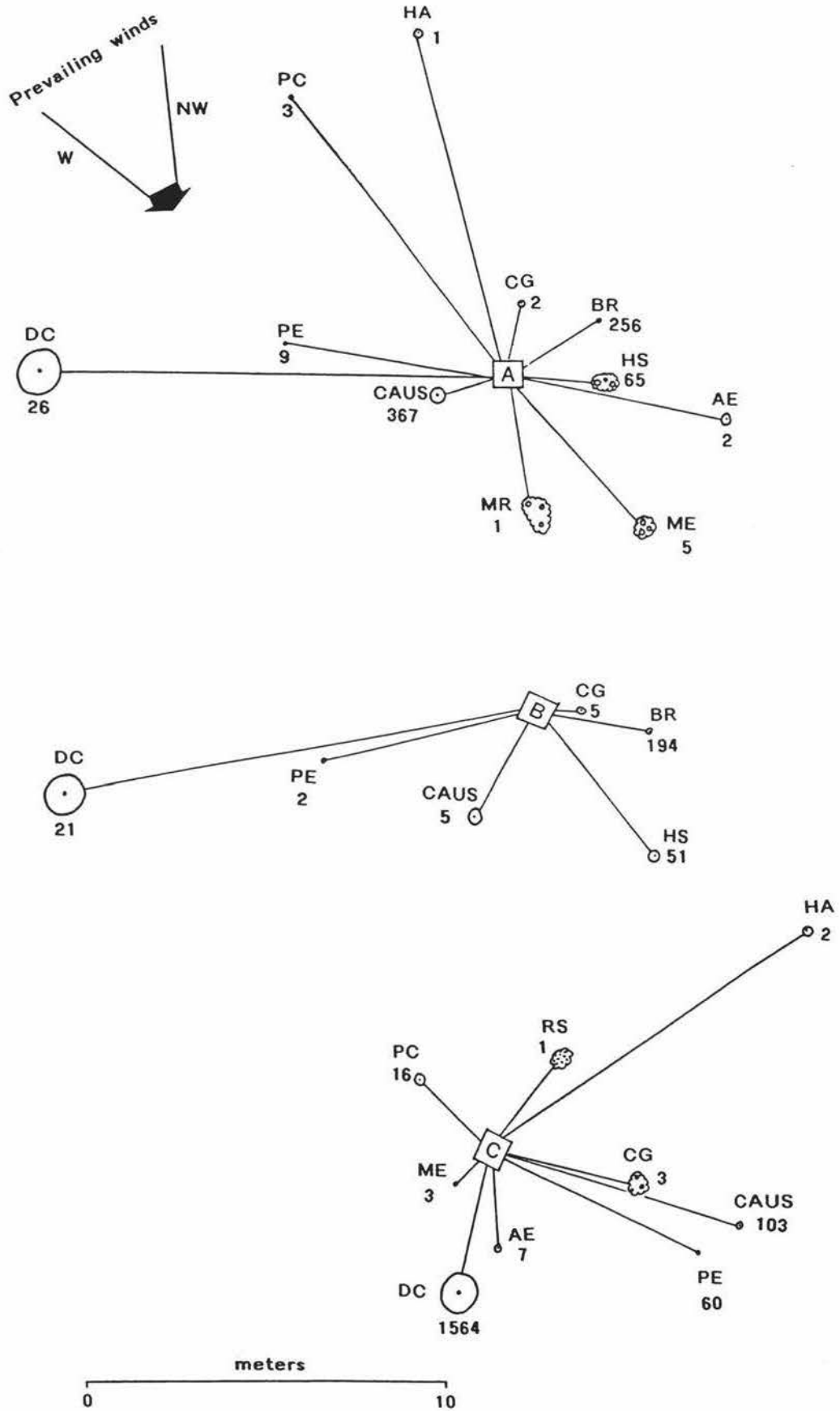
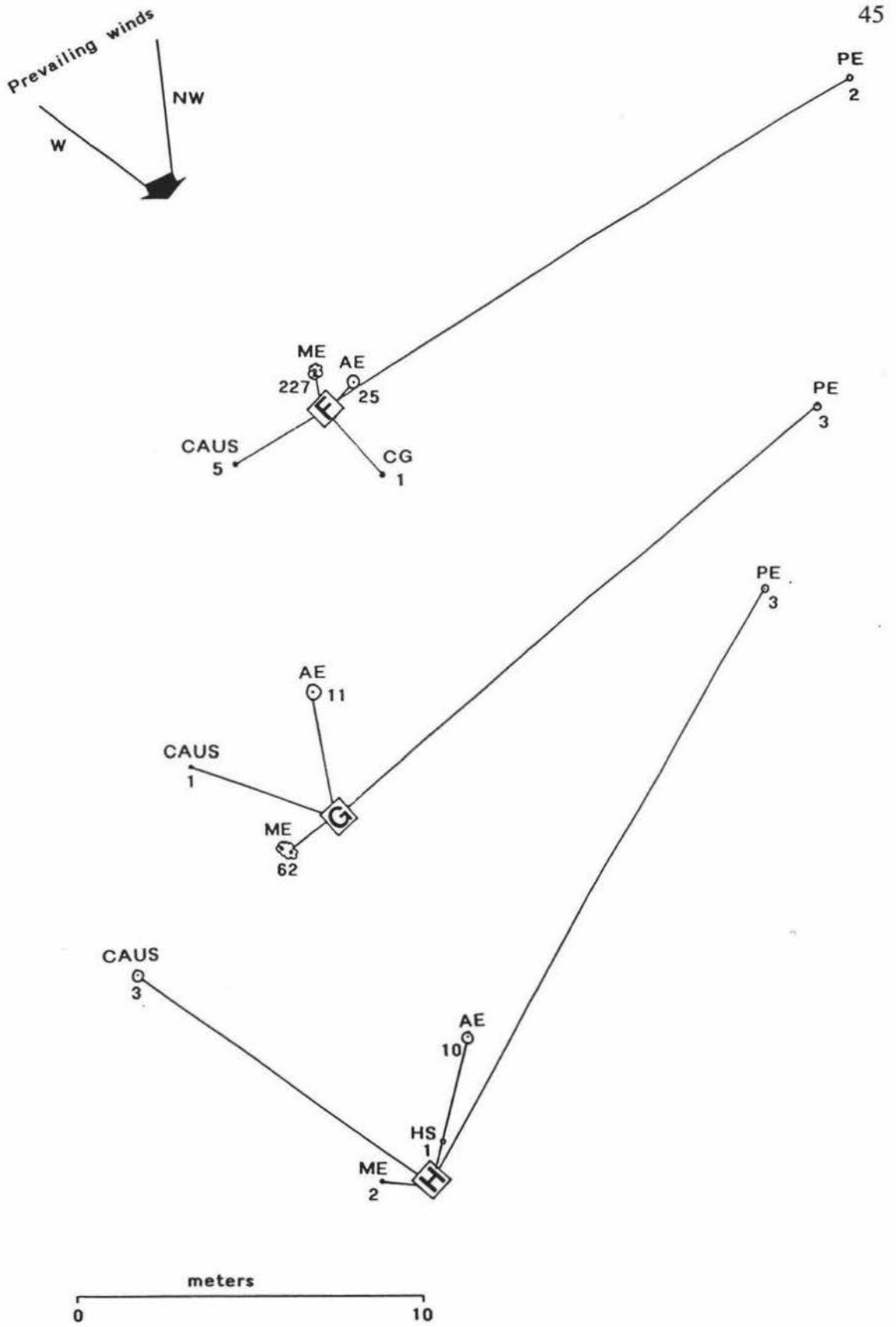


Fig. 3.7a The distribution of the nearest adult individuals that contributed seed to the three traps in Gap One.



**Fig. 3.7b** The distribution of the nearest adult individuals that contributed seed to the three traps in Gap Two.

### 3.3.7 Dispersal modes

Of the identified species trapped in the seed rain, over half (51.6%) were primarily bird dispersed (Table 3.5). The proportion of their different colours are given in Table 3.6.

**Table 3.5** Dispersal modes of the identified species in the trapped seed rain. (x) adventive species.

DISPERSAL AGENTS	Trees	Shrubs	Lianes	Herbs	TOTAL
Birds	10	3	3	0	16 (51.6%)
Wind	2 (2)	1	2	2 (4)	13 (41.9%)
Other	0	0	0	1 (1)	2 (6.5%)
TOTAL	14	4	5	8	31

The majority of the bird dispersed species caught in the traps however, had seeds which were less than 10 mm in size. Few are primarily dispersed by kereru, and those that are can also be potentially dispersed by a range of smaller native and introduced bird species.

**Table 3.6** Proportions of different colours represented in the bird dispersed aril/fruit/seeds collected in the seed rain.

RED	RED/ORANGE	ORANGE	PURPLE	BLACK	WHITE
4	3	1	2	4	2

### 3.4 Discussion

There are only a small number of studies on seed rain into lowland forest communities in New Zealand for comparison with this study, and only one other study within New Zealand has sought to investigate seed rain entering natural gaps (kauri forest; Ogden *et al.*, 1987). The seed rain estimates presented here are comparable with those made in other lowland forests in New Zealand (Hinds & Reid, 1957; Beveridge, 1964; James & Franklin, 1978; Norton & Kelly, 1988; Burrows, 1994b). They differ from estimates of seed rain entering non-forest vegetation communities, usually by being significantly higher in abundance (Connor, 1966; Mark, 1965; Allen & Platt, 1990; Spence, 1990a) and from tropical rain forests (Young *et al.*, 1987; Denslow & Gomez-Diaz, 1990), by being very much less diverse. Because most of the seed rain investigations in temperate forests are made at the species, not the community level, comparisons are difficult.

Seeds of 40 plant species were trapped during the study year, nine of which remain unidentified. This total species number is comparable to the 56 species per year trapped in other areas of lowland forest in New Zealand (Burrows, 1994b). It is low in comparison to the 150-160 species trapped per year in neotropical Mexican forest (Martinez-Ramos & Soto-Castro, 1993) and premontane wet tropical forest in Costa Rica (Denslow & Gomez-Diaz, 1990), yet significantly higher than the 19 species trapped in a New Zealand alpine community (Spence, 1990a). The total numbers trapped in the various habitats gives a good indication of the available species diversity.

No single kind of trap has been developed that will trap seeds of the many different kinds of dispersal categories (Spence, 1990a), however traps similar to the one used in this study (Beveridge, 1964; 1965; Burrows, 1994b) have effectively trapped seeds in several different New Zealand forest communities. All eight traps used in this study successfully intercepted seeds, over the 13 sampling months.

Five key points have emerged from this seed rain investigation:

1. the patchiness/heterogeneity of seed rain over time and space,
2. the variability of the fruiting phenology,
3. local sources provide the majority of seeds in the seed rain,
4. only those bird dispersed species with seeds <5 mm appear to be successfully dispersed, and
5. the most common/dominant species in the surrounding forest are notably sparse or absent from the seed rain.

#### 3.4.1 Patchiness/heterogeneity of seed rain over time and space

Seed sources are often patchily distributed, and seed dispersal is to a great extent a stochastically-driven process. The high coefficients of variation of the nine most abundant species (range 119.3- 265) in this study support this, indicating considerable spatial patchiness in the seed rain. None of the species caught were found in all eight traps, and the species composition of the seed rain sampled by each of the eight seed traps varied widely (ranging from 7-21 species/trap). Patchiness has also been identified in the seed rain entering tropical forests (Martinez-Ramos & Soto-Castro, 1993; Young *et. al.*, 1987), montane mountain beech forest (Allen & Platt, 1990), and alpine communities (Spence, 1990a).

#### 3.4.2 Marked variability of the fruiting phenology

Strong season patterns were recorded in the fruiting phenology of the species trapped during the year. Seed from one species or another fell at virtually all times of the year. Seasonal patterns and fluctuations in seed production and viability have been well documented for many of New Zealand's mast fruiting species (*e.g.*, rimu, matai, *Nothofagus* spp.), with investigations often carried out over several decades. Rimu has been shown to have the most irregular seed crops of all the New Zealand podocarps (Beveridge, 1964; Beveridge, 1980; Herbert, 1978; James & Franklin, 1978; Norton & Kelly, 1988). Beech, the most irregular of

all species, exhibit the most marked periodic heavy (mast) seeding (Wardle, 1984; Allen & Platt, 1990). Variation in size and timing of seed production for masting species is thought

to be highly correlated with the mean daily temperatures at the time of floral primordia formation (Wardle, 1984). A limited number of studies on non-masting New Zealand flora have shown that they too display annual phenological variation, *e.g.*, *Melicytus* spp. (Powlesland *et al.* 1985).

Temperate Northern Hemisphere forests also display marked periodicity in seed production and viability, with many deciduous species also exhibiting mast fruiting (Weis & Hermanutz, 1988; Houle & Payette, 1991; Masaki *et al.*, 1994). By comparison seed rain investigations in tropical forests have found little evidence of strong seasonal patterns (Frankie *et al.* 1974; Hilty, 1980; Denslow *et al.*, 1986; Levey, 1988; Denslow & Gomez Diaz, 1990).

Little of the rimu seed collected was viable either, with high numbers of small persistent brown seeds and unripe green arillate rimu seeds trapped during the study, suggesting that rimu did not mast seed in the 1992-1993 season, in the Manawatu. The last heavy fruiting year was recorded in 1986 (M. Greenwood *pers. com.*). Norton & Kelly (1988) indicated that in non-masting years the viability of a rimu crop may be below 15%. Destruction of rimu seeds by wetas (*Hemideina* spp.) and ship rats may have contributed significantly to the low number of viable seeds intercepted (Beveridge, 1964). Weta eat the seeds of matai, rimu kahikatea and likely other soft seeded species, and considerable numbers of weta frass were recorded in the trap positioned beneath a rimu crown.

Many New Zealand species typically produce large quantities of seed, with only a low percentage of it intact or full (with a viable embryo), *e.g.*, *Olearia ilicifolia*, *Celmisia* spp., *Metrosideros umbellata* (Wardle, 1991). This was certainly true of the rangiora seed collected during this study, much of which was shrivelled and obviously empty.

### 3.4.3 Nearest seed source

The data suggests that those species overhanging or in close proximity to the traps contribute the majority of the seeds. A large proportion of the seed rain appeared to be from plants less than 50 m away from the traps, with the majority closer than 15 m. The distance from the nearest individual to the trap was not correlated with the number of seeds, however this is

likely to be because of interaction of many different factors, including the canopy height of the plant, the volume of seed produced during the trapping year, and its dispersal ability.

In contrast, work done in neotropical rainforest in Costa Rica indicated large proportions of the seed rain entering tree fall gaps is from plants at least 50 m away, and some considerably further (Denslow & Gomez-Diaz, 1990). This difference is likely to reflect the type, number and diversity of the dispersal agents, with large numbers of frugivorous mammals and birds acting within the rainforest compared to the depauperate avifauna present in Keeble's Bush. Both the size of the dispersing animal and the period of seed retention in the gut are important in determining how far a seed will travel (Fenner, 1985).

All those woody tree and shrub seeds originating from further than 50 m from the traps were from either large emergent podocarps (totara, kahikatea, and matai), wind dispersed canopy trees (pukatea), or common wind dispersed adventive tree species (radiata pine and silverbirch). Seeds of large podocarp trees, with their crowns above the main canopy, can disperse *via* gravity and strong prevailing winds, but not usually more than 20 m (Beveridge, 1980). With the assistance of bird dispersers, however, they are able to travel considerably farther (Beveridge, 1964).

Previous studies have shown that the seeds of kahikatea become detached from their arils following bird dispersal (Beveridge, 1964), and all seeds intercepted in the present study supported this observation. Therefore one of three things is likely to have occurred:

- The seeds were eaten and deposited in the traps by birds, such as blackbird or tui (Fountain *et al.*, 1989),
- The arils of the seeds were eaten *in situ* prior to the seeds dispersal, with the seeds then dispersed by wind/gravity (Fountain *et al.*, 1989), or
- the seed fell under gravity and the fleshy attachment was consumed while it was within the catching jar (by an insect).

#### 3.4.4 Adventive component

It was difficult to determine the exact numbers of adventives present in the seed rain of each site during the study period, because a proportion of the small number of seeds which remained unidentified may have been from adventive species. However, six of the eight traps caught seeds identified as adventives, virtually all were herbaceous and wind dispersed. Only those adventive herbs with explosive or wind dispersed seeds reached the traps, which stood one metre above the ground. All the herbaceous adventives were local in origin; *i.e.*, already growing within the gap sites at the time of trapping. It is probable that they originally dispersed into the gap sites from the surrounding farmland. Previous studies of seed rain across habitat margins have shown adventive species are able to travel 80 metres, from pasture into closed forest (*e.g.*, tropical Queensland rainforest, Willson & Chrome, 1989).

The Manawatu is representative of a fragmented landscape. In similar situations, higher edge:interior ratios are likely to increase the contribution of propagules from shade intolerant, edge species to gap successional processes in the forest interior (Ranney *et al.*, 1981). The potential therefore is high for new tree fall gaps within the bush to be invaded and dominated by adventives. In Keeble's Bush these include blackberry, elderberry, and nightshade. Wind dispersed adventive species appear to be the most mobile, with the ability to travel over a kilometre; pine seeds, for example reached five of the traps, covering an average of 30 m, and silver birch reached two, covering 500 m. Neither have, however, been successful in establishing within the canopy gaps.

#### 3.4.5 Many common species in the surrounding forest were notably absent

There was an notable absence or paucity in the trapped seed rain of species that are relatively common components of the surrounding vegetation (*e.g.*, *Fuchsia perscandens*, mahoe, New Zealand passionfruit, poataniwha, small-leaved milktree, and shrubby mahoe), despite the fact that in many cases mature adults over hang, or are close to, the traps. This may possibly be directly related to the lack of suitable frugivores amongst the depauperate bird fauna now inhabiting Keeble's Bush, as most of these common plant species have fleshy fruit.

The most important frugivores that are still quite common on mainland New Zealand (kereru, tui, bellbirds and silvereye) are, apart from silvereyes, uncommon or absent from Keeble's Bush (*pers. obs.*). Silvereyes have the smallest gape (5-6 mm) of the four, restricting them to dispersing seeds 6 mm and less in diameter (Clout & Hay, 1989; Burrows, 1994a). This was reflected by the size of the majority of bird dispersed seeds that reached the traps (*e.g.*, lemonwood); virtually all were <8 mm. Introduced blackbirds are generalistic frugivores (Snow & Snow, 1986; Burrows, 1994a), and are common throughout the Bush (*pers. obs.*). They have a larger gape (9 mm) and therefore may compensate for the lack of native birds by dispersing some of the larger fleshy fruits (Snow & Snow, 1986). Seed predators, like possums, have been implicated as dispersal agents for some species, but the effectiveness and importance of these exotic dispersal vectors has not yet been evaluated (Cowan, 1990).

In addition, if no effective dispersal mechanism is operating, *i.e.*, through loss of bird species, the seeds are more likely to fall via gravity, and accumulate beneath the parent (Herbert, 1978). This increases seed predation for some species because that seed which remains at the base of the parent tree is more vulnerable to seed predators, *e.g.*, mice, pigs, possums, and ship rats (Beveridge, 1964; Herbert, 1978). Seed predation, by ship rats, possums, and weta while the fruit is still on the plants may also have an enormous impact (Brockie, 1992).

Brockie (1992) has suggested that, in addition to direct seed predation, browsing, particularly by possums on the leaves and flowers of some of these species (*e.g.*, mahoe) may be reducing their vigour, and lessening the number of flowers available for pollination and subsequent seed set. A consequence of their reduction in vigour will mean they have little energy to partition into seed production. This seems a likely scenario for mahoe. Possum browse and bark biting is evident in most of the mahoe trees around the sites, and little ripe fruit was observed on these trees during the study.

# Chapter 4

## Seedling growth and mortality

### 4.1 Introduction

The probability of any species becoming established following a natural disturbance event (*e.g.*, windthrow, landslide, fire) depends largely upon how well its seedlings can withstand mortality risks imposed by an environment that changes as plants develop from seed to later life stages (Martinez-Ramos & Soto-Castro, 1993). A complex of traits, including the initial amount of maternal resources, antiherbivore defences (Dirzo & Dominquez, 1986), carbon balance, and seedling size, determines this probability (Martinez-Ramos & Soto-Castro, 1993). The complex of resources, required by seedlings of each species for further growth and development, is termed their 'biological space' (Ross & Harper, 1972). In addition, within species, other important influences include seed size, emergence time, growth rate, and proximity to neighbours.

#### 4.1.1 Factors effecting seedling survival

The early stages of seedling growth generally have high mortality rates (Ng, 1978; Fenner, 1985; Burrows, 1990). Factors limiting seedling establishment differ between sites and species, and include initial seed input and microsite availability (June & Ogden, 1975; Law, 1981). For woody tree and shrub seedlings factors that can cause seedling death include light regimes, desiccation, physical damage, burial, herbivory/predation, pathogens, competition, and allelopathy (June & Ogden, 1975; Ng, 1978; Streng *et al.* 1989; Lieberman & Li, 1992; Martinez-Ramos & Soto-Castro, 1993). Studies in a wide range of temperate and tropical forests have shown that physical damage by falling debris (tree, branch and litterfall) is also potentially a significant agent of seedling mortality (Clark & Clark, 1989).

#### 4.1.2 Light requirements

There are two principal classes of forest tree and shrub seedlings: primary or shade-tolerant species that persist as suppressed seedlings in the understorey until a canopy gap opens above

or near them and permits accelerated growth, and pioneers, or shade intolerant species, that germinate in gaps and grow rapidly (Brokaw, 1987; Swain & Whitmore, 1988; Canham, 1989). Studies of the light requirements of 18 rainforest tree seedlings found that survival in shade was related to the successional status of the species (Augsburger, 1984). Species characteristic of later stages of succession tend to have seedlings which are more tolerant of low light conditions, while those that require high light (shade-intolerant) tend to be colonisers (Swain & Whitmore, 1988). Those seedlings tolerant of low light conditions often exist for extended periods beneath intact canopies, comprising what is often called the "seedling bank" (Brokaw, 1985; Streng *et al.*, 1989).

The type of germination exhibited is also related to a seedling's light demands. Shade-intolerant or pioneer species tend to have epigeal germination and green cotyledons capable of photosynthesis (Swaine & Whitmore, 1988). In the New Zealand context titoki exhibits these characteristics. By comparison those species which are shade tolerant, and establish under closed canopy, have hypogeal germination, achieving initial height without having to photosynthesise (*e.g.*, tawa; Knowles & Beveridge, 1982). Shade tolerant species also tend to have larger seeds, and therefore greater initial food reserves to establish under low light conditions.

A whole suite of other characteristics (*e.g.*, seed dormancy, seed dispersal mechanisms, and light compensation points), have also been applied to the two classes of seedlings (Swaine & Whitmore, 1988).

#### 4.1.3 Seedling investigations in New Zealand

Much of the work done in New Zealand on seedling establishment and growth has been in relation to the re-establishment of podocarp seedlings following different logging methods (*e.g.*, clear felling, strip felling), to determine the feasibility of managing indigenous forests as timber resources (Beveridge, 1973; Herbert & Beveridge, 1977; Beveridge & Herbert, 1978; James & Franklin, 1978; James & Griffiths, 1978; Smale *et al.*, 1985; Baxter & Norton, 1989).

Other studies have looked at seedling growth and establishment of different tree species (*e.g.*, red beech [*Nothofagus fusca*]), as part of the larger questions of forest pattern and regeneration ecology (*e.g.*, June & Ogden, 1975; Herbert, 1978; Runkle & Veblen, 1992).

The main aim of this chapter was to determine the diversity, density, and survival rates of the woody tree and shrub species within two gap sites (G1 and G2). In addition, comparisons were made between the adult assemblages of the surrounding vegetation, and the current seedling population.

Survival and mortality factors were also investigated for seedlings of titoki, a dominant canopy tree in the study area.

## 4.2 Methods

### 4.2.1 Seedling survival

#### *Tagging and measurement*

All seedlings within Gaps One and Two were tagged with plastic bread tags, at the end of November 1992. (Descriptions, and location maps of Gaps One and Two; Fig. 2.3 & 2.4). Seedlings were arbitrarily defined in this study as individuals <2m in height, with a stem diameter of 1.5 cm or less (Herbert, 1978; Norton, 1991; Lieberman & Li, 1992). The species, its height (taken from the soil surface to the tip of the apical bud) and the basal stem diameter (measured 0.5 cm above the soil) of each seedling was recorded. The gaps were divided into metre quadrats and all seedlings were mapped, to aid in re-location. The tagged seedlings were re-measured late in November 1993, and new seedlings (those which had grown in the intervening year) were also recorded and measured.

#### *Adult assemblages*

At each site 30x30 m plots, divided into grids of 5x5 m squares, were laid out to include the gaps. All trees >1.5 cm d.b.h. (diameter at breast height) were measured and mapped. For those trees with multiple stems (*e.g.*, mahoe and titoki) the girth of each stem was measured separately. Fig. 2.3 and 2.4 are maps of the plots showing positions of all individual mature trees and shrubs. Podocarp species, represented as seedlings but not present within the plot were sought, and measurements were made from the gap to the nearest mature individual of each species. Those occurring further than 70 m away were not measured.

### 4.2.2 Titoki (*Alectryon excelsus*) seedling survival

One hundred titoki seedlings were tagged, as above; fifty each within Gap Two (G2), and in the understorey of Adjacent Forest (AF) (Descriptions and map of study area location can be found in Chapter 2; Fig. 2.2 & 2.4), in May 1993. Of the 100 seedlings tagged no seedling

was <30 mm in height, and all had either hypocotyl hooks and emerged cotyledons, or cotyledons and their first true leaves at their first measurement. The height and basal stem diameter (measured 0.5 cm above the soil) of the seedlings were measured, along with their stage of development, the number of cotyledons (none, one or two), and the length and condition of their first, and subsequent, leaves.

The probable cause of death was noted (*e.g.*, buried, cut off, pulled out, pulled out with leaves, stem, withered) unless the seedling had disappeared (no sign). The seedlings were re-measured, and re-examined, initially once a month for the first nine months, and intermittently over a further 21 months. The final measurements were made in July 1995.

#### 4.2.3 Analysis

Statistical analysis is limited as much of the data in this chapter is by nature descriptive. Chi-square ( $\chi^2$ ) analyses were used to compare differences in species and seedling number from year to year. Differences were regarded as significant if  $P \leq 0.05$ . Critical values for all statistics were obtained from Zar (1984).

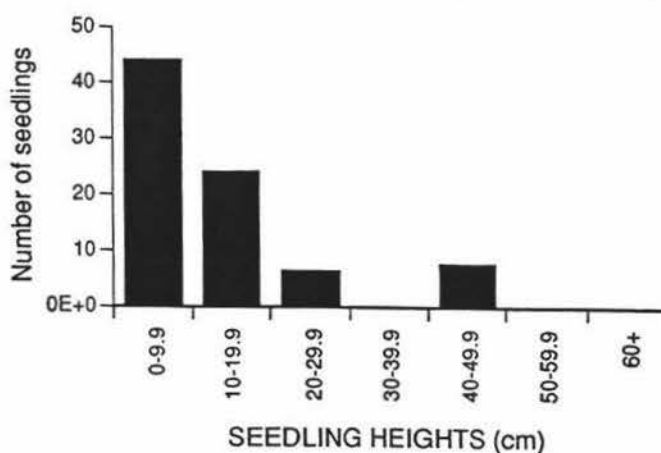
## 4.3 Results

### 4.3.1 Seedling composition and survival: Gap One

A total of 229 seedlings were recorded and tagged within Gap One, in 1992 (Table 4.1). Of those, 161 (70.3%) seedlings survived until 1993. The seedling survival rates of the species present varied between 0% and 100% (mean = 64.9%  $\pm$  7.7 SE). Most of the species that had high seedling survival rates (>60%) were either represented by small numbers of seedlings ( $n < 10$ ; pigeonwood, rewarewa, mapou and totara), and/or had high numbers of seedlings that were already well established in 1992 (*i.e.*, not cotyledonous, or not in their first year of growth when measured [ $>20$  cm]).

Most of the species that showed high seedling mortality (over 50%) were palatable to introduced browsers (Brockie, 1992); *e.g.*, 75% of kanono, 67% of kawakawa, 50% of rangiora and 67% of tawa seedlings.

Seedling mortality appeared to be size dependent (Fig. 4.1). The smallest, and presumably, the youngest seedlings had a higher probability of removal than larger ones. For example, in the 0-9.9 cm height class, 44% of the seedlings disappeared, whereas in the 40-49.9 cm height class the mortality figure was 7.7% over the same period. The differences in mortality between height classes were highly significant ( $\chi^2=1.729$ ;  $df=6$ ;  $0.95 < p < 0.90$ ). Virtually all (97%) the seedlings which died were  $<20$  cm in height when initially measured.



**Fig. 4.1** The percentage mortality for different height classes of seedlings in Gap One; 1992-1993.

By 1993 the total number of seedlings present within Gap One had increased to 252. This included the 161 surviving seedlings, as well as 91 newly established individuals. Kahikatea, kawakawa and kaikomako accounted for virtually half (49.5%) of the new seedlings.

The most abundant species in Gap One were kaikomako, kahikatea, houhere and titoki, together making up 67% in 1992, and 60% in 1993 of the total seedlings.

Many of the well established, presumably older, seedlings, particularly those of houhere, kaikomako, lemonwood and titoki were highly branched with thick stems, but did not attain a height of more than 30 cm. Their apical buds appeared to have been damaged on a number of separate occasions, allowing axillary bud development (*pers. obs.*).

The number of species of seedlings in Gap One did not differ significantly between years, with 17 species recorded in 1992, and 18 in 1993 ( $\chi^2=0.0142$ ;  $df=1$ ;  $0.5 < P < 0.25$ ). The change in species composition was also not significant. The single rimu seedling present in 1992 disappeared in the intervening year, while hangehange and *Coprosma areolata* seedlings became established. Seedling density increased by 1 seedling/m<sup>2</sup>, from 9.5 to 10.5 seedling/m<sup>2</sup>, with the number of species/m<sup>2</sup> increasing from 4.6 to 5.4 species/m<sup>2</sup>.

**Table 4.1** Gap One: Seedling numbers in 1992, survivorship from 1992-1993, those seedlings which established in the intervening year and seedling numbers in 1993.

(+) Increase in seedling number from 1992-1993 (-) Decrease in seedling number from 1992-1993

(=) Seedling number unchanged from 1992-1993

SPECIES	TOTAL 1992	Survivors	New 1993	TOTAL 1993	Change
<i>Coprosma areolata</i>	0	0	3	3	+
hangehange	0	0	1	1	+
houhere	33	30	8	38	+
lemonwood	11	11	1	12	+
kahikatea	45	21	19	40	-
kaikomako	52	45	12	57	+
kanono	16	4	8	12	-
kawakawa	6	2	14	16	+
mahoe	7	7	7	14	+
mapou	5	5	0	5	=
matai	2	1	1	2	=
pigeonwood	7	7	9	16	+
pukatea	2	1	1	2	=
rangiora	10	5	7	12	+
rewarewa	3	2	0	2	-
rimu	1	0	0	0	-
tawa	3	1	0	1	-
titoki	24	17	0	17	-
totara	2	2	0	2	=
<b>TOTAL</b>	<b>229</b>	<b>161</b>	<b>91</b>	<b>252</b>	

### *Turnover rate*

All of those species whose seedling number stayed the same (pukatea, mapou, totara and matai) were represented by fewer than 10 seedlings (two, five, two and two respectively). Of the nine increases, two were by species new to the gap in 1993 (*Coprosma areolata* and *hangehange*). None of the seedling numbers differed significantly between 1992 and 1993.

Kahikatea, kanono, matai, pukatea, and rangiora seedlings all exhibited a high turnover rate. That is, over half their seedlings disappeared and were replaced by at least that many again.

### *Comparison with the canopy and understorey of the surrounding forest*

All but four (kahikatea, pukatea, matai and totara) of the nineteen species represented as seedlings in Gap One, were present as mature individuals in the understorey and canopy of the surrounding forest. Three of the four occur within 70 m of the Gap, and the fourth, pukatea, is present on the lower terraces of Keeble's Bush.

Species proportions differed markedly between the seedlings within Gap One, and the forest surrounding it (Table 4.2). The most abundant species in the surrounding forest were kawakawa, mahoe, titoki, and kanono, together accounting for 70% of the trees and shrubs present. However, within the Gap, kaikomako, kahikatea, houhere and titoki dominated, making up over 65% of the seedlings in both years (refer Table 4.2).

**Table 4.2** Percentages of the four most abundant seedling species within Gap One, in 1992 and 1993, compared with their abundance in the surrounding forest (tree and shrub species >1.5 cm d.b.h; 30x30 m plot).

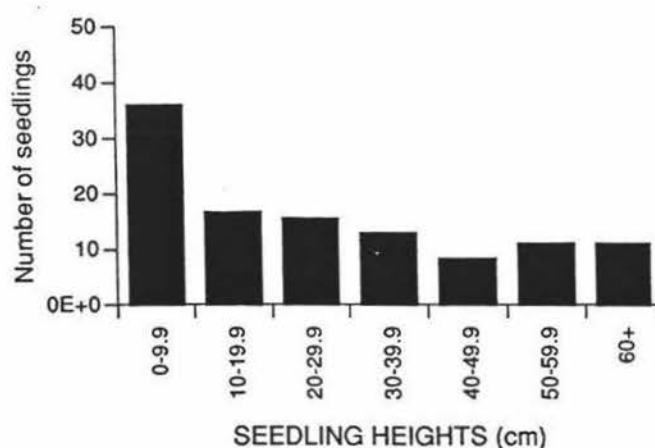
Species	Gap One 1992 (%)	Gap One 1993 (%)	Surrounding forest (%)
kaikomako	22.7	22.6	0.65
kahikatea	19.7	15.9	0
houhere	14.4	15.11	3.03
titoki	10.5	6.7	12.2

Of the woody tree and shrub species in the surrounding forest five did not occur as seedlings within the Gap. These were poataniwaha, shrubby mahoe, small-leaved milk tree, cabbage tree and wineberry. Poataniwaha was the only one of these making up >1% of the total individuals in the surrounding forest.

#### 4.3.2 Seedling composition and survival: Gap Two

In 1992 a total of 219 seedlings were tagged and measured, 169 (77%) of which were still present in 1993 (Table 4.3). Survival rates ranged between 0% to 100% (mean = 62%  $\pm$  10.85 SE). The same pattern as that recorded in Gap One for species with high seedling survival, occurred in Gap Two; *i.e.*, those with <10 seedlings and/or high number of seedlings that were already established in 1992 when first measured. The majority (62%) of the seedlings that died were <10 cm in height, and likely in their first or second growing season.

The differences in mortality between height size classes were not significant ( $\chi^2=4.215$ ;  $df=6$ ;  $0.75 < p < 0.5$ ). Seedlings of all ages and heights seemed just as likely to die, with a slightly higher probability for those in the 0-9.9 cm height class. For example, in the 0-9.9 cm height class 36% of the seedlings died, while in the 20-29.9 cm height class the figure was 15.6%.



**Fig. 4.2** The percentage mortality for different height classes of seedlings in Gap Two; 1992-1993.

The survivors, combined with the 108 new seedlings, gave a total of 277 seedlings in 1993. However, this increase was not statistically significant ( $\chi^2=3.39$ ;  $df=1$ ;  $0.10 < P < 0.05$ ). Species composition of the seedlings in Gap Two changed little between 1992 and 1993. The only

change was the addition of poataniwha in 1993. Mahoe, kawakawa and titoki accounted for nearly 90% of the total seedlings in both years (86.3% in 1992 and 88.4% in 1993), and 87% (94) of the 108 new seedlings (Table 4.3). All other species recorded were represented by fewer than 10 seedlings.

The total number of species/m<sup>2</sup> was low, and changed little between years; 3.2 species/m<sup>2</sup> in 1992 and 3.8 species/m<sup>2</sup> in 1993. Seedling densities however did increase, by 2.8 seedlings/m<sup>2</sup>, from 10.4 to 13.2 seedlings/m<sup>2</sup>. This increase was due largely to an influx (60) of newly established kawakawa seedlings.

**Table 4.3** Gap Two: Seedling numbers in 1992, survivorship from 1992-1993, those seedlings which established in the intervening year and seedling numbers in 1993.

(+) Increase in seedling number from 1992-1993 (-) Decrease in seedling number from 1992-1993

(=) Seedling number unchanged from 1992-1993

SPECIES	TOTAL 1992	Survivors	New 1993	TOTAL 1993	Change
<i>Coprosma areolata</i>	1	0	1	1	=
kahikatea	9	3	2	5	-
kaikomako	1	1	1	2	+
kanono	5	3	6	9	+
karamu	6	5	1	6	=
kawakawa	78	64	60	124	+
mahoe	95	77	13	90	-
matai	5	4	0	4	-
pigeonwood	0	0	2	2	+
poataniwha	0	0	1	1	+
shrubby mahoe	2	2	0	2	=
titoki	16	10	21	31	+
totara	1	0	0	0	-
<b>TOTAL</b>	<b>219</b>	<b>169</b>	<b>108</b>	<b>277</b>	

### *Turnover rate*

Of the 13 species whose seedlings were present in Gap Two, only kawakawa seedling numbers differed significantly between years ( $X^2=5.238$ ;  $df=1$ ;  $0.025 < P < 0.01$ ) (Table 4.3). Three species maintained the same number of seedlings; *Coprosma areolata*, karamu and shrubby mahoe, while six increased in number (Table 4.3). Two of the six species that increased in number were new to the Gap in 1993 (pigeonwood and poataniwha). Four species decreased in number, and one, totara, was no longer represented in 1993.

### *Comparison with the canopy and understorey of the surrounding forest*

Nine of the thirteen species represented as seedlings within Gap Two occur in the understorey or canopy of the surrounding forest. Kahikatea, totara, matai, and pigeonwood are all absent from the immediate vicinity, though the first three are present as mature individuals <70 m from Gap Two. Pigeonwood was not located in the vicinity, but is a fairly common component of the subcanopy throughout much of the forest.

The proportions of the three most abundant species (mahoe, kawakawa and titoki) within the Gap in both years, and in the surrounding forest (Table 4.4) were very similar; 86.3%, 88.5% and 87.4% respectively. The remaining species in all cases made up <5% of the total individuals.

**Table 4.4** Percentages of the seven most abundant seedling species within Gap Two, in 1992 and 1993, compared with their abundance in the surrounding forest (tree and shrub species >1.5 cm d.b.h.; 30x30 m plot).

Species	Gap Two 1992 (%)	Gap Two 1993 (%)	Surrounding forest (%)
mahoe	43.4	32.5	17.6
kawakawa	35.6	44.8	56.8
titoki	7.3	11.2	13
kahikatea	4.11	1.8	0
karamu	2.74	2.2	0.2
matai	2.28	1.4	0
kanono	2.28	3.2	0.6

#### 4.3.3 Comparison of the two sites: Gap One and Two

The total numbers of seedlings, and the seedling densities in the two sites were very similar in both years. Species diversity and numbers of species/m<sup>2</sup> however did vary. The seedling population of Gap Two was species poor in comparison with that in Gap One. In Gap Two only three species (kawakawa, mahoe and titoki) had >10 individuals, with the majority (62%) of species represented by 5 or less seedlings. On average there were 1.5 species/m<sup>2</sup> more in Gap One.

Ten species of seedlings were common to both Gap sites, with nine found only within Gap One (hangehange, houhere, lemonwood, mapou, pukatea, rangiora, rewarewa, rimu and tawa), and a further three occurring exclusively in Gap Two (karamu, poataniwha, and shrubby mahoe). However, three of the nine species only occurring within Gap One do grow in the forest surrounding Gap two. These are houhere, lemonwood and mapou.

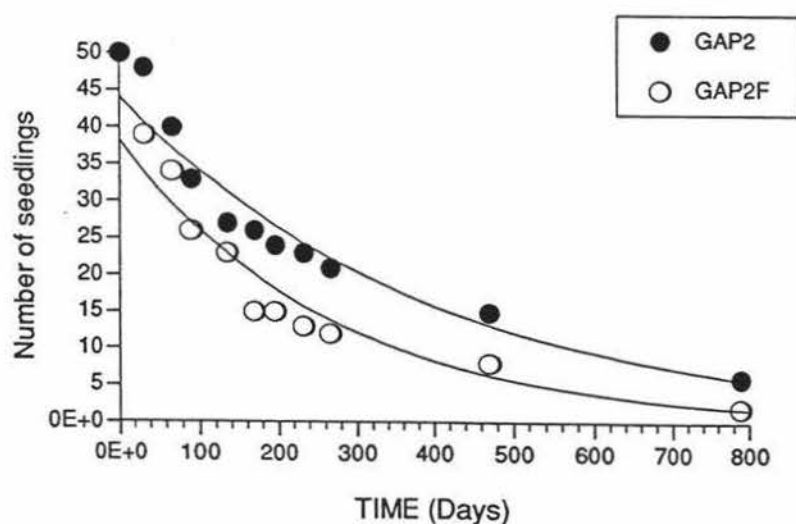
#### 4.3.4 Titoki seedling survival

##### *Seedling heights*

At the initial measurement seedlings in both sites ranged in their stage of development from those newly emerged (30–45 mm in height with remnants of hypocotyl hooks and leaves still tucked within their cotyledons), to those well established (>46 mm in height with cotyledons open and first leaves fully emerged). Their heights ranged from 40–110 mm (mean=77.34 mm) in Gap Two (G2), and from 30–115 mm (mean=72.14 mm) in the Adjacent Forest (AF).

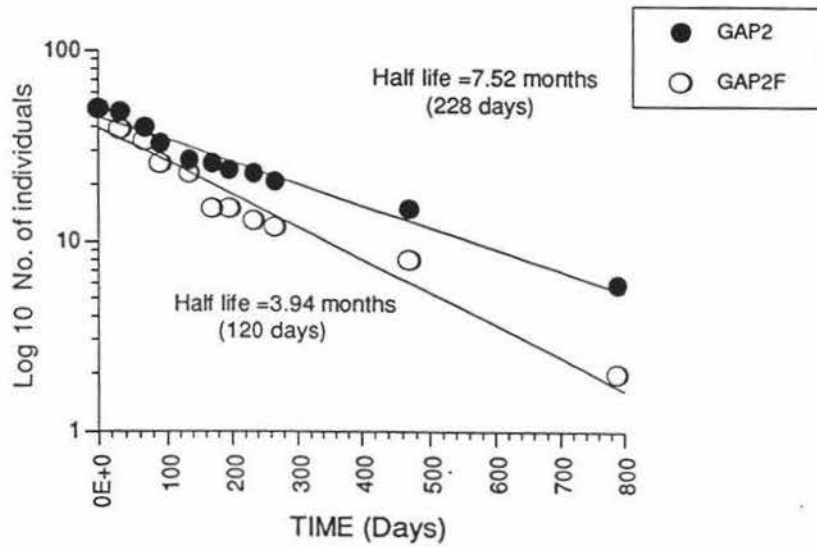
##### *Survival/mortality*

Initial monthly, and two subsequent annual measurements, provided survivorship data over a 30 month (789 day) period, for the 100 tagged titoki seedlings (Fig. 4.3). Mortality rates and the number of surviving seedlings differed between the two sites from the second month of assessment (Appendix 2). The Adjacent Forest site (AF) had consistently higher rates of seedling mortality throughout the investigation (Fig. 4.3). At the end of the first nine months (23/1/94) 42% of the seedlings in G2 were still alive, compared with only 24% in AF (Appendix 2). By the final measurement (1/7/95) only eight of the original 100 tagged titoki seedlings were still alive; six in G2 and two in AF (Fig. 4.3).



**Fig. 4.3** Survivorship curves for the 100 titoki seedlings tagged (Gap Two and Adjacent Forest), May 1993–July 1995.

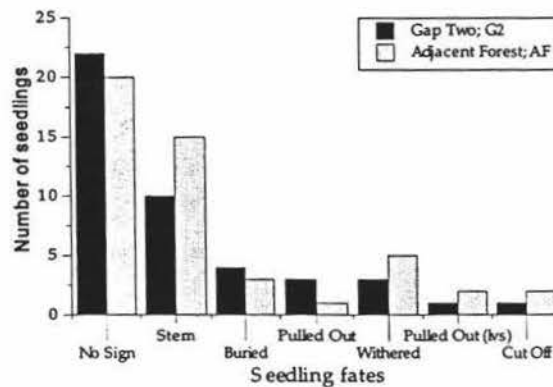
Decay rates for the 50 titoki seedlings tagged in each site could be derived by fitting linear regression lines, and are expressed as half lives (half-life being the time taken for the population size to halve during a period of exponential decline [June & Ogden, 1975]; Fig. 4.4).



**Fig. 4.4** Half-lives (time taken to reach 25 seedlings) indicated for titoki seedlings in Gap Two (G2) and Adjacent Forest (AF).

*Mortality factors*

The fates of the seedlings in the two sites are illustrated in Fig. 4.5. Despite initial monthly census intervals, a conclusive cause of death was not evident for many of the seedlings.



**Fig. 4.5** Presumed fates of the 92 titoki seedlings which died during the study period.

In both sites a third of the seedlings (36.1% in G2 & 33% in AF) disappeared, leaving either no trace, or just the plastic tag. A further third of the seedlings (30.6% in G2 & 35.7% in AF) were left as stems, with no leaves remaining.

A small number had been pulled out (8.3% in G2 & 2% in AF with leaves and 2.8% in G2 and 4.8% in AF without leaves) (Fig. 4.5). That is, they were found lying on the forest floor, with their roots undamaged, and either their leaves intact, or removed.

The remainder of the seedlings died through litter and debris burial (11.1% in G2 & 7.1% in AF), desiccation (withered) (8.3% in G2 & 11.9% in AF) and from being cut off (2.8% in G2 & 4.8% in AF). Litter burial was assumed to be the cause when the seedling was found completely covered by debris. Seedlings with wilted leaves and an intact root systems were presumed to have died through water shortage, and those seedlings with stems 'chewed' near the base were supposed to have been cut off.

Of those seedlings which died within Gap Two, 14 were growing beneath young kawakawa seedlings at the north-eastern end. All appeared etiolated and none had large vigorous leaf growth, as displayed by titoki seedlings in other parts of the Gap.

## 4.4 Discussion

### 4.4.1 Seedling composition and survival

Moore & Chapman (1986) noted that although the flux of individual plants into and out of populations may be substantial, the number of plants present at different censuses may remain relatively constant over considerable periods of time. This is because the majority of seedlings only survive for short periods, and thus have little impact upon population processes. This appears to be true of the seedling populations in both Gaps One and Two. Neither gap experienced significant variation in the total numbers of seedlings, or in the numbers of species of seedlings present between the successive years remeasurements.

Differences within the gaps from year to year would likely have been more substantial earlier in their histories, when the numbers of suitable microsites available were higher, and the amount of competition from existing vegetation less.

### 4.4.2 Mortality

The mortality pattern varied between the two sites, with seedling mortality within Gap One appearing to be size dependent. This fits the well documented phenomenon of huge seedling mortality during the initial period of establishment and growth which has been well documented in other forest types; *e.g.*, Malaysian rainforest [Ng, 1978; Kennedy & Swaine, 1992], Texan floodplain forest [Streng *et al.*, 1989], New Zealand podocarp forest [Beveridge, 1983], *Tsuga heterophylla* forest [Christy & Mack, 1984], and tropical dry forest in Ghana [Lieberman & Li, 1992]). The survivorship curves of the two populations of titoki seedlings also indicate that the youngest plants suffer the highest mortality risks, and that few individuals will achieve long life spans. The same type of curve has been documented for other forest tree and shrub species (van Valen, 1975; Sarukhán, 1980).

Within Gap Two however, the probability of seedling death appeared high in all height classes, with only slightly higher mortality for smaller seedlings (<10 cm). The high numbers

of seedlings which died in the >60 cm height class can be attributed to the size of the tags used; stems of fast growing mahoe >60 cm seedlings were restricted by the tags, caused ring-barking, stem breakage and death.

As Clark & Clark (1989) indicated, patterns of seedling mortality are a complex product of the activity of all mortality agents. Many of the mortality agents (*e.g.*, competition, drought, disease, predation/herbivory, burial) working on the seedlings would have been similar for both gap sites, however data was inadequate to permit assessment of the various causes of seedling death. The study of titoki seedlings, however, did provide insight into the mortality agents at work, though a large number of the seedlings disappeared leaving no trace. Mortality agents impacting on the seedlings beneath the canopy (AF) and within Gap Two were not significantly different.

#### 4.4.3 Competition

Competition from neighbouring plants (whether from pre-existing vegetation or contemporary individuals) is often the single greatest hazard faced by colonizing seedlings (Fenner, 1985). The seedlings of most species are far more sensitive to competition compared with mature individuals (Raven *et al.*, 1987), though seedlings of different species vary a great deal in their ability to cope (Fenner, 1985; Kolb & Steiner, 1990). For red beech seedling establishment, the least favourable gap sites are those where there is already a high density of established seedlings (June & Ogden, 1975). Older red beech seedlings occupy many of the limited number of favourable microsites, suppressing younger seedlings.

In Gap One there were a number of older seedlings (none >1 m), dense mats of *Hydrocotyle* spp., and patches of *Haloragis erecta*, bracken and *Carex* spp., which likely occupied suitable microsites and restricted seedling establishment. In addition, cabbage tree leaves, dropped by the tree in the centre of the Gap, formed an often dense mat, in a *c.* metre radius around the trunk. Low numbers of seedlings were recorded in this zone. The mat of old leaves may have impeded seed germination and seedling growth, either physically (they formed a dense layer of new, through to decomposing leaves, beneath the tree), by reducing the available light, or possibly by allelopathy. An additional study was carried out, with treatments designed to

investigate these possibilities. However, the commercial native seeds used (*Clematis paniculata*, *Metrosideros excelsa*, and *Fuchsia excorticata*) proved to have very low viability and the results were inconclusive (K.J. Whaley *unpubl. data*).

The north-easterly end of Gap Two was dominated by a fairly even-sized cohort of young kawakawa. The shaded environment beneath them which may have suppressed seedling establishment by reducing germination of light requiring species. The 14 tagged titoki seedlings in this area exhibited marked etiolation and all died, which indicates light was limiting. The taller mahoe seedlings that occurred on the south-eastern edge of the Gap, swards of the annual black (*Solanum nigrum*) and small-flowered nightshade (*Solanum americanum*), and patches of the fern *Phymatosorus scandens* may also have had a similar effects.

Below-ground (root) competition may also be an important factor (Wilczynski & Pickett, 1993). Trenching experiments carried out in forests both here (Cameron, 1963) and in Northern Hemisphere temperate forests (Christy, 1986) indicate seedling growth of many species improves with release from root competition. In some forest types (*e.g.*, Northern temperate forest) a below-ground gap in the fine root biomass has been shown to form, following windthrow and subsequent root death (Wilczynski & Pickett, 1993). This below-ground gap may have important implications for seedling recruitment providing a site relatively free from intense below-ground competition. When soil cores were taken from the Gaps being studied (refer Chapter 5), roots impeded the soil corer in most places. Indeed, the lack of seedlings immediately around the cabbage tree in Gap One could have less to do with the mat of leaves, and more to do with the tree's dense root system (Tomlinson & Esler, 1973). With roots penetrating throughout the soils within the Gaps, seedling drought stress (see below) is likely to be exacerbated.

The activity of soil organisms may also be an important influence on seedling survival within both Gaps. The topic has recently been reviewed in Brown & Gange (1990), who suggest that the effects of subterranean herbivores can be just as great as their foliar-feeding counterparts. It is highly likely that seedling establishment in general is significantly influenced by subterranean herbivory, though much of the data which exists originates from work in

agricultural rather than natural systems (Brown & Gange, 1990).

#### 4.4.4 Herbivory

Much interest in recent years has been focused on the impact of introduced herbivores on native forest ecosystems within New Zealand (*e.g.*, Meads, 1976; Coleman *et al.* 1980). Through the differential palatability of tree and shrub adults and seedlings the composition of New Zealand's forests have been and continue to be altered by their presence (Ogden, 1976).

In Gap One a number of seedlings (*e.g.*, lemonwood and kaikomako) suffered the loss of their apical buds on more than one occasion, or were browsed and hedged, as evidenced by their low (<30 cm in height) multi-branched habit. Foxglove (*Digitalis purpurea*) and *Carex* spp. within the Gap were also cropped. In addition, the highest seedling mortality (50%) was recorded for those species (*e.g.*, kanono, rangiora and tawa) known to be palatable to the introduced herbivores present (*i.e.*, possums and rabbits) (Brockie, 1992). In Gap Two, highly palatable karamu and kanono seedlings were only present within cages (Whaley, K.J., *Unpub. data*; enclosure cages designed to exclude possums and rabbits).

Those titoki seedlings left as just leafless stems were almost certainly browsed by rabbits. Fuentes *et al.* (1983) recorded seedling mortality in shrubland in Central Chile, and found those killed by rabbits were left as denuded dry stems. Several of the titoki seedlings appeared to have had their stems 'chewed' at ground level, leaving a distinct point. This was likely the work of native insects *e.g.*, wetas, and stick insects which are known to predate seedlings (Beveridge, 1973).

As well as direct browsing, blackbirds (*Turdus merula*) and other exotic bird species (*e.g.*, rook [*Corvus frugilegus*], Isabel Castro *pers. comm.*) which forage for insects in the litter, may inadvertently pull seedlings up or dislodge them (June & Ogden, 1975; John Ogden *pers. comm.*). Titoki seedlings found lying on the litter surface may have been pulled out in this way, as their root systems tend to be poorly anchored in the litter, and blackbirds which are common throughout the forest, were often observed feeding vigorously in the litter layer around Gap Two (*pers. obs.*).

#### 4.4.5 Drought stress

One of the most acute hazards for a seedling is desiccation at a time when their root system is scarcely established (Harper, 1977). Drought stress, in the form of extensive leaf wilt, was observed on mature kawakawa, mahoe and hen and chicken ferns during summer months around Gap Two. The litter around both Gaps was observed to be very dry during the same period. However, only a small proportion of the titoki seedlings which died likely succumbed to desiccation. That is, they showed no signs of being predated, and their leaves were withered.

The pines around the margin of the Bush, at the time of this study, probably utilised large quantities of soil water, which may have exacerbated drought stress among the plants growing nearby, especially in dry summer months. This would in part be balanced by the shelter provided, thus reducing transpiration. They also contribute large amounts of pine needles and spent male cones to the soil which in other cases has been shown to alter the pH and the soil chemistry (Hamilton, 1965; Will, 1967; McIntosh, 1980; Burrows, 1990). Several studies in forest communities have shown that plant litter exerts an important effect on seedling establishment (*e.g.*, Carson & Peterson, 1990; Peterson & Facelli, 1992). These changes may be inhibiting the seedling establishment, and seed germination of some species within Gap Two.

#### 4.4.6 Litter burial

Seven of the 98 titoki seedlings which died did so probably as the result of litter burial. A number of the seedlings within the Gaps may have died through burial also, as their tags had to be excavated during remeasurement. A species-independent assay, using inert 'artificial seedlings', could be employed to quantify the importance of litter burial as a mortality agent within the study sites (Clark & Clark, 1989).

In order to be more certain of the causes of death of the seedlings video footage, or direct observation of seedling predation, would be needed. The collection of environmental and edaphic site characteristics would also be helpful in elucidating mortality agents, particularly

in the cases of the titoki seedling cohort followed. A future study might be to locate sites in the adjacent forest understorey, to determine the densities and diversities of seedlings in the shaded environment as a comparison with the results of the present study.

#### 4.4.7 Comparison with the canopy and understorey of the surrounding forest

The diversity of species present as seedlings within natural gaps is heavily influenced by the diversity of species providing the initial seed input (June & Ogden, 1975). Analysis of the seed rain (Chapter 3) entering the two study sites indicated that the bulk of the seeds falling into the gaps were local (*i.e.*, came from the forest immediately surrounding the gaps). The fact that the seedling assemblage in Gap Two has low species richness (13 species) compared with that in Gap One (19 species), then is in part a reflection of the low diversity of mature individuals present in the immediate surrounding forest, *i.e.*, only three species, mahoe, kawakawa and titoki dominate both Gap Two and the surrounding forest.

The diversity of the forest surrounding Gap Two is low primarily because it is on the margin (Fig. 2.2). Differences in both microclimate, vegetation composition and structure exist between forest margins and forest interiors; these have been termed 'edge effects' (Young & Mitchell, 1994). Edge sites experience increased wind velocity, drought stress, lower relative humidity, greater light levels (PAR) and greater temperature fluctuations than sites in the forest interior (Williams-Linera, 1990) and are therefore dominated by species (*e.g.*, mapou) that can tolerate these conditions. These effects may be seasonal, with differences more extreme during the summer months, and may penetrate forest remnants for up to 50 m (Young & Mitchell, 1994).

The results presented here suggests that seedling communities in gaps differ between those gaps within the forest interior, and those at the forest margin. Other studies have also noted differences between seedling populations in interior forest and edge sites (*e.g.*, Williams & Linera, 1990).

# Chapter 5

## The soil seed bank.

### 5.1 Introduction

All viable seeds present on, or in, the soil or associated litter constitute the soil seed bank, *i.e.*, seeds which do not germinate at the soil surface and which escape predation and pathogens (Leck *et al.*, 1989). Their assimilation occurs slowly, by burial beneath litter, by incorporation during natural soil movement (*e.g.*, rain washing small seeds into coarse textured soil; Hopkins & Graham, 1983), or more rapidly because of the activities of soil animals (*e.g.*, earthworms; Lal, 1987) (Moore & Chapman, 1986). Factors which influence the seed burial rate include soil texture and structure, soil deposition and compression, seed size and other morphological characteristics (Thompson *et al.*, 1993), length of seed longevity, earthworm and other animal activity, and local environmental conditions that relate to seed longevity, such as cold or low pH (Parker *et al.*, 1989).

The soil seed bank is a product of site history (Livingston & Allesio, 1968; Kellman, 1974; Fenner, 1985), seed rain (previous seed input) (refer Chapter 3), and seed losses due to germination and mortality (Young *et al.*, 1987; Leck *et al.*, 1989). It may contain allochthonous seeds (*i.e.*, seeds that originate elsewhere and are dispersed onto the site) and/or autochthonous seeds (*i.e.*, seeds produced by plants growing on the site) (Young *et al.*, 1987).

Much early soil seed bank work focused on the commercially important seed banks of arable soils (Warr *et al.*, 1993), primarily as a result of long-standing concerns about the threat to agricultural crops presented by seed banks of weed species (McGee & Feller, 1993). In his review of the seed bank literature, Roberts (1981) observed that "it is only recently that much attention has been devoted to the role of seed banks in natural habitats as distinct from those of agricultural importance". Over the last decade, however, seed banks in a range of habitat types have been studied and the literature is now enormous and expanding rapidly. The aspects of the biology of seed banks covered range from detailed studies of the spatial distribution of buried seeds, to the evolutionary consequences of seed banks (Thompson, 1978). A comprehensive soil seed bank review has been produced in the form of a book (Leck

*et al.*, 1989).

Knowledge of soil seed banks is valuable in understanding aspects of vegetation change and plant succession (Partridge, 1989; McGee & Feller, 1993). They play a crucial role in the dynamics of most plant communities (Fenner, 1991). Models of forest succession suggest that initial phases of secondary succession are largely dependent upon the germination and establishment of plants derived from dormant propagules (Schiffman & Johnson, 1992). However, the relative importance of seed recruitment from the soil seed bank differs among plant species and among communities (Fenner, 1985). They also provide information about vegetation dynamics which may not be evident in the standing vegetation itself, *i.e.*, providing insight into communities which previously occupied a site (Howard, 1974). They are also essential elements in the management, conservation, and rehabilitation of forest ecosystems (Hopkins *et al.*, 1990).

#### 5.1.1 Transient and persistent soil seed banks

Soil seed banks occur in all plant communities, such as annual grasslands (Per & Hansson, 1993), pastures, cultivated land, waste places, wetlands, and forests (Baker, 1989). For species and vegetation communities in temperate zones Thompson and Grime (1979) distinguished four types: Type I, transient seed bank present during summer; Type II, transient seed bank present during winter; Type III and IV, persistent seed banks. Garwood (1989) described seven slightly different soil seed bank strategies present in tropical plant communities, based on germination behaviours and temporal patterns of seed dispersal: A, transient seed banks; B, transient seed bank replaced by a seedling bank; C-E, persistent seed bank; F, seasonal-transient seed bank; G, delayed transient seed bank. In species with transient seed banks, none of the seeds persist for more than one year, while in a species with a persistent seed bank, at least some of the seeds live for longer than a year (Baskin & Baskin, 1989).

The size and functional significance of the persistent seed bank varies between different types of vegetation and different environments (Hopkins *et al.*, 1990). The persistent seed bank is usually characterised by a preponderance of very small, light weight seeds, especially those of ephemeral and weedy species (*e.g.*, early successional species [*e.g.*, black nightshade] or those

of harsh or periodic environments) (Fenner, 1985), and represents only a subset of the plant species in a community over time (Louda, 1989).

As communities mature and long lived species tend to increase, the composition and relative abundance of species in the seed bank versus the above ground vegetation become increasingly different (Thompson & Grime, 1979; Fenner, 1985). Species with large seeds (*e.g.*, many primary forest tree species) generally do not have dormant seeds resident in the soil (Fenner, 1985). Large seeds, particularly those with thin seed coats, tend to attract high levels of predation pressure, compared with those with small or tough seeds (Louda, 1989).

The ability of plants to produce, through intrinsic or extrinsic mechanisms, a persistent seed population in effect becomes an additional habitat filter controlling species composition of vegetation composition. Species with transient seed banks may compensate with alternative mechanisms, such as long lived adults or persistent bulbs or rhizomes.

### 5.1.2 Seasonal variation/spatial heterogeneity

Processes such as dispersal, predation, germination and burial determine the spatial patterns of seeds in the soil, which are usually heterogeneous, both horizontally and vertically within the soil profile. The timing of seed dispersal, size of the seed crop, dispersal characteristics such as buoyancy or fruit quality (refer 3.1.1), and variations in environmental conditions such as inundation patterns or gaps can all influence the spatial distribution of seeds (Parker *et al.*, 1989). Predation of seeds and related activities of predators can also be of great importance. Predation intensity varies considerably within habitats; seed bank depletion can be sizeable and differential. Germination may often be the principle process by which seeds are lost from the soil seed bank. It is tightly coupled with spatial variation in microclimate that cue germination.

The interrelationship among environmental fluctuations, seed production, dispersal, habitat quality, and germination are responsible for most temporal patterns (Parker *et al.*, 1989).

### 5.1.3 Role of soil seed banks in regeneration/following disturbance

Studies from many plant communities have shown the importance of the soil seed bank to ecosystem development following disturbance (Looney & Gibson, 1995). However, the degree to which the soil seed bank is involved in regeneration succession and secondary succession seems to vary greatly (Skoglund, 1992). Gap size seems to be an important controlling factor concerning the relative contribution from the soil seed bank following disturbance (Garwood, 1989); regeneration from it is less important in small gaps but becomes predominant in large gaps.

Whether buried seeds contribute to regeneration depends on the depth from which they can germinate and the rate at which seeds in the soil are brought to the surface (Garwood, 1989). Ability of seeds to germinate usually decreases with depth and is influenced by soil type, seed size and species. The processes that bury seeds can also bring them to the surface, but probably don't account for much regeneration following gap creation except on bare soil around uprooted trees.

### 5.1.4 Seed longevity

Although considerable progress has been made in our understanding of soil seed banks, most work has focused on species composition and dynamics, either at a single point in time, or over a period of months or years. Less progress has been made in understanding the fates of individual seeds in the soil, due in part to the inherent difficulty of following the history of small objects like seeds in the complex environment of the soil (Spence, 1990*b*). Despite the difficulties, studies on seed fate provide valuable data on seed predation, viability, and longevity in the soil under relatively natural conditions.

Some indication of the normal period of seed viability of species under field conditions can be obtained by burying a known number of seeds and monitoring their germination over a period of years. Early interest in the longevity of seeds buried in the soil was generated by several studies; Beal in 1879 (Beal, 1905) and by Duvel in the early 1900's (1904). The work of these investigators included long-term experiments with buried seeds. The buried seed was

sampled at intervals, with large differences in the germination of species being recorded. It has now been established that the numbers of seed remaining viable tend to decline exponentially with time (Fenner, 1985).

Large seeds of climax (or at least late successional) taxa (*i.e.*, *Quercus* or *Beilschmeidia*) are rather moist, and this may be associated with their short lived survival if ungerminated (Baker, 1989). In the most extensive study of tropical seed longevity (Hopkins & Graham, 1987), seeds of primary species had a much shorter longevity than those of pioneer and late secondary species, and lacked facultive dormancy (Garwood, 1989). Longevity of large seeds in the soil is probably not limited by seed energy reserves (Garwood, 1989) *e.g.*, large dead seeds often have ample reserves remaining (Baker, 1989).

#### 5.1.5 Temperate and tropical rainforest soil seed banks

The soil seed banks of temperate woodland trees, are generally regarded as transient, or at most short-term persistent (Thompson, 1978). Seed banks of temperate forest tend to be dominated by herbaceous species, often with little similarity in species composition between the seed bank and extant vegetation (Thompson, 1978; Sem & Enright, 1995). This dissimilarity tends to increase with age of forest stands (Thompson, 1978). All studies of soil seed banks in tropical rainforests have shown the existence of significant pools, mostly composed of pioneer and early successional species, of viable seeds (Hopkins & Graham, 1984).

#### 5.1.6 Soil seed bank investigations in New Zealand

There is little published information concerning soil seed banks of New Zealand forests. (Herbert, 1976; Ogden, 1985; Partridge, 1989), with the soil seed banks under kauri (*Agathis australis*) forest most researched and perhaps best understood (Enright & Cameron, 1988; Sem & Enright, 1995). Emergence of native species from forest duff (the fragmented humified material and coarse surface litter which forms beneath a shrub or forest canopy) beneath podocarp-broadleaved forest has also been examined, to determine its feasibility as an alternative to fresh seed trapping for reforestation (Herbert, 1976).

Few studies have been carried out in New Zealand on the longevity of native seeds in the soil either, with most investigations having been made in regard to long term seed storage. Beveridge (1973) buried podocarp (matai, miro, rimu and totara) seeds in packets beneath litter and duff in Pureora forest, for different periods of time. Longevities of up to 4 years were recorded for miro and matai, with enhanced germination rates following burial in the case of miro. Spence (1990b) investigated the longevity of *Chionochloa rubra*, a large alpine tussock grass and found that its seed bank essentially declines to zero within two years in the absence of flowering. The greatest causes of seed removal are germination and death of the embryos due to factors other than predation.

The experiments described here were undertaken to examine the species composition and density of viable seeds at different depths, and the proportion of adventive species present in the soil seed bank, at various gap and forest sites within Keeble's Bush. The longevity, following artificial burial, of three native and one adventive species was also investigated.

## 5.2 Methods

### 5.2.1 Soil seed bank experiment

In late June 1993, soil was sampled in the four gap sites (refer Chapter 2), and in the adjacent closed canopy forest. Late June was chosen because the seeds present in the soil seed bank at that time would have had a period of stratification to assist in overcoming dormancy. There would also have been little fresh seed falling into the sites, as most fresh seed fell before July (refer Chapter 3).

A 30 mm diameter soil corer was used to collect samples from 0-2 cm (excluding litter), 2-4 cm, 4-10 cm and 10-20 cm depths, at each sample point. The 4-10cm and 10-20 cm samples were mixed, weighed, and divided by three and five respectively, so the subsample volumes were equal to those of the 0-2 cm and 2-4 cm samples. The samples were taken in ten randomly selected locations, in each of the four gap sites and in the adjacent forest. The exception was Blackberry Gap One, from which only three samples were taken. The nature of the soil and waterlogging of the site on the sampling days made sampling too difficult.

Three main methods are available for testing the presence of buried seeds in the soil. These either involve washing and sieving the seeds from samples of soil or floating the seeds out of the soil samples, followed by tests for viability, or germinating the seeds from within the soil sampled soil (Brown & Oosterhuis, 1981; Gross, 1990). In the present study the last (germination) method was used. Although this method may underestimate the seed bank, because germination requirements of all species may not be met by the experimental treatment, it does provide a estimate of the readily germinable fraction of the soil seed bank (Roberts, 1981; Gross, 1990; Dalling *et al.*, 1994).

The samples were kept in plastic bags at 4°C, for no more than two days, then transferred into the glasshouse. They were spread to a thickness of about 1 cm on two newspaper squares, within 10x10 cm plastic pots containing vermiculite. The samples were kept moist by an undermat capillary watering system, and an overhead mister. Additional hand misting was

carried out daily on pots which appeared dry.

The soil samples were examined for the presence of seedlings weekly for the first nine weeks, after which time new seedling emergence was infrequent. Seedlings were removed at each recording date, to prevent overcrowding in the small soil volumes and to allow unidentified seedlings to be grown on. The soil was stirred at week five to promote germination, but little additional seedling emergence resulted. Records of any further germination were noted for the next 16 weeks, until the experiment was dismantled on October 15th, 1993, due to time and space restriction.

Five control pots of sterilized soil from Keeble's Bush, placed randomly amongst the sample pots in the glasshouse yielded no seedlings, indicating that there was likely no contamination of samples by seeds entering the glasshouse.

### 5.2.2 Analysis

Chi-square ( $\chi^2$ ) analyses were used to compare seed numbers at the different sampling depths, and the number of seeds in gap and forested sites. Differences were regarded as significant if  $P \leq 0.05$ . Critical values for all statistics were obtained from Zar (1984).

### 5.2.3 Seed longevity experiment

In early March 1993 titoki, kawakawa and tawa seeds were collected from areas within Keeble's Bush, and radiata pine seeds from fresh cones on trees around the bush perimeter. Collected tawa seeds had fresh unwithered fruit flesh, apart from several with signs of superficial rat nibbling (as identified in Innes, 1977). Titoki seeds were collected both with and without red arils, with most free of their brown fruit coats. Kawakawa seed was collected in its ripe, bright orange fruit spikes ( $\geq 2$  cm in length), in most cases straight from the tree. Additional kawakawa fruit were collected to determine the average number of seeds per 2 cm fruit, approximately 200 seeds were counted. This result is similar to that obtained by Burrows (1995).

The experiment was set up under closed forest canopy in the eastern part of the bush (Fig. 2.2), and consisted of two replicates each with three burial depths (0 cm, 5 cm and 10 cm), and four lengths of burial time (3, 6 and 9 months). Each replicate had six tawa seeds, 10 titoki seeds, 10 radiata pine seeds, and one ripe 2 cm kawakawa spike. For the 5 cm and 10 cm depths, seeds of each species were buried in envelopes made of fibreglass mesh fine enough to allow water to pass through, and to allow easy seed retrieval. The envelopes were placed in trenches 5 and 10 cm deep. The soil removed was then carefully placed back in the trenches and firmed. The seeds in the 0 cm treatment were also placed in mesh envelopes, but were secured with a metal stake to the forest floor. A tunnel of fine chicken mesh was fixed over the 0cm seeds in order to deter predators, after several envelopes were damaged while the experiment was being set up.

At each time interval the seeds were excavated (3 months, May 1993; 6 months August 1993; 9 months, November 1993). The number of intact seeds and their condition were recorded on site. Seeds which were intact but had not germinated were taken back to the laboratory and placed in petri dishes, on moist filter paper. They were then kept in an incubator (set at 20°C) and checked at regular intervals, for germination. If after 6 months they had not germinated they were tested with tetrazolium stain to indicate if they were still viable.

## 5.3 Results

### 5.3.1 Soil seed bank composition

A total of 821 seedlings (mean=102.5; s.d.=72.1) germinated from the eight sampling sites (Table 5.1). From those seedlings 36 species were identified; 23 to species, 10 to genus, with the remaining three to family. Unknown (unidentified) seedlings made up only 8.5% of the total 821 recorded.

**Table 5.1** The numbers of species and seedlings (identified and unidentified) which germinated from soil samples from the eight different sites. (G1=Gap One, G1F=forest area adjacent to G1, G2=Gap Two, G2F=forest area adjacent to G2, BG1=Blackberry Gap One, BG1F=forest area adjacent to BG1, BG2=Blackberry Gap Two, BG2F=forest area adjacent to BG2).

Site	Total no. of identified species	Total no. of unidentified seeds germinated	Total no. of seeds germinated
G1	16	3	154
G1F	14	8	65
G2	10	1	37
G2F	7	8	34
BG1	21	25	251
BG1F	13	13	110
BG2	5	1	63
BG2F	16	11	107
TOTAL		70	751

Seeds were present in all samples from almost all sites, with only one sample each from G2 and BG1F, and two from G2F producing no seedlings. The numbers of viable seeds/m<sup>3</sup> of soil (269.5-2269.6 seed/m<sup>3</sup>; mean=1016.8 seed/m<sup>3</sup>) was markedly different between sites. Seed banks with the highest number of seeds germinating (Table 5.1) were found in the gap sites, *i.e.*, G1, BG1. The greatest seed diversity was also recorded from a gap site, BG1, that also produced the most seedlings (251) (Table 5.1). The low diversity of species and small number

of seedlings recorded for BG2 compared with other gap sites was due to the low volume of soil sampled; only two soil samples were taken from the site because of soil conditions at time of sampling. The number of seedlings which emerged of all species, and their contribution to the seed banks at the eight sampling sites, are listed in Appendix 4. No seedlings were recorded in the controls.

A mean of 12.6 species germinated per site. Collectively the seed bank included 26 herb, 2 shrub, 5 tree and 3 liane species (Table 5.2). Herbs were the most important life-form in the soil seed bank (Table 5.2); herbaceous species made up 77.5% of the total seedlings which emerged, and the total herbaceous seedling component of each site ranged from 53-92% (mean=73.2%; s.d.=14.01). Adventive species accounted for 16 of the 36 species identified, most (14) being herbaceous (*i.e.*, agricultural or naturalised adventive weeds) (Table 5.2). Seedlings of primary forest trees (mahoe, kahikatea and matai) contributed only 1.2% of the total, being present in samples at only 3 of the eight sites.

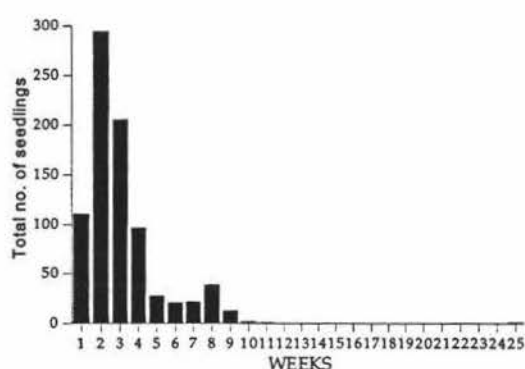
**Table 5.2** The life-form composition of the seeds which germinated from soil samples collected from all sites (identified seedlings only).

Growth form	Total no. of native species	Total no. of native seeds	Total no. of adventive species	Total no. adventive seeds
Trees	4	53	1	2
Shrubs	2	17	-	-
Herbs/grasses	12	325	14	309
Lianes	2	42	1	3

The species with the largest number of individuals germinating were the herbs black nightshade and *Cardamine debilis* agg.. They were the only species with >50 seeds, and were ubiquitous, *i.e.*, occurring in all or most of the eight sites (8 and 7 respectively). The majority of species (24 of the 36) appeared in only 1-3 sites, and were represented by <20 seedlings.

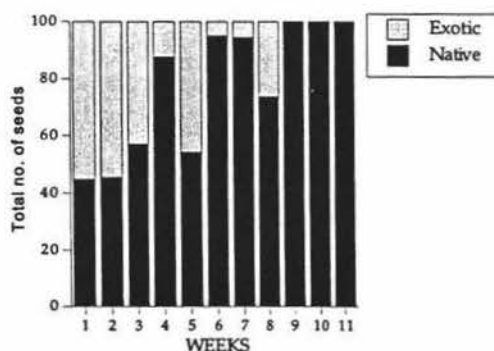
### 5.3.2 Timing of seedling emergence

In general germination was rapid, with the first seedlings emerging from the soil samples within 7 days of the start of the experiment. Over 86% (709 seedlings) of the total seedling emergence occurred within the first month (Fig. 5.1). This indicates that many seeds could respond immediately to the changed environmental conditions experienced in the glasshouse. Monitoring of the experiment was discontinued after 25 weeks as by that time only one new seedling had emerged in 14 weeks.



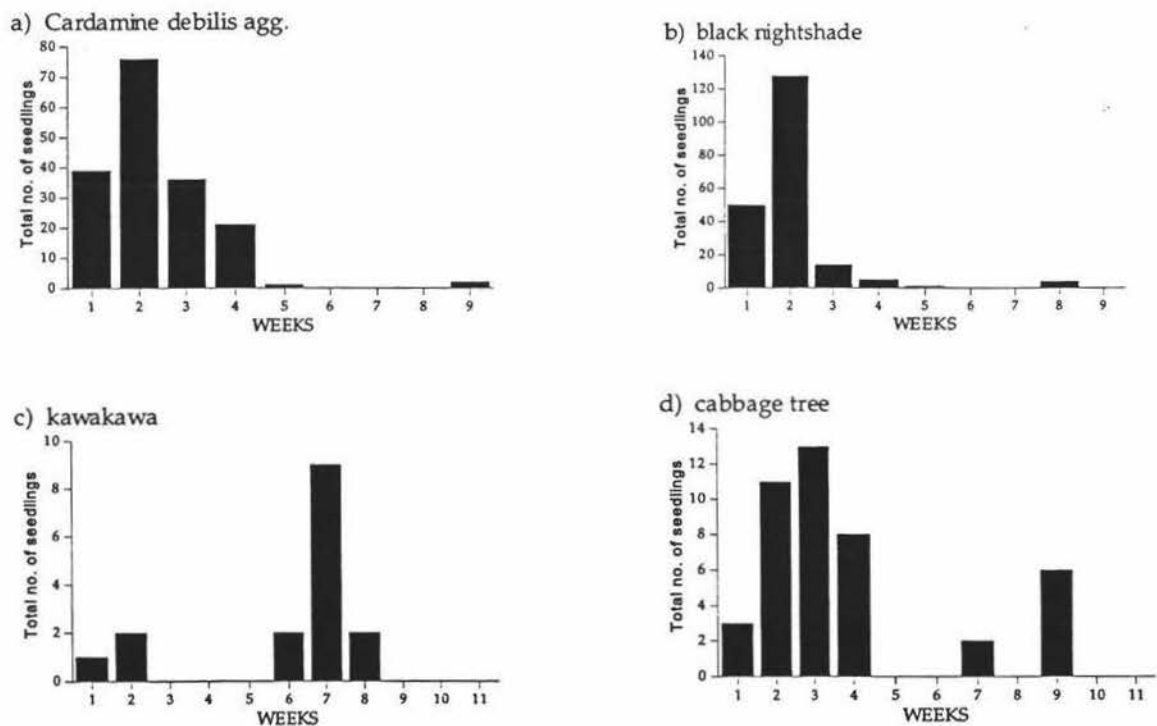
**Fig. 5.1** Total number of seedlings which emerged from all soil samples. (week 1 5-9 July - week 25 20-24 December).

Adventive species dominated the seedlings which emerged for the first 5 weeks (Fig. 5.2). Native species made up the bulk of seedlings which emerged after that time.



**Fig. 5.2** The proportion of native and adventive seedlings which emerged from the sampled soil (all sites inclusive) from weeks one to eleven. Only a single matai seedling germinated after week 11 (in week 25).

The bulk of the native and adventive seedlings which germinated within the first three weeks were early successional/colonising herbs (e.g., black nightshade, *Cardamine debilis* agg. and small flowered nightshade). Most herbaceous species exhibited similar emergence patterns (Fig. 5.3 a&b) with over 90% of their seedlings emerging by week four, and no further emergence after week nine. This pattern is characteristic of species that typically colonize recently disturbed sites (Schiffman & Johnson, 1992). In contrast seedlings of native shrub and tree species tended to occur either in low number throughout the experiment (weeks 1-11), or later in the experiment (from week 5-6) (Fig. 5.3 c&d)



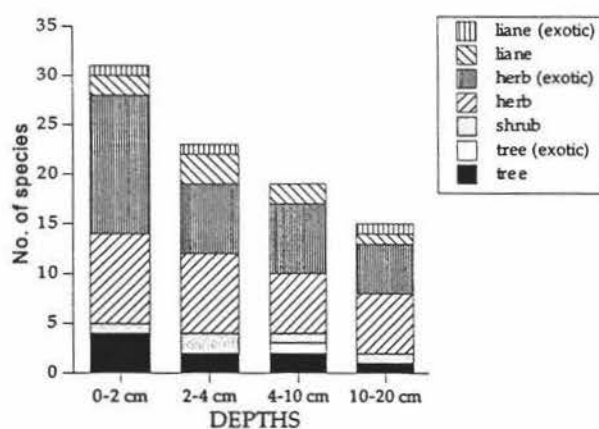
**Fig. 5.3 a, b, c & d** The seedling emergence pattern of herbaceous (native a) *Cardamine* sp. and adventive b) black nightshade), native shrub (c) kawakawa) and tree (d) cabbage tree) species from all soil samples.

### 5.3.3 Differences in relation to depth

The number of species and individuals which germinated decreased with soil sample depth (Table 5.3). The highest number of germinants was obtained from the 0-2 cm depth, and the lowest from the deepest layer (10-20 cm). Species richness for all life forms was also highest in the 0-2 cm layer and declined as depth increased. All life forms (trees, shrubs, herbs/grasses and lianes) were however still present at the 10-20 cm sampling depth (Fig. 5.4).

**Table 5.3** The total number of seeds, their percentage of the total, and the total number of species recorded at the four sampling depths (all sites inclusive).

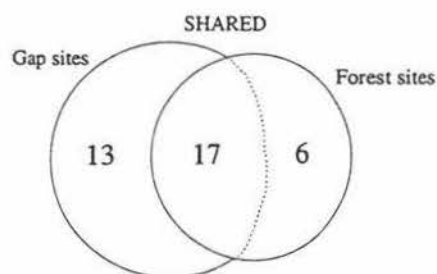
Depth (cm)	Total no. of seeds	% of total seeds	Total no. of species
0-2	451	55	31
2-4	201	24.4	25
4-10	117	14.3	22
10-20	52	6.3	16



**Fig. 5.4** Frequencies of life-forms at each soil depth (all samples inclusive).

### 5.3.4 Comparison of the soil seed banks of gap and forest sites

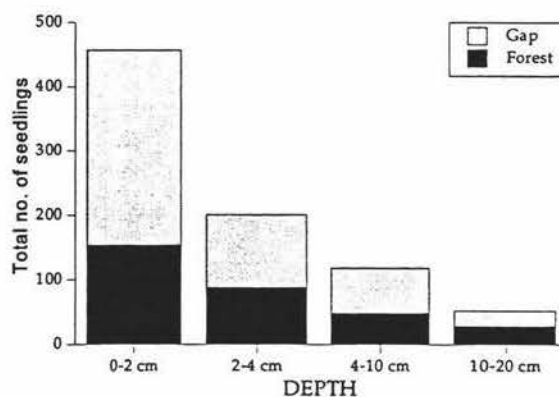
There were significant differences in the species composition of the forest vs the gap sites ( $\chi^2=199.1$ ;  $df = 34$ ;  $p \leq 0.0001$ ). The soil seed banks of the gap sites had greater species richness, with 30 species identified, compared with only 23 recorded in the forest soil sampled. Of those species present in each, 17 were shared, with 13 unique to the gap sites, and 6 to the forest sites (Fig. 5.5). Those species unique to the gap sites were predominantly adventive herbs (*e.g.*, grasses, thistles, ragwort, and sorrel), while those present only in the forest sites included several native tree and herbaceous species (*e.g.*, mahoe, matai, and *Psuedognaphalium luteo-album*).



**Fig. 5.5** The total number species unique to, and shared by the gap and forest sites (all samples inclusive).

Significantly more seedlings emerged from soil samples taken from the gap sites (505) than from the forest sites (316) ( $\chi^2=63.26$ ;  $df = 11$ ;  $p \leq 0.0001$ ). Herbaceous seedlings (black nightshade, *Cardamine debilis* agg., foxglove and *Hydrocotyle* sp.) accounted for the bulk of that difference (236 seedlings combined).

Differences also occurred at the four different sampling depths (Fig. 5.6). A greater proportion of the seeds in the gap sites germinated from the 0-2 cm layer. proportions in the 2-4, 4-10 and 10-20 cm depths were more similar.



**Fig. 5.6** The number of seedlings which germinated from the different sample depths, from the Gap and Forest sites ( $\chi^2=12.23$ ;  $df = 3$ ;  $p=0.0066$ ).

### 5.3.5 Seed longevity

Data from the seed burial experiment, including the percentage of seeds recovered during each time period, viability, and the number which germinated *in situ* and in the incubator are summarised in Appendix 5. *In situ* germination refers to those seeds which germinated while buried (at 5 and 10 cm) or while on the soil surface (0 cm) within the forest site. With only two replicates, only general trends can be inferred from this experiment, for each species.

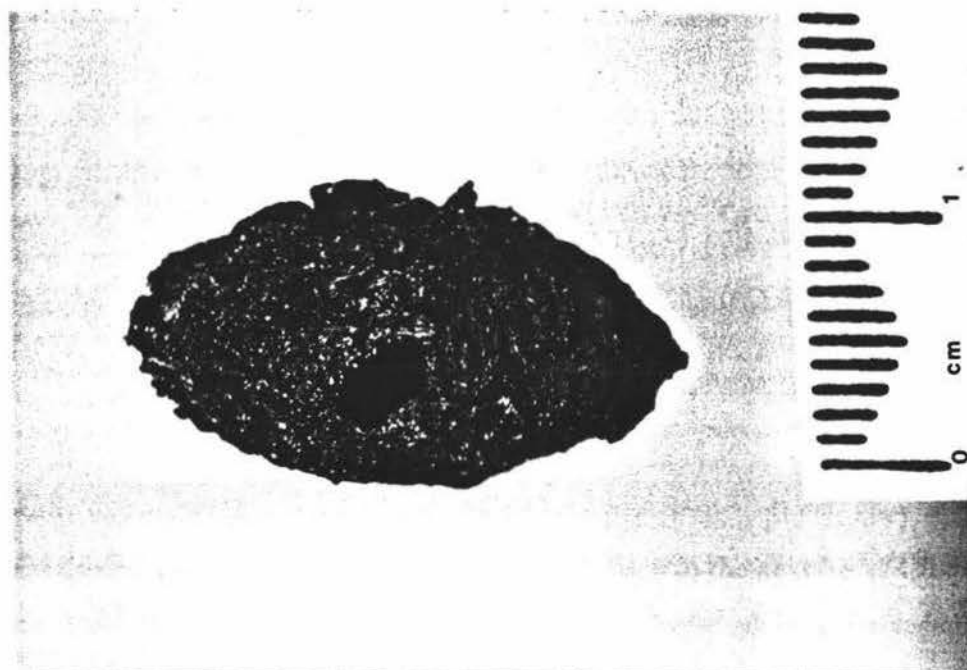
#### *Tawa*

In almost every treatment 100% (6/6) of the tawa seeds were recovered (60-100% mean=94%). This was primarily because they are large seeds (av. 2.8 x 1.0 cm) were easy to re-locate in the envelopes amongst the soil, and less likely (c.f. kawakawa) to have completely decomposed or removed by soil organisms.

**Table 5.4** Mean germination rate for those tawa seeds recovered during the burial experiment.

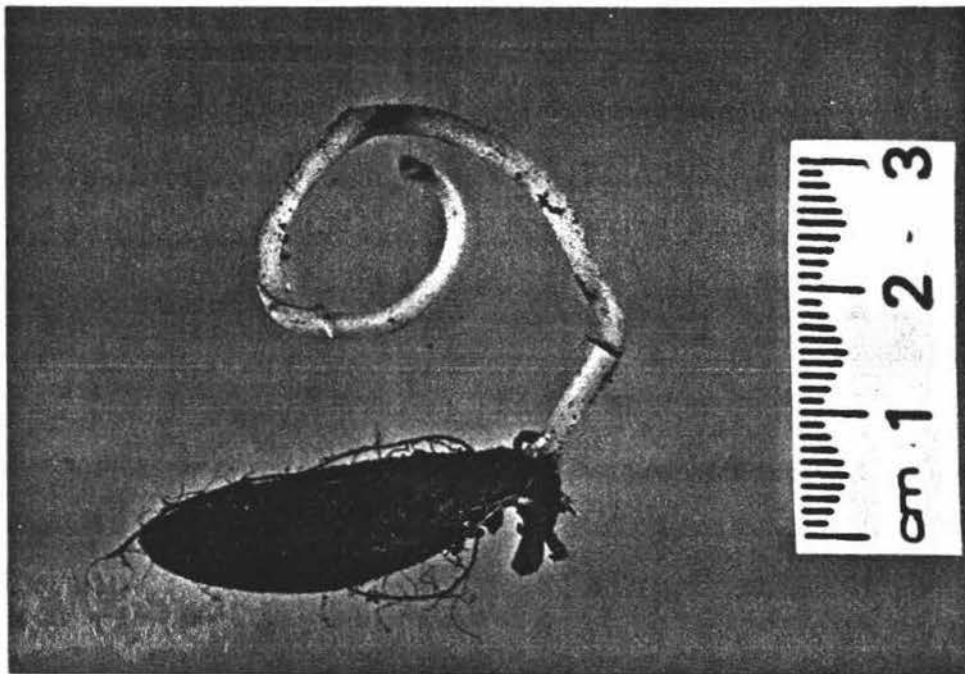
Sample depth (cm)	3 months (%)	6 months (%)	9 months (%)	mean (%)
0	16.5	74.9	18.4	36.6
5	100	73.4	91.5	88.3
10	100	90	74.5	88.2
mean (%)	72.2	79.4	61.5	

Tawa seed is suspected to be recalcitrant, *i.e.* to lose viability quickly when moisture content drops below a certain high level (Fountain & Outred, 1991). This loss of moisture likely occurred for many of the seeds that were laid in envelopes on the litter surface (0 cm) and lost their viability. Rapid burial, as occurred with seeds in the 5 and 10 cm trenches, would perhaps halt that rapid loss of viability by promoting moisture retention/reducing water loss. Buried seeds, in addition to perhaps having enhanced water retention, would have escaped the attack of above-ground insect predators (Fig. 5.4) (*e.g.*, from *Cryptaspasma querula*; Knowles & Beveridge, 1982) and fungi (*e.g.*, *Glomera cingulata*; Knowles & Beveridge, 1982), that would likely have affected the long-term viability of the seed on the soil surface.



**Fig. 5.7** One of the predated tawa seeds from the 0 cm (6 month) treatment. A large hole has been bored into the testa, perhaps by *Cryptaspasma querula* (Knowles & Beveridge, 1982), and the seed is empty.

The fact that the tawa seeds at the 5 and 10 cm burial depths began germinating *in situ* from 3 months suggests no inherent dormancy mechanism exists. All the tawa seeds that germinated *in situ* at 5 and 10 cm (at 3, 6 and 9 months) remained as 'buried seedlings' (Fig. 5.8). Their plumules were plump and white, with red coloration on their cataphylls (sessile outgrowths which drop off when foliage leaves develop; Knowles & Beveridge, 1982). Many were twisted, and most had retained their plumular hooks. Their radicles were often broken as the mesh of the envelopes had constricted them as they grew. All 'buried seedlings' were alive and produced green shoots when transplanted into trays following exhumation.



**Fig. 5.8** A buried tawa seedling following exhumation from the soil (5 cm depth) after 6 months. Note the swollen plumules with scale like reddish cataphylls, and short radicle broken at the point where it passed through the mesh.

*Titoki*

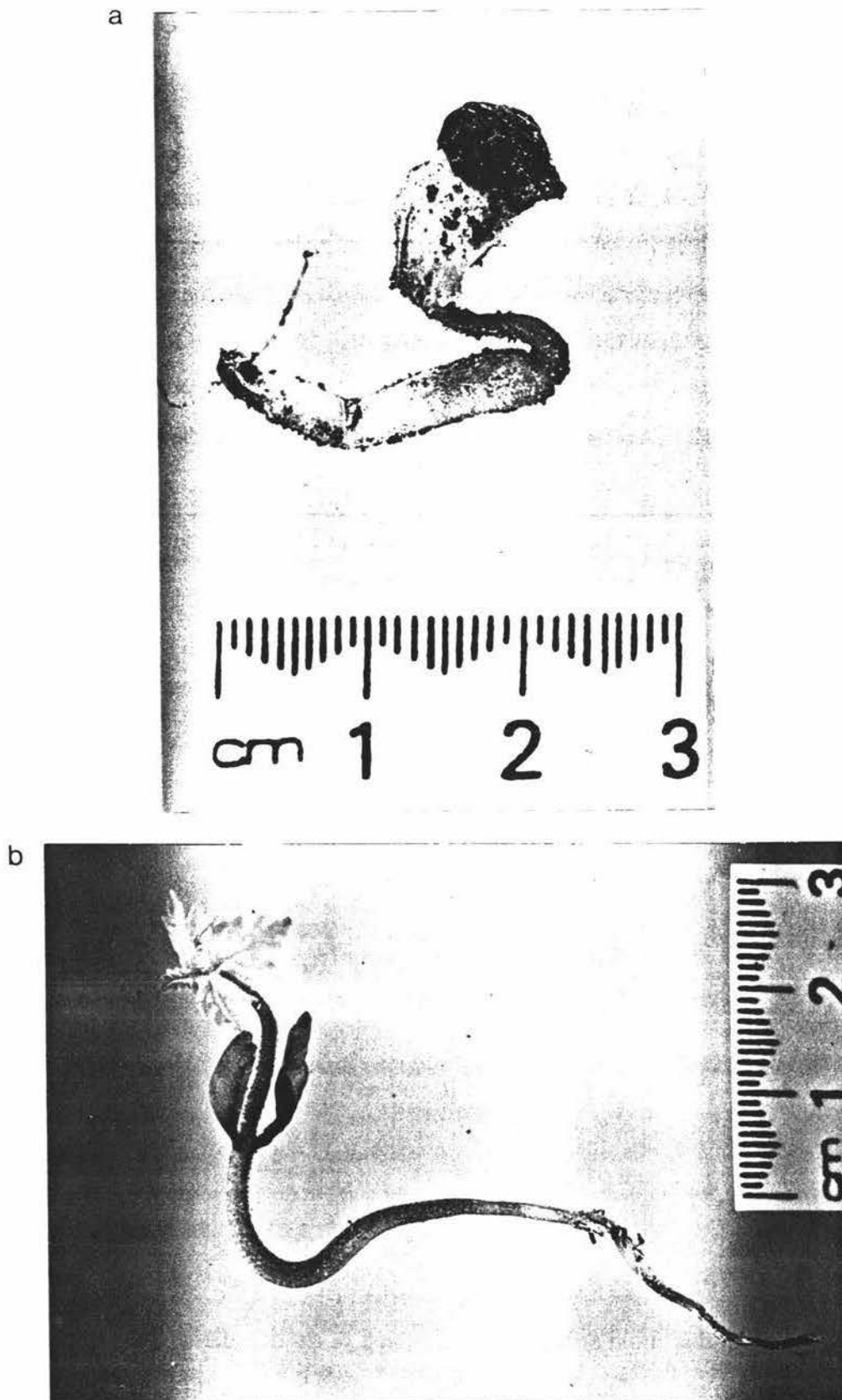
Titoki too have large conspicuous seeds (7 x 5 mm), and so also had high seed recovery rates (70-100%; mean=92.2%). Viable seeds were present at each time period, at all depths (Table 5.5). The low viability recorded at 6 months was due to the seeds in the second replicate, none of which were viable at any depth.

**Table 5.5** Mean germination rate for those titoki seeds recovered during the burial experiment.

Sample depth (cm)	3 months (%)	6 months (%)	9 months (%)	mean (%)
0	65	30	47.5	47.5
5	84.5	20	27.2	43.9
10	48.5	15	65	42.8
mean (%)	66	21.7	46.6	

*In situ* germination occurred only after 9 months, but at all depths (0, 5 and 10 cm). Seedlings which established on the litter surface (0 cm) at 9 months were 'normal' in appearance, *i.e.*, had green cotyledons and first true leaves, and a long primary root (mean = 76 mm) (Fig. 5.9a). By contrast those that had germinated beneath the soil (at 5 and 10 cm) at 9 months had yellow cotyledons, some still partly within their seed coats, and swollen short reddish white radicles with small lateral roots (mean = 28.4 mm) (Fig. 5.9b). Several of the buried seedlings were just beginning to produce their first true leaves, but they too lacked chlorophyll and were yellow. When placed in the glasshouse, following exhumation, all but two of the buried seedlings assumed 'normal' growth.

The results suggest that titoki seeds require a period of stratification. They appear able to remain viable on the soil surface from one fruiting season to the next (refer Chapter 3), with burial seeming not to increase their viability over time. The fact that viable buried titoki seeds germinated after 9 months also suggests that their seeds would form only a short term seed bank if any. Longer term data is needed however.



**Fig. 5.9 a & b** A comparison of titoki seedlings. a) is a buried titoki seedling exhumed from soil (10 cm depth) after 9 months. Note the yellow cotyledons still held within the testa, and the swollen reddish radicle with several small lateral roots. b) is a titoki seedling which established on the soil surface (0 cm) after 9 months. Note the 'normal'/un-swollen radicle, green cotyledons and first true leaves.

*Kawakawa*

Kawakawa seeds are small (averaging only 2 x 2 mm) and were therefore more difficult to retrieve from the soil following their release from their fruit. Being small they may also be more likely to be moved or eaten by soil organisms. The percentage of seeds recovered for each replicate and treatment reflected this and was generally low (0-46% mean= 18.5%). The rates of germination/viability of the recovered seeds decreased over time, and with depth of burial (Table 5.6).

**Table 5.6** Mean germination rate for those kawakawa seeds recovered during the burial experiment. (none) = no seeds recovered.

Sampling depth (cm)	3 months (%)	6 months (%)	9 months (%)	mean (%)
0	70.5	89.9	98.75	86.4
5	88.8	100	43	77.3
10	0 (none)	50	11.2	20.4
mean (%)	79.7	78	50.98	

*In situ* germination occurred from the third month suggesting that no dormancy mechanism was present, though some seeds on the surface (0 cm ) remained ungerminated and viable for 9 months. It would appear then that kawakawa seeds are able to remain viable between fruiting periods, but more are likely to be on the soil surface, beneath litter, than incorporated into the soil. However, results from the soil seed bank experiment (5.3.1) , indicate that kawakawa seeds do occur in the soil below 10 cm, though in very low numbers.

*Radiata pine*

The viability of the radiata pine seeds decreased rapidly with both length of burial, and burial depth (Table 5.7). At 6 months none of the ungerminated seeds remained viable, with one seedlings at 0cm and one at 5 cm. By 9 months none of the recovered seeds were viable. Many of them appeared to have germinated and died during the time between exhumation; one

end of the testa was frayed giving the impression that the radicle had emerged and rotted.

**Table 5.7** Mean germination rate for those radiata pine seeds recovered during the burial experiment.

Sample depth (cm)	3 months (%)	6 months (%)	9 months (%)	mean (%)
0	40	5	0	15
5	50	5	0	18.3
10	0	0	0	0
mean (%)	30	3.3	0	

The results then suggest, in keeping with what is already known, that radiata pine seeds have a short period of viability, and lack a dormancy mechanism, *i.e.*, they either germinate immediately and establish or die. They would therefore not form a persistent seed bank, with fresh seed fall being required to colonise an area.

## 5.4 Discussion

Although the germination method is the simplest and fastest method of estimating seed bank composition and density (Brown, 1992), a number of methodological problems became apparent during the course of this study. For example, the soil seed bank is described here in terms of germination but it must be remembered that some viable seed may not have germinated, because the correct germination cue for all species may not have been provided (*e.g.*, cold stratification, scarification, heat treatments, fluctuating temperatures, light exposure (Brown 1992)) (Enright & Cameron, 1988). In addition, much non-viable seed may also have been present in the soil samples, though careful examination of each sample was made for ungerminated seeds prior to it being discarded. Further, taking the samples in July precluded the presence of some species in the samples, *i.e.*, those fruiting in summer and autumn and having a short seed life (Enright & Cameron, 1988).

Soil seed bank composition and size are usually patchy and spatially variable (Marquis, 1975; Matlack, 1987; Bigwood & Inouye, 1988), though previous work has shown a range of seed patterns, from regularly spaced to strongly clustered (Matlack & Good, 1990). Given this inherent variability it also cannot be assumed that the variation within each site was represented adequately in the samples.

Another area of uncontrolled variability, inherent in the experimental design, was the quality of seed crops, which could be expected to vary significantly between conspecific adults (Hopkins & Graham, 1987). Although seed from a number of conspecific trees were included in the samples, there was no measure of the degree to which the seed samples examined were representative of the variability in species' seed behaviour.

To evaluate the role of the persistent and transient soil seed banks in regeneration, it is necessary to identify the proportion of the seeds or species in the soil seed bank in the persistent seed bank as opposed to the various transient seed banks. At least two of the following criteria must be known to identify seed bank strategies: seasonal changes in the seed bank, seasonal timing of dispersal, or the presence of seasonal or facultative dormancy

(Garwood, 1989). Most studies document only one criterion. In this study a single sampling date meant that none of the criteria were evaluated.

#### 5.4.1 Soil seed bank composition

The sampled soil seed bank from each of the eight sites had markedly different species combinations. This variability may be linked to the compositional and structural (*e.g.*, vegetation age and height) differences in the extant vegetation among sites, though this was not assessed quantitatively in this study. Few similar studies in either tropical or temperate forests have found close floristic similarities between soil seed banks and standing vegetation (Thompson, 1978; Hopkins *et al.*, 1990; Matlack & Good, 1990; Russell-Smith & Lucas, 1994; Looney & Gibson, 1995; Sem & Enright 1995).

Density estimates were also highly variable, with a range of 269.5-2269.6 seeds/m<sup>3</sup> (mean=1016.8 seeds/m<sup>3</sup>) in the eight sampling sites. It is difficult to make direct comparisons between these densities and soil seed bank densities in other plant communities as most studies express their seed densities as seeds/m<sup>2</sup>.

Converting the seed densities from m<sup>3</sup> to m<sup>2</sup> assumes that the soil samples taken have captured the entire seed compliment of the soil. This assumption is likely mabe because the majority of soil seed banks studies have shown that the top 5 cm of soil, which is most often sampled, holds the bulk of viable seeds (forests [*e.g.*, Southern Appalachian oak forest; Schiffman & Johnson, 1992] savanna, regrowth [*e.g.*, secondary vegetation on Banks Peninsula, New Zealand; Partridge, 1989] and farmland). This was found to be true in this study, with 80% of seeds were recorded between 0 and 4 cm.

Comparisons are also made difficult by the fact that enormous variation is encountered in sampling, with often too few samples being taken for accurate determination (Fenner, 1985), and that there is no standard depth of sampling amongst studies.

Unpublished densities estimates, based on data collected by students at Auckland University, of the soil seed banks in forests around the upper North Island, has shown that they are of

similar magnitudes to those in temperate forest communities elsewhere in the world (Ogden, 1985), and to those recorded in this study.

The high variability in seed density and species composition, as described here and for soil seed banks both in New Zealand (Ogden, 1985) and overseas, makes characterisation of forest seed banks difficult and complicates interpretation of how seed banks may contribute to secondary succession following forest disturbance (Sem & Enright, 1995).

A general trend, exhibited at all sites, was a decrease in species diversity with soil depth. Differences in the depth profile of the soil seed bank within and between sites have been attributed to differences in forest soil texture (Hopkins & Graham, 1983), and successional changes in seed rain (Young *et al.*, 1987), but differences within a given profile must reflect variation among species in seed rain, rates of incorporation, and/or seed longevity.

The seed flora at all sites consisted largely of herbs. Woody species flora were the most poorly represented of the life-forms, comprising only 1%, the same figure attained by Russell-Smith & Lucas (1994) in northern Australian monsoon rain forest. Only four native primary tree species were represented, many of which have an early successional or gap colonising role; *e.g.*, cabbage tree, kahikatea, mahoe and matai. In these respects, it is also similar to many temperate (*e.g.*, Thompson & Grime, 1979; Hill & Stevens, 1981; Matlack & Good, 1990), and tropical (*e.g.*, Rico-Gray & García, 1992) forest soil seed banks, and those of other vegetation types (*e.g.*, coastal barrier island, Florida; Looney & Gibson, 1995).

#### 5.4.2 Adventive species

Adventive species occurred in the soil seed bank of all sites sampled. Most of those species are common components of the surrounding scrubby forest margins/pasture, with many occurring within gaps in the Bush (*e.g.*, black nightshade, foxgloves, sorrel, thistles and grasses). The strong dominance in the soil seed bank by weedy species appears to reflect the remnant nature of the study area and its closeness to the sources of these adventives (Enright & Cameron, 1988). In addition the numerous gap sites within Keeble's Bush (Abrahams, 1981) may provide 'stepping stones' which facilitate penetration of the adventive species into

the remnant (Sem & Enright, 1995).

#### 5.4.3 Timing of emergence

As with other similar soil seed bank investigations (*e.g.*, Hill & Stevens, 1981; Enright & Cameron, 1988) most seeds germinated within a month of sampling. Weed/ephemeral seeds (*e.g.*, *Cardamine deblis* agg., black nightshade and *Hydrocotyle* spp.) germinated first. This rapid germination response under glasshouse conditions indicates that they require a shorter time between germination cue (provision of light) and germination. Native woody species, in contrast, require at least several weeks of exposure to break dormancy. This pattern is similar to that described for soil seed banks from a kauri (*Agathis australis*) forest remnant near Auckland by Enright and Cameron (1988). Dominance of early stages of succession by weedy species may be partly attributed to this ability to break dormancy almost immediately upon exposure to the appropriate cue, since this gives them a competitive advantage, in addition to the advantage derived from a rapid growth rate (Sem & Enright, 1995).

#### 5.4.4 Seed longevity

Burying seeds in the soil directly measures longevity. However, estimates of longevity are biased compared to those for naturally dispersed seeds. This is because seed buried in containers may exclude many seed predators, change the microenvironment, and affect pathogen infection (Vazquez-Yanes & Smith, 1982). The effect of the burial technique used in this study on seed longevity is not known.

Due to the small sample sizes in this study it is difficult to generalise about differences in survival/longevity and germination between different depths and burial periods for the four species. However, supposition can be made about the type of seed bank they might be likely to form, given their behaviour in this study, and what is known about their regeneration strategies.

Tawa seed is able to germinate and establish in the low light conditions of a forest understorey, and persist as a seedling bank. Therefore a persistent seed bank is unnecessary for the long

term maintenance of the species. In addition, the recalcitrant nature of the seeds precludes them for surviving for long (>1.5yrs) periods of time after dispersal from the parent (Fountain & Outred, 1991). However, tawa may be able to form a short-term transient seed bank for up to nine months, with viable seed existing as 'buried seedlings' for some of that time; this is assuming that the tawa seed has escaped predation by rats, possums, pigs, and insects, and is buried rapidly so as to retain adequate moisture content and thus viability (Fountain & Outred, 1991). The phenomenon of germinated seeds surviving as 'buried seedlings' has also been recorded for some other large-seeded primary rainforest species; *e.g.*, *Castanospermum australe* (Hopkins & Graham, 1987). Some of these 'buried seedlings' have remained alive and been transplanted successfully even after 2 years of burial. Rapid burial of tawa seed, via 'normal' animal activity and litter build up, to 5 or 10 cm, may be a fairly uncommon occurrence for tawa seeds.

The results suggest that titoki seed too might form a short-term transient seed bank, with viable seeds remaining in the soil from one fruiting period to the next. It also appears able to survive for some time as 'buried seedlings' beneath the soil, but again rapid burial, as occurred during the longevity experiment may be uncommon. This supports observations made during this study that titoki produces abundant seed (refer Chapter 3) which germinates in pulses, the following autumn and winter after dispersal. Titoki seedlings are not as shade tolerant (refer Chapter 4) as tawa and therefore do not tend to have large seedling banks beneath intact forest canopies.

Kawakawa seed remained viable for 9 months within the soil, so could feasibly persist for up to a year in the soil, forming a transient seed bank. Being small, the seeds would probably be incorporated into the soil relatively rapidly (Thompson *et al.*, 1993) (compared to say tawa or titoki), through litter fall and movement of soil organisms. Burrow's work on the kawakawa seed germination behaviour, however, suggests that they possess no primary dormancy mechanism and would be unlikely to form anything more than a short term seed bank of a few months (Burrows, 1995). Burial rate may be a crucial factor in determining their length of survival. The low recovery rate of the kawakawa seeds suggests that they either decomposed or were predated. However, virtually nothing is known about those agents which predate kawakawa seeds (T. Crosby, *pers. comm.*).

Radiata pine (*Pinus radiata*) on the other hand is unlikely to produce any sort of soil seed bank, with its seeds losing viability rapidly after dispersal, even following rapid burial. With high annual seed production, widely disseminated seeds, and a long life span, pine does not require the maintenance of a persistent or even transient seed bank.

# Chapter 6

## **General summary**

### **6.1 Introduction**

Keeble's Bush, a 14.3 ha remnant of lowland podocarp-broadleaved forest, is the finest remaining piece of the forest type that was once widespread on lowland alluvial terraces throughout the Manawatu (Esler, 1978). The Bush contains more vascular plant species than any of the other surviving remnants of the same forest type in the Manawatu Plains Ecological District, with all five species of lowland podocarp present (rimu, matai and kahikatea the most abundant). It also supports a number of plants which now occur naturally nowhere else in the district. For these reasons it is an important part of the protected natural area network within the Manawatu Plain Ecological District (Ravine, 1995), deserving all attempts to maintain it in perpetuity.

The aim of this study was to assess the ecological integrity of Keeble's Bush. To achieve that aim the seed rain (fresh seed input), seedling diversity and survival, and soil seed bank composition were all assessed. This chapter summarises the major findings of the study.

### **6.2 Conclusions**

#### **6.2.1 Seed rain diversity**

1. The nine most abundant species trapped from the seed rain during the period of this study exhibited high coefficients of variation, indicating considerable spatial patchiness. None of the species caught were found in all eight traps, with the species composition varying widely.
2. Strong seasonal patterns were recorded in the fruiting phenology of the species intercepted, with seed from one species or another present at all times during the year. Rimu, the most irregular mast seeder of all New Zealand's podocarps, did not fruit heavily during 1992-1993, with only small numbers of viable seed, and few red arilled seeds trapped.

3. Those species overhanging or in close proximity (<50 m with most <15 m away) to the traps contributed the majority of seeds. The distance from the nearest individual to the trap was not correlated with the numbers of seeds. However, this is likely to be because of the interaction of many different factors, including the canopy height of the plant, the volume of seed produced, and its dispersal ability. All those species originating from further than 50 m away were either from large emergent podocarps, wind-dispersed canopy trees, or common wind dispersed adventive tree species. The kahikatea seeds trapped all appeared to have been bird dispersed.

4. Six of the eight traps caught seeds of adventive species, virtually all of which were herbaceous and wind dispersed. All adventive species were local in origin, *i.e.*, present within the gap sites at the time of trapping. The higher edge:interior ratios of Keeble's Bush compared with continuous forest tracts increases the potential for disturbed sites to be invaded and dominated by adventives.

5. Many of the species that are common components of the surrounding vegetation (*e.g.*, *Fuchsia perscandens*, mahoe, New Zealand passionfruit, and shrubby mahoe) were notably absent or present only in low numbers in the trapped seed rain. This is despite the fact that in most cases mature adults overhang or are close to, the traps. Virtually all the seed dispersed species that reached the traps were <8 mm in diameter, which is probably directly related to the paucity of native bird dispersers that are able to disperse larger seeds. Introduced blackbirds partly compensate by dispersing seeds up to 9 mm, and possums may also be acting as dispersal vectors, though their importance requires investigation.

If the complement of frugivorous birds still present on the mainland were still active in Keeble's Bush one might expect the data collected from the seed rain investigation to have been significantly different. For example, with greater diversity and density of seed dispersing native frugivores, more of the seeds would have originated from greater distances from the seed traps, instead of the majority originating from overhanging or adjacent individuals (<50 m), and higher numbers of certain species (*e.g.*, kawakawa) would have reached traps, defaecated in clumps (Burrows, 1994a). Also larger fruits (>8 mm; *e.g.*, tawa), and common species like mahoe and New Zealand passionfruit would likely have made up a greater

proportion of the seed rain.

The implications of changes in forest avifauna are only beginning to be recognised. This is in part because we are still learning about the relationships between native frugivorous birds and the fruits they disperse, and also because forest bird diversities and densities comparable with those of pre-human forests now occur on only a few offshore islands, like Kapiti and Little Barrier. The importance of extinct frugivores can now never be evaluated.

### 6.2.2 Seedling diversity and survival within Gaps One and Two

1. The density and diversity of the seedling populations within Gaps One and Two appear to be stable, with the rate of flux into and out of the population similar.
2. Mortality within Gap One appeared to be size dependent, *i.e.*, with greatest mortality during the initial period of establishment and growth. This phenomenon is well documented for seedling populations in other forest types. The same type of survivorship was recorded for the titoki seedling population followed. By contrast, in Gap Two, the probability of mortality appeared to be high in all height classes. Those mahoe seedlings in the >60 cm height class showed higher mortality as a result of stem breakage caused by restriction of the tags used.
3. The dense ground cover over some of Gap One appear to be restricting the establishment of seedlings. In addition, cabbage tree leaves from the tree in the centre of the gap form a dense mat around the base of the trunk, that may also be impeding seedling growth and development. In Gap Two the north-easterly end is dominated by young kawakawa seedlings, which produce a shaded environment that may suppress seedling establishment by reducing the germination of light requiring species. Titoki seedlings in this area showed marked etiolation, and all subsequently died.
4. Below ground root competition may also be an important factor in seedling establishment and survival, though it was not assessed during this study. When soil cores (refer Chapter 5) were taken within the gaps, roots impeded penetration in many places.

5. A number of seedlings appeared to have been browsed and hedged, as evidenced by their low (<30 cm in height) multi-branched habit. The highest seedling mortality was recorded in those species known to be palatable (e.g., kanono, rangiora, and tawa) to introduced browsers (i.e., possums and rabbits). Foxglove and *Carex* spp. within the gaps were also cropped. Much of the seedling mortality could be attributed to introduced browsers, but the exact proportion is very difficult to establish. Blackbirds foraging for insects and disturbing the litter could also be affecting seedling survival.

6. Only a small proportion of the tagged titoki seedlings which died likely succumbed to desiccation. A greater proportion died through litter burial. In order to be more certain of the roles of the different mortality factors video photography, direct observation or daily records would be needed.

7. The low species richness (13 species) of the seedling assemblage in Gap Two, compared with that in Gap One (19 species), is in part a reflection of the low diversity of mature individuals present in the immediate surrounding forest (refer Fig. 2.3 & 2.4). This low diversity is probably due to the fact that the site is near the forest margin and therefore subject to 'edge effects' (Young & Mitchell, 1994).

Data obtained are in agreement with Moore & Chapman (1986) that most seedlings in many plant communities survive for only a short time, and thus have little impact upon population processes. This was reinforced by the low survival rates of the titoki seedlings tagged, and of some of the species within Gaps One and Two. The seedling populations in both Gaps appear to be stable. In Gap One none of the seedlings had attained a height in excess of 1 m, the height at which many authors measure recruitment (e.g., Brokaw, 1987; Uhl *et al.*, 1988), with browsing appearing to prevent height increases. Mahoe and kawakawa seedlings were the only species in Gap Two to have increased in height. Both Gaps One and Two appear to be decreasing in area not because of seedling growth, but rather via the lateral growth of surrounding vegetation. Visits to the sites in 1995 confirm this with stakes marking the original gap margins now overgrown. In tropical forests tree sprouts at gap edges are often a hugely important part of gap succession (Young *et al.* 1987).

As expected many of the species present as seedlings within the gaps were those that require the higher light environments of canopy gaps or forest margins to establish, e.g., titoki, mapou (Pook, 1978), rewarewa (Smale & Kimberley, 1983), and totara (Beveridge, 1973).

Despite prolific germination of titoki seed, mortality factors particularly rabbits (*pers. obs.*) appear to be preventing seedling recruitment. Neither seedlings within Gap Two or in the adjacent forest thrived, with high mortality occurring in both. This lack of establishment is likely to have a significant impact on future forest composition, as titoki is a major component of the present canopy of the forest on the upper terrace in Keeble's Bush (location of the study sites).

### 6.2.3 Podocarp regeneration within Keeble's Bush

Esler (1978) noted that podocarp regeneration within Keebles Bush was negligible, except for several isolated saplings, and this still appears to true almost thirty years later (especially for rimu, miro and kahikatea).

Although a mature rimu tree grows 12 m away from Gap one, only one rimu seedling was recorded in 1992 (which had died by 1993). This is despite the fact that, as Herbert (1978) indicated, rimu seedlings grow well within canopy gaps. Gap size may be a crucial factor with both Gaps One and Two being too small to permit podocarp establishment. Podocarp seedlings are averse to root competition (Cameron, 1963), which may be significant within the gaps. Other factors, such as lack of viable seed (refer Chapter 3), lack of recent soil disturbance, the proximity to a mature adult, and the presence of exotic herbivores may also help to explain their absence.

James & Franklin (1978) indicated that a moderate degree of soil disturbance is necessary to obtain good recruitment of rimu seedlings, but the soil within Gap One has not been disturbed for some time. Podocarp seedlings do not normally successfully establish under canopy of their own kind (Burke, 1973; Herbert, 1978), and part of the rimu crown overhangs Gap One. All podocarps are relatively unpalatable to browsing mammals, with establishment often aided by removal of the more palatable broadleaved species (McKelvey, 1963), which compete with

podocarp seedlings for light and space (Beveridge, 1983). However, podocarps may be browsed when other palatable species have been depleted. Rimu are comparatively free from insect damage as small seedlings (Franklin, 1968; Beveridge, 1983), though totara, and to a lesser extent, kahikatea seedlings are sometimes subject to defoliation, mainly by tortricid and geometrid caterpillars (Beveridge, 1973).

Kahikatea seeds typically have high viability (refer Chapter 3) with resultant masses of small seedlings, which mostly die during dry periods in the summer (Beveridge, 1983). This was observed in Gap One where almost half the tagged kahikatea seedlings died and were replaced by a similar number the following season.

The suite of factors affecting podocarp seedling establishment is also acting on the broadleaved seedlings within the Gaps, though less is known about their establishment requirements compared with podocarps.

#### 6.2.4 Soil seed bank

1. Glasshouse conditions may not have been correct to cue the germination of all seeds present in the soil seed bank samples. In addition, taking the samples in July may have precluded the presence of some species in the samples, *i.e.*, summer fruiting species. Finally given the heterogeneity of the sampled soil seed bank it can not be assumed that the variation within each site was represented adequately or that
2. The species compositions and seed densities were highly variable between the eight sampling sites. Seed densities are comparable to those in seed banks beneath other North Island forests (Ogden, 1985).
3. A general trend, exhibited by all sites, was a decrease in species diversity and density with soil depth. Almost all (80%) of the seed germinated from the top 4 cm of the soil profile.
4. The seed flora of all sites consisted largely of herbs. Woody species flora were the most poorly represented of the life-forms, comprising only 1%. Only four native primary tree

species were represented, many of which have a gap colonising or early successional role; *e.g.*, cabbage tree, kahikatea, mahoe and matai.

5. Adventive species were present in the soil seed banks of all sites, with most common components of the surrounding scrubby forest margin/pasture, with many occurring within gaps in the bush (*e.g.*, black nightshade, foxglove, sorrel, thistles, and grasses). The numerous gap sites within the bush likely act as 'stepping stones, facilitating adventive penetration into the remnant.

6. Rapid germination occurred with most seedlings emerging from the samples by the end of the first month. Ephemeral species (*e.g.*, *Cardamine debilis* agg.) germinated first, with native woody species requiring several weeks of exposure to break dormancy. This rapid germination in ephemeral species gives them a competitive advantage following disturbance.

7. Tawa and titoki appear able to maintain short term transient soil seed banks, following rapid seed burial. Both are capable of below ground germination, subsequently surviving as 'buried seedlings' which are able to assume 'normal' growth if transplanted. Kawakawa seeds may persist for slightly longer, however low recovery rates suggest high decomposition/predation following burial. Radiata pine does not form a transient or persistent soil seed bank.

Newly formed treefall gaps within Keeble's Bush are likely to be dominated immediately by both native and ephemeral weedy species; with components originating from both the soil seed bank, and fresh seed rain. However, it would appear that the timing of the disturbance is crucial in determining what species are able to capitalise on a newly disturbed site. Those species that do not maintain a persistent or longer-term transient seed bank would only be able to establish from fresh seed rain, vegetative spread, or from a dormant seedling bank (*e.g.*, tawa). If the seed rain is reduced, *i.e.*, through flower or seed predation, lack of dispersal vectors (*e.g.*, kereru or tui) then these species are likely not to regenerate. From the data it would seem that many of the common tree and shrub (*e.g.*, tawa) species may have limited re-establishment following canopy disturbance.

Some of the more problem/aggressive weed species present within Keeble's Bush are present in the soil seed bank, and from the depth they occur are likely to be persistent in the long-term. They therefore pose a continuing threat long after the parent plants have been removed, *e.g.*, blackberry and elderberry.

As with most other sampled soil seed banks, that in Keeble's Bush appears to have both a transient and persistent component.

### 6.3 Management implications

Keeble's Bush is already in a much modified state. It has passed from being a small area in a larger continuous forest, where natural disturbance regimes maintained species diversity, to an isolated fragment in which even small natural disturbances (*e.g.*, windthrow of several large podocarps) could potentially have substantial impacts on its long-term sustainability. From the results presented here it is evident that many of the natural processes are still functioning, but with the added influences of adventive weed species, and introduced mammals and birds; the seed rain is still diverse and relatively abundant, the gaps maintain a fairly stable assemblage of seedlings, and the soil seed bank holds the seeds of many species.

In small gaps, like Gaps One and Two, closure appears to be more a result of the growth of surrounding vegetation and the expansion of the canopy, than the establishment of sapling within the gaps. Natural canopy replacement of titoki and tawa does not appear to be occurring, with no seedling/sapling bank of either present.

This is also true for many of the podocarp species. The main reason for this is not lack of seeds, but rather lack of disturbance on a large enough scale, and of the right type, to promote seedling establishment.

Recommendations are made for:

- (i) The continued and intensified monitoring and control of possums, and the control of rats, rabbits, and hares.
- (ii) The monitoring and control of invasive and aggressive weed species (*e.g.*, wandering willy, old man's beard, and Japanese honeysuckle) ; in particular elderberry, which is re-establishing in and around Gap Two, and is present in the soil seed bank, and blackberry which is also present in the soil seed bank.
- (iii) Active management, *i.e.*, the planting of canopy tree and understorey species, is recommended in the larger gaps (*e.g.*, podocarps, titoki and tawa in BG2) to ensure their presence in the future forest composition. The seed rain will provide ample seed for growing on.

An area of ca. 3 ha adjacent to and downstream from the Bush is currently being planted with indigenous vascular species natural to the Manawatu Plains Ecological District. This area will buffer the Bush along its northwestern edge, in addition to acting as a seed source for many of the species now uncommon or absent following animal damage, and changing environmental conditions.

#### 6.4 Directions for future research

This research has highlighted a number of areas of New Zealand forest ecology for which there is a paucity of information. In particular:

- The seed ecology of many of our forest tree and shrubs is poorly understood *e.g.*, their pollinators, seed predators and pathogens, seed dispersal mechanisms, and their abilities to form soil seed banks,
- The requirements of the seedlings of most species for establishment and subsequent growth,
- The influence of exotic tree litter and the trees themselves on indigenous forests, *e.g.*, alteration of soil pH and water holding capacity. This is particularly pertinent for

small remnants where, as with Keeble's Bush, exotic trees have been planted as fast growing shelter belts, or in larger tracts of forest that abut exotic plantations.

The role of possums as dispersal vectors, particularly in regard to those plant species dispersed by kereru (>10 mm).

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**Appendix 1** List of scientific and common names used in the text.

\* exotic species

Common name	Scientific name
beech	<i>Nothofagus</i> spp.
*blackberry	<i>Rubus fruticosus</i>
*black nightshade	<i>Solanum nigrum</i>
bracken	<i>Pteridium esculentum</i>
cabbage tree	<i>Cordyline australis</i>
*Californian thistle	<i>Cirsium arvense</i>
*elderberry	<i>Sambucus nigra</i>
*eucalypt	<i>Eucalyptus</i> sp.
*foxglove	<i>Digitalis purpurea</i>
hangehange	<i>Geniostoma rupestre</i>
houhere	<i>Hoheria populnea</i> var. <i>sexstylosa</i>
*Japanese honeysuckle	<i>Lonicera japonica</i>
*Jerusalem cherry	<i>Solanum pseudocapsicum</i>
kahikatea	<i>Dacrycarpus dacrydioides</i>
kaikomako	<i>Pennantia corymbosa</i>
kamahi	<i>Weinmannia racemosa</i>
kanono	<i>Coprosma grandifolia</i>
karaka	<i>Corynocarpus laevigatus</i>
karamu	<i>Coprosma lucida</i>
kauri	<i>Agathis australis</i>
kawakawa	<i>Macropiper excelsum</i>
kohekohe	<i>Dysoxylum spectabile</i>
koromiko	<i>Hebe stricta</i>
lemonwood	<i>Pittosporum eugenioides</i>
*macrocarpa	<i>Cupressus macrocarpa</i>
mahoe	<i>Melicytus ramiflorus</i>
mangrove	<i>Avicennia marina</i> var. <i>resinifera</i>

Common name	Scientific name
mapou	<i>Myrsine australis</i>
matai	<i>Prumnopitys taxifolia</i>
miro	<i>P. furruginea</i>
New Zealand jasmine	<i>Parsonsia heterophylla</i>
New Zealand passionfruit	<i>Passiflora tetrandra</i>
ngaio	<i>Myoporum laetum</i>
Northern rata	<i>Metrosideros robusta</i>
*old man's beard	<i>Clematis vitalba</i>
*penny royal	<i>Mentha pulegium</i>
pigeonwood	<i>Hedycarya arborea</i>
*pine	<i>Pinus radiata</i>
poataniwha	<i>Melicope simplex</i>
pohuehue	<i>Muehlenbeckia australis</i>
pukatea	<i>Laurelia novaezelandia</i>
rangiora	<i>Brachyglottis repanda</i>
red beech	<i>Nothofagus fusca</i>
rewarewa	<i>Knightia excelsa</i>
ribbonwood	<i>Plagianthus regius</i>
rimu	<i>Dacrydium cupressinum</i>
shrubby mahoe	<i>Melicytus micranthus</i>
*silver birch	<i>Betula pendula</i>
*small-flowered nightshade	<i>Solanum americanum</i>
small-leaved milktree	<i>Streblus heterophyllus</i>
supplejack	<i>Ripogonum scandens</i>
taraire	<i>Beilschmeidia taraire</i>
tawa	<i>B. tawa</i>
titoki	<i>Alectryon excelsus</i>
tree fuchsia	<i>Fuchsia excorticata</i>
totara	<i>Podocarpus totara</i>

Common name	Scientific name
*wandering willy	<i>Tradescantia fluminensis</i>
*wattle	<i>Racosperma</i> spp.
wineberry	<i>Aristotelia serrata</i>
*Yorkshire fog	<i>Holcus lanatus</i>

**Appendix 2** Seed rain: total number of seeds intercepted by each trap (December 1992-December 1993).

\* Adventive species

SPECIES	G 1		BG1	BG2	G 2			TOTAL	% of TOTAL SEEDS	
	A	B	C	D	E	F	G			H
<i>Alectryon excelsum</i>	2	0	7	0	0	25	11	10	55	1.5
* <i>Betula pendula</i>	0	0	0	1	0	1	0	0	2	0.05
<i>Brachyglottis repanda</i>	256	194	0	0	0	0	0	0	450	12
* <i>Cardamine hirsuta</i>	0	0	0	0	13	0	0	0	13	0.3
* <i>Cirsium vulgare</i>	0	0	0	13	1	0	0	0	14	0.4
<i>Clematis</i> sp.	0	0	0	6	1	0	0	0	7	0.2
<i>Coprosma grandifolia</i>	2	5	3	0	0	1	0	0	11	0.3
<i>Coprosma</i> sp.	0	0	0	0	0	0	1	0	1	0.03
<i>Cordyline australis</i>	367	5	103	0	6	5	1	3	490	13
<i>Dacrycarpus dacrydioides</i>	24	3	22	0	0	5	2	0	56	1.5
<i>Dacrydium cupressinum</i>	26	21	1564	0	0	1	0	0	1612	42.8
* <i>Epilobium erectum</i>	0	0	0	2	0	0	0	0	2	0.05

SPECIES	G 1		BG1	BG2	G 2			TOTAL	% of TOTAL SEEDS	
	A	B	C	D	E	F	G			H
<i>Hedycarya arborea</i>	1	0	2	0	0	0	0	0	3	0.08
<i>Hoheria populnea</i> var. <i>sexstylosa</i>	65	51	0	17	3	0	0	1	137	3.6
* <i>Holcus lanatus</i>	0	0	0	0	0	0	1	0	1	0.03
<i>Laurelia novaezelandia</i>	0	1	1	0	0	0	0	0	2	0.05
<i>Macropiper excelsum</i>	5	0	3	0	0	227	62	2	299	7.9
<i>Melicytus ramiflorus</i>	1	0	0	0	0	0	0	0	1	0.03
<i>Muehlenbeckis austraslis</i>	5	2	37	0	0	110	165	33	352	9.4
<i>Parsonsia heterophylla</i>	1	2	1	0	0	0	0	0	4	0.1
<i>Pennantia corymbosa</i>	3	0	16	2	0	0	0	0	21	0.56
* <i>Pinus radiata</i>	0	0	1	3	1	0	1	1	7	0.19
<i>Pittosporum eugenioides</i>	9	2	60	0	0	2	3	3	79	2.1
<i>Podocarpus totara</i>	7	1	30	0	0	5	3	1	47	1.2
<i>Prumnopitys taxifolia</i>	0	0	1	5	0	0	0	0	6	0.16
<i>Ripogonum scandens</i>	0	0	1	0	0	0	0	0	1	0.03

SPECIES	G 1		BG1	BG2	G 2			TOTAL	% of TOTAL SEEDS	
	A	B	C	D	E	F	G			H
<i>Rubus</i> sp.	0	0	0	0	0	5	4	2	11	0.29
<i>*Taraxacum officinale</i>	0	0	0	0	0	0	2	1	3	0.08
<i>Uncinia</i> sp.	0	0	0	0	0	1	0	0	1	0.03
<b>Family</b>										
Asteraceae	0	0	0	0	0	1	0	0	1	0.03
Asteraceae	0	0	0	0	0	1	0	0	1	0.03
<b>Total Identified</b>	763	287	1851	49	25	394	257	57	3690	98.02
<b>Unknown</b>										
1	22	1	0	0	0	0	0	0	23	0.6
2	5	18	0	0	0	0	0	0	23	0.6
3	1	0	0	0	0	0	0	0	1	0.03
4	3	0	9	0	0	0	0	0	12	0.31
5	1	0	0	0	0	0	0	0	1	0.03
6	3	0	1	1	0	1	0	0	5	0.13
7	0	0	0	0	0	1	0	0	1	0.03

SPECIES	G 1		BG1	BG2	G 2				TOTAL	% of TOTAL SEEDS
	A	B	C	D	E	F	G	H		
8	0	0	0	0	1	0	0	0	1	0.03
9	0	0	0	0	0	6	1	0	7	0.19
<b>Total unknown</b>	35	19	10	1	1	8	1	0	74	1.95
<b>TOTAL</b>	798	306	1862	50	26	398	257	57	3764	100%

**Appendix 3** Numbers of surviving titoki seedlings in the two study areas (G2 & G2F), at each measurement date.

DATE	Gap Two	Gap Two Forest	TOTAL
2/5/93	50	50	100
2/6/93	48	39	88
8/7/93	40	34	74
1/8/93	33	26	59
13/9/93	27	23	50
18/10/93	26	15	41
14/11/93	24	15	39
21/12/93	23	13	36
23/1/94	21	12	33
16/8/94	15	8	23
1/7/95	6	2	8



SPECIES	G1	G1F	G2	G2F	BG1	BG1F	BG2	BG2F	TOTAL
*ragwort					1				1
*small-flowered nightshade		2	1		1	2		1	7
*sorrel					1		1		2
<i>Spurgularia</i> sp.	3	1	6		18	8		13	49
*tall willow herb						1			1
*thistle				2					2
*yorkshire fog					2				2
UNKNOWN	3	8	1	8	25	13	1	11	70
	154	65	37	34	251	110	63	107	821



**Appendix 5** Summary of results on survival of buried tawa, titoki, kawakawa and pine seeds in two replicates. The initial fruit numbers were: tawa, 6; titoki, 10; kawakawa, 2 cm fruit spike (approx. 200 seeds); pine, 10. \*pine = *Pinus radiata*. *in situ* = those seeds which germinated in the field

Sample Depth (cm)		3 months				6 months				9 months			
		Recovered		Germinated		Recovered		Germinated		Recovered		Germinated	
		(%)	Viable	<i>in situ</i>	incubator	(%)	Viable	<i>in situ</i>	incubator	(%)	Viable	<i>in situ</i>	incubator
Rep 1													
0	tawa	100	2/6	2	-	100	5/6	5	-	100	1/6	1	-
	titoki	100	7/10	-	7	100	6/10	-	6	100	7/10	5	2
	kawakawa	34	56/68	32	24	5.5	9/11	-	9	40	78/80	59	19
	*pine	100	4/10	3	1	100	0/10	-	-	100	0/10	-	-
5	tawa	100	6/6	5	1	60	4/6	4	-	83	5/5	5	-
	titoki	80	5/8	-	5	100	4/10	-	4	90	4/9	4	-
	kawakawa	0.5	1/1	1	-	0.5	1/1	1	-	0	-	-	-
	*pine	40	4/4	4	-	100	0/10	-	-	40	0/4	-	-

Sample Depth (cm)		3 months				6 months				9 months			
		Recovered		Germinated		Recovered		Germinated		Recovered		Germinated	
		(%)	Viable	<i>in situ</i>	incubator	(%)	Viable	<i>in situ</i>	incubator	(%)	Viable	<i>in situ</i>	incubator
10	tawa	100	6/6	6	-	100	6/6	6	-	100	5/6	5	-
	titoki	80	6/8	-	6	100	3/10	-	3	90	9/9	5	4
	kawakawa	0	-	-	-	0	-	-	-	24.5	11/49	-	11
	*pine	0	-	-	-	0	-	-	-	40	0/4	-	-
Rep 2													
0	tawa	100	0/6	-	-	100	4/6	3	1	83	1/6	-	1
	titoki	100	6/10	-	6	100	0/10	-	-	40	1/4	-	1
	kawakawa	41	48/82	9	39	27.5	54/55	-	54	26	52/52	-	52
	*pine	100	4/10	3	1	100	1/10	1	-	70	2/7	2	-

Sample Depth (cm)		3 months				6 months				9 months			
		Recovered		Germinated		Recovered		Germinated		Recovered		Germinated	
		(%)	Viable	<i>in situ</i>	incubator	(%)	Viable	<i>in situ</i>	incubator	(%)	Viable	<i>in situ</i>	incubator
5	tawa	100	6/6	6	-	83	4/5	4	-	100	5/6	5	-
	titoki	90	2/9	-	2	100	0/10	-	-	100	1/10	1	-
	kawakawa	42.5	66/85	-	66	43.5	87/87	41	46	46	79/92	-	79
	*pine	90	0/9	-	-	100	1/10	1	-	100	0/10	-	-
10	tawa	100	6/6	6	-	83	4/5	4	-	100	4/6	4	-
	titoki	90	2/9	-	2	100	0/10	-	-	100	3/10	3	-
	kawakawa	0	-	-	-	1	2/2	-	2	0	-	-	-
	*pine	10	0/1	-	-	10	0/1	-	-	0	-	-	-