INVASION OF WOODY SPECIES INTO WEED INFESTED AREAS

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**Patch of broom-dominated vegetation with Mount Tongariro and
Mount Ngauruhoe in the distance.**

*"I'm planting a haycorn, Pooh, so that it can grow up into an oak tree, and
have lots of haycorns just outside the front door instead of having to walk for
miles and miles, do you see Pooh?"*

*"Well," said Pooh, "if I plant a honeycomb outside my house,
then it will grow up into a beehive."*

But Piglet wasn't quite sure about this...

A.A. Milne 1928. The House at Pooh Corner.

ABSTRACT

When studying plant dynamics and succession, it is important to determine potential limiting factors affecting recruitment (Crawley 1990). The purpose of this study was to investigate factors affecting the establishment and survival of woody species in weed infested areas around the central volcanic plateau. This was achieved by first describing these communities, and quantifying the number of native seedlings and saplings found in both forested and non-forested (weedy) areas. Seed input was measured with seed traps, and factors affecting recruitment of seedlings were investigated by manipulative field experiments.

Although some native woody species were dispersed into weedy areas, both seed and seedling densities of most species declined rapidly with increasing distance from the forest margin. Sowing seeds at densities equivalent to 625 per m^2 significantly increased seedling establishment of *Griselinia littoralis* and *Coprosma* 'taylorii' but not *Pittosporum tenuifolium* var. *colensoi*. Removal of exotic grasses (clearing treatment) that dominated in non-forest areas resulted in much greater establishment of all woody seedlings, including introduced broom (*Cytisus scoparius*) and several native species that had dispersed naturally. Most species also showed greater establishment in plots that were caged to prevent predation. However, the effects of clearing and caging treatments on survival of seedlings were not as apparent as they were for establishment. In addition, experimental clearing increased the growth of transplanted *G. littoralis* seedlings. Overall, most native species had much lower seedling establishment and survival in weedy areas compared with native forest. This is explained by a combination of both seed and microsite limitation in weedy areas.

In another experiment designed to test the effects of bird consumption on seed germination, bird dispersers increased germination percentages of native species by removing fruits from seeds. All species examined (*G. littoralis, Coprosma robusta, Pseudopanax crassifolius,* and *P. tenuifolium* var. *colensoi*) showed very low germination of seeds within fruit, and much greater germination of seeds that were cleaned either by passage through birds or by hand. For *C. robusta, G. littoralis,* and *P. tenuifolium* var. *colensoi*, passage through birds also significantly increased germination of seeds compared with those cleaned by hand. The rate of germination was less affected by different treatments than the absolute

percentage germinating, but was generally faster in bird-voided compared to hand-cleaned seed. Seeds in both of these latter treatments germinated considerably faster than seeds within fruit.

Invasion of native woody plants in weedy areas appears to be constrained by a combination of low rates of seed dispersal for most species, and low probabilities of seedling establishment and survival in areas without disturbance. The most likely future scenario for the majority of weedy areas studied is continued dominance of exotic species in the short term, with slow succession to native shrubland as well-dispersed, frost-resistant native species such as manuka (*Leptospermum scoparium*) establish after disturbance. Management options are discussed with the aim of accelerating the rate of succession in weedy areas to native forest.

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Chapter 1

PLANT COMMUNITY ANALYSIS

"An advantage of studying plants is that they sit in one place and wait to be counted."

John Harper (1977)

1.1 INTRODUCTION

Substantial areas of native forest on the central volcanic plateau have been affected by disturbances. These include human induced disturbances such as fires and logging operations, and natural events such as volcanic eruptions. Many of these areas are still devoid of forest today and consist of a mosaic of vegetation types including native shrub and tussockland species and introduced invasives such as broom (*Cytisus scoparius*), heather (*Calluna vulgaris*), and exotic grasses. Broom is considered to be a serious 'problem weed' on conservation land in the central north island and is currently being controlled by the Department of Conservation around Tongariro National Park (Jones 1995). However, there are some areas where broom has not been controlled and is unlikely to be controlled in the future due to its large extent and a lack of funding (Peter Morton pers. comm.). These are mostly older stands of broom with exotic grasses and/or heather (*C. vulgaris*) forming the dominant ground cover (Photo 1.1). The assumption is that these weedy areas are undergoing succession to native forest. But are they? Since most native trees live longer and grow taller than broom, one might expect an eventual succession to native forest, but this is only one of a number of possible scenarios. As Cooper (1926) so eloquently stated, 'succession is like a braided stream with many possible pathways'.

A major motivation behind the study of succession is an increased ability to predict and manipulate successions (Glenn-Lewin *et al.* 1992). Thus, one of the main aims of this study is to use the information collected to address ways of managing weedy areas to encourage and accelerate succession to native forest. Before carrying out manipulative experiments to test what affects seedling recruitment (Chapter 4), it is important to review existing knowledge about succession, and in particular, succession from broom and exotic grasslands to native forest.

Succession can be defined as a directional change in the structure and species composition of a community over time (Glenn-Lewin *et al.* 1992). Although humans have long recognised the phenomenon of succession, the scientific study of succession only began at the end of the 19th century. Despite one hundred years of research, the factors that influence rates, dynamics, and patterns of vegetation change are still not well understood (Glenn-Lewin *et al.* 1992, Weltzin & McPherson 1999). It is thought that the importance of different mechanisms may change at different spatial scales. For example,

environmental factors such as disturbance are important determinants of vegetation pattern at landscape scales. At more local scales, plant interactions and the availability of suitable 'microsites' are sometimes more important (Weltzin & McPherson 1999). A microsite can be defined as the nature of the environment immediately surrounding a seed or seedling (Harper et al. 1977). Disturbance can also act at smaller spatial scales because it often affects the availability of microsites.

In 1977, Connell and Slatyer proposed three models of succession that have had a large influence on subsequent studies. The first, commonly known as the facilitation model, involves species altering an environment in a way that favours later successional species. In contrast, the tolerance model outlines a process of species replacement based on life histories. In other words, slower growing more tolerant species replace faster growing but less tolerant species. The third model is usually known as the inhibition model, and is the opposite of the facilitation model. It predicts that early successional species will inhibit the growth of later successional species. Each of these models is really a combination of several mechanisms that often act together to produce the observed effect (Glenn-Lewin et al. 1992), and they are not mutually exclusive (Connell & Slatyer 1977, Pickett et al. 1987, Walker & Chapin 1987). In fact, many successional processes occur simultaneously and cannot always be grouped into alternative models (Walker et al. 1986, De Steven 1991b, Gill & Marks 1991). This could occur if species A facilitates the establishment of species B by inhibiting species C. For example, Walker et al. (1986) found components of all three models to be important causes of successional change from alder (Alnus incana) to spruce (Picea glauca) on an Alaskan floodplain. In addition, the relative importance of successional processes may change through time (Connell & Slatyer 1987). Walker & Chapin (1987) suggest that succession involves a continuum from early stages where factors governing colonisation are most important, to later stages where factors governing senescence and mortality predominate.

There is still debate over whether facilitation is common during secondary succession (Pickett et al. 1987, Berkowitz et al. 1995). Most authors have found facilitation to be more important in severe environments (Lawrence et al. 1967, Connell & Slatyer 1977, Finegan 1984, Glenn-Lewin et al. 1992). In general, published studies have tended to favour inhibition over facilitation, with less evidence for the tolerance model (Hils & Vankat 1982). One would normally assume tolerance in the absence of evidence for either facilitation or inhibition, however De Steven (1991b) pointed out that the tolerance

model only holds if the species involved reach maturation. Simple coexistence alone, especially for the short time of many successional studies, is not sufficient to label an interaction as tolerance (Glenn-Lewin *et al.* 1992). This could explain the difficulties some have had in testing the applicability of Connell and Slatyer's three models.

The relative importance of facilitation, competition (inhibition model), and life history traits (tolerance model) can best be determined experimentally - either by removing species that establish in early succession that may facilitate or compete with species that establish later, or by sowing seeds or transplanting seedlings into successional communities. If removal of species A causes increased establishment, survival, or growth of species B, then competitive inhibition is likely. If species A removal causes a decrease in recruitment or growth of species B, then facilitation is probably occurring. If there is no change in species B, then one cannot reject the null hypothesis of no interaction between species A and B, although the same result could be obtained by an interaction between competition and facilitation (Walker & Chapin 1987). Seed sowing and grass removal experiments are presented in Chapter 4 and discussed further in Chapter 5.

It should be remembered that the effects of intact vegetation on establishment and survival of tree seedlings probably vary significantly among species. This is because of differences in life history traits that determine their responses to environmental conditions (Berkowitz *et al.* 1995). As a result, an evaluation of the likelihood of succession must take into account the traits of species dispersing into the community (Pickett 1976). These will be discussed in more detail in Chapters 4 and 5.

Management of weedy species depends on an understanding of their ecology, especially their role in succession to native vegetation (Williams 1983). The introduced broom, *Cytisus scoparius*, is a globally invasive European shrub which is now naturalised in Australia, Hawaii, North America, South Africa, Chile, Iran, India, and Japan (Allen *et al.* 1995, Hosking *et al.* 1996, Peterson & Prasad 1998). Broom also covers extensive areas of waste land, river beds, native grasslands, and previously forested hill country throughout New Zealand. Around Tongariro National Park, broom typically occupies disturbed sites and invades short-stature communities (Buddenhagen 1996).

Broom is a leguminous shrub (nitrogen-fixer) that is drought resistant because of its sparse leaves and photosynthetic stems bearing sunken stomata beneath thick epidermal

wax (Williams 1981, Hosking *et al.* 1996). Broom normally flowers in its second or third year. After flowering, broom plants produce large numbers of seeds that mostly fall within 1 m of the parent plants (Smith & Harlen 1991). Broom seeds are hard-coated and can stay viable for many years (Smith & Harlen 1991, Bossard 1991, Parker *et al.* 1994). Generally, only a small proportion of the seed bank emerges as seedlings each year (Williams 1981), and large seed banks accumulate beneath stands (Partridge 1989, Hosking *et al.* 1996). Broom often forms dense thickets when young, and can grow up to 4 m high at maturity (Hosking *et al.* 1996). Broom plants are often deciduous in winter, and sometimes in summer in drought-prone areas (Hosking *et al.* 1996). Published data on the demography of broom suggests that broom can achieve higher fecundities and live longer where it has become naturalised than in its native range. For example, plants live approximately 10-15 years in England and other European countries but can live longer than 23 years in Australia and New Zealand (Williams 1981, Hosking *et al.* 1996, Rees & Paynter 1997).

Several authors consider broom to be a good 'nurse' species (Williams 1983, Porteous 1993, Wilson 1994) and it has been successfully used as such in India (Chinnamani *et al.* 1965). Williams (1983) described a succession of broom to introduced elder (*Sambucus nigra*), which is in turn invaded by mahoe (*Melicytus ramiflorus*) and other native species on the Port hills in Canterbury. He also compared broom favourably to gorse (*Ulex europaeus*) as a nurse species because broom has a shorter lifespan, more readily decomposable litter, and allows more light to reach seedlings of later successional species. On the other hand, broom has been described as a serious weed that competes with other species (Johnson 1982, Bossard 1991, Jones 1995, Hosking *et al.* 1996, Buddenhagen 1996). For example, it can invade short-stature native communities and shade them out (Jones 1995, Timmins & MacKenzie 1995, Hosking *et al.* 1996). It can also cause reductions in the growth of the economically important *Pinus radiata* in New Zealand (Richardson *et al.* 1997).

Broom is often found growing in association with heather and exotic grasses. European heather (*Calluna vulgaris*) is another widespread weed in the central volcanic plateau that competes aggressively with native species (May 1993, Rogers 1996). Once heather has become established, it influences both the composition and structure of the vegetation it has infested (May 1993, Keesing 1995). It can also modify the soil environment by reducing the pH, and has effects on the underlying microclimate (May 1993). The most

obvious factors that influence species composition and the amount of heather within existing communities are altitude, soil moisture, and disturbance (May 1993). The ability of native species to invade heather and the rate of succession in heather-dominated areas will be commented on further in the discussion (section 1.5).

It is thought that exotic grasses inhibit the recruitment of native woody species by competing for available moisture in the soil and by overtopping and smothering seedlings (Evans 1983, Porteous 1993). However, results of many studies carried out in overseas old-fields (agricultural land that has been abandoned) prove that secondary succession does occur eventually, although this process may take many decades and sometimes hundreds of years (Myster 1993).

In order to investigate successional sequences in the study area it is firstly important to quantify the existing plant communities. Hence the first aim of this chapter was to describe and quantify plant communities in the study area. Since succession to native forest depends on the availability of native seedlings and saplings in weedy areas, the second aim was to quantify these. The third aim of this chapter was to investigate whether the current pattern of native seedlings in weedy areas is related to distance from a seed source.

1.2 STUDY SITES

All field work was carried out on the central volcanic plateau in the North Island of New Zealand (Fig. 1.1). Several study sites were situated in broom (*Cytisus scoparius*) dominated vegetation on the western slopes of Mount Tongariro, adjacent to Tongariro National Park. These sites will hereafter be referred to as the Mangatepopo sites (Fig. 1.2). Further study sites were located at latitude 39° 23.4' and longitude 175° 26.1' E in retired farmland adjacent to Raetihi hill, near Ohakune (Fig. 1.1, Photo 1.2).

1.2.1 Soils

At the Mangatepopo sites on the north-western slopes of Mount Tongariro, the soils are derived from Taupo pumice (Froggatt 1981) overlain with 0.5-1 m of free-draining andesitic Ngauruhoe ash (Topping 1973). Chunks of Taupo pumice (originating from the Taupo volcanic centre 50 km to the north) are often evident where the topsoil is very thin. In contrast, the soils on the southern slopes of Ruapehu at Raetihi hill show less evidence of the Taupo eruptions and are composed mainly of material from andesitic eruptions of the neighbouring volcanoes; Ruapehu, Ngauruhoe, and Tongariro (Topping 1973).

1.2.2 Climate

Tables 1.1 and 1.2 in Appendix 1 summarise climate measurements collected from May 1999 to April 2000 at the closest weather stations to the Mangatepopo and Raetihi hill study areas. Long-term averages for Whakapapa (the nearest weather station to Mangatepopo) show a high annual precipitation (2913 mm) with rain spread relatively evenly throughout the year, although somewhat lower during the three summer months (Thompson 1984). In comparison, total annual rainfall was lower in the year of study both at Mangatepopo (2332 mm) and Raetihi hill (1789 mm) (Appendix 1.1, 1.2). Mean annual air temperatures ranged from 2.9°C (mean minimum) to 11.3°C (mean maximum) (Thompson 1984). Both sites generally have a cool spring and early summer (October to December), with January to March being the warmest months (Thompson 1984). Although winter snow falls only occasionally in both study areas, it can persist at higher elevations well into October. The prevailing wind is westerly (Thompson 1984).
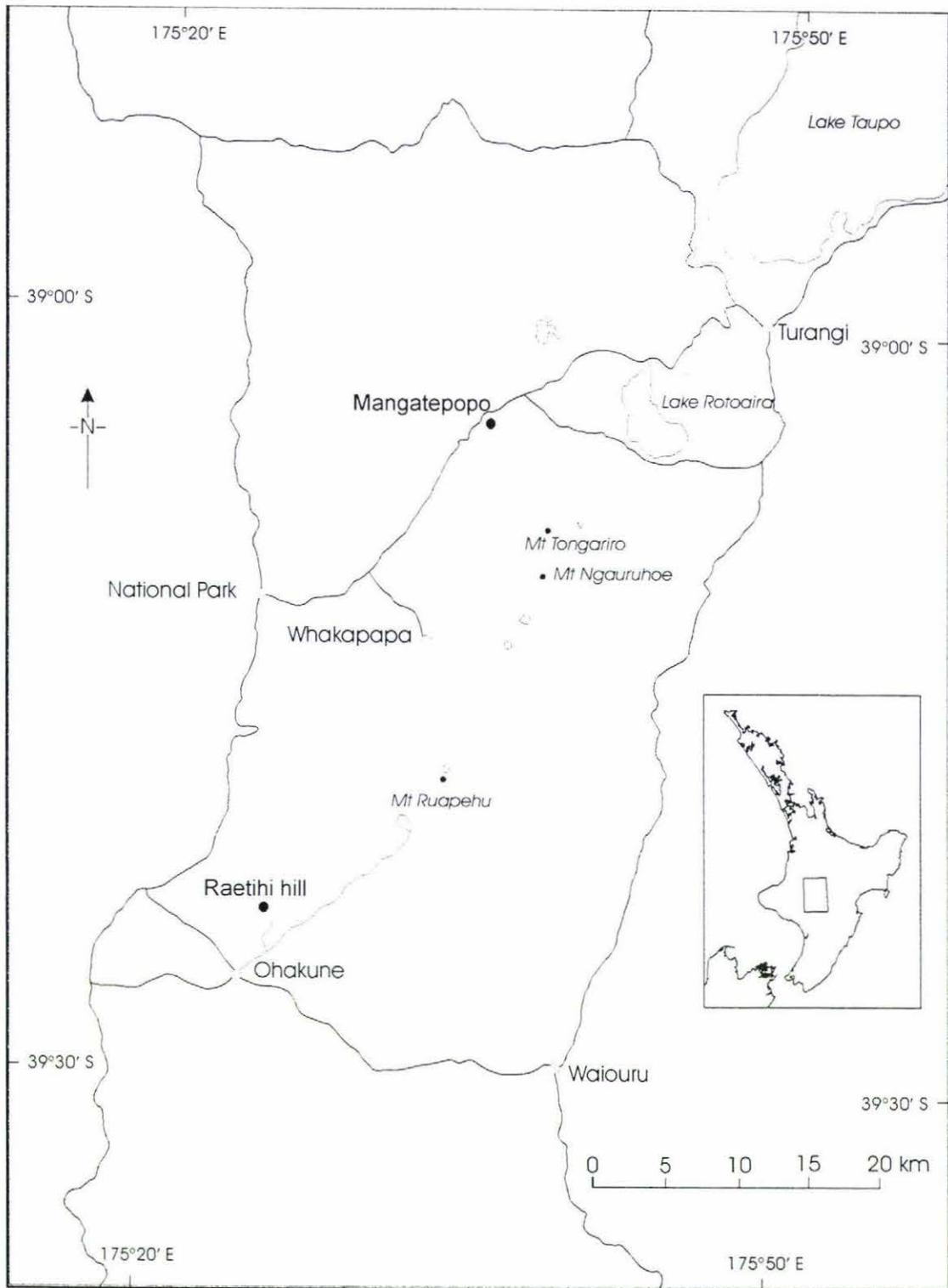
Fig. 1.1 Locations of study sites (Mangatepopo and Raetihi hill) on the central volcanic plateau, situated in the north island of New Zealand.
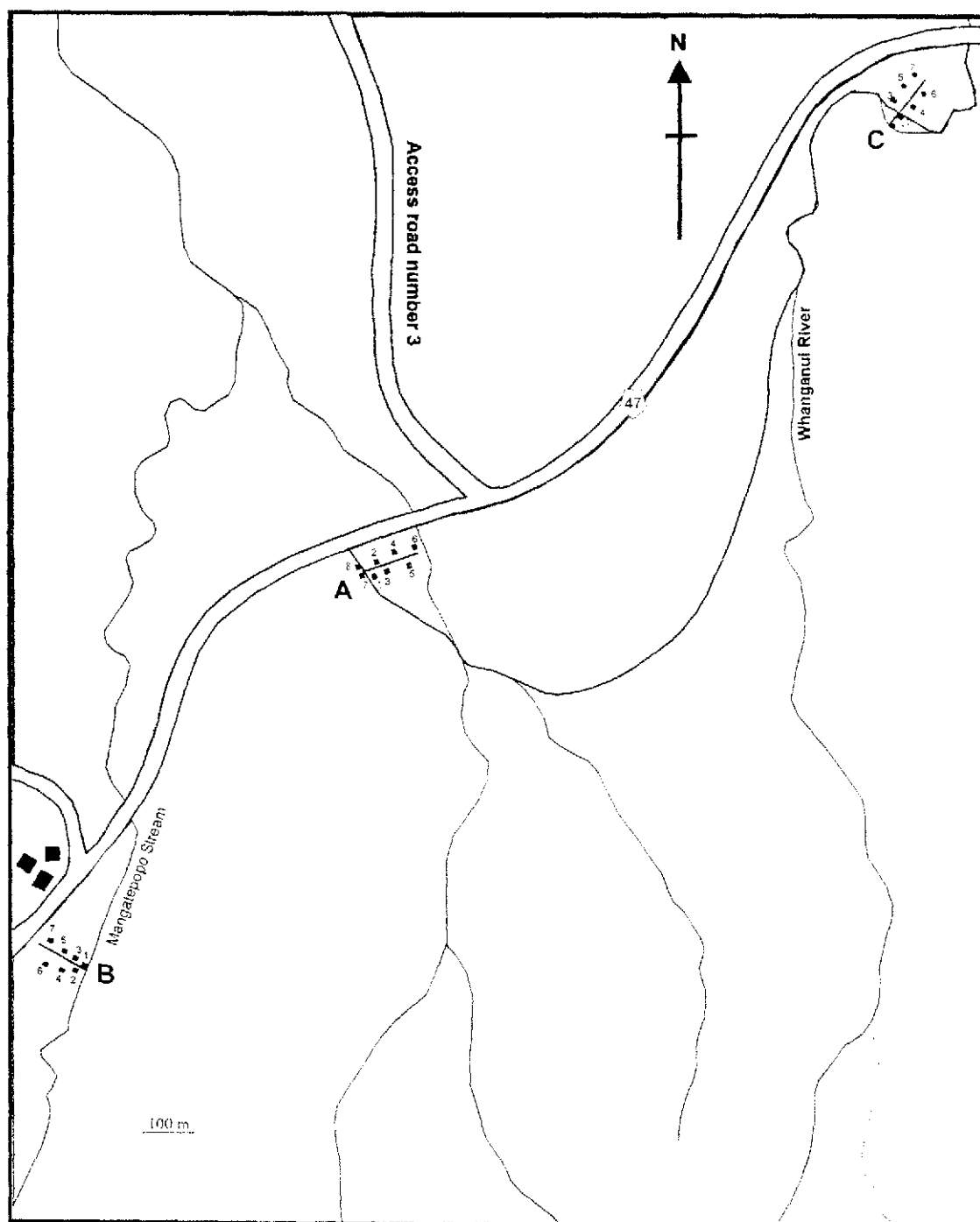
Fig. 1.2 Location of transects A, B, and C in broom-dominated vegetation at the Mangatepopo sites. These sites are located between latitudes 39° 03.7' and 39° 04.6' S and longitudes 175° 34' and 175° 35.5' E. NB: Dark shading = exotic forestry, light shading = broom-dominated vegetation, no shading = native shrubland and tussock grassland.

1.3 METHODS

1.3.1 Community description

In order to describe the current plant communities, a combination of transects and plots were used to sample the vegetation and environmental components of the landscape. Typical broom stands were chosen at the Mangatepopo sites, along with other weedy areas adjacent to patches of native bush (Raetihi hill). Randomly selected transects were located within each area. Five 100 m long transects were set up perpendicular to and including the forest edge, and running into adjacent weedy vegetation. Seven to eight permanently marked 5x5 m plots were established along each transect. These plots were placed randomly but restricted to be at least 7 m apart. Plots were placed within 20 m of each transect alternately to the left and to right of the transect line (Fig. 1.2).

Percent cover was estimated for all plant species, litter, bare soil, logs, rocks, and bryophytes in each plot. Total percent cover of the canopy, vegetation less then 1 m, and exotic grasses was also recorded for each plot. Litter depth was measured by a metal probe at eight random points within each plot, and a mean depth calculated. In addition, altitude, aspect, and slope were recorded at each plot. Slope was defined as the maximum slope in the plot, with aspect defined as the direction looking down the line of maximum slope.

A further eight belt transects were set up in the weedy areas to describe and quantify native sapling patterns more broadly. These transects were 5 m wide and 100 m long. The number, height and position of all saplings (classified as > 1 m) was recorded in the area within each transect.

1.3.2 Demography of woody species

Diameter at 10 cm above the ground and height was recorded for all woody species in each 5x5 m plot. Transverse sections were taken from a total of 47 live broom trees of a variety of sizes to determine their ages. Harvested broom trees were randomly located from each transect. Growth rings were clearly visible for most discs, enabling reasonably accurate age determinations. The largest discs provided the minimum age of the current broom stands, but did not assess whether previous generations had grown in the area. There was a significant relationship between diameter and age of harvested broom, and

the regression equation (age=1.76*diameter + 1.65, N = 47, P<0.001, R^2=0.79) was used to predict ages of all other broom plants (Fig.1.1 in Appendix 1).

All seedlings (classified as < 1 m) of woody species were identified, their height measured (in cm), and microsite recorded. Seven categories of microsite were used; bare ground, litter on ground, moss on ground, grass, bare log, litter on log, moss on log. Seedlings of species that could not be identified at the time of survey were removed, numbered, and grown in the glasshouse until they were large enough to be identified.

1.3.3 Statistical analyses

Survey results were analysed using ordination and classification procedures. Ordinations were carried out using Detrended Correspondence Analysis (DECORANA) with the statistical program PCORD 4.0 (1999). Data used were percent cover of all species. A cluster analysis (Ward's minimum variance method and Euclidean distance measures) was also carried out using PCORD and the resulting groupings were superimposed on the ordination diagram. The frequency of seedlings in each microsite was analysed separately for each species using loglinear models (SAS Institute 1996). This method took into account the different expected numbers of seedlings due to differences in percent cover of various microsites. All other analyses (regressions and simple ANOVAS) were carried out using SYSTAT (1996).

Photo 1.1 Aerial view of a typical senescent broom stand with an understorey of exotic grasses at Mangatepopo. Transect A starts at the large totara on the forest margin and runs into the adjacent broom dominated vegetation.

Photo 1.2 Raetihi hill site showing the mixed podocarp/broadleaf forest on the hill and the patchy nature of native shrubs invading exotic grassland retired from farmland 40 years ago. Transect E runs from the forest margin at the top of the picture downslope to the manuka shrub in the foreground.

Photo 1.3 Disturbance in the broom stand sampled by transect C caused by heavy machinery during realignment of state highway 47.

1.4 RESULTS

1.4.1 PLANT COMMUNITY ANALYSIS

1.4.1.1 Species richness

A total of 81 species were found within the 35 five by five metre plots (not including exotic grasses or bryophytes). Detailed lists of species found at each site are included in Appendix 1 (Tables 1.9 & 1.10). Species richness (mean number of species per 5x5 m plot) was much higher in forest plots than in plots located in either broom or grass habitats (Fig. 1.3), and these differences were significant at the 1% level (Appendix 1.3). However, forest habitats at the two different sites were not significantly different from each other in terms of mean number of species. Similarly, species richness between broom and grass habitats was not significantly different (Appendix 1.3).
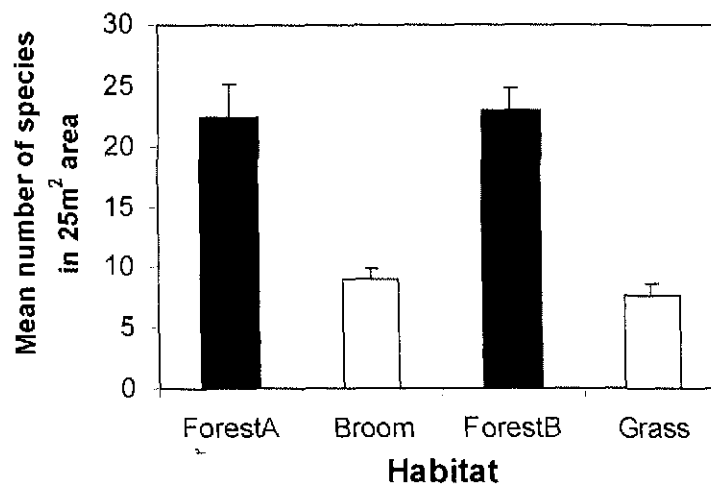
Fig. 1.3 Mean species richness per plot (excluding introduced grasses and bryophytes) in four different habitat types. ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill. Black bars = forest habitats, open bars = non-forest habitats.

1.4.1.2 Community description

An ordination of all plots based on percent cover of all species revealed which plots were similar to each other (Fig. 1.4). Axis one explained approximately 40% of the total variation, while axis two explained 26%. All grassy plots at Raetihi hill were quite similar, although some of the forest plots at this site included exotic grasses and were thus more similar to the grassy plots than to other forest plots. Most of the forest plots at Mangatepopo were very similar in that they consisted of dense communities of manuka (*Leptospermum scoparium*) and *Phyllocladus aspleniifolius* var. *alpinus*. However one forest plot at Mangatepopo (A7) was more similar to some of the forest plots at Raetihi hill. This was probably because this plot had a few large trees of *Griselinia littoralis*, *Podocarpus totara*, and other species that were more commonly found at Raetihi hill.

Axis one was strongly correlated with combined basal area of all woody species (r = 0.82), canopy cover (r = 0.71), percent cover of litter (r = 0.68), and was negatively correlated with ground cover (r = -0.69). The total number of native seedlings (excluding *Coprosma* 'taylorii') was also correlated with axis one (r = 0.58). Thus, on the left of the ordination are broom and grass plots with low basal area, low percent cover of litter and canopy, but a high proportion of ground cover. In contrast, forest plots with high basal area, high percent cover of canopy and litter, and greater densities of native seedlings are grouped on the right of the diagram. Other significant correlations with axis one include; maximum plant height (r = 0.56), slope (r = 0.60), and percent cover of logs (r = 0.55). Maximum vegetation height was generally greater in forest plots, although some old broom trees were taller than manuka trees found in forest plots at Mangatepopo (B2, C1, and C2). Naturally, maximum height was much lower in the grassy plots, although sometimes a few individual shrubs or saplings caused greater heights in these plots. For example, plot E7 had a very low canopy cover, but contained one tall spindly lancewood that had a height of 3.5 m (Appendix 1.7).
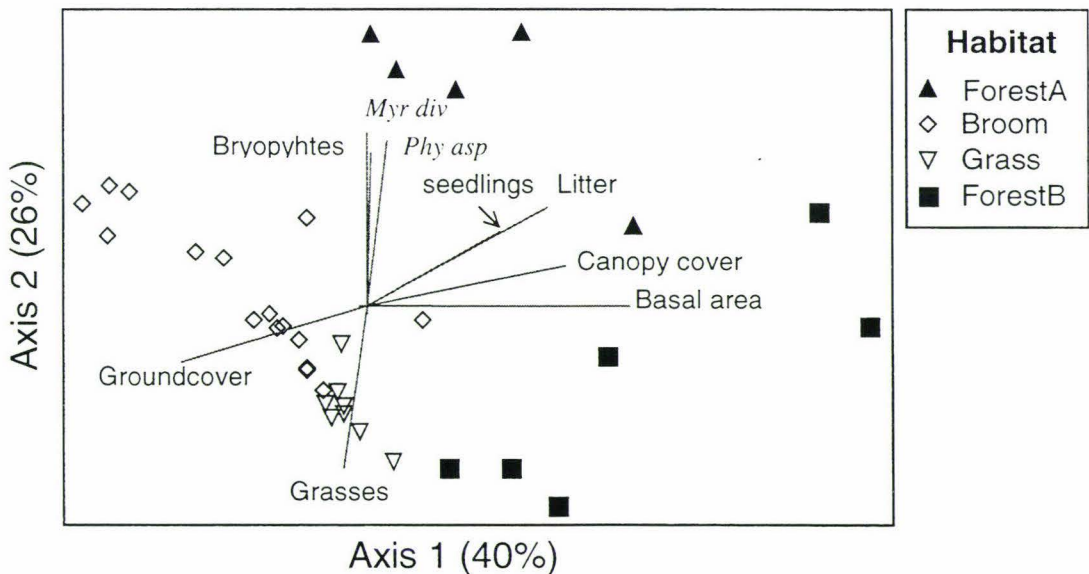
Fig. 1.4 Detrended correspondence analysis of all plots (based on percent cover of all species) at both sites (PCORD 1999). ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill. Vectors with correlations > 0.58 are superimposed on the diagram. The direction of the vectors indicates the maximum change of the variable across the diagram, and the length of the vector indicates the magnitude of that change.

The highest correlations with axis two were percent cover of bryophytes ($r = 0.62$) and exotic grasses ($r = -0.64$). Percent cover of bryophytes was greater in forest plots situated at the top of the diagram whereas exotic grasses were more prevalent in plots near the bottom of the ordination. Native seedling densities of two species were also correlated with axis two, *Phyllocladus aspleniifolius* var. *alpinus* ($r = 0.66$) and *Myrsine divaricata* ($r = 0.65$).

1.4.1.3 Species composition

A cluster analysis of all plots separated communities into four broad groups: I, II, III and IV which were superimposed on the ordination diagram (Fig. 1.5).

<u>Vegetation type I – low density/high basal area native forest</u>

This first group consists mostly of native forest plots from Raetihi hill. These plots have a variety of native tree species forming the canopy including *Griselinia littoralis*, lancewood (*Pseudopanax crassifolius*), ducksfoot (*Pennantia corymbosa*), putaputaweta (*Carpodetus serratus*), black maire (*Nestegis cunninghamii*), and kahikatea (*Dacrycarpus dacrydioides*) (Appendix 1.4 and 1.5). Compared to the other groups, this vegetation type has a low proportion of introduced heather, broom and exotic grasses. Plots in this cluster also had a high percent cover of litter compared to other vegetation types. Many native fern and climber species were only found under a canopy of native forest. Surprisingly, one broom plot was also included with this group. This plot (A1) had a high proportion of the native ferns *Histiopteris incisa* and bracken (*Pteridium esculentum*), and thus a higher proportion of litter than the other broom plots, which made it more similar to forest plots.

<u>Vegetation type II – high density manuka/*Phyllocladus* forest</u>

This small group consists of four forest plots from Mangatepopo. The main canopy species in these plots were manuka and *Phyllocladus aspleniifolius* var. *alpinus* (Appendix 1.4). These plots had higher stem densities than the other forest plots but lower basal areas. They also had a higher percent cover of bryophytes and orchids, especially *Pterostylis* species. Plots in this group also contained more *Myrsine divaricata* and *P. aspleniifolius* var. *alpinus* seedlings than any other community.

Axis 1 (40%)
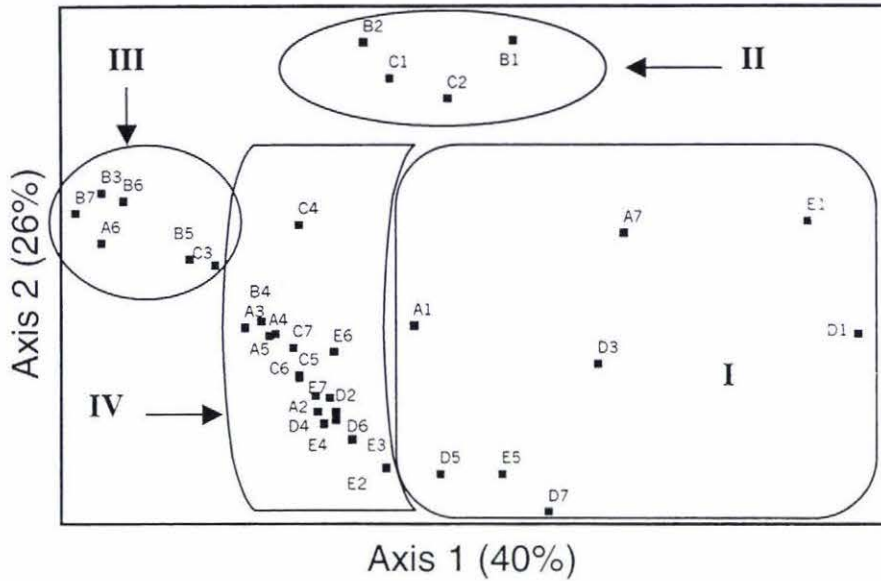
Fig. 1.5 A detrended correspondence analysis of the same data as Fig. 1.4 (based on percent cover of all species), showing plot labels and communities from a classification analysis superimposed (Cluster analysis using PCORD, Euclidean distance, Ward's minimum variance method). Plot labels beginning with A-C are from Mangatepopo while those beginning with D and E are from Raetihi hill.

Vegetation type III – Broom/heather community

The third group consists of broom plots that have a high percent ground cover of introduced heather. The colonising native ferns bracken (*Pteridium esculentum*) and *Polystichum vestitum* were occasionally found in this vegetation type. *Coprosma* 'taylorii' seedlings were present in all six plots and four of these plots also contained seedlings of *P. aspleniifolius* var. *alpinus*. Very few other species were present in this vegetation type, apart from a few more invasive weeds such as blackberry (*Rubus fruticosus*), *Pinus contorta*, and the garden escapees' *Cotoneaster simonsii* and *C. franchesii*.

Vegetation type IV– Broom/grass community

All of these plots have a high percent cover of exotic grasses. Some have no canopy at all, while others have an aging and collapsing canopy of broom. Some plots also have small proportions of toetoe (*Cortaderia toetoe* and *C. fulvida*) and the occasional seedling of *Coprosma* 'taylorii' and *G. littoralis*. Several of the grassy plots from Raetihi hill also have a few native shrubs such as *C.* 'taylorii', *C. tenuifolia*, *Hebe stricta*, lancewood, and manuka. Quite a few of the grassy plots in this group contain bracken and many weed species are also present (Tables 1.9, 1.10 in Appendix 1).

1.4.1.4 Changes in broom community with age

Another ordination was constructed using only plots containing broom (Fig. 1.6). In this case, the first axis explained almost all of the total variation. There were high correlations of litter depth (0.83), percent cover of exotic grasses (-0.97), heather (0.99), bryophytes (0.61) and light levels (-0.60) with the first axis. Other correlations of interest are maximum age of broom trees (-0.58), basal area of dead stems (-0.58) and bare soil (-0.56). Plots on the left of the ordination are older broom stands with less canopy and thus higher light levels, more exotic grasses, and a higher basal area of dead broom. In contrast, plots on the far right of the ordination are younger broom stands with a high percent cover of heather, deeper litter, more bryophytes and less grass. Comparing the different areas studied, transect A had the highest mean maximum age of 16 years, C the next highest at 14 years, and B the lowest at 10 years (Appendix 1.6). The latter value excludes one very large broom tree in forest plot B2, because this individual was almost dead, overtopped by native trees, and assumed to be a member of the previous generation of broom in the area.

Because axis one explains such a high proportion of the total variation, the effect of axis two actually has a negative percentage (Fig. 1.6) and is not worth commenting on further.
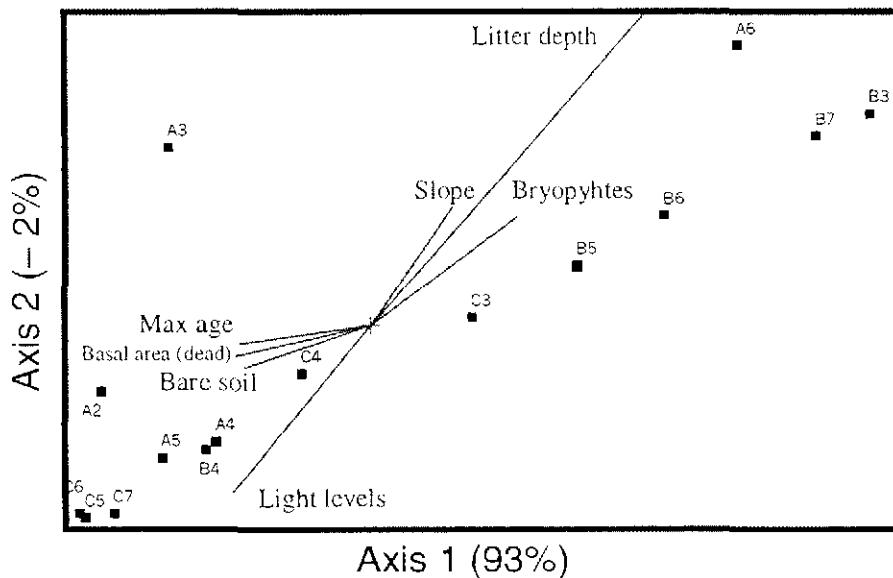
Fig. 1.6 Detrended correspondence analysis of broom plots only (Mangatepopo) based on percent cover of all species present (PCORD 1999). Vectors with correlations > 0.50 are shown. The direction of the vectors indicates the maximum change of the variable across the diagram, and the length of the vector indicates the magnitude of that change.

Litter depth varied with the dominant species at different sites. The greatest depth of litter (mean = 8.2 cm) was found in broom sites that had an understorey predominantly of heather (*Calluna vulgaris*). In comparison, broom plots with a ground cover of exotic grasses had a mean litter depth of 5.2 cm. Litter depth was not highly correlated with the first ordination (Fig. 1.3), because the grassy habitat at Raetihi hill had a high mean litter depth (8.3 cm) similar to that beneath heather. Interestingly, mean litter depth in forest plots at Mangatepopo is only 4.1 cm compared with a mean of almost 8 cm in the same habitat type at Raetihi hill (Appendix 1.5, 1.6).

1.4.2 SEEDLING PATTERNS

1.4.2.1 Habitat and site differences

The seedlings of the majority of native species were only found in very low densities, in the plots sampled, although a few species were more common. Overall, *Coprosma* 'taylorii' seedlings were the most abundant (Table 1.1), while the next most abundant were those of *Griselinia littoralis*. Total density of native seedlings was much higher in forest plots than in non-forest plots at both sites.

Considering only forest plots, the total density of all native seedlings found at the Mangatepopo sites (12 m^{-2}) was higher than at Raetihi hill (4 m^{-2}). In addition, some seedlings were more commonly found at Mangatepopo, than at Raetihi hill. These species include *Phyllocladus aspleniifolius* var. *alpinus, Myrsine divaricata*, lancewood (*Pseudopanax crassifolius*), five finger (*Pseudopanax. colensoi*), and manuka (*Leptospermum scoparium*). In contrast, seedlings of ducksfoot (*Pennantia corymbosa*) and horopito (*Pseudowintera colorata*) had higher densities in forest plots at Raetihi hill than at Mangatepopo.

Generally, native species were very rarely found in broom habitats (1.5 m^{-2}) and were even rarer in grass habitats (0.2 m^{-2}). An exception was *Coprosma* 'taylorii', which reached slightly higher densities in broom than it did under a canopy of native forest at Raetihi hill (Table 1.1). *C.* 'taylorii' was also the most common native species found in the grass habitat. The other exceptions were manuka (*Leptospermum scoparium*) and introduced broom (*Cytisus scoparius*), which were found in greater densities in the broom habitat than in forest plots.

Table 1.1 Density of naturally occurring seedlings of different species in different habitats. Data are pooled within each habitat, then converted to per m^2. * denotes naturalised exotic species.

	Density of seedlings per m^2			
Site	Mangatepopo		Raetihi hill	
Species	ForestA	Broom	ForestB	Grass
Aristotelia fruticosa	0.01	0	0	0
Aristotelia serrata	0	0	0.01	0
Brachyglottis repanda	0	0	0.03	0
Carpodetus serratus	0.02	0.004	0.18	0
Coprosma foetidissima	0	0	0.02	0
Coprosma grandifolia	0	0	0.13	0
Coprosma propinqua	0.22	0.01	0	0
Coprosma propinqua x robusta	0	0.004	0	0
Coprosma rhamnoides	0	0.02	0	0
Coprosma robusta	0.02	0.02	0.01	0
Coprosma 'taylorii'	6.76	1.16	0.92	0.15
Coprosma tenuifolia	0.66	0.02	0.43	0.01
Cotoneaster franchesii*	0	0.01	0	0
Cyathodes juniperina	0	0.01	0	0
Cytisus scoparius*	2.54	3.50	0	0
Dracophyllum filifolium	0	0.004	0	0
Elaeocarpus hookerianus	0	0	0.02	0
Gaultheria depressa	0.04	0	0	0
Gaultheria rupestris	0.02	0	0	0
Griselinia littoralis	2.06	0.09	0.89	0.01
Hebe stricta	0	0	0.08	0.01
Leptospermum scoparium	0.03	0.05	0	0
Leucopogon fasiculatus	0	0	0.02	0
Melicytus ramiflorus	0	0	0.09	0
Melicope simplex	0.01	0	0	0
Myrsine divaricata	0.46	0.004	0.01	0
Nestegis cunninghamii	0.01	0	0.02	0
Olearia arborea	0.01	0	0	0
Pennantia corymbosa	0.02	0	0.51	0.01
Phyllocladus aspleniifolius	0.76	0.11	0	0
Pittosporum tenuifolium	0.03	0.004	0	0
Podocarpus totara	0.12	0	0	0
Prumnopitys ferruginea	0	0	0.01	0
Prumnopitys taxifolia	0.08	0	0	0
Pseudopanax crassifolius	0.58	0	0.13	0
Pseudopanax colensoi	0.24	0	0	0
Pseudowintera colorata	0.02	0.01	0.52	0
Schefflera digitata	0	0	0.01	0
TOTAL (native species only)	12.19	1.52	4.04	0.19

1.4.2.2 Are seedling densities related to distance from a seed source?

Examining the three transects at Mangatepopo only, there is a significant negative relationship between distance from the margin of native forest and the total number of seedlings (after $\log_{10}$ transformation) (Fig. 1.7). The plots at Raetihi hill were excluded from this analysis because the situation there is quite different (ie: patches of forest remnants interspersed in a matrix of exotic grasses), making distance along a transect less useful as a measure of distance from the nearest seed source.
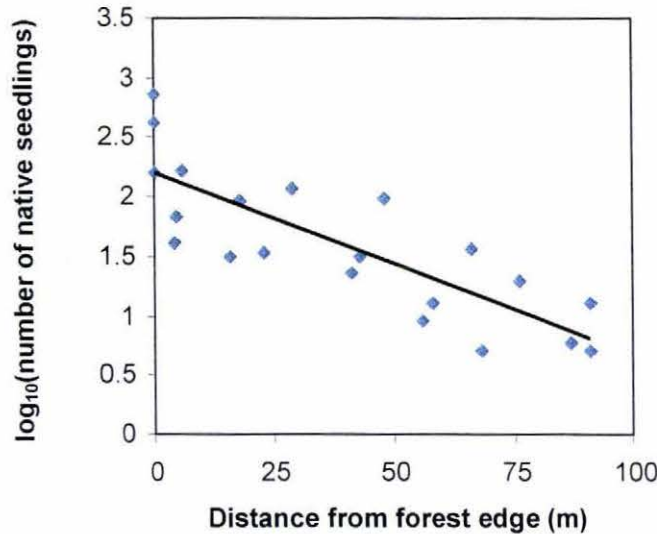
Fig. 1.7 Density of all native seedlings ($\log_{10}$ transformed) along three transects running from the forest edge into adjacent broom dominated vegetation at Mangatepopo. (y=-0.015x + 2.20, N=21, P<0.001, R^2=0.66).

The general pattern of decreasing seedling density with increasing distance from the forest edge was observed for the most common native species. However, *C.* 'taylorii' seedlings did not follow such a clear pattern (Fig. 1.8b). The highest seedling densities of this species were found in transect A. The difference between transects was significant at the 1% level (Appendix 1.8). In fact, the forest plot in this transect had 26 seedlings of this species per m^2 (Fig. 1.8b). Excluding transect A, the trend towards lower densities of *C.* 'taylorii' seedlings further away from the forest is clearer.

a) *Griselinia littoralis*   **b)** *Coprosma* 'taylorii'
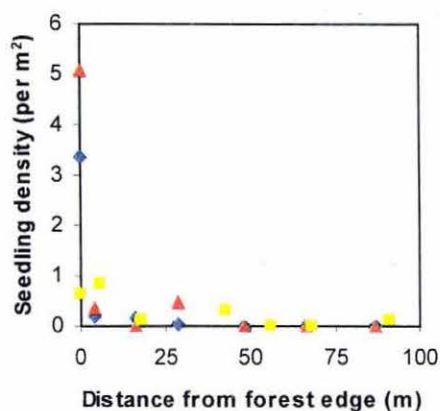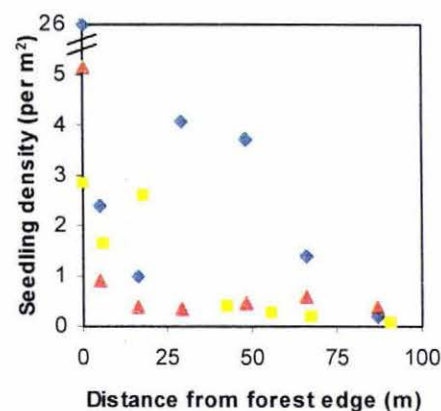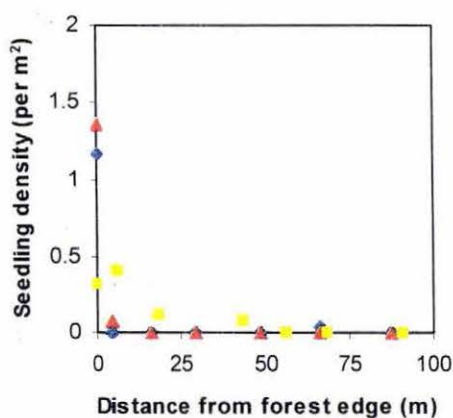
c) *Coprosma tenuifolia*   **d)** *Phyllocladus aspleniifolius* var. *alpinus*
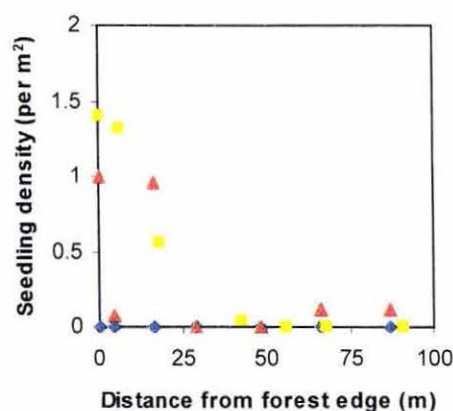
Fig. 1.8 Density of seedlings of a) *Griselinia littoralis*, b) *Coprosma* 'taylorii', c) *Coprosma tenuifolia* and d) *Phyllocladus aspleniifolius* var. *alpinus* along three transects running from the forest edge into adjacent broom dominated vegetation at Mangatepopo. Note the expanded scale for graphs c) and d).

Seedling densities of most other native species rapidly decreased in plots further than a few metres away from the forest edge. Seedlings of *P. aspleniifolius* var. *alpinus* were found in similar densities to *C. tenuifolia* in forest plots (Fig. 1.8c,d). Although no seedlings of *P. aspleniifolius* var. *alpinus* were found in transect A (Fig. 1.8d), there was a less rapid decline in seedling densities with increasing distance from the forest edge for this species. For example, reasonable densities of *P. aspleniifolius* seedlings were found around 20 m from the forest margin in transects B and C.

In contrast to the native species, there was no discernible pattern of broom seedling density with distance from the forest edge. Transect C showed much higher densities overall than the other two transects (Fig. 1.9) and this difference was highly significant (Appendix 1.8).
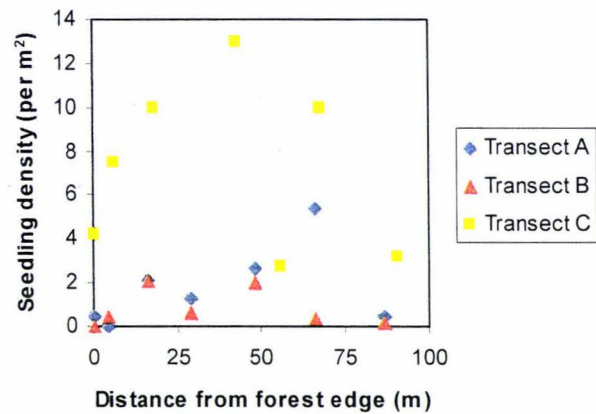
Fig. 1.9 Density of broom seedlings (*Cytisus scoparius*) along three transects running from the forest edge into adjacent broom dominated vegetation at Mangatepopo.

1.4.2.3 Microsites

The majority of native seedlings were found in microsites characterised by litter (Table 1.2). One exception was manuka (*Leptospermum scoparium*), in which over 50% of seedlings were found growing in moss (Table 1.2). Of all the species examined manuka and *Carpodetus serratus* had the highest proportions of seedlings growing in bare ground (approximately 13%). Both *Pseudowintera colorata* and ducksfoot (*Pennantia corymbosa*) also had around 10% of seedlings found in this microsite.

Most native seedlings were not found very often on logs, although approximately 22% of *Pseudowintera colorata* seedlings and 19% of *Carpodetus serratus* seedlings were found in this microsite. Almost half of the broom seedlings were found in grassy microsites, with 30% in litter, 15% in moss and the remainder mostly growing in bare ground. The only native species to have over 10% of seedlings found in the grassy microsite was *Coprosma* 'taylorii'.

Table 1.2 Summary of microsite data for the most common species (where n>20). Percentage of total seedlings that were found in different microsites. G=grass, L=litter, M=moss, B=bare ground, LL=litter on log, ML=moss on log, BL=bare log, * denotes naturalised exotic species.

Species	G	L	M	B	LL	ML	BL	Total number of seedlings
Carpodetus serratus	0	64.5	3.2	12.9	16.1	0	3.23	31
Coprosma propinqua x robusta	0	66.7	33.3	0	0	0	0	45
Coprosma 'taylorii'	10.7	63.2	18.4	3.0	2.8	0.9	1.0	1474
Coprosma tenuifolia	0.7	77.3	8.4	8.4	1.2	2.0	2.0	154
*Cytisus scoparius**	48.7	28.7	14.5	7.1	0	0.9	0.1	1719
Griselinia littoralis	0.2	80.2	8.9	3.3	4.9	0.2	2.3	429
Leptospermum scoparium	0	24.8	52.2	13.0	0	0	0	23
Myrsine divaricata	0	80.7	19.3	0	0	0	0	62
Pennantia corymbosa	0	76.2	3.8	10	10	0	0	80
Phyllocladus aspleniifolius	0	67.9	32.1	0	0	0	0	140
Pseudowintera colorata	1.2	58.8	7.1	10.6	11.7	1.2	9.4	85
Pseudopanax colensoi	0	100	0	0	0	0	0	30
Pseudopanax crassifolius	1.1	68.9	21.1	4.5	1.1	0	3.3	90
Availability of microsite (%)	57.5	31.7	5.0	2.4	1.2	1.2	0.9	

Because each plot had varying amounts of each microsite, these data were analysed using loglinear models that took this into account (see section 1.3 methods). The analysis tested if there were more seedlings than would be expected on the basis of area of each microsite. Microsites can be listed from ones with more seedlings than expected to ones with less seedlings than expected (Table 1.3). For *C.* 'taylorii', more seedlings occurred on logs, bare ground and litter than was expected from the area occupied by these microsites. This was especially noticeable at Raetihi hill where many more seedlings were found growing on scattered logs compared with other microsites which were far more abundant (eg: exotic grasses). In fact grass was the least preferred microsite for this species, even though it was still able to grow in this microsite. *G. littoralis* showed basically the same order of microsite suitability as *C.* 'taylorii'. In contrast, broom (*Cytisus scoparius*) did not show any significant differences between microsites after area was taken into account.

Table 1.3 Results of loglinear analyses on seedling microsites for the three most commonly occurring species (where n>400). NB: Log = pooled data for the three different log microsites LL, BL, and ML (log litter, bare log, moss on log respectively). * denotes naturalised exotic species. Microsites in the same row with the same letter are not significantly different.

	Microsites arranged in decreasing order of suitability ⟶				
Species					
Coprosma 'taylorii'	Log[a]	Bare[a]	Litter[a]	Moss[b]	Grass[b]
*Cytisus scoparius**	Log[a]	Bare[a]	Litter[a]	Moss[a]	Grass[a]
Griselinia littoralis	Litter[a]	Log[a]	Bare[a]	Moss[b]	Grass[b]

1.4.3 SAPLING PATTERNS

Overall, the highest densities of native saplings (>1 m in height) were found in broom stands sampled by transects B_1 and B_2. This was mostly because of high densities of manuka (*Leptospermum scoparium*) found in this area (Table 1.4). Densities of manuka saplings at other sites were much lower. *Coprosma* 'taylorii' had the next highest sapling densities in transects A_1 and A_2. In comparison, other transects had much lower sapling densities of this species. Very few saplings of other native species were found at all.

Table 1.4 Sapling density (number per m^2) of the most common native species in broom and grassy habitats. A_1 = 5x5 m belt transect set up along the same line as the original transect A, A_2 = additional 5x5 m belt transect set up parallel to transect A etc.

Site	Mangatepopo						Raetihi hill	
Transect	A_1	A_2	B_1	B_2	C_1	C_2	D	E
Coprosma 'taylorii'	0.12	0.08	0.02	0.01	0.04	0.02	0.04	0.03
Coprosma tenuifolia	0	0	0	0	0	0	0.004	0.004
C. propinqua x robusta	0.004	0.004	0	0	0.004	0.004	0	0
Dracophyllum filifolium	0.02	0	0.03	0.01	0	0	0	0
Griselinia littoralis	0	0	0.002	0	0	0	0.01	0.002
Hebe stricta	0	0	0	0.01	0.004	0	0.002	0.01
Leptospermum scoparium	0.03	0.004	0.35	0.18	0.02	0	0	0
Pittosporum tenuifolium	0	0	0.01	0	0.004	0	0	0.002
TOTAL	0.17	0.09	0.41	0.21	0.07	0.02	0.06	0.05

1.5 DISCUSSION

Changes in the distribution and abundance of woody plants are ultimately dependent on recruitment of individuals into the population (Weltzin & McPherson 1999). Thus, by investigating seedling patterns of woody species in weedy areas an insight can be gained into possible future patterns of vegetation structure and composition.

1.5.1 Native seedling patterns

The majority of native seedlings were found under a canopy of forest with very few native seedlings found in broom-dominated areas. Smith (1994) found a similar result in broom infested areas in Australia, as did Partridge (1992) in New Zealand. Even fewer native seedlings were found in the grassy habitat at Raetihi hill. This pattern could have been caused by low densities of seed dispersed into these areas ('dispersal limitation' see Chapter 2). Alternatively, conditions in weedy areas may have been less suitable for establishment and survival of native seedlings ('microsite limitation' see Chapter 4). Compared to forest areas, the total number of native seedlings declined rapidly with increasing distance from the forest edge in broom habitats. The majority of seedlings of most native species were found within 25 metres of the forest margin. However, *Coprosma* 'taylorii' was a notable exception. This small-leaved shrub may have more seed being dispersed into weedy areas than other native species, or perhaps it is more able to successfully establish and survive in these conditions. In fact, probably a combination of the above factors cause this species to occur more often than other native species in weedy areas.

1.5.2 Microsites

The nature of the environment immediately surrounding a seed or seedling can influence the establishment and survival of that seedling (Grubb 1977, Harper 1977, Fowler 1988). Thus, the availability of suitable microsites will influence seedling recruitment. Microsites have degrees of suitability that are reflected in probabilities of germination, seedling survival, and seedling growth rates (Fowler 1988). In this study, the majority of native seedlings were found on litter. However, once the area occupied by each microsite (ie: the proportional availability) was taken into account, several species showed preferences for other less common microsites such as logs, and bare ground. For example, even though *Coprosma* 'taylorii' seedlings were found growing in the grassy microsite, they were disproportionately more common on logs, especially at Raetihi hill.

This may be due to a combination of greater seed input (from birds using logs as perching sites), and from less competition from the thick swards of exotic grasses surrounding the logs.

Most authors have found that broom seedlings establish best after disturbance of the soil or vegetation (Bossard 1991, Smith 1994, Hosking *et al.* 1996). However, results from this chapter show that although more broom seedlings were found growing amongst exotic grasses, there were no significant differences between microsites when the area each occupied was taken into account. The effects of experimental disturbance on establishment of broom seedlings are presented in Chapter 4. Characteristics of microsites necessary for successful establishment might vary seasonally as environmental factors, such as water availability, fluctuate (Fowler 1988). For example, bare ground may be suitable for seedling establishment when soil moisture is readily available, but not when water is limiting. Seedlings growing on bare ground may have died during the summer drought before the area was surveyed. As the survey was carried out in mid-summer (1998), many of the native woody seedlings observed were very young. For succession to occur, some of these seedlings would have to survive to maturity.

1.5.3 Native sapling patterns

The density of native saplings in weedy habitats varied in the different areas sampled. By far the highest density of saplings was recorded in transect B (broom habitat). Most of these were manuka (*Leptospermum scoparium*). It seems likely that some sort of disturbance initiated the establishment of this wind-dispersed species at the same time as broom established. As a result, although this site has the youngest population of broom of the three areas studied, it also appears to be the most likely to succeed into native forest in the near future. The other native species found in relatively high densities was *Coprosma* 'taylorii'. Saplings of this species were especially dominant in the broom habitat sampled by transect A. This corresponds with higher seedling densities of *C.* 'taylorii' also found in this area. Compared to the broom habitats, grassy habitats at Raetihi hill had even lower densities of native shrubs. However, because transects were randomly positioned, patches of native vegetation that were non-randomly aggregated on and around logs were often missed. These patches may provide centers for radial spread of woody species into surrounding grassland.

1.5.4 Broom cycles

Broom stands are usually even-aged (Williams 1983, Smith & Harlen 1991). Although small seedlings can be present beneath different aged stands, the absence of 1-2 year old plants in all but the oldest stands shows that broom cannot regenerate successfully without disturbance or stand senescence. Changes in the density of broom stems, canopy cover, light levels, and litter depth appear to influence the ability of native woody seedlings to establish. Most of these parameters change with the age of the broom community. Density of stems and canopy cover was highest in young broom stands, and declined until broom plants were over 10-15 years old. Understorey cover increased with broom age, as exotic grasses increased with higher light availability. Broom normally reaches its maximum height of about four metres before it starts to lean and topple over. The collapse of older broom plants means that shading of the ground is reduced (Smith 1994, Hosking *et al.* 1996). As the canopy opens up, more broom seedlings may be able to establish (Wilson 1994). However, less native seedlings are likely to establish in these senescent stands as the protective canopy cover is gone, and exotic grasses form a thick sward.

1.5.5 Succession in weedy areas

This leads to predictions about the future of broom-dominated vegetation at the Mangatepopo sites. From the evidence so far, it seems likely that broom and exotic grasses will continue to dominate the vegetation in the short term due to low densities of most native species. Although saplings of manuka (*Leptospermum scoparium*), *Dracophyllum* species and *Coprosma* 'taylorii' were found scattered throughout broom-dominated vegetation, these species do not normally grow much taller than broom so are unlikely to overtop it. However, these native species will probably provide more suitable microsites for establishment of other native species as they ameliorate conditions beneath their canopies. Manuka is known to be a good 'nurse' species (Evans 1983, Porteous 1993). *C.* 'taylorii' attracts bird dispersers, especially silvereyes (*Zosterops lateralis*) (personal observation), which may enhance the seed rain of other native species.

Evidence of charcoal was found in the broom habitat sampled by transect C and this area was grazed 10-15 years ago (Mike Brown pers. comm.). It is likely that a fire cleared the original vegetation and broom probably invaded after grazing was abandoned at this site. Whether this site was dominated by broom before this is difficult to ascertain without historical records or aerial photographs.

During this study, an area of broom at transect C was bulldozed due to realignment of state highway 47. Only one month after this disturbance, thousands of broom seedlings were released from the seed bank (personal observation). It is highly likely that broom will again form the dominant canopy cover in these disturbed areas. Since most native woody species do not form a long-lived seed bank (Enright & Cameron 1988, Burrows 1994c), they are unlikely to benefit from such a large scale disturbance, except perhaps manuka which has a large seed source available year round (Mohan *et al.* 1984).

The situation at Raetihi hill is slightly different, as broom is not present at this site. The area was milled at the start of the 20th century by Gammon and Co. and again between 1952 and 1954 by Punch and Co. (George 1990). The flat area around the hill was farmed from 1943 to around 1956 (Merrilyn George pers. comm.). This land was retired from farming by the early 1960's when it was bought by the former Tongariro National Park Board (Evelyn Cooper pers. comm.). Today, exotic pasture still dominates the previously farmed areas 40 years after grazing ceased. As thick swards of exotic grasses usually inhibit establishment, survival and growth of most woody seedlings (Evans 1983, Porteous 1993), a slow spread of native shrubs from forest margins is the most likely scenario. Charcoal was also found on some of the old logs at this site, although it is not known at what time and on what scale fire might have occurred. Fires were probably lit deliberately after logging had ceased in order to clear the area before sowing pasture seed, as this was common practise at the time (Allen 1984).

1.5.6 Rate of succession

In an experimental study on secondary succession after disturbance, Rydgren *et al.* (1988) found that the rate of succession depended on the severity of disturbance, the area of the disturbed patch, and the distance to intact vegetation. Results from the current study indicate that distance to a seed source affects the rate of succession, with more native seedlings found in weedy areas adjacent to forest margins than further away from these margins. There are two hypotheses that might explain this; a lack of seed dispersal into weedy areas (see Chapter 2), or a lack of suitable microsites in weedy areas (Chapter 4).

The presence of broom at a site appears to increase the rate of succession to native shrubland compared with areas of grassland that have very little or no canopy (eg: at Raetihi hill). However, broom does not seem to enhance the establishment of native woody species as well as other species can, especially in old stands that are in a state of

senescence. As already discussed, broom seems to be in a cyclic phase of re-establishment after senescence of even-aged stands. This observation is similar to a suggestion by Partridge (1992) that vegetation dominated by broom and bracken on the Port hills in Canterbury is likely to persist as a relatively stable community. However, Williams (1983) suggested that if broom is left alone it will succeed to native forest relatively quickly. In a similar situation, Lee *et al.* (1986) estimated that the establishment of a native canopy above gorse (*Ulex europaeus*) on an undisturbed site would take no more than 50 or 60 years. They also suggest that where manuka establishes with gorse on a newly cleared site, native species would displace gorse in about half that time. This latter situation is probably similar to the area sampled by transect B where broom and manuka occur together. However, the rate of succession is likely to be slower in other weedy areas because of low densities of native seedlings and saplings. Succession from manuka to later successional species generally takes another 100 years, but can be faster on more fertile sites (Porteous 1993).

Rates of succession of native shrubs in heather dominated vegetation are similar to those under gorse. For example, based on historical fires and the likely date for heather invasions, Rogers and Leathwick (1996) estimated that it takes 38-75 years for manuka (*Leptospermum scoparium*) and *Dracophyllum* species to colonise and exceed the cover of heather at 900 m above sea level. At higher elevations the times for this succession are almost doubled (Rogers & Leathwick 1996). They also found that although rates of native shrub invasion into tussock grassland without heather showed somewhat faster initial rates, there was little difference after 70-80 years. These results suggest that succession of heather to native shrubland and ultimately forest is inevitable. However, interpretation of their results must be treated with caution as there is now a much bigger seed source of heather than was the case 70-80 years ago.

In this study, seedlings of both native species and broom were occasionally found under a canopy of heather. However, the number of seedlings seemed to depend on the density and age of the heather (personal observation). Young stands of heather are often very dense and can form a barrier to seedling establishment. Light levels are also very low, and only the hardiest seedlings can grow through the dense layers of heather. Given that heather is usually able to invade and displace grasses (Rogers & Leathwick 1996), why is it not more widely distributed in broom-dominated vegetation in the study area? It is possible that it is still invading these areas, and is thus patchily distributed. In Scotland,

the same species of heather is likely to be out competed by grasses only when there are gaps in the canopy, resulting either from heavy grazing or from the heather being in the mature or degenerate phase (Alonso & Hartley 1998). However, this 'degenerate phase' is not as common in New Zealand (Keesing 1995). Thus, it seems less likely that exotic grasses can out-compete heather in this country.

One of the other species commonly present in the surveyed plots was native bracken (*Pteridium esculentum*). This species is especially common at Raetihi hill where it is invading grassland (Photo 1.2). Bracken is usually able to out-compete grasses and herbs (Evans 1983, Porteous 1993), however its effect on broom is more complicated. In a study in Canterbury, Partridge (1992) found that removing bracken affected only the growth form of broom but not survival. In addition, experimental sowing of broom into areas with and without bracken resulted in better recruitment of broom in the latter case. Hence, the effect of bracken on broom fits the tolerance model of interaction for established plants, and the inhibition model for recruitment (Partridge 1992).

1.5.8 Conclusions

While other authors have found broom to be a relatively good nurse plant and to encourage succession to native forest, the association of broom with a dense ground cover of exotic grasses (especially prevalent in the senescent stages of broom) appears to be restricting establishment of native seedlings in the study area. A similar situation was observed in retired farmland at Raetihi hill, where native seedlings and saplings were mostly found growing under a canopy of forest or in microsites such as logs where exotic grasses were not present. The native small-leaved shrub *Coprosma* 'taylorii' was the only woody species that was found in reasonable densities in grassy habitats.

Chapter 2

SEED DISPERSAL

"That a ripe strawberry is as pleasing to the eye as to the palate, that the gaily coloured fruit of the spindle-wood tree and scarlet berries of the holly are beautiful objects, will be admitted by everyone. But this beauty serves merely as a guide to the birds and the beasts, in order that the fruit may be devoured and the manured seeds disseminated."

Charles Darwin (1859) **The Origin of Species**.

2.1 INTRODUCTION

The pattern of seed rain is an important factor affecting the rate of secondary succession (De Steven 1991a). Dispersal patterns can be divided into two main groups based on dispersal vector: 1) wind dispersed species with high fecundities, long distance dispersal and low clumping of seeds, 2) animal dispersed species with low fecundities, short distance dispersal and a high degree of clumping of seeds (Clark *et al.* 1998).

The important role birds play in the dispersal of plant seeds is well documented (McDonnell & Stiles 1983, Murray 1988, Medellín & Gaona 1999). However, the extinction of half of New Zealand's native frugivorous (fruit-eating) birds since the arrival of humans in this country, and the decline of others has reduced the number of potential seed dispersers (Clout & Hay 1989, Lee *et al.* 1991). Given that 70% of native trees have fruits suited for vertebrate dispersal (Burrows 1994c), birds are likely to be important in secondary successional processes.

The spatial structure of vegetation and the behaviour of birds also influence seed dispersal patterns (Hoppes 1988, Glenn-Lewin *et al.* 1992, Kollmann 1995). Frugivorous birds often have favoured flight paths and preferred perching locations after feeding in fruiting trees (Herrera & Jordano 1981). Trees often serve as important 'recruitment foci' for seed deposition because they provide perching and roosting sites for seed-dispersing birds and other animals (McDonnell & Stiles 1983, Herrrera *et al.* 1994, Wunderle 1997, Toh *et al.* 1999, Harvey 2000, Robinson & Handel 2000). Hence, the presence of woody species often encourages natural successional processes both by increasing seed deposition into the site and by providing more favourable microsites for seedling establishment and survival (Harvey 2000).

The actual area over which seeds are dispersed (seed shadow) can vary widely between species. Seed shadows resulting from vertebrate dispersed species do not always show the regular pattern that results from dispersal by wind (Glenn-Lewin *et al.* 1992). In fact, seed dispersal by vertebrates can show a combination of patterns:

1) an exponential decrease in density in relation to the distance to the maternal plant similar to most wind dispersed species (Izhaki *et al.* 1991, Debussche & Isenmann 1994),

2) a localised increase in density in relation to perching places situated in open areas

(Janzen *et al.* 1976, McDonnell & Stiles 1983), and 3) an increase in seed density in relation to vegetation height (Glyphis *et al.* 1981, Gleadow & Ashton 1981, Debussche & Isenmann 1994, Robinson & Handel 2000). Thus, frugivorous birds may influence vegetation patterns, but existing vegetation may also influence recruitment of new individuals by affecting bird movement and subsequent seed dispersal patterns (McDonnell & Stiles 1983). Similarly, seed availability, bird availability, and the patterns of fruit choice influence the temporal pattern of seed deposition in weedy areas by birds (Stiles 1980). However it is important to note that these periods of dispersal may or may not coincide with favourable establishment conditions.

Of special interest is the dispersal of broom (*Cytisus scoparius*) which is a 'problem weed' growing around Tongariro National Park. It is generally accepted that broom spreads slowly but persistently over short distances. Most broom seeds fall within 1 m of parent plants, although sometimes dehiscence can fling them up to 4.5 m (Smith & Harlen 1991). Bossard (1991) reported ant dispersal of broom seeds up to 5 m from parent plants in California. Ants were also seen carrying broom seed on two occasions during the current study (personal observation). Some isolated plants occur as far as 50-100 m away from the nearest visible seed source in Tongariro National Park (Buddenhagen 1998). This sort of longer distance dispersal may occur by movement of seeds: 1) in mud attached to vehicles, machinery, footwear and animals, 2) internally by animals eg: possums, birds, rats, pigs, deer, or 3) by streams in flood which carry the non-buoyant seeds by bedland saltation (Smith & Harlen 1991). Birds have been known to disperse broom in the United States, but how well the seeds survive digestion varies with the species of bird (Parker *et al.* 1994). Mice have eaten broom seeds in California (Bossard 1991), although seeds are generally not viable after digestion. The relative importance of different dispersal vectors of broom in New Zealand no doubt varies with location, and availability of different vectors.

Since seed dispersal is a key factor affecting the invasion of woody species and the rate of succession, it is important to measure the dispersal of seed into weedy areas. A lack of native seeds may be limiting succession in weedy areas around Tongariro National Park. This study was designed to investigate the following questions: 1) what is the input of seeds into the study areas? 2) does this input differ in different habitats and with successional increases in structural complexity, such as maximum vegetation height? 3) does seed rain decrease with increasing distance away from a seed source?

2.2 METHODS

2.2.1 Seed traps

Twenty seed traps were used to determine the quantity and composition of the seed rain in different habitats. At each transect (see section 1.3 for location and description of transects), four seed traps were sited in a restricted random fashion, two under a native forest canopy and two under either a canopy of broom (transects A, B and C) or in the open grassy habitat (transects D and E). Seed traps were set up in the broom transects at Mangatepopo on 19th May 1999, and on 16th June 1999 at Raetihi Hill near Ohakune.

Each seed trap consisted of a metal funnel, with a catching area of 0.2 m², supported on a metal tripod so that the mouth of the funnel was 1 m above the ground surface (Photo 2.1). The total area sampled by 20 seed traps was 4 m². Seed and litterfall was collected in a metal can attached to the bottom of the funnel. Cans had holes drilled in the bottom to allow water to drain away. To prevent escape of smaller seeds, muslin bags were placed inside each can and changed on emptying.

2.2.2 Seed sorting and identification

Seed traps were emptied monthly (on average every 29 days) over 9 months. Seed trap samples were stored at 4°C and processed as soon as possible after collection. Seeds were sorted and identified under a dissecting microscope. Identification was primarily by comparing seeds found in the seed traps with those collected from plants growing in the study areas. Unknown seeds were sent to Colin Webb at the Foundation for Research, Science, and Technology in Wellington for identification. A reference collection of seeds is kept at the Seed Technology building, Massey University, Palmerston North.

Trapped seeds of each species were counted and categorised according to dispersal mode; 1) wind dispersed, 2) bird dispersed, 3) unknown. Species that were known to be bird dispersed were then identified as either a) cleaned by passage through a disperser b) still contained within fruit (either fleshy or dry). All seeds regardless of dispersal mode were then further divided into the following categories:

(i) empty or immature seeds; (ii) full or viable seeds (determined by eye only, not viability tests), (iii) damaged seeds (mostly from attack by invertebrates). Generally, full

or viable seeds (with embryos) were clearly distinguishable from empty seeds because they were much fatter. Immature seeds were smaller in size than mature seeds, and attacked seeds were distinguished by the presence of holes in the seed coat, a dark colour within the seed, or if the seed was able to be squashed with gentle pressure from tweezers.

2.2.3 Statistical analyses

Linear regressions were carried out in SYSTAT (1996). Differences in the number of species caught per trap and their dispersal modes were analysed with a loglinear model using SAS (SAS Institute 1996).

Photo 2.1 Example of a seed trap located in the broom-dominated vegetation sampled by transect A.

2.3 RESULTS

2.3.1 SPECIES RICHNESS

A total of 36 species (excluding exotic grass seeds) were caught in 20 seed traps over nine months of trapping. This total represents 25 bird dispersed species, seven wind dispersed species and four species which could not be identified and whose dispersal mechanism was not apparent. Twenty of the 32 species identified were native. Seed size ranged from approximately 1-2 mm for manuka (*Leptospermum scoparium*), *Hebe stricta* and *Carpodetus serratus* seeds to 5 mm for *Griselinia littoralis* seeds.

Generally, more species were caught in seed traps under a canopy of native forest than in broom or grassy habitats (Fig. 2.1). Analysis of these results with a loglinear model confirmed that the effect of habitat was highly significant (Appendix 2.1a) and explained the largest amount of deviance in the model. Forest habitats at Mangatepopo and Raetihi hill were not significantly different from each other in terms of species richness. However, more species were caught under a canopy of broom than in open grassland (Fig. 2.1, Appendix 2.1b). Overall, there were significantly less wind dispersed species than bird dispersed species (Appendix 2.1b).
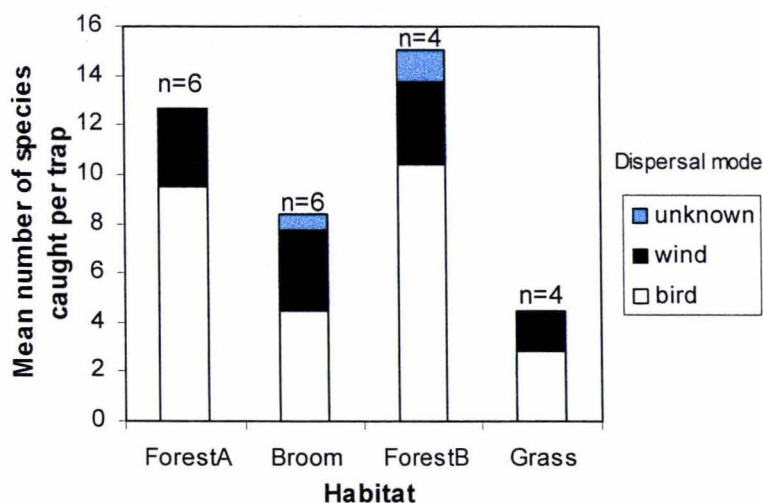
Fig. 2.1 Species richness of seeds caught in four different habitats over 9 months of seed trapping. NB: ForestA = native forest at Mangatepopo, ForestB = native forest at Raetihi hill. The number of seed traps in each habitat is presented above each bar.

The proportion of wind dispersed to bird dispersed species was generally higher in the non-forest habitats. A significant interaction between habitat and dispersal mode confirms this (Appendix 2.1a). In fact, significantly more wind dispersed species were caught in broom and grass habitats than under a canopy of native forest (Appendix 2.1b). Species richness increased with the number of seeds caught per seed trap (after $\log_{10}$ transformation). Although this relationship was significant, the amount of variation explained by the line was not that high (Fig. 2.2).
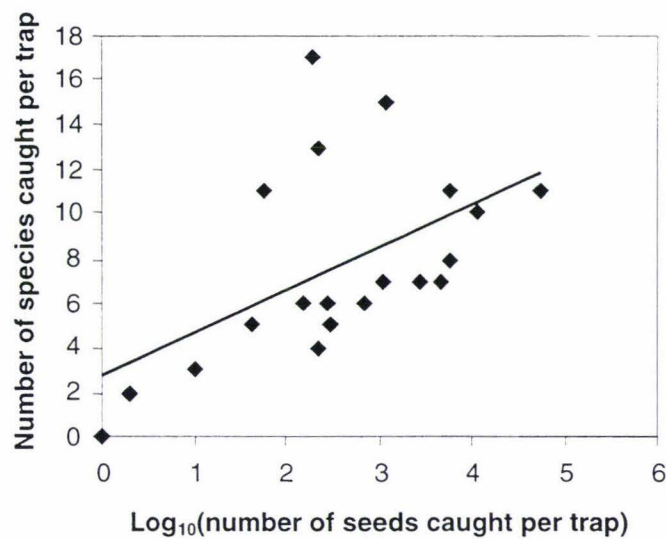
Fig. 2.2 The relationship between number of seeds caught per trap over 9 months ($\log_{10}$transformed) and species richness. ($y = 1.9x + 2.8$, N=20, R^2=0.30, P=0.014).
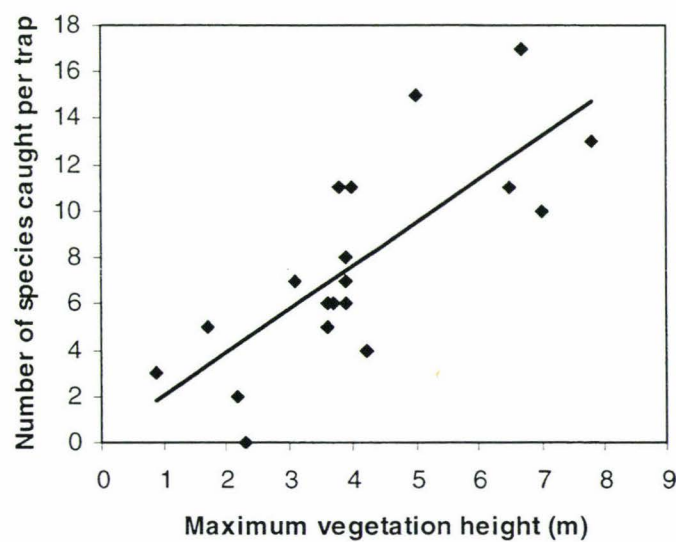
Fig. 2.3 The relationship between maximum vegetation height per plot and species richness. ($y = 1.9 + 0.1$, N=20, $R^2 = 0.60$, P<0.001).

There was also a significant positive relationship between the number of species caught per trap and the maximum vegetation height of the plot in which the seed trap was placed (Fig. 2.3).

2.3.2 SEED AVAILABILITY

The density of seed rain also increased with increasing maximum vegetation height in the vicinity of the seed traps (Fig. 2.4).
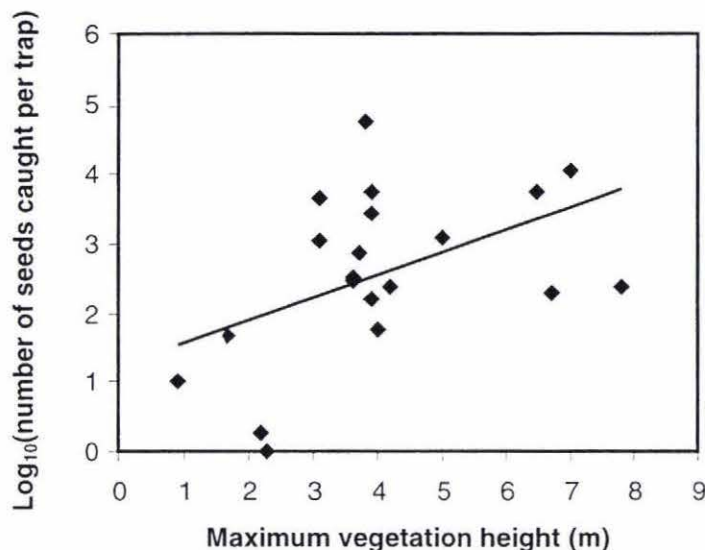
Fig. 2.4 The relationship between number of seeds caught per trap over 9 months ($\log_{10}$ transformed) and maximum vegetation height. ($y = 0.32x + 1.26$, N=20, R^2=0.23, P=0.034).

The density of dispersed seeds was very heterogenous in space. It varied from 0 per m^2 to over 60,000 per m^2 over nine months. As the mean statistic is not very useful in instances of high data variability such as this, data are pooled within each habitat then converted to number of seeds per m^2.

2.3.2.1 Bird dispersed species

There were obvious differences in seed rain between sites. Overall, the total density of seeds caught at Raetihi hill was six times that caught at Mangatepopo (Table 2.1). However, both *Coprosma* 'taylorii' and *Griselinia littoralis* had much higher seed densities at Mangatepopo compared with Raetihi hill (Table 2.1). In fact, some species were only caught at Mangatepopo, for example *Phyllocladus aspleniifolius* var. *alpinus*, *Melicytus lanceolatus*, and *Myrsine divaricata*. In contrast, lancewood (*Pseudopanax crassifolius*), and *Carpodetus serratus* had much higher seed densities at Raetihi hill.

Rimu (*Dacrydium cupressinum*), cabbage tree (*Cordyline indivisa*), and *Pittosporum tenuifolium* var. *colensoi* were among other species caught only at Raetihi hill. Overall, lancewood was the most abundant bird dispersed species reaching very high densities at Raetihi hill (Table 2.1). *Carpodetus serratus* and *Coprosma* species had the second and third highest densities at Raetihi hill (approximately 316 and 19 per m^2 respectively).

Table 2.1 Seed densities of species known to be dispersed by birds (per m^2) caught over 9 months of seed trapping at Mangatepopo and Raetihi hill. NB: Filled = whole seed, unfilled = empty or immature seed, attacked = seed damaged by insect larvae. Percentage of seeds attacked is calculated from the raw data (counts) not from the data in the table (converted to per m^2). *Coprosma* seeds other than *C.* 'taylorii', *C. tenuifolia* and *C. rigida* were difficult to tell apart and were thus grouped under '*Coprosma* species'. This group includes various *C. robusta* x *propinqua* hybrids, and *C. foetidissima*.

Site	Mangatepopo				Raetihi hill			
Species	filled	unfilled	attacked	% attacked	filled	unfilled	attacked	% attacked
Carpodetus serratus	0.4	0	0	0	310	5.6	0	0
Coprosma rigida	0	0	0	0	0.6	0	0	0
Coprosma 'taylorii'	59	13	11	16	14	0.6	3	21
Coprosma tenuifolia	10	0.4	3	24	0	0	0	0
Coprosma species	24	2	11	44	19	0.6	4	19
Cordyline indivisa	0	0	0	0	2	0	0	0
Dacrydium cuppressinum	0	0	0	0	1	0	0	0
Griselinia littoralis	230	0	15	7	6	0	0	0
Melicytus lanceolatus	4	0	0	0	0	0	0	0
Myrsine divaricata	0.4	0	0	0	0	0	0	0
Phyllocladus aspleniifolius	61	1	5	8	0	0	0	0
Pittosporum tenuifolium	0	0	0	0	2	0	0	0
Pseudopanax colensoi	0	0	0	0	2	0	0	0
Pseudopanax crassifolius	35	13	3	6	2227	898	29	1
Pseudowintera colorata	4	0	0	0	9	0	0	0
Rubus schmidelioides	1	0	0	0	0	0	0	0
TOTAL	429	29	48		2593	905	36	

2.3.2.2 Predation

The level of seed predation was very species specific, with species of *Coprosma* being the most affected (Table 2.1). *Coprosma tenuifolia* and other *Coprosma* species in the *propinqua x robusta* group had especially high levels of predation by unidentified larvae at Mangatepopo (24 and 44% respectively). In fact, *Coprosma tenuifolia* was observed to have much higher levels of predation than displayed in Table 2.1 in fruit harvested from mature trees for germination pilot trials (personal observation). There was also some predation of *Griselinia littoralis* seeds by the larvae of a moth (thought to be a species of *Heterocrossa,* Carposonidae). Lancewood (*Pseudopanax crassifolius*) and *Phyllocladus aspleniifolius* var. *alpinus* were the only other species to show damage from unidentified larvae.

2.3.2.3 Wind dispersed species

Densities of wind dispersed seed from native species were generally much higher than bird dispersed seed (Tables 2.1, 2.2). The most abundant wind dispersed species was clearly manuka (*Leptospermum scoparium*), although this species had a very high proportion of unfilled seeds (Table 2.2). Interestingly, manuka was much more commonly caught at Mangatepopo than at Raetihi hill. In fact, all other wind dispersed species except *Clematis* seeds were caught in higher densities at Mangatepopo than at Raetihi hill. There was no insect predation of any wind dispersed seeds, and empty or unfilled seeds were only observed for manuka. Surprisingly, only 11 broom (*Cytisus scoparius*) seeds were caught per m^2 at Mangatepopo. This is probably because the main period of seed dispersal for this species occurred after sampling had ceased.

Table 2.2 Seed densities of wind dispersed species (per m^2) caught over 9 months of seed trapping at Mangatepopo and Raetihi hill. NB: Filled = whole seed, unfilled = empty or immature seeds. Percentage of seed filled was calculated from raw data (counts) not from data in the table (converted to per m^2). * denotes naturalised exotic species.

Site	Mangatepopo			Raetihi hill		
Species	filled	unfilled	% filled	filled	unfilled	% filled
Calluna vulgaris *	11	0	100	0	0	0
Clematis species	0	0	0	11	0	100
Cortaderia toetoe	747	0	100	88	0	100
Cytisus scoparius *	11	0	100	0	0	0
Hebe stricta	2828	0	100	1569	0	100
Leptospermum scoparium	5603	25318	22	0	6	0
TOTAL	9200	25318		1668	6	

2.3.2.4 Cleaned seeds vs those in fruit

By far the highest densities of seeds from fleshy fruited species were caught in seed traps situated under a canopy of native forest at Raetihi hill (Table 2.3). The total density at this site reached almost 7000 seeds per m^2 over 9 months. Lancewood seeds (*Pseudopanax crassifolius*) contained within fruits made up a large proportion of the seeds caught at this site. This was due to one seed trap that was situated under an adult female lancewood (plot E1) at Raetihi hill.

All of the seeds from fleshy fruited species caught by seed traps in both broom and grassy habitats had been cleaned by passage through a disperser. Lancewood (*Pseudopanax crassifolius*), *Carpodetus serratus*, and *Coprosma* 'taylorii' were the only species caught in seed traps in the open grassy habitat. Lancewood also had the highest

seed densities of all fleshy fruited species caught in the broom habitat, in fact more were caught in this habitat than under a forest canopy at the same site (Table 2.3). There were also reasonable densities of *C.* 'taylorii' seeds deposited under a canopy of broom, while other species present had lower densities (Table 2.3).

Table 2.3 Densities of viable seeds cleaned by passage through a disperser (C) and seeds still contained within fruit (F) of bird-dispersed species in four different habitats. All seeds were caught over 9 months of seed trapping at Mangatepopo and Raetihi hill. NB: ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill. Data were pooled within each habitat and converted to per m^2. Percentage of cleaned seeds is calculated from the raw data (counts) not from the data in the table (converted to per m^2). *Coprosma* seeds other than *C.* 'taylorii', *C. tenuifolia* and *C. rigida* were difficult to tell apart and were thus grouped under '*Coprosma* species'. This group includes various *C. robusta* x *propinqua* hybrids, and *C. foetidissima*.

Site	Mangatepopo						Raetihi hill					
Habitat	ForestA			Broom			ForestB			Grass		
Species	C	F	%C	C	F	%C	C	F	%C	C	F	%C
Carpodetus serratus	1	0	100	0	0	-	629	0	100	4	0	100
Coprosma rigida	0	0	-	0	0	-	1	0	100	0	0	-
Coprosma 'taylorii'	133	3	98	9	0	100	29	0	100	1	0	100
Coprosma tenuifolia	9	10	31	2	0	100	0	0	-	0	0	-
Coprosma species	42	7	87	2	0	100	26	13	68	0	0	-
Cordyline indivisa	0	0	-	0	0	-	4	0	100	0	0	-
Dacrydium cuppressinum	0	0	-	0	0	-	3	0	100	0	0	-
Griselinia littoralis	152	307	33	2	0	100	11	1	90	0	0	-
Melicytus lanceolatus	7	0	-	0	0	-	0	0	-	0	0	-
Myrsine divaricata	0	0	-	1	0	100	0	0	-	0	0	-
Phyllocladus aspleniifolius	51	63	45	0	0	-	0	0	-	0	0	-
Pittosporum tenuifolium	2	0	100	0	0	-	4	0	100	0	0	-
Pseudopanax colensoi	0	0	-	0	0	-	4	0	100	0	0	-
Pseudopanax crassifolius	30	0	100	67	0	100	306	5933	5	10	0	100
Pseudowintera colorata	7	0	100	0	0	-	11	6	64	0	0	-
Rubus schmidelioides	2	0	100	0	0	-	0	0	-	0	0	-
TOTAL	436	390		83	0		1028	5953		15	0	

Considerably more seeds dispersed by birds (cleaned) were caught in forest habitats compared to non-forest habitats (Table 2.3). The total number of cleaned seeds caught under a canopy of broom was $83/m^2$, and $15/m^2$ in the open grassy habitat, compared to $436/m^2$ and $1028/m^2$ under a canopy of forest at Mangatepopo and Raetihi hill respectively. When seeds within fruits are added to these forest figures, seed density of native species is doubled at Mangatepopo and is almost 7 times the density of cleaned seeds at Raetihi hill.

2.3.3 SEED SHADOWS – PATTERNS IN SPACE

In order to investigate seed shadows, a discrete seed source must be identified. Because the grassy habitat at Raetihi hill also contains patches of native vegetation (Photo 1.2), the seed rain may originate from a variety of sources in addition to the main forest patch. Hence, only the seed shadows at the broom sites (Mangatepopo) will be analysed. The influence of distance from the seed source on the density of seed rain was estimated by regressing the total number of seeds caught (after $\log_{10}$ transformation) with distance from the forest edge (Fig. 2.5). The result was a statistically significant negative relationship.
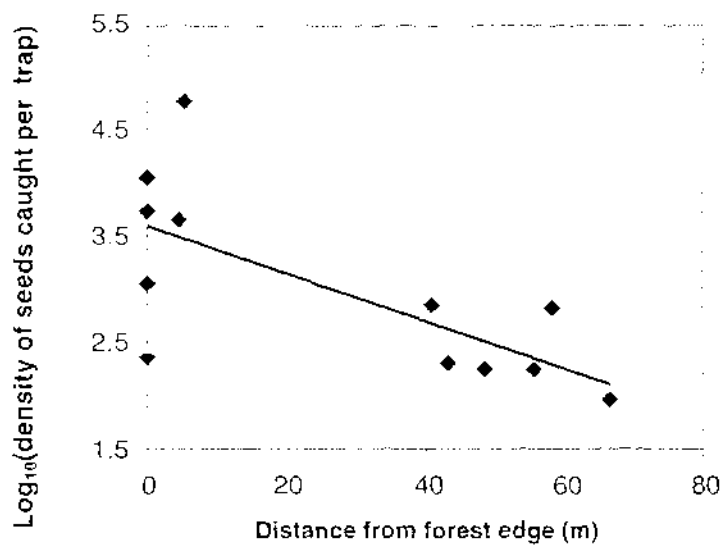
Fig. 2.5 Density of all seeds caught per seed trap over 9 months with distance from the forest edge. $(y=0.02x + 3.6, N=12, R^2=0.49, P=0.02)$.

Similar patterns were observed for most of the commonly dispersed species in that they exhibited much lower seed densities further away from the forest edge. However, lancewood (*Pseudopanax crassifolius*) had higher numbers of viable seeds caught in the broom habitat 40 metres from the forest edge than under the forest canopy in transect B (Fig. 2.6a).

Seed densities for other species had to be log transformed as they exhibited very high densities in seed traps under forest compared to seed traps further away from this seed source. Of the species graphed, manuka (*Leptospermum scoparium*) had the highest number of seeds dispersed into the broom habitat. Seeds of lancewood (*P. crassifolius*) were the next most abundant, then those of *Coprosma* 'taylorii', and *Griselinia littoralis* (Fig. 2.6b,c,d). Generally, seed traps in transect B caught more seeds under a canopy of broom than in any other transect.

a) *Pseudopanax crassifolius*

b) *Leptospermum scoparium*

c) *Coprosma* 'taylorii'

d) *Griselinia littoralis*
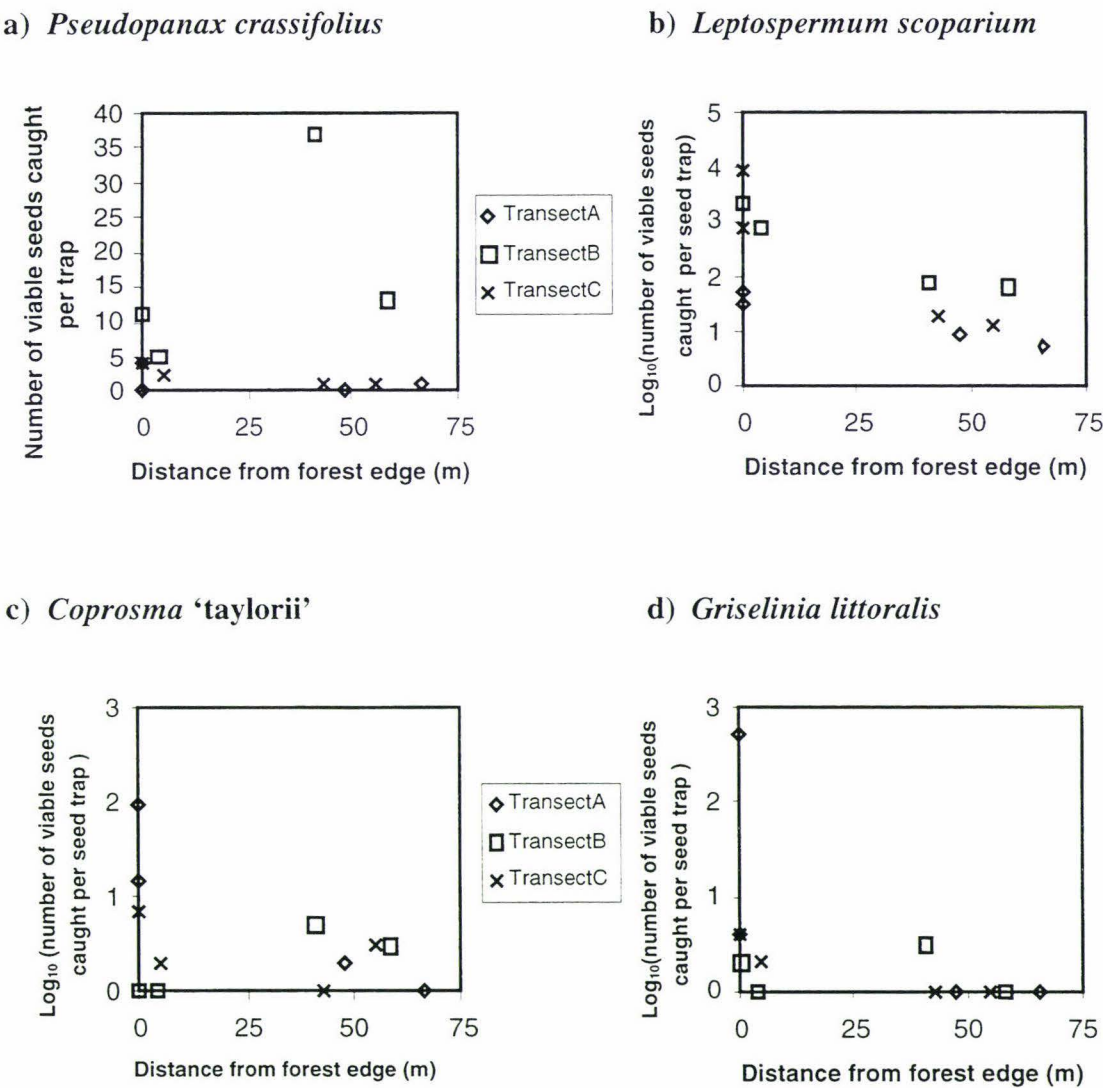
Fig. 2.6 Seed shadows for a) lancewood (*Pseudopanax crassifolius*), b) manuka (*Leptospermum scoparium*), c) *Coprosma* 'taylorii', and d) *Griselinia littoralis*. Number of viable seeds caught per seed trap over 9 months of seed trapping at Mangatepopo, against distance from the forest edge (seed source).

2.3.4 FAECAL SAMPLES

Vertebrate faecal samples containing seeds were collected as encountered from both sites. A total of 34 faecal samples were collected containing seeds of six species. The most common species found in bird droppings was lancewood (*Pseudopanax crassifolius*).

Table 2.4 Contents of discrete bird droppings collected opportunistically from different habitats. NB: Br = broom habitat, G = grass habitat, and F = forest habitat. Those with the same symbol are from the same faecal sac. Plots along transects A, B, and C are located at Mangatepopo, plots along transects D and E are situated at Raetihi hill. For more detailed descriptions of plots see Appendix 1, and Chapter 1.

Species	Number of viable seeds	Unfilled or attacked seeds	Date of collection	Place of collection	Possible disperser
Coprosma 'taylorii'	22	2	23 Mar '99	Plot B4 (Br)	Possum
Pseudopanax crassifolius	6	0	12 Aug '99	Plot E3 (G)	Bellbird/tui?
Pseudopanax crassifolius	4	0	12 Aug '99	Plot E3 (G)	Bellbird/tui?
Pseudopanax crassifolius	7	1	12 Aug '99	Plot E3 (G)	Bellbird/tui?
Griselinia littoralis[°]	3[°]	0[°]	12 Aug '99	Plot D2 (G)	Kereru
Pseudopanax crassifolius[°]	14[°]	4[°]	12 Aug '99	Plot D2 (G)	
Griselinia littoralis[α]	2[α]	0[α]	12 Aug '99	Plot D2 (G)	Kereru
Pseudopanax crassifolius[α]	18[α]	3[α]	12 Aug '99	Plot D2 (G)	
Pseudopanax crassifolius	10	0	13 Aug '99	Plot D2 (G)	Bellbird/tui?
Griselinia littoralis	6	0	13 Aug '99	Plot A8 (F)	Bellbird/tui?
Pseudopanax crassifolius	10	0	13 Aug '99	Plot A7 (F)	Bellbird/tui?
Coprosma robustaxpropinqua	25	22	13 Aug '99	Plot A7 (F)	Possum
Coprosma robustaxpropinqua	8	0	13 Aug '99	Plot A7 (F)	Bellbird/tui?
Pseudopanax crassifolius	9	0	13 Aug '99	Plot A2 (Br)	Bellbird/tui?
Pseudopanax crassifolius	5	0	13 Aug '99	Plot B2 (F)	Bellbird/tui?
Pseudopanax crassifolius[β]	12[β]	2[β]	13 Aug '99	Plot B2 (F)	Kereru
Griselinia littoralis[β]	2[β]	0[β]	13 Aug '99	Plot B2 (F)	
Pseudopanax crassifolius	7	1	13 Aug '99	Plot B4 (Br)	Bellbird/tui?
Pseudopanax crassifolius	6	0	13 Aug '99	Plot B4 (Br)	Bellbird/tui?
Griselinia littoralis	7	0	13 Aug '99	Plot C1 (F)	Kereru
Griselinia littoralis	6	0	13 Aug '99	Plot C1 (F)	Kereru
Carpodetus serratus[*]	64[*]	0[*]	9 Sep '99	Plot D7 (F)	Kereru
Pseudopanax crassifolius[*]	18[*]	4[*]	9 Sep '99	Plot D7 (F)	
Pseudopanax crassifolius	7	0	9 Sep '99	Plot E1 (F)	Bellbird/tui?
Pseudopanax crassifolius	18	4	9 Sep '99	Plot E3 (F)	Kereru
Pseudopanax crassifolius	10	0	9 Sep '99	Plot D3 (F)	Bellbird/tui?
Pseudopanax crassifolius	14	1	9 Sep '99	Plot D3 (F)	Bellbird/tui?
Pseudopanax crassifolius	20	2	9 Sep '99	Plot D7 (F)	Kereru
Pseudopanax crassifolius	8	0	10 Sep '99	Plot B2 (F)	Bellbird/tui?
Pseudopanax crassifolius	12	2	10 Sep '99	Plot B2 (F)	Bellbird/tui?
Pseudopanax crassifolius	6	0	10 Sep '99	Plot B4 (Br)	Bellbird/tui?
Pseudopanax crassifolius	5	0	10 Sep '99	Plot B4 (Br)	Bellbird/tui?
Pseudopanax crassifolius	10	1	10 Sep '99	Plot B5 (Br)	Bellbird/tui?
Pseudopanax crassifolius	12	2	10 Sep '99	Plot C1 (F)	Bellbird/tui?
Pseudopanax crassifolius	11	3	10 Sep '99	Plot C1 (F)	Bellbird/tui?
Coprosma tenuifolia	22	18	17 Sep '99	Plot C2 (F)	Possum
Carpodetus serratus	116	0	6 Oct '99	on track at Raetihi hill (G)	Kereru
Pseudopanax crassifolius	11	2	7 Oct '99	Plot C6 (Br)	Bellbird/tui?

There were also large numbers of small *Carpodetus serratus* seeds found on two occasions in the large faecal sacs of the native wood pigeon (kereru or *Hemiphaga novaeseelandiae*).

The size of the droppings suggests that most are derived from native bellbirds or tuis (*Prosthemadera novaeseelandiae* and *Anthornis melanura* respectively). It is also possible that these droppings could have originated from introduced species of a similar size such as blackbirds, although no individuals of this species were seen at either site during the course of this study.

The kereru was the only species that dispersed more than one plant species at a time. The average number of seeds per faecal sac for this disperser (excluding the very small seeds of *Carpodetus serratus*) was 17. In comparison, medium sized droppings of tui or bellbird contained only nine seeds on average. Unfortunately, it was not possible to distinguish between these two dispersers as their faecal sacs were of very similar sizes.

Coprosma seeds were found in droppings of the introduced possum (*Trichosurus vulpecula*) on several occasions. However, most of them had been partly digested and were not viable, due to longer gut retention times of this introduced marsupial. An exception was one sample in which some *Coprosma* 'taylorii' seeds were found to be viable and capable of germinating.

The majority of faecal samples were collected from under a canopy of native forest (Table 2.4). More droppings were found at Mangatepopo than at Raetihi hill. These faecal samples contained a greater variety of species than those collected in weedy habitats. However, eight samples were also found in both broom and grassy habitats.

2.4 DISCUSSION

Seed dispersal is the last step in the reproductive cycle of plants, but also the starting point in the process of population renewal and recruitment (Herrera *et al.* 1994). It is thus an important step in studying succession. Obviously, seed has to first arrive at a site before it can germinate. If native seed is not represented in the seed rain or seed bank in weedy areas it can be assumed that these areas will continue to be dominated by naturalised exotic species.

2.4.1 Species richness

More species were caught in seed traps under a canopy of native forest than in weedy habitats. There was also a relationship between the number of species caught and maximum vegetation height. A similar result was found by McDonnell & Stiles (1983) who reported greater species diversity of seed rain in American old fields with taller vegetation. Although more bird dispersed species were caught overall, the proportion of wind dispersed species caught in non-forest habitats was higher than under a canopy of forest. This was probably due to a combination of less bird dispersal in weedy areas, and exotic species such as broom (*Cytisus scoparius*) and heather (*Calluna vulgaris*) being present in the seed rain in weedy areas but not under a canopy of forest. Note that although broom has no specific adaptations for wind dispersal, it can be blown further than it would normally disperse under gravity alone (Smith & Harlen 1991), and is thus included in this category.

2.4.2 Seed availability

Generally, wind dispersed species had higher seed densities than bird dispersed species, both within the forest and in non-forest habitats. This could be because many of the wind dispersed species caught have small seeds, and species with small seeds often have a high seed production (Stöcklin & Bäumler 1996, Clark *et al.* 1998). Another possible reason is that the abundance of mature wind dispersed species is greater than the abundance of fleshy fruited species in the study area. This may be the case at the Mangatepopo sites, but not at Raetihi hill where wind dispersed species were less common. As a dispersal mechanism, wind is also more ubiquitous than bird vectors, which appear to deposit seeds in clumps and non-randomly within different habitats (Glenn-Lewin *et al.* 1992). Manuka (*Leptospermum scoparium*) had by far the highest

seed densities, despite the fact that many of the seeds dispersed were empty and thus inviable. Manuka has a high seed production (Porteous 1993) and also has seed available for dispersal year round (Mohan *et al.* 1984) which could explain its dominance in the seed trap samples.

Seed density also increased with maximum vegetation height. Other authors have found a similar sort of relationship (Glyphis *et al.* 1981, Gleadow & Ashton 1981, Debussche & Isenmann 1994, Robinson & Handel 2000). This observation could be partly due to higher seed production and dispersal in forests compared with shorter shrub and grassland vegetation. For fleshy fruited species, it may be possible that birds are more attracted to taller vegetation. Herrera *et al.* (1994) found that the abundance of fruit crops was related to plant height. Birds are often attracted to trees with more abundant displays of fruit (Glenn-Lewin *et al.* 1992). In fact, Sallabanks (1992) found that dispersal success was most strongly correlated with fruit abundance on hawthorn bushes.

2.4.3 Dispersal in weedy areas

Introduced broom (*Cytisus scoparius*) does not offer any attractive rewards to bird dispersers other than use as a potential perching site. Not surprisingly, seed deposition in this habitat was lower than under a taller canopy of native forest. A notable exception was lancewood (*Pseudopanax crassifolius*) seed, which was locally abundant in particular seed traps situated under good perching sites in the broom habitat. The higher densities of lancewood seeds caught under a canopy of broom compared to other fleshy fruited species may be partly due to the abundant fruiting of this species in the year in which the seed traps were run. Or it could be due to the greater palatability of this species over other fleshy fruits.

Many more seeds were caught in seed traps under a canopy of broom, than in the open grassy habitat at Raetihi hill. A similar result was reported by McDonnell & Stiles (1983) who found significantly more seeds in a 13 year old field that had structurally complex vegetation, than in a 3 year old field with a single layer of vegetation. They also found more seeds in 2 year old field which had artificial structures (simulating saplings) placed in it, than in an adjacent control field of the same age (McDonnell & Stiles 1983). In addition, Kollmann (1995) found that seed rain density was highest

beneath mature scrub and lowest in grassland, thus the spatial pattern of seed dispersal may be dependent on the successional stage.

Unfortunately the degree to which birds use weedy habitats such as broom in New Zealand is not well known. Williams (1983) described broom plants as providing roosting points for birds that are vectors of elder in Canterbury. He also suggested that birds might prefer to perch in the open crowns of broom compared to other introduced woody species such as gorse, which is a lot pricklier! During this study, very few birds other than the native fernbirds (*Bowdleria punctata*), tomtits (*Petroica macrocephala*), and silvereyes (*Zosterops lateralis*) were observed in broom habitats. Although the first two species are primarily insectivorous (Heather & Robertson 1996), silvereyes have been reported to feed on a wide range of indigenous and exotic fruits in other parts of the country (Burrows 1994a, O'Donnell & Dilks 1994, Williams & Karl 1996). In this study, flocks of silvereyes were seen feeding on the small fruits of *Coprosma* 'taylorii'. Of all the bird dispersed species caught in the broom habitat, *C.* 'taylorii' had the second highest seed densities. Thus, this species appears to be one of the better dispersed native woody plants in the broom habitat. Although the number of animal dispersed seeds may be higher under perches or in more complex vegetation, recruitment may still be limited by other barriers such as seed predation and a lack of suitable microsites. Such a result was found by Holl (1998) in abandoned pastures in Costa Rica.

Although bird droppings were found in the open without any overhead perching sites on several occasions, the voiding of seeds by birds as they fly across open spaces is probably a relatively rare event. Several authors agree that birds generally defecate seeds from a perched position thus dispersing seeds primarily when not in flight (Charles-Dominique 1986, Burrows 1994, Medellín & Gaona 1999). In addition, Izhaki *et al.* (1991) and DaSilva *et al.* (1996) found that scrub clearings were largely avoided by birds overseas. If these observations are also true for birds in New Zealand, perching sites may be a limiting factor for the dispersal of native fleshy fruited species in early successional vegetation such as the exotic grassland at Raetihi hill.

2.4.4 Seed shadows – patterns in space

Seed density often depends on distance to the maternal plant (Debussche & Isenmann 1994). Generally, seed rain decreased with increasing distance from the forest margin in this study. Other authors have found that the majority of bird dispersed seeds are deposited within 100 m of the maternal plant (Hoppes 1988, McDonnell & Stiles 1983, Myster 1993, Robinson & Handel 1993, Debussche & Isenmann 1994, Robinson & Handel 2000). As the seed traps in this study were placed no more than 60 m away from the forest edge it was not possible to determine if any seed dispersal occurred at greater distances. However, seed densities were many times lower only 10 to 20 metres away from the seed source for most species. Wenny (2000) reported a similar pattern (80% of seeds were dispersed within 25 m of parent trees and under high canopy cover) in Costa Rica. In contrast, Harvey (2000) found no relationship between seed deposition and distance from the forest. However, this could be because the vegetation pattern at his study sites was similar to that at Raetihi hill where patches of native trees occur within a matrix of exotic species and seed rain may originate from a variety of sources in addition to the main forest patch.

Even within the same habitat, seed rain in individual traps was very variable. It is clear from the literature that great variability of seed fall, often on small spatial scales, is common (Burrows 1994b, Herrera *et al.* 1994). In fact this is a product of non-random influences on seed deposition. Factors that may influence the seed rain that reaches a given place on the forest floor include; whether it is located beneath fruiting plants or sites that are attractive to birds as perching places, differing palatability of fleshy fruited species, foraging behaviour and digestive rates of bird dispersers. Wind velocity and direction will also affect the spatial and temporal pattern of wind dispersed species (Burrows 1994b).

2.4.5 Disperser limitation

Not surprisingly, considerably more seed was caught under fruiting female trees than under non-fruiting trees. Because the proportion of seeds within fruit compared to those cleaned by birds was much higher underneath fruiting parent trees, the most common fate of fruits was to simply fall to the ground. It is possible that low numbers of frugivorous birds in the study areas may be limiting seed dispersal of native woody species. Although disperser abundances were not quantified in this study, very few frugivorous

birds were seen or heard at Mangatepopo. Native frugivorous birds such as bellbird, kereru, tui and silvereye appeared to be more common at Raetihi hill. However, more bird droppings containing seeds were found at Mangatepopo. The reason for this inconsistency is not apparent. Bird dispersers may be more conspicuous but less common at Raetihi hill, or droppings may have been easier to find at Mangatepopo and may not necessarily reflect disperser abundances.

The decline of native birds since the arrival of humans in this country has reduced the number of potential dispersers. Kate McNutt (1998) found evidence that smaller bird populations were limiting seed dispersal on the mainland compared with offshore islands with no introduced predators. She found that more fruit was dispersed and at a faster rate on islands with abundant bird populations (McNutt 1998) than on the mainland where disperser populations have been depleted. Similarly, Sandra Anderson (1997) reported lower fruit take of several native species at a modified mainland site near Auckland than on a nearby offshore island.

2.4.6 Seed predation

Moth larvae were the main predators of seed caught in seed traps. However, only six species appear to have been affected by attack from invertebrates. The worst affected were species of the genus *Coprosma*. Apart from these species, pre-dispersal predation of seeds was negligible and probably would not have a lasting effect on plant populations. Surprisingly, levels of larval attack were observed to be much higher in fruits harvested from mature *Coprosma tenuifolia* plants than bird dispersed seed caught in seed traps for this species (personal observation). The seed trap results may have underestimated the amount of predation if birds preferentially feed on non-attacked fruits. Other authors have reported similar results (Traveset *et al.* 1995, Garcia *et al.* 1999)

Many of the seeds found in possum (*Trichosurus vulpecula*) droppings in seed traps and on the ground were damaged by passage through the gut of this introduced marsupial. Possums are known to disperse viable seeds in their native Australia (Bass 1990) however, not much work has been done on their potential role as dispersers in New Zealand. Although Cowan (1990) found that possums ate fleshy fruits from most species available in the Orongorongo valley near Wellington, they did not always eat the seeds.

Of the seeds that were ingested, pigeonwood (*Hedycarya arborea*), kawakawa (*Macropiper excelsum*), ducksfoot (*Pennantia corymbosa*) and native passionfruit (*Passiflora tetranda*) were mostly broken by passage through the digestive system of possums. Similarly, Mason (1958) recorded destruction of pigeonwood and tutu (*Coriaria arborea*) seeds after egestion by possums. Despite this, some ducksfoot seeds were capable of germinating (Cowan 1990). Burrows (1994b) found apparently undamaged seeds of *Fuchsia* in possum droppings, but seeds of lancewood and *Coprosma lineariifolia* were crushed. In this study, some *Coprosma* 'taylorii' seeds were capable of germinating after passage through the gut of a possum. Indeed the increased dispersal of this species in weedy areas could be partly due to deposition by possums, although only one dropping containing *C.* 'taylorii' seeds was found! Generally, it seems that possums may be regarded as seed predators for most species.

2.4.7 Succession and nucleation processes

Pioneer woody plants that act as perching sites for bird dispersers may initiate 'nucleation' processes in plant succession (Yarranton & Morrison 1974, McDonnell & Stiles 1983, Robinson & Handel 2000). In other words, isolated trees can serve as a centre for invasion, establishment, and subsequent growth of bird dispersed species in weedy areas. Patches or clumps of vegetation may arise and slowly expand until they eventually join together. This appears to be the case at Raetihi hill. Yarranton & Morrison (1974) have discussed the effect these patches have on the spatial dynamics of succession in their nucleation theory. Although Williams (1983) suggested that broom might act as a perching place and nurse species in the Port hills near Christchurch, Partridge (1992) found no evidence of broom facilitating successful dispersal and establishment of woody species in the same area. In fact, Partridge reported no other woody species entering the succession in eight years of monitoring broom-dominated vegetation. However, he did not directly measure seed rain so it is possible that native species were being dispersed into this area but did not establish.

2.4.8 Limitations

Seed traps allow one to document where seeds go but not their origin (Levey & Sargent 2000). The assumption that seeds arriving in seed traps were from the nearest available seed source may not have always been correct. However, in this study, the emphasis was on quantifying the current seed rain in weedy areas regardless of seed origin. Some

authors have reported increased dispersal at forest edges compared with the forest interior (Hoppes 1988, Herrera *et al.* 1994, Restrepo *et al.* 1999). If this finding can be applied generally, seed densities caught under a canopy of forest in this study may overestimate seed dispersal, as seed traps were situated in plots on the margin of the forest not the interior.

2.4.9 Conclusions

Generally, more seeds were caught under a canopy of native forest than in weedy areas. Some native woody species were dispersed into weedy areas although densities of most species declined rapidly with increasing distance from the forest margin in broom habitats. Much less seed was dispersed into open grassland, probably because of a lack of perches. Overall, seeds of wind dispersed species, especially manuka (*Leptospermum scoparium*), had the highest densities. However, there were more species dispersed by birds than by wind, even though bird-dispersed seeds were less abundant. Lancewood (*Pseudopanax crassifolius*) had the highest seed densities of all the fleshy fruited species caught. Pre-dispersal predation of most species was minimal and is unlikely to affect plant populations.

On a final note, one must remember that only part of the colonisation process has been completed once seeds reach a site. After being dispersed, they must still germinate and survive and these stages will be dealt with in Chapters 3 and 4 respectively.

Chapter 3

EFFECTS OF BIRD CONSUMPTION ON SEED GERMINATION

"Hence the seed, if unable to generate, would be in vain, since it is always aimed at generation and produced by nature to achieve it." Theophrastus, 4th Century B.C.

3.1 INTRODUCTION

The consumption of fleshy fruits by vertebrate dispersers is a well-known mutualism in which the disperser obtains a meal and the plant gets an opportunity to disperse its seeds (Howe & Smallwood 1982). A key question is whether seeds germinate better after passage through the digestive system of a disperser. There are few examples of plants whose seeds apparently fail to germinate without treatment by a vertebrate gut (Noble 1975, Temple 1977, Howe & Vande Kerckhove 1979). Debate continues over one of these examples, concerning the extinct dodo and the massive seeds of the tambalacoque tree (Temple 1977, Owadally 1979, Wyse Jackson *et al.* 1988, Witmer & Cheke 1991). However, the requirement of fruit pulp removal for successful germination of seeds of rain forest trees has been noted (Howe & Vande Kerckhove 1981, Ng 1983, Jackson *et al.* 1988, Wenny 2000). Similarly, there have been reports of strong effects of gut treatment on both final germination percentage and the rate of germination (Rick & Bowman 1961, Noble & Whalley 1978, Applegate *et al.* 1979, Izhaki & Safriel 1990, Murray *et al.* 1994, Traveset & Willson 1997, Traveset 1998, Wenny 2000).

A confounding factor in most of the literature is a tendency to lump both increases in the proportion of seeds that eventually germinate and the rate of germination together as 'germination enhancement'. It is important to distinguish between these two components of germination performance, as they have quite different ecological consequences (Traveset 1998). Increases in the number of seeds that germinate is generally a good thing, whereas faster germination rates over the short time scales of most experiments is less clearly 'enhancement'. Faster germination rates of seeds could in fact be detrimental if they germinate in unfavourable conditions. In fact, many species have an inbuilt dormancy or delaying mechanism that prevents them germinating under conditions which are unsuitable for establishment (Fenner 1985). On the other hand, early germination has been shown to be advantageous for a few species (Ross & Harper 1972, Cook 1980, Garwood 1983). Loiselle (1990) suggested that more rapid germination might promote competitive superiority among different plant species contained in bird droppings.

In a recent review of nearly 200 plant species, Anna Traveset (1998) found that frugivores (fruit-eating animals) significantly influenced the germination patterns of nearly half the species they consume. Of these affected species, final germination percentage was increased by ingestion about twice as often as it was reduced. Germination rate was also accelerated by ingestion much more commonly than it was delayed. However, the diversity of animal species tested so far is still rather low (42 bird species, 28 non-flying mammals, 10 bats, 12 reptiles, 2 fishes). Interestingly, germination percentage was increased more frequently in temperate zones compared to tropical regions. This result supports the hypothesis that enhanced germination may be more advantageous in unpredictable or less constant environments (Traveset 1998). In both tropical and temperate zones, tree seeds appear to be more affected by ingestion than shrub or herb seeds. This may reflect a thicker seed coat, or a higher frequency of seed-coat dormancy in tree species (Traveset 1998).

Unfortunately, the majority of studies used only manually cleaned seeds as controls instead of seeds contained within fruits as they would fall from the parent plant. Thus, most studies tested the possible abrasive (scarifying) effect that ingestion by vertebrates has on seed coats rather than the effect frugivores have in separating the fruit pulp from the seeds. Because of this, the importance of consumption of seeds by frugivores on germination is probably underestimated in most studies reported in Traveset's review.

In New Zealand, the effect of fruit pulp removal appears to have a large effect on final germination percentage of the majority of species tested so far. Over the past decade, Colin Burrows has conducted germination experiments on over 50 species from a range of native trees, shrubs, and vines in New Zealand (Burrows 1994-1999). His treatments include seeds left within intact fruit and seeds cleaned by hand to simulate passage through the digestive system of a disperser. Nearly all of the species exhibited increased germination percentages when fruit was removed. In addition, germination rates were almost always slower for seed within fruits compared with those cleaned by hand, or by passage through birds. However, only twelve of a total of 51 native fleshy fruited species directly tested the effect of frugivores

on seed germination. Most studies only simulated passage through a disperser by removing seed from fruit by hand. Hence, there is a lack of data on seed germination patterns following passage through vertebrate dispersers in New Zealand. Thus, the main aim of my experiments is to test if passage through the digestive tracts of frugivorous birds affects germination of seeds of five native woody species, and if so, how they are affected.

3.2 METHODS

3.2.1 Species and treatments

Ripe fruits from *Griselinia littoralis,* lancewood *(Pseudopanax crassifolius), Pittosporum tenuifolium* var. *colensoi,* and *Carpodetus serratus* were collected from adult trees at the Raetihi hill site (see section 1.2 for location) on 12 August 1999. Fruits and bird-voided seeds of *Coprosma robusta* were also collected, as this species was already present in aviaries at Mount Bruce National Wildlife Centre and Kowhai Park in Feilding. All species were subjected to three treatments;

1) fruit fed to captive native birds; kereru *(Hemiphaga novaeseelandiae),* tui *(Prosthemadera novaeseelandiae),* and hihi *(Notiomystis cincta),* and defecated seeds collected.

2) fruit flesh manually removed and seeds extracted by hand.

3) seeds left within intact fruits.

Fruits were offered to two individuals of each bird species at Mount Bruce National Wildlife Centre (hihi) and Kowhai Park, Fielding (kereru and tui). The birds were kept under continuous observation and the time between fruit consumption and defecation recorded. Thus, it was possible to calculate mean minimum seed passage times for each individual bird. Defecated seeds were collected and moist stratified at 4°C for five weeks (Metcalf 1995, Porteous 1993). Seeds were manually extracted from fruits by hand on the same day that bird-defecated seeds were collected and kept under the same conditions.

3.2.2 Experimental conditions

Before the germination experiments began, all seeds and fruits were soaked in tap water for 12 hours then sorted. Any small, empty or damaged seeds were discarded at this stage. This

was not possible for the in-fruit treatment, but these types of seeds were removed from the totals at the end of the experiment. Each replicate of bird-voided, hand-cleaned seeds and intact fruit were placed onto two sheets of moistened seed germination blotter (0.7 mm thick) in tupperware containers to minimise moisture loss. The containers were placed in two environments: a fully lit (no dark cycle) constant temperature room kept at 20°C, and an unheated glasshouse subject to natural photoperiods (see Appendix 3, Fig 3.1 for temperatures in the glasshouse). These facilities were located in the Seed Technology building at Massey University, Palmerston North.

In these experiments, germination was defined as the first sign of radicle emergence (when radicles had visibly protruded at least 1 mm beyond the testa). Seeds were checked every 2-3 days for signs of germination and individual seeds were removed upon germination to reduce their effect on remaining, ungerminated seeds. When no more germination occurred for over three months, the final germination percentage for each treatment and species was calculated. The viability of remaining seeds was tested by gently squeezing seeds between tweezers, those that collapsed were assumed to be dead (Baskin & Baskin 1998). For treatments in which 50% or more seeds germinated, the rate of germination, ie: 'time to 50% radicle emergence' (T_{50}) was calculated according to the formula given by Coolbear et al (1984) as follows:

$$T_{50} = t_i + \frac{\frac{(N+1)}{2} - n_i}{n_j - n_i} \times (t_j - t_i)$$

N = final number of seeds that germinate
t_i = days from start of experiment until immediately prior to 50% radicle emergence
t_j = days from start of experiment until immediately subsequent to 50% radicle emergence
n_i = number of seeds germinated at time t_i
n_j = number of seeds germinated at time t_j
Where $n_i < (N+1)/2$; and n_i and n_j are adjacent counts.

3.2.3 Statistical analyses

Average seed passage times were compared between different species and individuals of birds using analysis of variance and Tukey's Studentized Range Test (SAS Institute 1996). At the end of the experiment the total number of seeds that had germinated and the number that remained ungerminated were compared between treatments. Since these data were binary, they were analysed by a generalised linear model with a binomial error distribution. Each plant species was analysed separately. The effect of different treatments on percentage germination was ascertained from the 'parameter estimates' in output produced by the model (SAS Institute 1996). Separate ANOVAs for each species compared a measure of germination rate (time to 50% germination) between treatments. Mean rates for each treatment were compared using Tukey's Studentized Range Test.

Photo 3.1 Woody capsules of *Pittosporum tenuifolium* var. *colensoi* that open to reveal black seeds covered with a sticky mucilage attractive to birds. NB: white square = 1 cm^2.

3.3 RESULTS

3.3.1 SEED PASSAGE RATES

Of the three species of bird used, the smallest species, the stitchbird or hihi (*Notiomystis cincta*), had the shortest passage times (Table 3.1). Average seed passage times of the medium sized tui (*Prosthemadera novaeseelandiae*) were just over half an hour. In comparison, the largest species, the native wood pigeon or kereru (*Hemiphaga novaeseelandiae*) had the longest seed passage times. In fact, on several occasions, Kereru #1 was apparently constipated and seeds took over five hours to pass through its digestive system, hence the large standard deviation for this individual (Table 3.1). Bird species had a highly significant effect on seed passage times (DF = 2, P = 0.0001). Kereru passage times were significantly different from both tui and hihi, however the difference between the latter two species was not significant (Tukey's Studentized Range Test). The effect of individual birds was only significant for kereru (DF = 3, P = 0.0001).

Table 3.1 Average minimum seed passage times through the digestive systems of different bird species and individuals.

	Hihi #1	Hihi #2	Tui #1	Tui #2	Kereru #1	Kereru #2
Average minimum seed passage time (minutes)	15	12	33	35	192	45
Standard deviation	4.2	2.9	5.2	7.6	116.3	10.3

3.3.2 FINAL GERMINATION PERCENTAGES

For all species, final germination percentages were generally much higher for bird-voided and hand-cleaned seeds than for in-fruit treatments (Table 3.2, Fig. 3.1). In fact, very few seeds germinated inside fruit. In some cases, significantly more bird-voided seed germinated than hand-cleaned seed (Table 3.2). This was especially noticeable for *Pittosporum tenuifolium* var. *colensoi* in which no hand-cleaned seed germinated at all (Fig. 3.1). Despite the fact that mean passage time differed between bird species, the final germination percentage of bird-voided seeds was not affected by bird species.

Table 3.2 The effect of fruit, fruit removal (hand-cleaned), and passage through birds, on final germination percentage for four native species. NB: *Coprosma robusta* fruits collected from two different provenances (Feilding in the Manawatu, and Mount Bruce in the Wairarapa) behaved differently and hence were analysed separately. Values in the same row and sharing a common letter are not significantly different (*P*>0.05) from each other (parameter estimates from generalised linear models), - = not applicable.

| Species | In-fruit | Mean final germination percentage | | | |
		Hand-cleaned	Kereru	Tui	Hihi
Coprosma robusta (Feilding)	3[a]	74[b]	93[c]	94[c]	-
Coprosma robusta (Mount Bruce)	4[a]	96[b]	-	-	96[b]
Griselinia littoralis	2[a]	97[b]	100[c]	-	100[c]
Pittosporum tenuifolium	0[a]	0[a]	68[b]	-	52[b]
Pseudopanax crassifolius	3[a]	100[b]	100[b]	-	-

The effect of different treatments on the final number of germinated seeds was highly significant for all species examined (Table 3.3). Treatment also explained the largest amount of total deviance in the models for all species (Appendix 3.1). Only two species showed a significant difference between place of germination (Table 3.3). Both lancewood (*Pseudopanax crassifolius*) and *Pittosporum tenuifolium* var. *colensoi* had very few seeds germinate in the unheated glasshouse compared to the constant temperature room.

One species, *Carpodetus serratus*, did not germinate sufficiently for analysis. Although a few seeds of this species germinated in October 1999, the main flush of germination did not start until June 2000 and so could not be presented here. However, it is interesting to note that the only seeds that had germinated at the time of writing were bird-voided seeds in the unheated glasshouse.

The effect of different individuals of the same bird species on final germination percentage was not significant for any plant species. In some instances, only one individual bird was willing to consume certain fruits, hence the effect of different individual birds could not be tested for all species.

Table 3.3 Results of general linear models (with binomial error distribution) on final germination percentages for four native species. NB: *Coprosma robusta* fruits collected from two different provenances (Feilding in the Manawatu, and Mount Bruce in the Wairarapa) behaved differently and hence were analysed separately. Place = unheated glasshouse or constant temperature room kept at 20°C, both at Massey University, Palmerston North. Treatment = bird-voided, hand-cleaned or in-fruit. **= 0.01>P>0.001, ***= P<0.001, NS = not significant, - = not applicable.

Species	Place	Treatment	Place x treatment	Individual bird
Coprosma robusta (Feilding)	NS	***	**	NS
Coprosma robusta (Mt Bruce)	NS	***	NS	NS
Griselinia littoralis	NS	***	NS	-
Pittosporum tenuifolium	***	***	NS	-
Pseudopanax crassifolius	***	***	NS	NS

3.3.3 GERMINATION RATES

Of the cases in which more than 50% of seeds germinated, there were significant effects of treatment on germination rate for three species (Table 3.5). In most cases, the rate of germination was faster in bird-voided seeds compared with hand-cleaned seeds (Table 3.4). Generally, seeds voided by smaller bird species germinated faster than larger species. For instance, seeds voided by tui germinated slightly quicker than seeds voided by kereru. Although this difference was statistically significant, the time to 50% germination only differed by a few days (Table 3.4). Germination rate was exceptionally fast in *Coprosma robusta* seeds collected from Mount Bruce compared with all other species, including the a different provenance of the same species collected from Feilding (Fig. 3.1b,c).

Coprosma robusta seeds collected from Feilding germinated faster at a constant temperature of 20°C than in the unheated glasshouse (Fig. 3.1b). Again, the effect of individual birds was not significant except for *Coprosma robusta* seeds collected from Feilding. In this case, seeds that were eaten by the kereru with the extra long passage time (Table 3.1) did not germinate as quickly as seeds eaten by the other kereru.

Table 3.4 The effect of cleaning by hand and passage through three different bird species on the rate of germination (T_{50} = time to 50% germination in days) for four native species. NB: *Coprosma robusta* fruits collected from two different provenances (Feilding in the Manawatu, and Mount Bruce in the Wairarapa) behaved differently and hence were analysed separately. Values in the same row and sharing a common letter are not significantly different ($P>0.05$) from each other (Tukey's Studentized Range Test). - = not applicable, * = did not germinate.

Species	Time to 50% germination (days)			
	Hand-cleaned	Kereru	Tui	Hihi
Coprosma robusta (Feilding)	12.4[a]	7.9[b]	4.4[c]	-
Coprosma robusta (Mount Bruce)	2.9[a]	-	-	2.4[a]
Griselinia littoralis	12.9[a]	7.8[b]	-	8.6[b]
Pittosporum tenuifolium	*	20.8[a]	-	17.8[a]
Pseudopanax crassifolius	11.5[a]	8.1[b]	-	-

Table 3.5 Results of ANOVAs on germination rate (time to 50% germination) for four native species. NB: *Coprosma robusta* fruits collected from two different provenances (Fielding in the Manawatu, and Mount Bruce in the Wairarapa) behaved differently and hence were analysed separately. Place = unheated glasshouse or constant temperature room kept at 20°C. Treatment = bird-voided, hand-cleaned or in-fruit.
**= 0.01>P>0.001, *** = P<0.001, NS = not significant, - = not applicable.

Species	Place	Treatment	Place x treatment	Individual bird
Coprosma robusta (Feilding)	***	NS	**	*
Coprosma robusta (Mt Bruce)	NS	**	NS	NS
Griselinia littoralis	NS	**	-	-
Pittosporum tenuifolium	-	NS	-	-
Pseudopanax crassifolius	-	***	-	-

a) *Griselinia littoralis*

(i) 20°C constant temperature room
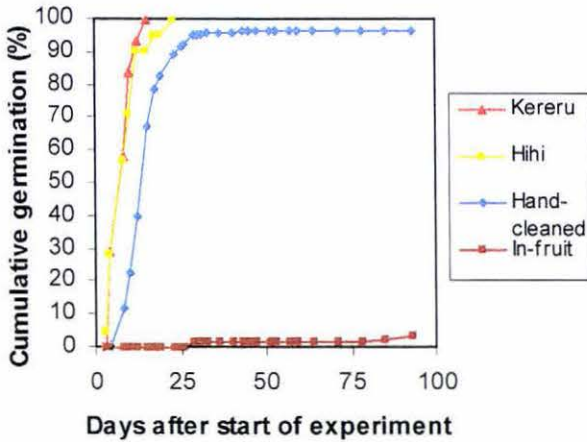
(ii) unheated glasshouse
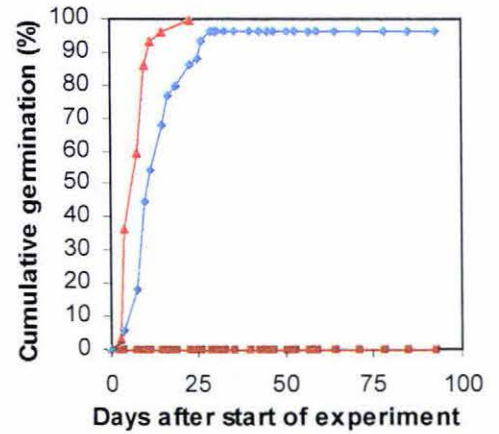
b) *Coprosma robusta* (Fielding)

(i) 20°C constant temperature room
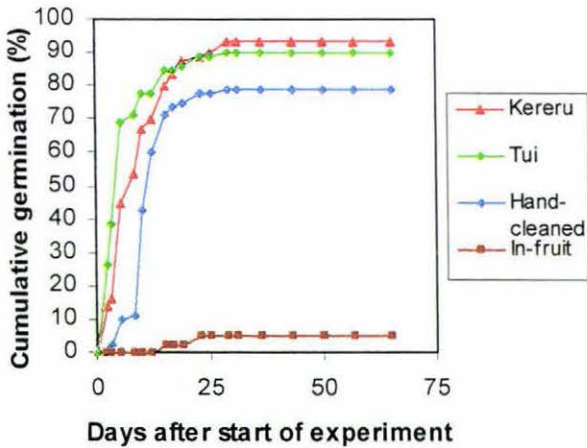
(ii) unheated glasshouse
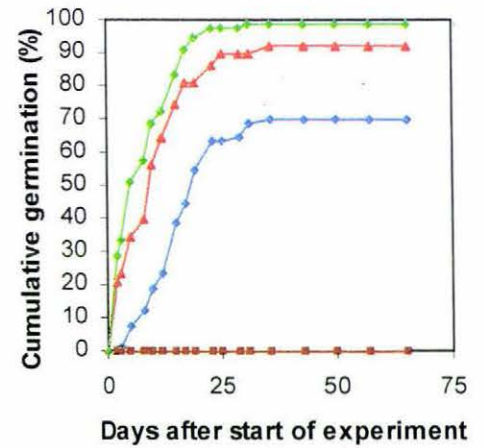
Fig. 3.1 Germination curves for native seeds subjected to different treatments.
NB: Kereru = seeds defecated by native wood pigeons (*Hemiphaga novaeseelandiae*), Tui =
seeds defecated by tui (*Prosthemadera novaeseelandiae*), Hihi = seeds defecated by stitchbird
or hihi (*Notiomystis cincta*), Hand-cleaned = seeds removed from fruit by hand, In-fruit =
seeds left within whole fruit. N = 80 for each line except for *Griselinia littoralis* seeds
consumed by birds (N= 30 for kereru, N = 21 for hihi). Values were averaged when more
than one bird of the same species consumed fruits, as there were no significant differences
between them.

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c) *Coprosma robusta* (Mount Bruce)
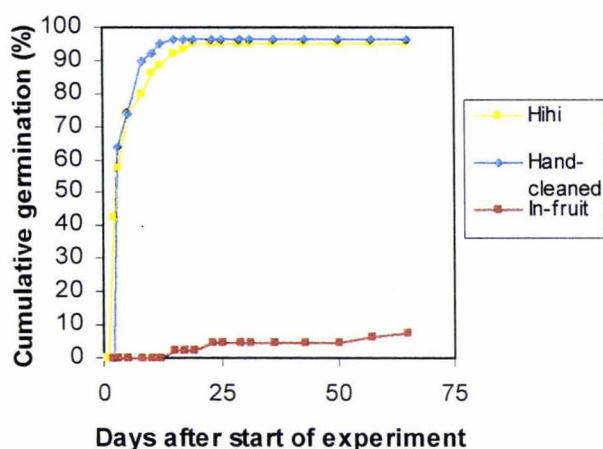
(i) 20°C constant temperature room   (ii) unheated glasshouse
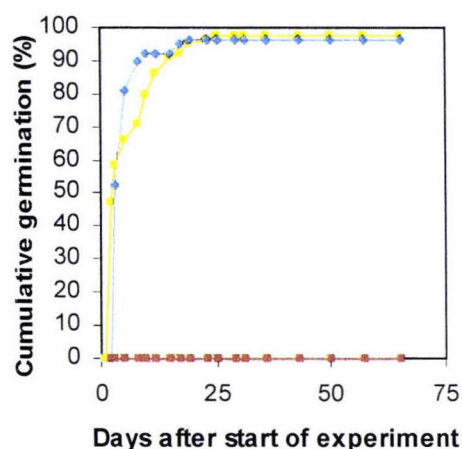
d) *Pittosporum tenuifolium* var. *colensoi*

(20°C constant temperature room)
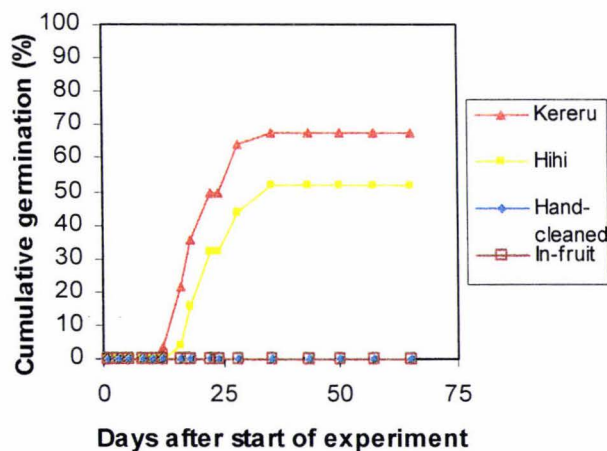
e) *Pseudopanax crassifolius*

(20°C room)
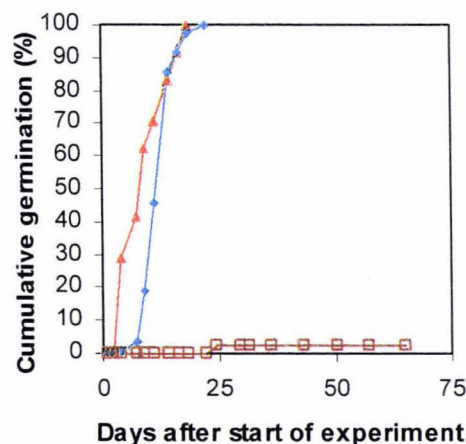
Fig. 3.1   cont.   Germination curves for three more native species subjected to different treatments.   NB: Kereru = seeds defecated by native wood pigeons (*Hemiphaga novaeseelandiae*), Tui = seeds defecated by tui (*Prosthemadera novaeseelandiae*), Hihi = seeds defecated by stitchbird or hihi (*Notiomystis cincta*), Hand-cleaned = seeds removed from fruit by hand, In-fruit = seeds left within whole fruit. N = 80 for each line, except for seeds of *Pittosporum tenuifolium* consumed by birds (N = 30 for kereru, N = 25 for hihi) and *Pseudopanax crassifolius* (N = 25 for kereru). Values were averaged when more than one bird of the same species consumed fruits, as there were no significant differences between them.

3.4 DISCUSSION

3.4.1 Germination percentages

All of the species examined had much higher germination percentages in bird-voided and hand-cleaned seeds (most over 90%) compared with those contained within fruits. In fact very few seeds germinated in the in-fruit treatment. For example, *Coprosma robusta* exhibited the highest final germination percentage within fruit of only 4%! A similar result for this species was found by Roger James (unpublished data presented in Bannister & Jameson 1991). However, he also reported 20% less germination in bird-voided compared with hand-cleaned seeds, which is opposite to my findings. In contrast, Burrows (1995b) reported a much higher germination percentage within *C. robusta* fruit (from Canterbury) of 72%. The reason for this inconsistency is not clear, as my experimental conditions were very similar to those used by Burrows. The only difference was that he used petri dishes while I used tupperware containers, and the temperatures in the glasshouses (both unheated) were slightly different. The difference in germination percentage within fruit between our two studies might be partly explained by the different provenances from which the seeds were collected, as I found that *C. robusta* seed collected from Feilding behaved differently to seeds collected from Mount Bruce National Wildlife centre in the Wairarapa.

Overall however, results from my experiments are in agreement with the majority of other New Zealand studies, in that much higher germination percentages were achieved when seeds were removed from fruit (Bannister & Bridgman 1991, Bannister & Jameson 1991, Bannister *et al.* 1996, Ladley & Kelly 1996, Burrows 1991-1999, see table 3.6 overleaf for a summary). Both *Griselinia littoralis* and lancewood (*Pseudopanax crassifolius*) had close to 100% germination in both bird-voided and hand-cleaned seeds, but very low germination within fruit. Although Bannister and Bridgeman (1991) reported a similar result for this species, Burrows (1996c) again reported higher germination percentages within fruit (20%).

Table 3.6 Summary of seed germination experiments for native species including this study (values in bold). DFG=days to first germination: DFLG=days from first germination to last germination (timespread of germination). Fruit = seeds contained within fruit. Bird = bird-voided seeds. Hand = seeds cleaned by hand. * time taken for the average seed to germinate (refer Bannister & Bridgman 1991). ** fruit broken open but still in contact with the seeds. Unless stated otherwise all publications by Colin Burrows (unpublished data by Roger James presented in Bannister & Jameson 1991, Clout & Tilley 1992, Ladley & Kelly 1996, Anderson 1997).

Species	Number of seeds per treatment Fruit	Bird	Hand	Mean germination % TREATMENT Fruit	Bird	Hand	Germination rate DFG/DFLG Fruit	Bird	Hand	Year of publication
Alectryon excelsus	50		100	8		48	19/44		2/42	1996d
Alepis flavida	95	223	199	0	26	17	-	-	-	L&K 1996
Alseuosmia macrophylla	-		100	-		99	-		115/201	1999b
Alseuosmia pusilla	-		50	-		98	-		113/167	1999b
Aristotelia serrata	50		100	10		96	69/		17/69	1995b
Ascarina lucida	25		100	48		91	165/		41/175	1996f
Beilschmiedia tawa	10		80	0		96.5	-		40/14	1999a
Carpodetus serratus	50		100	0		99	-		68/83	1996c
Carpodetus serratus	**240**	**360**	**240**	**0**	**26**	**0**	-	**16/**	-	**this study**
Coprosma foetidissima	25		50	4		98	146/		105/55	1996e
Coprosma grandifolia	25		100	4		91	59/162		23/44	1996f
Coprosma lucida	50		100	0		95	-		99/65	1996c
Coprosma rhamnoides	-	50	50	-	2	0	-	-	-	Anderson 1997
Coprosma robusta	50		100	72		90	62/108		17/68	1995b
Coprosma robusta	?	?	?	0	80	100	-	-	-	B&J 1991
Coprosma robusta (F)	**160**	**320**	**160**	**3**	**94**	**74**	**15/50**	**2/29**	**3/29**	**this study**
Coprosma robusta (Mt B)	**160**	**320**	**160**	**4**	**96**	**96**	**15/50**	**2/17**	**3/17**	**this study**
Coprosma robusta/lucida?	-	40	40	-	37	38	-	-	-	Anderson 1997
Cordyline australis	50		100	0		96	-		26/73	1995b
Cordyline banksii	25		100	0		100	-		26/149	1999b
Corynocarpus laevigatus	25		50	0		94	-		2/148	1996d
Dysoxylum spectabile	25		100	0		100	-		12/13	1999a
Dysoxylum spectabile	-	50	50	-	100	98	-	-	-	Anderson 1997
Freycinetia baueriana	50		100	0		92	-		101/21	1996e
Fuchsia excorticata	50		100	54		100	26/62		12/31	1995a
Geniostoma rupestre	50		100	0		99	-		57/63	1999b
Geniostoma rupestre	-	50	50	-	98	100	-	-	-	Anderson 1997
Griselinia littoralis	50		100	2		92	29/70		9/25	1995a
Griselinia littoralis	**160**	**50**	**160**	**2**	**100**	**97**	**29/64**	**3/20**	**8/35**	**this study**
Griselinia lucida	25		100	0		100	-		8/24	1999a
Hedycarya arborea	50		100	2		100	81/97		33/90	1995d
Ileostylus micranthus	40	142	146	0	53	46	-	-	-	L&K 1996
Macropiper excelsum	50		100	0		100	-		20/13	1995a
Melicytus lanceolatus	25		100	20		100	119/76		68/86	1996f
Melicytus ramiflorus	50		100	24		99	29/57		11/18	1995a
Melicytus ramiflorus	?	?	?	0	56	60	-	-	-	B&J 1991
Muehlenbeckia australis	50		100	88		97	54/148		35/166	1996a
Muehlenbeckia ?	-	50	50	-	50	60	-	-	-	Anderson 1997

Species	Number of seeds per treatment			Mean germination % TREATMENT			Germination rate DFG/DFLG			Year of publication
	Fruit	Bird	Hand	Fruit	Bird	Hand	Fruit	Bird	Hand	
Myoporum laetum	?	?	?	4	16	35	-	-	-	B&J 1991
Myoporum laetum	50		100	0		90	-		!55/648	1996b
Myrsine australis	25		100	16		100	-		112/290	1996e
Myrsine divaricata	50		100	24		92	76/		55/1551	1996b
Myrtus bullata	25		100	0		97	-		56/63	1999b
Myrtus obcordata	50		100	12		100	113/		34/64	1995b
Pennantia corymbosa	50		100	36		100	140/71		122/67	1995d
Peraxilla colensoi	21	169	157	0	41	83	-	-	-	L&K 1996
Peraxilla tetrapetala	80		152	0		96	-		-	L&K 1996
Pittosporum tenuifolium	50		100	0		80	-		83/81	1996c
Pittosporum ten. var. col.	**160**	**53**	**160**	**0**	**60**	**0**	**-**	**12/23**	**-**	**this study**
Pittosporum eugenioides	50		100	0		95	-		58/221	1996c
Prumnopitys ferruginea	67	80	-	33	45	-	840/120	840/120	-	C&T 1992
Pseudopanax arboreus	50		100	0		100	-		46/67	1996c
Pseudopanax arboreus	80	80**	80	19	26**	28	97*	86*	86*	B&B 1991
Pseudopanax arboreus?	-	50	50	-	10	23	-	-	-	Anderson 1997
Pseudopanax crassifolius	50		100	20		100	38/81		27/14	1996c
Pseudopanax crassifolius	80	80**	80	6	6**	49	105*	66*	39*	B&B 1991
Pseudopanax crassifolius	**240**	**50**	**240**	**3**	**100**	**100**	**24/41**	**4/14**	**4/18**	**this study**
Pseudopanax ferox	80	80**	80	6	6**	19	95*	60*	66*	B&B 1991
Pseudowintera colorata	50		100	0		98	-		139/360	1995d
Ripogonum scandens	50		100	0		98	-		18/137	1996a
Rhopalostylis sapida	50		100	2		95	345/35		303/65	1995d
Rubus cissoides	50		100	38		82	112/226		57/607	1996a
Schefflera digitata	50		100	60		98	73/?		41/65	1995b
Solanum aviculare	50		50	0		82	-		18/125	1999b
Solanum laciniatum	25		100	12		98	228/?		62/125	1996f
Streblus heterophyllus	50		100	0		100	-		14/189	1995d
Tetrapathaea tetranda	50		100	-		98	-		30/61	1996a
Tupeia antarctica	120	133	120	0	50	83	-	-	-	L&K 1996

In my experiments, although over half of the bird-voided seeds of *Pittosporum tenuifolium* var. *colensoi* germinated, no hand-cleaned seeds germinated at all. This result is unusual because Burrows (1996c) reported 80% germination of the closely related *Pittosporum tenuifolium* seeds cleaned by hand in similar conditions (Table 3.6). Seeds of this species were very difficult to clean, as they are contained within a capsule surrounded by a sticky mucilage that defies removal! However, natural removal of this mucilage by passage through birds is usually quite effective. Despite hand-cleaning efforts (including a sand treatment described by Porteous 1993), some residues may have remained on the seeds possibly preventing their germination. In fact, Burrows (1999c) found that leachate from capsules of *Pittosporum* species inhibited seed germination of several species. However, some seeds of *P. tenuifolia* var. *colensoi* subjected to the same hand-cleaning process, did germinate in the

field during my planting experiments (see chapter 4). Perhaps any residues remaining on seeds were leached away in this more natural environment, allowing germination to occur. Another explanation for this apparent anomaly is that seeds sown in field conditions (Chapter 4) were stratified for longer than seeds in the germination experiments (this chapter). Moore *et al.* (1994) found that more seeds of *Pittosporum tenuifolium* germinated after eight weeks or more of low temperatures, compared with shorter periods.

Because conditions were not completely sterile. colonies of fungi and bacteria sometimes became established on seeds or fruits. Colonies were especially common on capsules of *Pittosporum tenuifolium* var. *colensoi* in which they appeared to be feeding on the mucilagenic substance produced by this species. Seeds that were covered with fungi often collapsed when pinched gently with forceps and were presumed to he dead (Baskin & Baskin 1998). As time went on, more and more seeds became infected with fungal colonies. By the end of the experiments, most seeds thus affected were dead. However, most naturally occurring fungi are not seed pathogens (Baskin & Baskin 1998). In fact, fungi do a very thorough job of testing for dead seeds in that they generally only infect dead or damaged seeds (Baskin & Baskin 1998). It is likely that some of the seeds became too old, lost viability, and then succumbed to microbial attack. Other possible causes of seed death are discussed below.

Alternating temperatures are usually more favourable for germination than constant ones (Baskin & Baskin 1998). However. in this study, seeds germinated better in the constant temperature room at 20°C. In fact, *Pittosporum tenuifolium* var. *colensoi* and lancewood (*Pseudopanax crassifolius*) failed to germinate in the unheated glasshouse. High temperatures during the day (Fig 3.1 in Appendix 3) may have caused these seeds to die. All ungerminated seeds in the glasshouse were dead on inspection at the end of the experiment and were presumed to have died some time during the experiment as they became soft after a few months. In comparison, ungerminated seeds in the constant temperature room were still hard and did not collapse when squeezed with tweezers at the end of the experiment.

3.4.2 Germination inhibitors

There are several reasons why seeds contained within fleshy fruits are unlikely to germinate. They may be physically constrained from germinating if the radicle cannot penetrate through the intact fruit, or chemically constrained if the fruit juice has an osmotic potential too negative to allow germination to occur (Salisbury & Ross 1985). Other causes of germination inhibition include the exclusion of oxygen by seed coats or pericarps, or the presence of particular compounds such as coumarin, ferulic acid and the growth inhibitor abscissic acid (Burrows 1999c). In some cases, there is evidence that the fruit flesh may contain inhibitors. For example, Bannister and Bridgman (1991) found that when the fruits of *Pseudopanax crassifolius* and *Pseudopanax ferox* were broken open but still in contact with the seeds, final germination percentages were considerably lower than those that were completely removed from fruit. Germination of seeds in contact with fruit flesh was also delayed, especially in *P. crassifolius*. Inhibition by fruit flesh has also been reported for taraire (*Beilschmiedia taraire*) (Myers 1984). However, in mahoe (*Melicytus ramiflorus*), the seed itself is thought to be the source of inhibition as no unleached seeds germinated while germination in leached seeds averaged 72% (Partridge & Wilson 1990). These same authors also found that leachate from mahoe seeds prevented seed germination of *Fuchsia excorticata, Kunzea ericoides,* and two introduced plants *Bromus unioloides* and *Spergula arvensis*. However, in a similar bioassay experiment by Burrows (1999c), leachate from mahoe, *Coprosma robusta,* and pigeonwood (*Hedycarya arborea*) seeds had negligible effects on the germination of lettuce seeds, compared with the effects of leachate from the pericarps of these species, which significantly inhibited germination. Ingestion by vertebrate dispersers is likely to remove inhibitors present in fruit flesh, although inhibitors in the seed itself are probably leached out in natural environments by precipitation or by the enzymal activity of fungi, bacteria and other microorganisms (Bryant 1985, Burrows 1999c).

3.4.3 Germination rates

Generally, germination rate was less affected by different treatments than final germination percentage. However, this could have been due to an inability to statistically test those treatments that did not reach 50% germination. Of the species that did show significant

effects, germination rate was generally faster in bird-voided seeds than hand-cleaned seeds. Unfortunately, none of the in-fruit treatments had enough seeds germinate for statistical analysis. Other authors have found that seeds within fruits generally take a lot longer to germinate (Table 3.6). For example, Burrows' experiments on *Coprosma robusta* (1995b) demonstrate that all hand-cleaned seeds had finished germinating before seeds within fruit had even started!

Apart from *Carpodetus serratus*, which started germinating seven months after the start of the experiment (data not presented), *Pittosporum tenuifolium* var. *colensoi* had the slowest rate of germination. Burrows (1996c) reported embryo immaturity of some *Pittosporum* species which may contribute to the delayed germination of *P. tenuifolium* var. *colensoi*. In contrast, Burrows (1996c) reported faster germination rates for *Carpodetus serratus* than observed in this study. This may have been due to different starting dates of our experiments (June – Burrows, and October – current study). Therefore, seeds of *C. serratus* in Burrows experiments would have been subject to greater periods of cold treatment over winter (as they were contained in an unheated glasshouse). Although I stratified my seeds for a period of five weeks at 4°C, this may not have been enough to stimulate germination of this species. Interestingly, no *C. serratus* seeds germinated in the constant temperature room, which lends weight to the theory that seeds in the glasshouse could not germinate until the following autumn after they were subjected to cooler temperatures. As the seeds in the constant temperature room were also kept in continual light, another possibility is that this species has a short day requirement in order to overcome dormancy.

Sandra Anderson (1997) compared seed germination of karamu (either *Coprosma robusta* or *Coprosma lucida*, scientific names not specified), *Coprosma rhamnoides*, a species of *Muehlenbeckia* (not specified), fivefinger (*Pseudopanax arboreus*), kohekohe (*Dysoxylum spectabile*) and hangehange (*Geniostoma rupestre* var. *ligustrifolium*) after consumption by different bird species. However, she had no control of intact fruit, instead using seeds cleaned from fruit by hand. As anticipated, her data indicated little difference between the bird-voided and hand-cleaned treatments for all plant species except kohekohe for which seed germination was more rapid and more synchronised in bird-voided than hand-cleaned seeds.

An interesting result was obtained for *Coprosma robusta*, where seed voided by native tui (*Prosthemadera novaeseelandiae*), bellbird (*Anthornis melanura*) and saddleback (*Philesturnus carunculatus*) germinated more quickly than hand-cleaned seed or blackbird-voided seed (Anderson 1997). Unfortunately, it is not known whether this difference is significant as no statistical analyses were performed on the data. However, the apparent difference in germination response for karamu observed by Anderson may have been a result of shorter passage time in the exotic blackbird compared with the native birds used.

3.4.4 Seed retention times

In this study, retention times differed between bird species, and this sometimes affected both germination percentage and rate. Generally, seeds eaten by the kereru (*Hemiphaga novaeseelandiae*) showed slightly higher germination percentages than smaller species (tui and hihi). Seed voided by kereru also had slightly slower germination rates (measured as time to 50% germination), although this difference was only significant for *Coprosma robusta* collected from Feilding. However, this difference was only a matter of a few days, and the ecological significance of these slightly faster germination rates is not known. In a recent review, Traveset (1998) reported that for most plant species, an effect on germination is associated positively or negatively with the time that seeds remain in the digestive tract of dispersers. In general, seeds which stay longer in a dispersers' digestive system become more abraded. This presumably increases permeability of the seed coat, thus increasing germination percentage or rate (Izhaki & Safriel 1990, Barnea *et al.* 1990 Barnea *et al.* 1991). On the other hand, while investigating a natural fruit laxative in *Witheringia solanacea*, Murray *et al.* (1994) discovered that seeds voided rapidly were far more likely to germinate than those remaining longer in the gut of their disperser the black-faced solitaire bird (*Myadestes melanops*). In contrast to both of these results, Traveset and Willson (1997) found no differences in germination of six plant species between bear and bird treated seeds in southeast Alaska. They conclude that seed retention time in the gut (which is much greater in bears than birds) does not affect germination in this case. Obviously, gut passage time has different effects on seeds of different species.

A long retention time in a vertebrate gut (and thus a prolonged exposure to digestive fluids) may damage the seed embryo, especially in seeds with soft seed coats (Murphy *et al.* 1993, Traveset 1998). Thus, vertebrates that have longer food retention times may act as seed predators by causing mortality of seeds that cannot withstand long periods of acid treatment. Although there was no evidence of seed mortality occurring from bird consumption in my germination experiments (this chapter), I have observed that seeds of the genus *Coprosma* are often destroyed when egested by possums (Chapter 2). Although some authors have reported undamaged seeds of small seeded species (Bass 1990, Cowan 1990, Burrows 1994b), generally possums may be regarded as seed predators. On a larger scale, Dinerstein and Wemmer (1988) found significant seed mortality in the alimentary canal of the *Rhinoceros* for *Trewia nudiflora* (26.7 and 47.7% in two trials), although they point out that these animals are still important in removing fruit pulp from these seeds and dispersing them.

3.4.5 Other effects of frugivore consumption

Besides the discussed effects of dispersers on germination performance, there are also a number of other ways in which frugivores can influence establishment success. These include the site or 'microsite' where seeds are defecated. For example, a frugivore may enhance seed germination in the lab but this may be irrelevant if the animal is inefficient as a disperser and voids most seeds at high densities in places that are unsuitable for seedling establishment (Traveset 1998). Furthermore, the time in a season when fruit is consumed and dispersed can be crucial for germination and seedling establishment. Seed predation, for instance, can be either smaller (Schupp 1988) or greater (Traveset 1998) for early dispersed seeds than for those dispersed later in the season. Frugivores may select for particular traits within a species, for example some researchers have found that birds consumed significantly less insect-infested fruits than uninfested ones (Traveset *et al.* 1995, Garcia *et al.* 1999). Another way in which dispersers can affect seedling establishment is by influencing the number of seeds per dropping as well as the seed composition of those droppings. Loiselle (1990) found that the survival of certain shrubs depended on which other species it was associated with in droppings. Certain species combinations are more common than others, as frugivores do not choose fruits randomly (Traveset 1998). Lastly, different species of frugivores with different

diets can affect the plant nutrient content of the frugivore's faeces, which may in turn be important for seedling establishment and growth (Traveset 1998).

3.4.6 Limitations

My study joins the majority of experiments performed thus far in that it was carried out in relatively artificial conditions, and may not represent what happens in the field. There is a real lack of field experiments designed to test any potential differences between germination of bird or hand cleaned seed and seed inside intact fruit on the forest floor. Although there is a reasonable amount of international literature on seed planting/seedling emergence experiments, most authors used either cleaned seed or intact fruit but not both. It is possible that seeds within fruit may show better germination in more natural situations, especially if the fleshy tissues surrounding seeds are partially broken down by soil invertebrates and microorganisms. For example, some authors found a significant effect of ingestion by mammals on germination in the laboratory but not in the field, where germination varied depending on habitats (Bustamante *et al.* 1992, Figueiredo & Perin 1995). They attributed this to factors such as variation in temperature, chemical characteristics of the soil, and soil-borne pathogens that kill the embryos in different habitats.

3.4.7 Conclusions

Bird dispersers have an important effect of increasing germination percentages in native species by removing fruits from seeds. In some instances, bird-voided seeds showed greater final germination percentages than seeds cleaned by hand. This is probably due to abrasion of the seed coat by the birds' digestive fluids. Overall, germination rate was less affected by different treatments. Of the species that did show a significant difference between treatments, germination rate was generally faster in bird-voided than in hand-cleaned seeds. Thus, the importance of native birds for fleshy-fruited native plants should not be underestimated. Not only do they generally increase both final germination percentage and germination rate of seeds, but they also act as dispersal agents for many fleshy-fruited species.

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Chapter 4

EXPERIMENTS ON FACTORS AFFECTING SEEDLING ESTABLISHMENT AND SURVIVAL OF WOODY SPECIES IN WEEDY AREAS

"....rather than concentrating on a search for the ways in which organisms are perfectly suited to their environments, we might more healthily concentrate on the nature of the limitations that constrain where they live." Harper (1982).

4.1 INTRODUCTION

When studying plant dynamics and succession, it is important to determine potential limiting factors affecting recruitment (Crawley 1990). Recruitment is dependent on both seed availability and microsite availability (Eriksson & Ehrlén 1992). Seed and microsite availability in turn may be determined by factors such as dispersal, seed predation and disturbance frequency (Eriksson and Ehrlén 1992).

In his seminal review, Crawley (1990) noted: "It is curious that the simple experiment of sowing extra seeds and recording the number of recruits has been carried out so seldom". In the last decade however, there have been numerous published examples of such experiments (Kelly 1989, Peart 1989b, Silvertown & Tremlett 1989, De Steven 1991, Barrett & Silander 1992, Eriksson & Ehrlén 1992, Primack & Miao 1992, Thompson & Baster 1992, Ribbens *et al.* 1994, Crawley & Long 1995, Eriksson & Froborg 1995, Robinson *et al.* 1995, Ackerman *et al.* 1996, Burke & Grime 1996, Ehrlén & Eriksson 1996, O'Connor 1996, Tilman 1997, Holl 1999, Weltzin & McPherson 1999). These studies and more are reviewed in Turnbull *et al.* (2000).

Seed sowing experiments can be very useful in unravelling the extent of seed limitation in natural systems. Experimental manipulations within such seed sowing experiments are also useful for teasing out factors important for seedling establishment and survival. A plant population is said to be seed limited when it experiences an increase in population size following the addition of seed. A very recent review by Turnbull *et al.* (2000) distinguishes between seed augmentation and seed introduction experiments where the former involves adding seed to existing populations, and the latter occurs where seeds are sown in sites from which the species is known to be absent. Turnbull *et al.* (2000) found that approximately 50% of seed augmentation studies showed evidence of seed limitation. They also found that seed limitation was more common in early successional species and habitats.

The availability of native seed in the weedy habitats studied in this project has already been discussed in Chapter 2. Seed rain of native species was found to decline with distance from the forest edge. Thus, it is possible that invasion of native species into

weedy areas is limited by a lack of seed. Other possibilities include microsite limitation, a combination of both seed and microsite limitation, or no limitation.

As already mentioned, if recruitment is seed limited then sowing seeds should increase seedling density. If recruitment is limited exclusively by the availability of microsites, seedling density should be affected only by experimental treatments such as disturbance (under the assumption that suitable microsites become available under these treatments). If seed addition and disturbance both have a positive effect on seedling recruitment, then populations may be affected by a combination of seed and microsite limitation (Eriksson & Ehrlén 1992).

Although Crawley (1990) suggested that microsite limitation is generally predominant in plant populations, many authors have since found that a combination of both seed and microsite limitation is more common (Louda et al. 1990, Eriksson & Ehrlén 1992, Van Der Meijden et al. 1992, Scherff et al. 1994, Crawley & Brown 1995, Ehrlén & Eriksson 1996, Eriksson & Froborg 1996, Gray & Spies 1996, Hilton & Boyd 1996, Nepstad et al. 1996, O'Connor 1996, Holl 1998, Edwards & Crawley 1999ab, Holl 1999, Kiviniemi & Eriksson 1999, Weltzin & McPherson 1999, Robinson & Handel 2000). Others have reported only seed limitation (Hawthorn & Cavers 1976, Greig-Smith & Sagar 1981, Louda 1982, Fowler 1986, Shaw & Antonovics 1986, Hughes et al. 1988, Peart 1989a, Ackerman et al. 1996) or only microsite limitation (Gross 1980, Gross & Werner 1982, Louda 1983, Crawley & Nachapong 1985, Reader 1991a,b, Jordan & Hartman 1995, Reader et al. 1995, Rydgren et al. 1998).

In fact, multiple mechanisms often interact in complex ways to influence emergence and survival rates of seedlings (De Stevens 1991a), and teasing these mechanisms apart is one of the many challenges of ecological research! The main aims of this chapter are to test whether recruitment of native woody species in weedy areas is seed limited and/or microsite limited.

4.2 METHODS

4.2.1 Seed sowing experiments

Seed was manually extracted from ripe fruits collected in February/March 1999 from female *Griselinia littoralis, Coprosma* 'taylorii' (Photo 4.1), and *Pittosporum tenuifolium* var. *colensoi* (Photo 3.1) trees at both sites and stored at 4°C until sowing.

A total of 23 plots were established for the planting experiments, mostly within existing 5x5 m plots along original transects (section 1.3 methods). There were six plots under a canopy of native forest, and nine under a canopy of introduced broom (*Cytisus scoparius*) at the Mangetepopo sites. At Raetihi hill, four plots were established in native forest, and another four in exotic grasses with no overhead canopy. Each 5x5 m plot had four 40x40 cm subplots that were positioned within it in a restricted random fashion (Fig. 4.1). The plots were restricted to flat ground to prevent sideways movement of sown seeds. Each subplot was randomly assigned to one of four combinations of the two experimental treatments outlined below.

(i) ground cover, roots and litter were manually removed to expose the mineral soil. Subsequent litterfall and weed growth was removed at monthly intervals.

(ii) animal exclosure cages constructed out of wire mesh were used to prevent browsing by hares, possums and other large animals, but not mice and invertebrates. These cages were 40x40 cm wide and 20 cm high (Photo 4.2).

In summary, within each 5x5 m plot, there was one subplot with no treatment, one subjected to clearing only, one with caging only, and one subjected to both clearing and caging treatments (Fig. 4.1). Each 40x40 cm subplot was further divided into four 20x20 cm sections that were randomly assigned to the three aforementioned plant species, leaving one section empty. At the end of May 1999, 25 seeds of each species were sown in the 20x20 cm sections using a custom made grid.

Photo 4.1 Twig and berries of *Coprosma* 'taylorii' (species 27 in Wilson & Galloway 1993) showing three different colour morphs. NB: white square = 1 cm^2.

Photo 4.2 An example of an exclosure cage designed to prevent access by hares, possums, and other large animals, but not excluding mice and invertebrates.
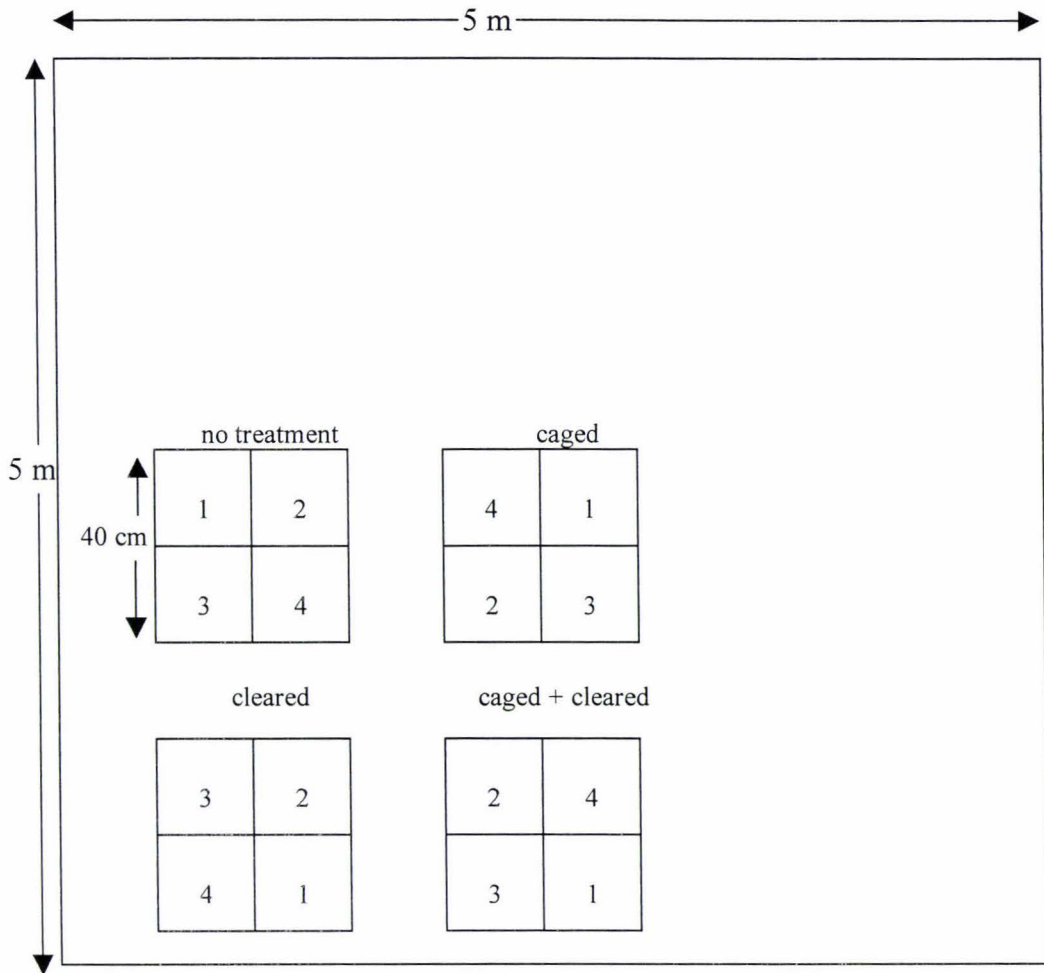
Fig. 4.1 Block design for the planting experiments, with four treatment combinations of the two experimental factors of vegetation cover (cleared or not cleared) and predator access (caged or not caged). Numbers one to three correspond to three tree species which were randomly assigned to a 20x20 cm subplot within each treatment combination (*Griselinia littoralis, Coprosma* 'taylorii', and *Pittosporum tenuifolium* var. *colensoi*). The number four corresponds to transplanted *G. littoralis* seedlings.

Seedlings were tagged with fine wire-wrap wire and the section in which they emerged was recorded. Seedlings were considered 'established' and counted if they were erect and rooted. Plots were checked monthly and a different colour of wire was used at each visit so that the month of establishment could be identified for each seedling (Photo 4.3). When a seedling died, its death was recorded and the coloured wire around it removed. Seedlings were considered to be dead when they were missing, cut at the stem or entirely lacking in green colour. The plots were monitored for 11 months after sowing.

Photo 4.3 Tagged native seedlings established from sown seed in an uncleared forest plot. The four-leaved seedlings on the right of the photo are *Pittosporum tenuifolium* var. *colensoi*, and the ones on the left are *Griselinia littoralis* seedlings. The small seedling in the middle is a naturally dispersed lancewood (*Pseudopanax crassifolius*).

4.2.2 Seedling transplants

In addition, seedlings of *Griselinia littoralis* were transplanted into the remaining empty section of each subplot from nearby locations and the number of leaves and height recorded over 11 months. Two size classes of transplants were used, those with 1-2 leaves (approximately 4 cm high) and those with 4-5 leaves (approximately 6 cm high). The root systems were trimmed to approximately the same size (within each size class) before transplantation.

4.2.3 Light meters

In most environments, light levels usually undergo rapid temporal fluctuations as a result of cloud cover, branch and leaf movement, so instantaneous measurements of light intensity at selected points are of little value in determining the light regime and its effect on seedling germination and growth (Ebbett & Ogden 1998). Therefore, in this study, integrated measurements of light levels over time were made using a simple photographic light sensor originally described by Friend (1961).

This method uses booklets 15 sheets thick of photosensitive ammonium diazo paper that chemically reacts upon exposure to light. Each meter consisted of a booklet sitting on a sponge pad inside a small petri dish (see Friend 1961 for a diagram and more detailed methods). To prevent exposure to moisture, which deleteriously affects the photosensitive paper, each petri dish was sealed with black electrical tape.

The light meters were constructed in the dark room and transported to the field in black plastic bags. One light meter was placed at ground level in each treatment, so that each quadrat had four meters, two inside exclosure cages and two outside, to detect any differences in light received caused by the wire mesh. To determine percent of full sunlight, two replicate meters were placed in the open at the beginning of each transect. The meters were left out for seven days and booklets were developed by exposure to ammonia fumes for 15 minutes. They were stored in a dark place until they could be scored.

A set of standards was made by constructing a large booklet (14x10 cm) four sheets thick, and marking off seven 2 cm wide strips. Each strip was exposed to light for an increasing period of time. The first strip was exposed for 0 minutes; the second for 8 minutes; third 10 minutes and 1 second; fourth 12 minutes and 2 seconds; fifth 16 minutes and 1 second; sixth 24 minutes and 26 seconds and the last for 41 minutes. This time scale is logarithmic since there is a logarithmic relationship between the number of sheets exposed and the total irradiance received during the exposure period. After development, the second page of this booklet was used as a standard for scoring between the sheets of other booklets. A fully exposed sheet is scored as 1, and partially exposed sheets scored on a scale of 0.1 to 0.9 by visual comparison with a set of prepared standards. All booklets were scored blind (ie: not knowing which treatment they came from) and twice. Thus the final result is an average of two scores.

To calibrate the paper light meters, 20 were placed in full sunlight with a licor light sensor attached to a data logger which measured average light levels in microeinsteins per m^2 over 15 minute intervals. Two replicate paper light meters were pulled in at each of 10 time intervals. These booklets were developed and scored using the prepared standard. The linear regression equation for the calibration was: $y = 0.47x + 3.56$

(R^2=0.996) where y is the light integral received (microeinsteins $m^{-2}s^{-1}$) and x is the "score" or number of pages exposed obtained from the booklets (see Fig 4.1 in Appendix 4).

4.2.4 Statistical analyses

To test if species were seed limited, loglinear models were used (SAS Institute 1996). The response factors were the establishment and survival of seedlings, and the treatment factors included site, habitat (nested within site), transect (treated as a block), and position in the subplot in which seedlings were found (ie: sown or unsown). Each species was analysed separately, and the number of seedlings that established and survived in the section in which the species was sown was compared to the section diagonally opposite and the two sections adjacent to the sown section. The reason the results were analysed in this manner was because of the possibility that some seed may have moved between sections and was more likely to have moved from the sown section to the adjacent sections than the diagonally opposite section. All other analyses on seedling establishment, including that of naturally occurring seedlings was performed with general linear models (poisson error distribution). The poisson distribution was preferred, because overall there was a low success rate for unsown seeds but occasionally more seedlings established from naturally dispersed seeds beneath fruiting trees. Since seedling survivorship data were binary, they were analysed by a generalised linear model with a binomial error distribution. Survival of transplanted *G. littoralis* seedlings was analysed in the same way. Of the transplanted seedlings that survived to the last sampling period, the final number of leaves of the larger and smaller size classes were analysed separately (ANOVAs with a poisson error distribution). Relative height growth was calculated by the change in height divided by the starting height of seedlings, and analysed in the same way as before separating larger and smaller size classes. Loglinear models were used to analyse the relationship between measured light levels and the total number of seedlings that established (poisson) and survived (binomial).

4.3 RESULTS

4.3.1 SOWN SPECIES

4.3.1.1 Seed limitation

Sowing seeds at densities equivalent to $625/m^2$ dramatically increased the number of seedlings that established compared to plots that were unsown (Table 4.1a). Overall, this difference was significant for *Griselinia littoralis* and *Coprosma* 'taylorii' but not for *Pittosporum tenuifolium* var. *colensoi*. However, very low overall establishment of the latter species made it difficult to detect statistical significant differences between sown and unsown plots. For the other two species, differing establishment between unsown and sown sections was especially noticeable in non-forest habitats. In unsown plots, very few naturally established seedlings were found in the broom habitat (<1 per m^2), and none at all in grassland (Table 4.1a). In comparison, reasonable densities of seedlings germinated from sown seed in these habitats. Overall however, all three sown species had much lower seedling densities in the broom and grass habitats than under a canopy of native forest.

Of the three species sown, *Griselinia littoralis* showed the best establishment with the highest number of seedlings found in the forest plots at Mangatepopo (Table 4.1a). This species also showed the highest density of seedlings establishing from naturally dispersed seed in the same habitat. In the broom habitat however, compared to other species, *C.* 'taylorii' had the greatest densities of seedlings establishing in unsown plots at one per m^2 (Table 4.1a). *Pittosporum tenuifolium* var. *colensoi* showed much less establishment than the other two species, in both sown and unsown plots.

The only significant difference between survival of seedlings in sown and unsown plots was for *G. littoralis* that established in forest habitats (Table 4.1b). However, because fewer seedlings established from natural seed rain, densities of surviving seedlings were still much less in unsown plots than sown plots. Survival of *G. littoralis* was also significantly higher in forest habitats than in broom and grassy habitats (Table 4.1b).

Table 4.1 Densities of seedlings a) establishing and b) surviving in sown and unsown sections. Seed was sown on 20 May 1999 and the plots were monitored for 11 months subsequently. Most seed established between four to nine months after sowing. ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill. The overall effect of seed addition on establishment and survival of seedlings is denoted by *0.05>P>0.01, **0.01>P>0.001, ***P<0.001, NS = not significant.

a) **Establishment** (defined as seedlings that had germinated and were erect and rooted). Within each species, values with the same letter are not significantly different from each other at the 5% level (loglinear analysis with a poisson error distribution).

	Number of seedlings per m^2					
	Griselinia littoralis ***		*Coprosma* 'taylorii' ***		*Pittosporum tenuifolium* NS	
Habitat	Sown	Unsown	Sown	Unsown	Sown	Unsown
ForestA	115^a	63^b	84^a	17^b	15^a	0.3^a
ForestB	82^a	6^b	60^a	5^b	9^a	0^a
Broom	50^c	0.2^d	15^c	1^c	3^a	0.4^a
Grass	26^e	0^e	2^d	0^d	2^a	0^a

b) **Survival** (seedlings surviving at the last recording episode). Within each species, values with the same letter are not significantly different from each other at the 5% level (loglinear analysis with a binomial error distribution).

	Number of seedlings surviving per m^2 (percent surviving in brackets)					
	Griselinia littoralis *		*Coprosma* 'taylorii' NS		*Pittosporum tenuifolium* NS	
Habitat	Sown	Unsown	Sown	Unsown	Sown	Unsown
ForestA	60 (52%)^a	17 (30%)^b	33 (39%)^a	11 (65%)^a	6 (40%)^a	0.3 (100%)^a
ForestB	40 (49%)^a	5 (83%)^b	29 (48%)^a	4 (80%)^a	2 (22%)^a	0
Broom	9^c (18%)^b	0.2 (100%)^b	4 (27%)^a	1 (100%)^a	0.2a (7%)^a	0.4 (100%)^a
Grass	0.4 (2%)^d	0	1 (50%)^a	0	0.4 (20%)^a	0

4.3.1.2 Seedling responses to experimental treatments and other factors

Caging and clearing treatments had significant effects on establishment of most species. Of the three sown species (*G. littoralis*, *C.* 'taylorii', and *P. tenuifolium* var. *colensoi*) and the most common naturally occurring species, clearing of litter and ground vegetation had significant effects on seedling establishment of all but one (Table 4.2a). The effect of the caging treatment on seedling establishment was also significant for all species except *C.* 'taylorii'. However, only two species showed a significant caging by clearing interaction. The effect of habitat was highly significant for all species examined, and the effect of site was significant for most species that occurred at

sites. There was also a significant transect effect for the majority of species examined. Of all the other interactions, the effect of clearing in different habitats was significant for the greatest number of species.

Survival of seedlings is ultimately more important than establishment as long as some seedlings establish. For most species there was less evidence for significant treatment effects on survival. However, due to lower sample sizes there is less statistical power for detecting significant differences. Despite this, survival of *G. littoralis* and *C.* 'taylorii' showed significant effects of both treatments. Generally, more seedlings survived under a canopy of native forest in plots that were both caged and cleared (Figs. 4.2b, 4.3b). There was also a significant caging by clearing interaction for three species (Table 4.2b).

4.3.1.3 Griselinia littoralis

Of all the treatments, plots that were both caged and cleared showed the greatest establishment and survival of *G. littoralis* seedlings, with the clearing treatment generally being the next best (Fig. 4.2). Surprisingly, in the broom habitat, more seedlings established in subplots with no treatment than in those with a caging treatment imposed (Fig. 4.1a). Generally, seeds sown in the broom and grass habitats had much less establishment overall than seeds sown under a canopy of native forest. In addition, a greater proportion of seedlings survived in forest plots. This effect of habitat (nested within site) was highly significant and explained the largest proportion of deviance in the model (Table 4.2 and Appendix 4.2a). Significant effects of site and transect on seedling establishment showed that transects A and B at Mangatepopo were better than other areas for establishment of *G. littoralis* seedlings (Table 4.2a).

Table 4.2 Effects of experimental treatments and other factors on **a) seedling establishment** (defined as seedlings that had germinated and were erect and rooted at the time of recording) and **b) seedling survival** (surviving at the last recording episode). The first three species established from sown seed, the remaining species established from naturally dispersed seed. NB: *Coprosma* species other than 'taylorii' are *C. grandifolia, C. robusta, C. tenuifolia,* and *C. foetidissima.* Cl = clearing treatment, Ca = caging treatment, Cl x Ca = clearing by caging interaction *0.05>P>0.01, **0.01>P>0.001, ***P<0.001, NS = not significant.

a) Seedling establishment (ANOVAs with poisson error distributions)

Species	Cl	Ca	Cl x Ca	Site	Habitat	Transect	Site x Cl	Site x Ca	Site x Cl x Ca	Habitat x Cl	Habitat x Ca	Habitat x Ca x Cl
Griselinia littoralis	***	**	NS	***	***	***	NS	**	***	***	NS	***
Coprosma 'taylorii'	***	NS	NS	***	***	***	***	NS	NS	***	NS	NS
Pittosporum tenuifolium	***	***	*	NS	***	NS	NS	**	**	*	NS	NS
Leptospermum scoparium	***	***	NS	-	***	***	-	-	-	**	*	-
Pseudopanax crassifolius	***	***	***	***	***	***	***	NS	***	**	NS	NS
Coprosma species	NS	*	NS	***	***	NS	**	NS	NS	-	-	-
Cytisus scoparius	***	***	NS	-	***	***	-	-	-	***	***	*

b) Seedling survival (ANOVAs with a binomial error distributions)

Species	Cl	Ca	Cl x Ca	Site	Habitat	Transect	Site x Cl	Site x Ca	Site x Cl x Ca	Habitat x Cl	Habitat x Ca	Habitat x Ca x Cl
Griselinia littoralis	***	***	*	NS	***	NS	NS	NS	NS	NS	**	NS
Coprosma 'taylorii'	***	***	NS	**	NS	***	NS	***	NS	*	**	NS
Pittosporum tenuifolium	NS	NS	NS	NS	*	*	NS	NS	NS	NS	-	-
Leptospermum scoparium	NS	NS	-	-	***	NS	-	-	-	-	**	-
Pseudopanax crassifolius	NS	NS	***	***	NS	NS	NS	NS	-	NS	NS	-
Coprosma species	NS	NS	***	NS	-	*	NS	-	NS	-	-	-
Cytisus scoparius	***	***	NS	-	***	***	-	-	-	***	***	*

4.3.1.4 *Coprosma* 'taylorii'

In keeping with the general pattern, establishment of *Coprosma* 'taylorii' seedlings was much greater in forest habitats than in broom or grassy habitats (Fig. 4.3a, Table 4.2a). Again, the effect of habitat was highly significant and explained over half of the total deviance in the model (Table 4.2a, Appendix 4.2b). Within the forest and broom habitats, more seedlings established and survived in plots that were both caged and cleared. The difference between cleared and uncleared plots was most pronounced in the forest habitat at Raetihi hill. This was confirmed by a significant habitat by clearing interaction for both establishment and survival of seedlings (Table 4.2). Interestingly, this species also showed a significant site by clearing interaction for seedling establishment. There were also significant effects of site and transect on establishment and survival of *C.* 'taylorii' seedlings, with transects A and B showing the greatest recruitment. For survival, the effect of transect was the single most influential factor although it only explained 15% of the total deviance (Appendix 4.2b). In contrast, for seedling survival there were significant interactions of site by caging and habitat by caging.

4.3.1.5 *Pittosporum tenuifolium* var. *colensoi*

Overall, very few *Pittosporum tenuifolium* var. *colensoi* seedlings established, although more were found in forest plots at Mangatepopo than in any other habitat (Fig. 4.4a). This effect of habitat was highly significant and explained the greatest amount of deviance (Table 4.2a, Appendix 4.2c). Both treatments (clearing and caging) had significant effects on seedling establishment, but not on survival of this species (Table 4.2). There was also a weaker clearing by caging interaction for seedling establishment. This combination of caging and clearing resulted in greater establishment in most habitats (Fig. 4.4a). However, percentage survival appears greatest in plots with no treatment (Fig. 4.4b), this is because of very low establishment of seedlings in these plots. For example, 100% survival of *P. tenuifolium* seedlings in forest plots at Raetihi hill only corresponds to one established seedling! The only statistically significant effects on survival of seedlings were habitat and transect which explained an equal amount of deviance (Table 4.2b, Appendix 4.2c). More seedlings survived under a canopy of native forest than in other habitats (Fig. 4.4b).

a) established
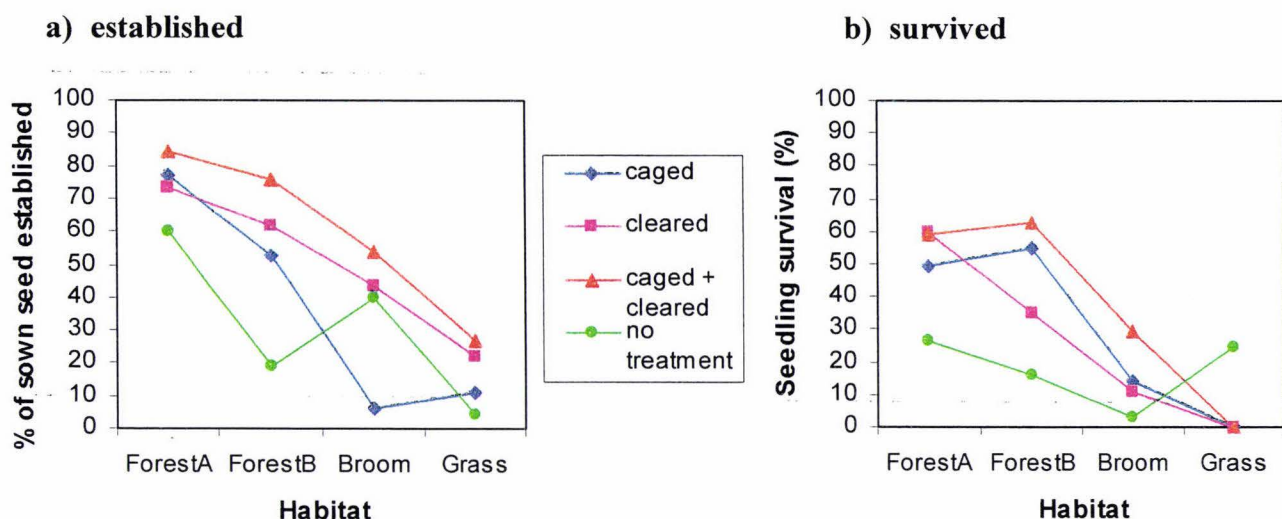
b) survived

Fig. 4.2 Percentage of *Griselinia littoralis* seedlings that a) established and b) survived in different habitats and subjected to different treatments. ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill.

a) established
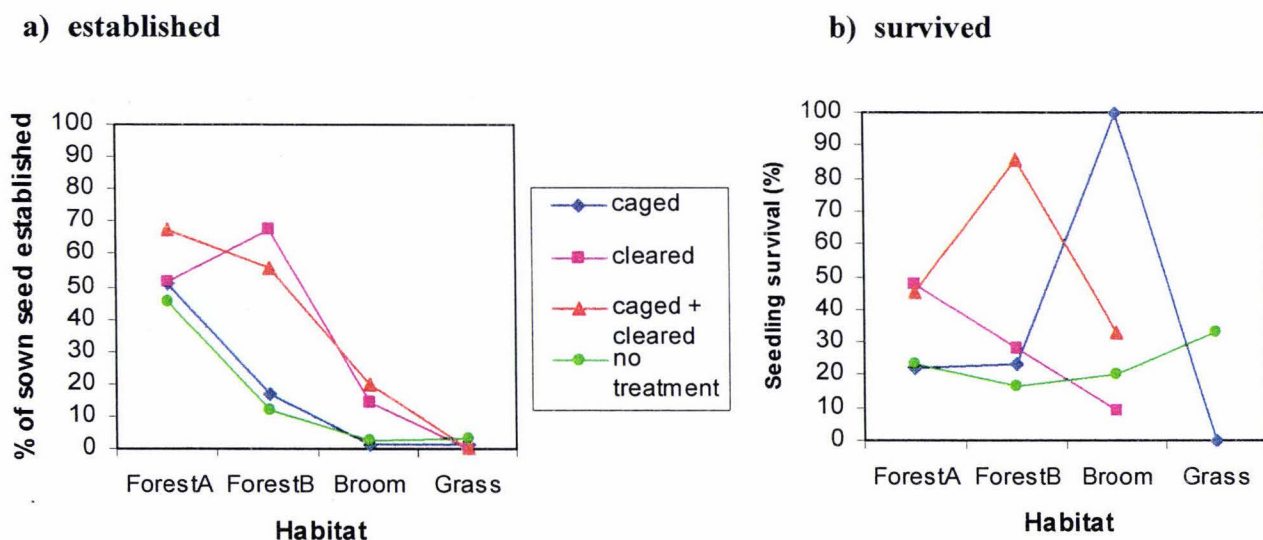
b) survived

Fig. 4.3 Percentage of *Coprosma* 'taylorii' seedlings that a) established and b) survived in different habitats and subjected to different treatments. ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill.

a) established   b) survived
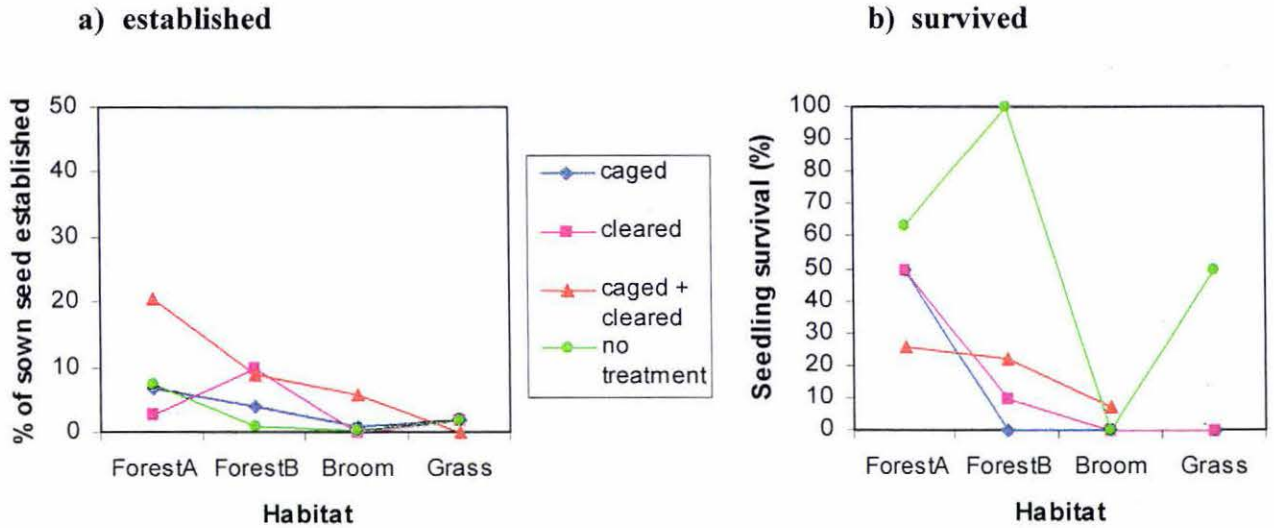
Fig. 4.4 Percentage of *Pittosporum tenuifolium* var. *colensoi* seedlings that
a) established and b) survived in different habitats and subjected to different treatments.
ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill. Note the
expanded scale on the y-axis for graph a).

4.3.2 UNSOWN SPECIES

Over the course of this study, some other species established from naturally dispersed
seed or from the seed bank. The greatest densities of native seedlings established and
survived in forest habitats at Raetihi hill. The most common species include broom
(*Cytisus scoparius*), manuka (*Leptospermum scoparium*) and lancewood (*Pseudopanax
crassifolius*) at the Mangatepopo sites (Table 4.3). Lancewood was also abundant at
Raetihi hill. Other common species found here were ducksfoot (*Pennantia corymbosa*)
and various *Coprosma* species. Apart from broom, most species occurred more often in
the forest habitats and only in very low numbers in the broom habitats. Within the
broom habitat, manuka was the most abundant native seedling in terms of establishment.
This species also survived relatively well under a canopy of broom. The only other
native species to establish naturally in the broom habitat (apart from the aforementioned
G. littoralis, C. 'taylorii' and *P. tenuifolium* var. *colensoi* Table 4.1) were *Phyllocladus
aspleniifolius* var. *alpinus* and lancewood. Unfortunately no seedlings of these latter
two species survived after 11 months. No woody seedlings established naturally in the
grass habitat over the duration of this study.

Table 4.3 Density of naturally occurring seedlings of different species in different habitats. E=established, S=survived to the last recording episode (survived for at least 2 months). NB: *Coprosma* species are *C. grandifolia, C. robusta, C. tenuifolia,* and *C. foetidissima.* * denotes naturalised exotic species, - = not applicable.

	Number of seedlings per m^2							
Site	Mangatepopo				Raetihi hill			
Habitat	FOREST		BROOM		FOREST		GRASS	
Species	E	S	E	S	E	S	E	S
Carpodetus serratus	0.3	0	0	0	6	5	0	0
Coprosma species	5	2	0	0	13	7	0	0
*Cytisus scoparius**	61	-	134	-	0	0	0	0
Leptospermum scoparium	52	19	15	11	0	0	0	0
Melicytus ramiflorus	0	0	0	0	2	2	0	0
Nestegis cunninghamii	0	0	0	0	2	2	0	0
Pennantia corymbosa	0	0	0	0	14	11	0	0
Phyllocladus aspleniifolius	4	3	1	0	0	0	0	0
Pseudopanax crassifolius	34	16	2	1	77	53	0	0
Pseudowintera colorata	0.3	0	0	0	1	0.4	0	0
TOTAL (natives only)	**96**	**40**	**18**	**12**	**115**	**80**	**0**	**0**

The most common naturally dispersed fleshy fruited species was lancewood (*P. crassifolius*). The greatest number of lancewood seedlings established and survived in forest plots at Raetihi hill (Fig. 4.5). In contrast, establishment and survival of seedlings in non-forest habitats was very low. The effects of both site and habitat were highly significant for the establishment of lancewood seedlings (Table 4.2a). Habitat had by far the greatest explanatory power for establishment, whereas site was more important for seedling survival (Appendix 4.3a, Table 4.2). More lancewood seedlings established in transect B than any other transect (Appendix 4.3a). Plots that were cleared generally had higher densities of establishing seedlings (Fig. 4.5a). Effects of both treatments (clearing and caging) on seedling establishment were significant, as was an interaction between them (Table 4.2a). Similarly, a greater proportion of lancewood seedlings survived in plots that were both cleared and caged compared to plots that were cleared only. A significant clearing by caging interaction supported this observation (Table 4.2b).

Seedlings of the genus *Coprosma* (not including *C.* 'taylorii') also established in greatest densities in forest plots at Raetihi hill (Fig. 4.6a). In contrast, there was no establishment in the non-forest habitats and very little in forest plots at Mangatepopo. The effects of both habitat and site were significant, with habitat explaining almost half of the deviance (Appendix 4.3b). Most seedlings established in forest plots that were cleared, or both

caged and cleared. Very few were found in plots that had no treatment or that were caged only. Overall however, there was no significant effect of the clearing treatment on establishment and only a weak effect of the caging treatment (Table 4.2a). Similar to the pattern for establishment, survival of *Coprosma* species was greatest in plots that were both caged and cleared (Fig. 4.6b). This interaction was significant and explained the largest amount of deviance for seedling survival (Table 4.2b, Appendix 4.3b).

Manuka seedlings were only found at the Mangatepopo sites (Table 4.3). This species showed the greatest establishment in forest plots that were both caged and cleared (Fig. 4.7a). Clearing was the single most important factor affecting seedling establishment, although caging was also significant (Table 4.2a, Appendix 4.3c). Although there was no general pattern for survival of manuka seedlings, more survived under a canopy of broom in plots that were both caged and cleared than in any other treatment (Fig.4.7b). The only factors significantly affecting survival of this species were habitat (which explained over half of the total deviance) and an interaction between habitat and the caging treatment which was less influential (Table 4.2b, Appendix 4.3c).

a) established   **b) survived**
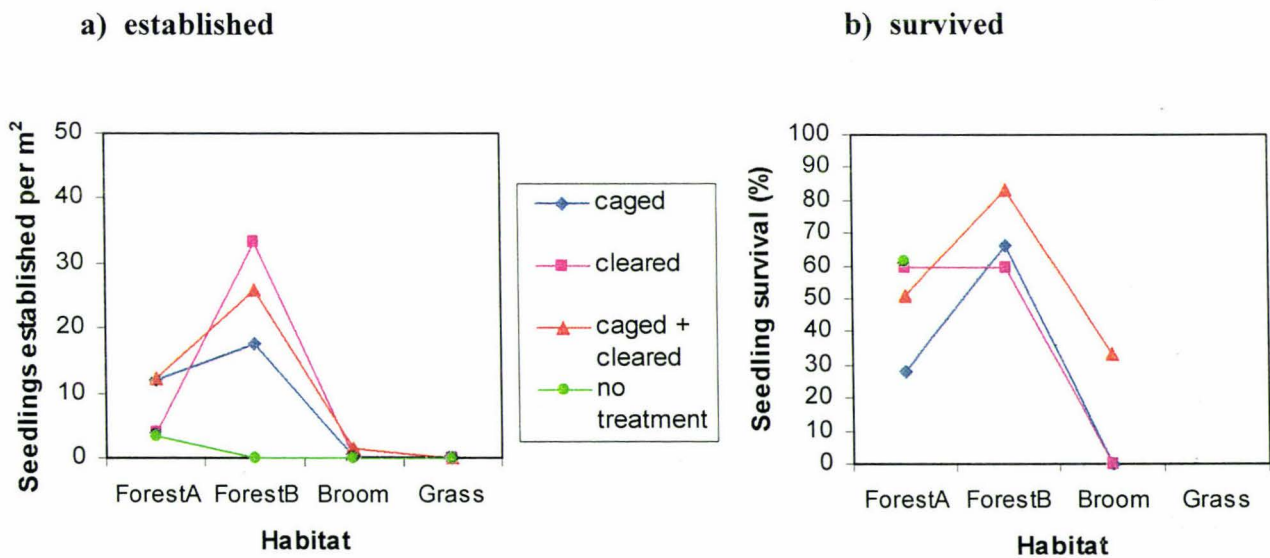
Fig. 4.5 Seedlings of naturally dispersed *Pseudopanax crassifolius* that a) established and b) survived in different habitats and subjected to different treatments. ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill.

a) established
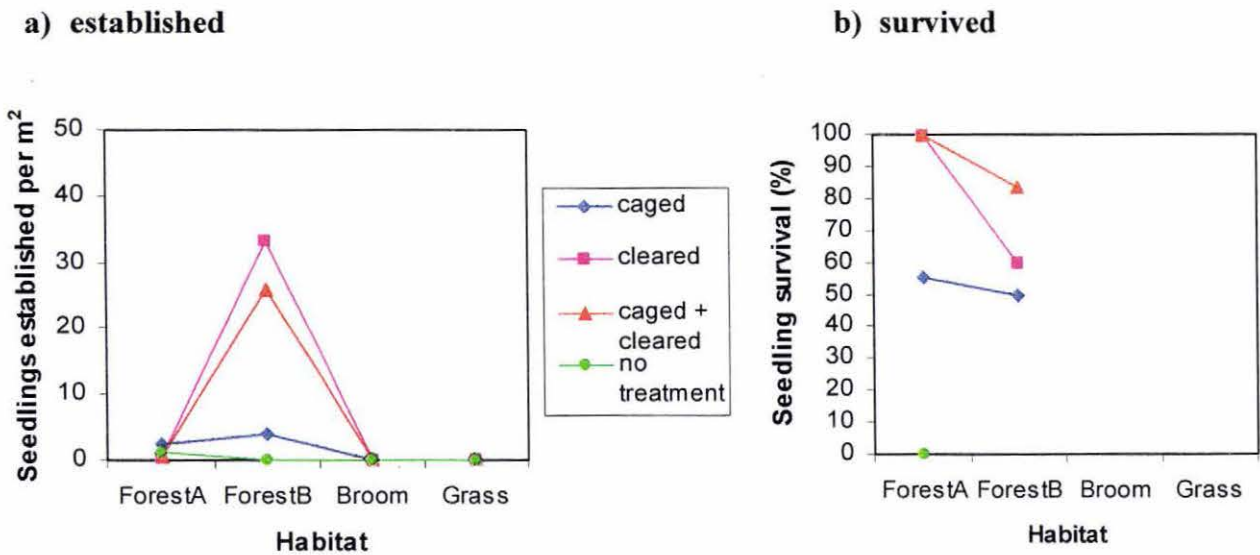
b) survived

Fig. 4.6 Seedlings of the genus *Coprosma* that a) established and b) survived in different habitats and subjected to different treatments. Includes *C. grandifolia, C. robusta, C. tenuifolia,* and *C. foetidissima.* ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill.

a) established
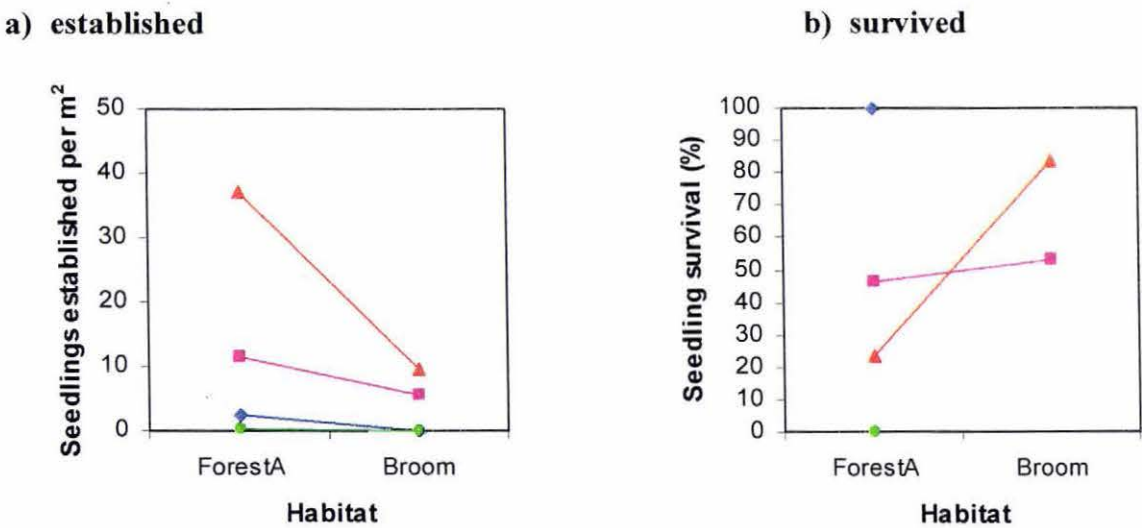
b) survived

Fig. 4.7 (above) Seedlings of manuka (*Leptospermum scoparium*) that a) established and b) survived in two habitats and subjected to different treatments.
ForestA = forest plots at Mangatepopo,
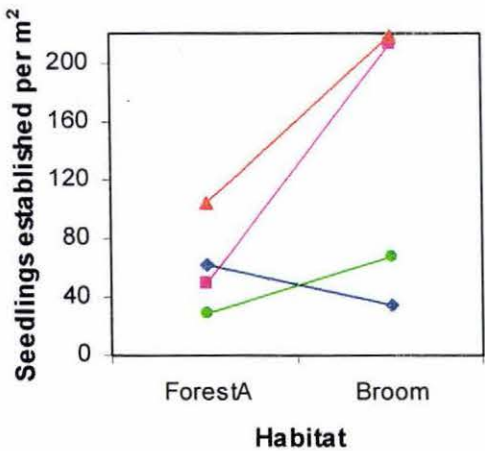
Fig. 4.8 (at left) Establishment of broom (*Cytisus scoparius*) seedlings at Mangatepopo. ForestA = forest plots at Mangatepopo.Note the expanded scale on the y-axis.

Broom seedlings were significantly more abundant under a canopy of adult broom where there was a greater seed bank (Table 4.2, Table 4.3, Fig. 4.8). In this habitat, the difference between cleared and uncleared plots was quite obvious (Fig. 4.8). Cleared plots showed much greater densities of established seedlings than uncleared plots and this difference was highly significant (Table 4.2a). In addition, the effect of clearing was the single most influential factor affecting the model (Appendix 4.3d). Caging also had a significant effect, but there was no clearing by caging interaction (Table 4.2a). Other significant effects include that of habitat, transect and interactions between habitat and treatments (Table 4.2a). Transects listed in order from greatest to least densities of broom seedlings - A, C, and B.

4.3.4 LIGHT LEVELS

Light levels were generally much lower in forest habitats than broom or grass habitats at both sites. In fact, some plots at Raetihi hill showed less than 1% of full sunlight (Fig 4.9a). Generally, the lower the light level, the greater the number of seedlings established. Results from a loglinear analysis confirmed that light was the most important factor explaining over 65% of the total deviance in densities of established seedlings (Appendix 4.4). Although habitat, site, and transect also had significant effects they were much less influential. There was no appreciable difference between measured light levels under cages compared to plots that were uncaged, suggesting that the presence of cages had a negligible effect on the amount of light reaching seedlings.

There was also a significant relationship between light levels and seedling survival (Appendix 4.4). Thus, more seedlings survived in the lower light levels found under a canopy of native forest than in broom or grass habitats (Fig. 4.9b). Again, light was the most influential factor explaining approximately 35% of the total deviance (Appendix 4.7).

a) establishment

b) survival
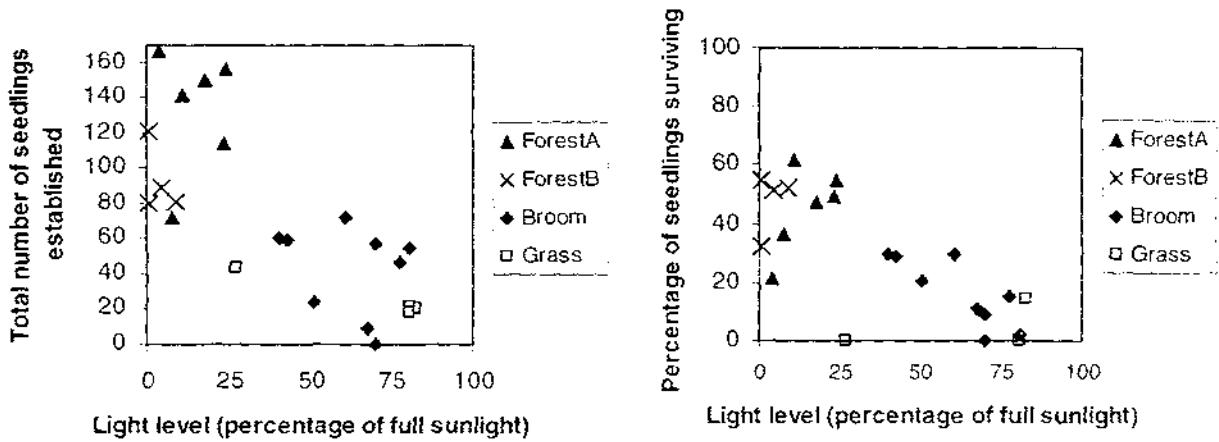
Fig 4.9 Total number of seedlings that a) established from sown seed and b) survived, compared with light levels expressed as a percentage of full sunlight (each point is a mean of four paper light meters). ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill.

4.3.3 TRANSPLANTED SEEDLINGS

4.3.3.1 Survival

More *G. littoralis* seedlings survived 11 months after transplant in forest habitats than in any other habitat (Fig. 4.10). Survival of transplanted seedlings was generally poor in the broom habitat and even worse in open grassland. This effect of habitat was highly significant (Table 4.4) and explained the largest amount of deviance (Appendix 4.5). There was also a significant transect effect for the larger size class of transplanted seedlings, with more seedlings surviving in transect B than any other area. Survival of transplants in the smaller size class (1-2 leaves initially) was generally less than that of the larger size class (4-5 leaves initially) especially in the broom habitat (Fig. 4.10). Within the broom habitat, larger seedlings transplanted into the caged and cleared treatment survived better than in any other treatment. However, only the effect of clearing was significant in this case (Table 4.4). For the smaller size class of transplants, a significant interaction between caging and clearing was detected (Table 4.4).
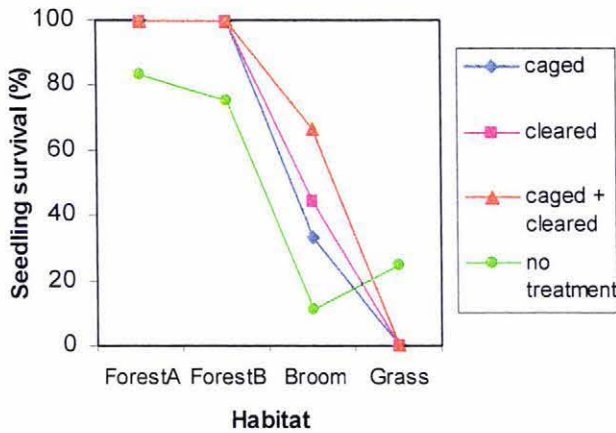
a) **larger size class of transplants**   b) **smaller size class**
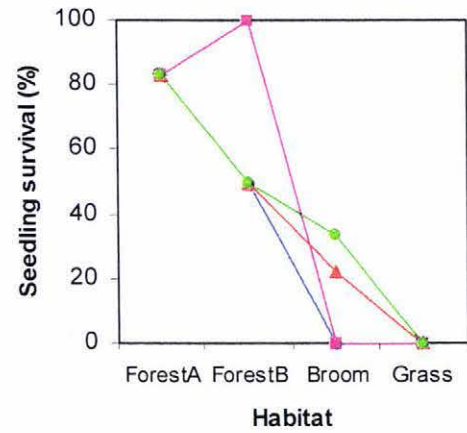
Fig. 4.10 Survival of transplanted *Griselinia littoralis* seedlings in different habitats and treatments for a) larger size class of seedlings, b) smaller size class. ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill.

Table 4.4 Effects of treatments and other factors on survival and growth of transplanted *Griselinia littoralis* seedlings. L=larger size class (4-5 leaves initially), S=smaller size class (1-2 leaves initially) of transplanted seedlings. *0.05>P>0.01, **0.01>P>0.001, ***P<0.001, NS = not significant.

Source	Survival		Final number of leaves		Relative height growth	
	L	S	L	S	L	S
Cleared	*	NS	***	*	*	NS
Caged	NS	NS	NS	NS	NS	NS
Clxcaged	NS	*	NS	*	NS	NS
Site	NS	NS	***	**	NS	NS
Habitat	***	***	***	***	***	***
Transect	**	NS	**	**	NS	NS
SxCl	NS	NS	**	NS	NS	NS
SxCa	NS	NS	NS	NS	NS	NS
SxClxCa	NS	NS	NS	*	NS	NS
HxCl	NS	NS	***	NS	NS	NS
HxCa	NS	NS	***	NS	NS	NS
HxClxCa	NS	NS	***	***	NS	NS

4.3.3.2 Growth

For both size classes of transplanted seedlings that survived until the last sampling period, there were significant effects of site, habitat, transect, and the clearing treatment on the final number of leaves (Table 4.4). The most influential of these was habitat, which explained 22% and 37% of the total deviance for larger and smaller size classes respectively (Appendix 4.6).

a) larger size class of transplants　　　　**b) smaller size class**
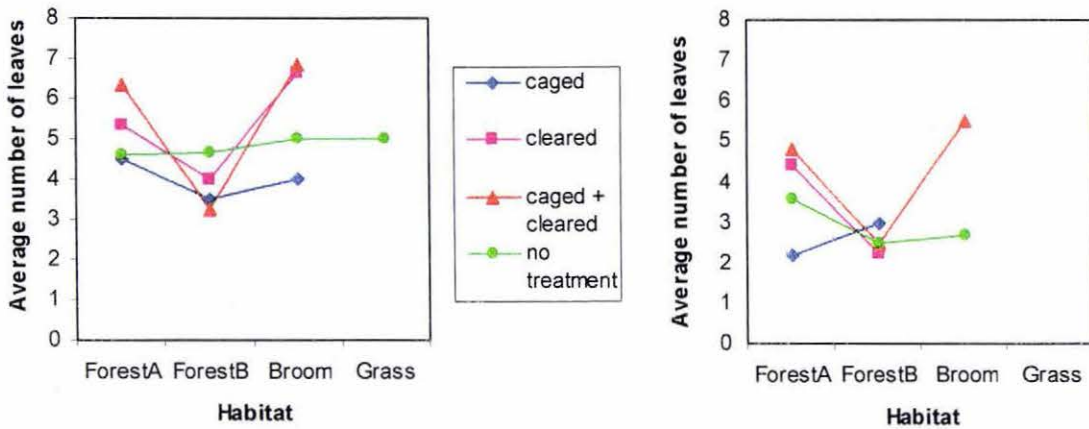
Fig 4.11 Average final number of leaves per seedling in a) larger size class and b) smaller size class of transplants. ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill.

Comparing forest habitats, seedlings transplanted at Raetihi hill had fewer leaves on average than those transplanted at Mangatepopo (Fig. 4.11). Since all seedlings of the smaller size class that were transplanted into the grass habitat died, the average final number of leaves could not be included in the analysis or the graphs. Within the broom habitat, seedlings of both size classes had more leaves on average in plots that were both caged and cleared than most other treatments (Fig 4.11). This was confirmed by significant habitat, clearing and caging interactions (Table 4.4).

Surprisingly, the highest relative height growth was observed in the grass habitat (Fig. 4.12). However, this was because of the exceptional growth of one surviving individual in the larger size class, which increased in height by seven centimetres over 11 months. Relative height growth was slightly greater for transplanted seedlings in forest plots at Mangatepopo compared with those in forest plots at Raetihi hill. The effect of habitat on

relative height growth of transplanted seedlings was significant for both size classes and also had the greatest explanatory power (Table 4.4, Appendix 4.7a,b). Interestingly, the smaller size class of transplanted seedlings grew comparatively taller than the larger size class in the broom habitat.
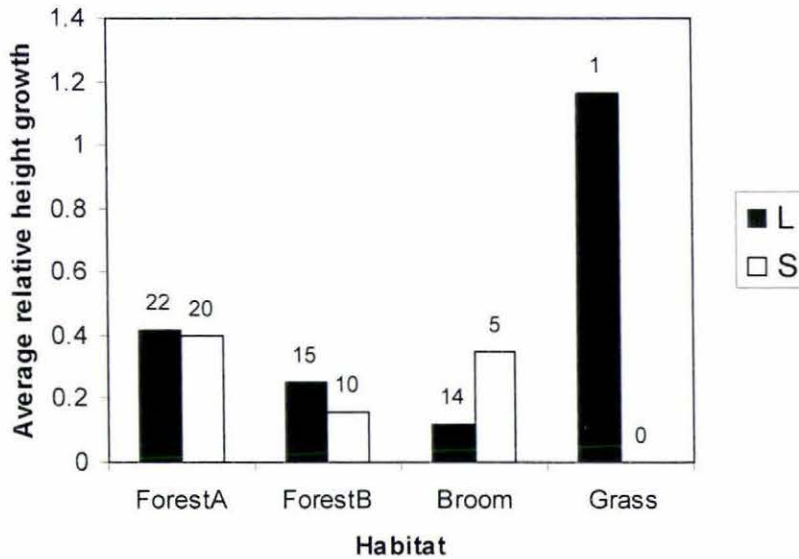
Fig. 4.12 Relative height growth of surviving transplanted *Griselinia littoralis* seedlings in different habitats. NB: relative height growth was calculated by change in height divided by starting height, L=larger size class, S=smaller size class, ForestA = forest plots at Mangatepopo, ForestB = forest plots at Raetihi hill. Numbers above each bar indicate how many individuals were surviving after 12 months.

Photo 4.4 Example of disturbance caused by feral pigs in broom-dominated vegetation at the Mangatepopo site sampled by transect A.

4.4 DISCUSSION

4.4.1 Seed and microsite limitation

Recruitment rate is a function of both seed availability and microsite availability (Eriksson & Ehrlén 1992). Therefore, to find out if recruitment is limiting, one must test if the population is seed limited and/or microsite limited. In this study, two of the three native species examined (*Griselinia littoralis* and *Coprosma* 'taylorii') were seed limited because the number of seedlings that established and survived was significantly greater in sown sections than unsown sections. Very low establishment of the third species (*Pittosporum tenuifolium* var. *colensoi*) made it difficult to detect any statistically significant differences. There was also evidence of microsite limitation, as the number of seedlings that established from sown and unsown seed was generally greater in cleared than in undisturbed areas.

It is interesting to note that although both *Griselinia littoralis* and *Coprosma* 'taylorii' were seed limited overall, the difference between seedling establishment in sown and unsown sections was not significant in grassy habitats. This is probably because very few seedlings established in this habitat at all. Likewise, there was no difference in establishment or survival between sown and unsown sections in the broom habitat for *C.* 'taylorii'. In these cases, clearing of the ground vegetation was required before seedling establishment and survival could occur.

In a recent review by Turnbull *et al.* (2000), a statistical interaction between seed sowing and disturbance was detected for 20 out of 29 cases where a disturbance treatment was applied. In 19 of these, recruitment in disturbed and sown treatments was higher than in plots receiving either seed additions or disturbance alone (Turnbull *et al.* 2000). This implies that the removal of herbaceous vegetation often provides additional microsites, but that seeds are not always present to take advantage of such events. Myster (1993) and Robinson and Handel (2000) further expand this idea, concluding that most woody species must be present to take advantage of a 'narrow window of opportunity for establishment' in order to successfully invade grassland.

4.4.2 Effects of the clearing treatment

Removing the ground vegetation and litter nearly always resulted in greater establishment of woody seedlings. This suggests that exotic grasses and deep litter have an inhibitory effect on seedlings of native woody species and of introduced broom (*Cytisus scoparius*). This effect was especially noticeable for two naturally establishing species, manuka (*Leptospermum scoparium*) and broom. Both of these species have been found to establish preferentially in disturbed sites (Grant 1967, Bossard 1991, Porteous 1993, Hosking *et al.* 1996). For example, the number of broom seedlings was at least ten times lower in undisturbed pasture compared with disturbed plots in Australia (Hosking *et al.* 1996). Similarly, I found that the number of broom seedlings was six times lower in plots dominated by exotic grasses compared with plots in which these grasses were removed. Preliminary observations of seedlings of introduced heather (*Calluna vulgaris*) revealed that this species only established in cleared plots, and that no seedlings were found in uncleared plots. (NB: this species only started germinating near the end of monitoring and was not included in the results).

There is a growing view that small-scale disturbances that disrupt the dominant ground cover such as animal diggings can act as important microsites for seedling recruitment (Kotanen 1995, Edwards & Crawley 1999b). In this study, feral pigs caused considerable disturbance by uprooting grasses and shrubs in some areas of the broom habitat (Photo 4.4). In a detailed study of the effects of feral pig disturbance in a Californian prairie, Kotanen (1995) found that grubbing had significant effects on vegetation composition. This author reported increased establishment of both native and non-native plants in disturbed areas (Kotanen 1995). Similarly, I found that both native and non-native species with high seed availability such as manuka, broom, and heather had greater seedling densities in these disturbed areas (personal observation). Although other native species also showed greater establishment in disturbed areas, the probability of bird dispersed species being deposited in these more suitable microsites is much lower than that of wind dispersed species (section 2.3.2.3). Thus, the timing of disturbance relative to the availability of seeds capable of germination is also important (Edwards & Crawley 1999b).

The impact of vegetative ground cover preventing the establishment of woody species

has been frequently noted (Evans 1983, Gill & Marks 1991, Magee & Antos 1992, Berkowitz *et al.* 1995). Magee & Antos (1992) suggest that dense herbaceous vegetation can create obstacles to tree seedling establishment through competition for resources, physical barriers, or by mechanical damage from burial by litter. Generally, above-ground competition is thought to be more important than below ground competition in the early seedling stages (Gill & Marks 1991).

Disturbance treatments may have had different effects in different habitats, as clearing in forest plots generally only involved removal of litter, whereas clearing in broom and grassy habitats involved complete removal of the vegetation cover. Significant interactions between clearing treatment and habitat for seedling establishment supports this theory, although only one species (*Coprosma* 'taylorii') showed a significant interaction for seedling survival.

Within the forest habitat, establishment of most native seedlings was increased when litter was removed. Significant site by clearing interactions for *Coprosma* species and lancewood (*Pseudopanax crassifolius*) suggest that these species were less able to establish in uncleared forest plots at Raetihi hill compared with the same situation at Mangatepopo. This is probably because of deeper litter at Raetihi hill (section 1.4.1.4). Similarly, Bartlett *et al.* (1991) found that deep litter limited recruitment of forest tree seedlings on cliff edge communities in Canada, and even small amounts of litter reduced survival rates of grass seedlings in Texas (Fowler 1988). As well as having a physical effect of burying seeds, sometimes litter may inhibit germination of seeds by leaching of allelopathic chemicals (Bosy & Reader 1995). A study on the effects of broom litter suggested that it has an allelopathic effect on some other species but not on its own seedlings (Nemoto *et al.* 1993). On the other hand, sometimes burial of seeds by litter may improve a seed's chance of survival and germination, but only if they are not buried too deeply. This is because they are less likely to be eaten, or to dry out (Glenn-Lewin *et al.* 1992).

Overall, the effect of the clearing treatment on seedling survival (rather than establishment) was only significant for *G. littoralis* and *C.* 'taylorii'. This result is unusual as other studies have found that disturbance to the ground cover has beneficial

effects on seeding survival as well as establishment. However, De Steven (1991b) reported no significant effect of clearing on survival but an effect of competition with herbaceous vegetation on height growth of seedlings. In this study, clearing had a significant effect on the final number of leaves and relative height growth of *G. littoralis* transplants.

4.4.3 Effects of caging treatment

Rodents and other predators may also have considerable impact on seed populations and seedling survival. In this study, a caging treatment was imposed that prevented access by hares, possums, rats and other large animals, but not mice and invertebrates. Most species had greater establishment in caged compared to uncaged plots, although the effect was not as apparent for seedling survival. This suggests that seed predation was more important than herbivory for most species. While rats probably ate some seed, seed predation by invertebrates such as slugs also appeared to affect seedling establishment. Invertebrate seed predation seemed to occur more in the broom and grassy habitats than under a canopy of native forest (personal observation). Similarly, several authors have reported higher rates of seed removal and consumption by predators in abandoned pasture than under a forest canopy (Nepstad *et al.* 1986, Ostfeld *et al.* 1997, Manson & Stiles 1998). Invertebrate predation appeared to affect *Coprosma* 'taylorii' and *Pittosporum tenuifolium* var. *colensoi* the most. Seeds of *Griselinia littoralis* were also affected but were still able to establish as invertebrates very rarely ate all of the seed (personal observation). Thus, seedlings with holes in their cotyledons were seen emerging from invertebrate attacked- seed.

As already noted, predation effects are often species specific (Meiners & Stiles 1997). They can also be related to seed size. For example, Reader (1993) reported no significant effect of excluding vertebrates on seedling emergence in four species with small seeds, but increased emergence in species with larger seeds. Contrary to theoretical predictions and this empirical finding, Blate *et al.* (1998) reported lower predation on larger seeds in Indonesian tropical rain forest. This was also the case in the present study, where the larger *Griselinia littoralis* seeds were less affected by invertebrate predation than the smaller seeds of *Coprosma* 'taylorii' and *Pittosporum tenuifolium* var. *colensoi*.

Interestingly, *C.* 'taylorii' and *G. littoralis* were the only two species that showed a significant positive effect of caging on survival. These two species are considered to be quite palatable to herbivores (the former to hares, and the latter to deer and goats). Seedlings of *Coprosma* 'taylorii' were often observed to have evidence of hare browse (stem clean-cut on an angle), especially at Raetihi hill (personal observation). Seedling survival of this species also showed a significant site by caging interaction. This suggests that there was more herbivory at one site than the other. Indeed, hares and their sign were observed more often in grassland at Raetihi hill than at the Mangatepopo sites. A significant habitat by caging interaction for seedling survival of these two species suggests that browsers are more common, or are more likely to eat seedlings in weedy areas than under a canopy of forest.

It is possible that caging may also have had an effect on the survival of broom seedlings, however survival of this species was not monitored (they were removed monthly as the high numbers establishing may have affected the other species). Broom is grazed readily by vertebrate herbivores in Australia, especially as seedlings (Smith 1994). Williams (1998) reported browsing of broom seedlings by hares (*Lepus europaeus*) and broom has also been identified in stomach contents of the introduced possum in New Zealand (Warburton 1978). Broom is also likely to be browsed upon by deer in the study area (Chris Buddenhagen pers. comm.). It should be noted that although seed predation and seedling herbivory can exert strong effects on seedling recruitment these effects may disappear by the time of plant maturation (Sork 1987, Edwards & Crawley 1999a).

Groundcover could also inhibit recruitment of seedlings by providing a habitat for seed and seedling predators. Consistent with this hypothesis, some studies show that predators remove more seeds and seedlings where ground cover was present than absent, thereby reducing seedling emergence (Gill & Marks 1991, Reader 1991b). This was probably not the case in the present study as there were few significant interactions between caging and clearing treatments. Occasionally, establishment and survival of seedlings was lower in plots that were caged only than in plots with no treatment. This could be because grass grows more rankly in caged plots without grazing pressure.

Edwards and Crawley (1999b) also found lower survival of seedlings in rabbit fenced plots where non-grazed biomass accumulated.

4.4.4 Effects of habitat

Habitat was found to be one of the most universal and important factors affecting the establishment and survival of seedlings, at least up to the age of 11 months. All species (except broom) had much greater establishment under a canopy of native forest than in the broom or grassy habitats. Similarly, other authors have found that the establishment of fleshy-fruited plants is favoured when seeds are deposited under trees rather than in open areas (Werner & Harbeck 1982, Walker & Vitousek 1991, Debussche & Isenmann 1994, Herrera *et al.* 1994, Meiners & Gorchov 1998). A number of factors might explain this differential establishment and survival including; improved water relations, better protection from frost, more available nutrients, presence of mycorrhizal fungi, and suppression from competing ground vegetation.

4.4.5 Shade and water relations

The presence of adult trees often facilitates the growth and survival of seedlings by ameliorating local microclimatic conditions (Harvey 2000). It is likely that a canopy cover of native forest provides an improved local water balance in the upper soil layer, particularly during summer, which is a critical period for the seedlings in the study region. This localised improvement in water relations is often explained by the shading effect of canopy plants (Debussche & Isenmann 1994, Herrera *et al.* 1994). For instance, several authors have found that artificial shading dramatically increased the emergence and survival of seedlings (Walker & Vitousek 1991, O'Connor 1995, Weltzin & McPherson 1999). Similarly, in this study, there appeared to be a relationship between measured light levels (a measure of canopy cover) and total seedling establishment and survival. Many more seedlings established and survived under more shaded conditions in the forest compared to the higher light levels found in broom and grassy habitats. In fact, the greatest establishment and survival of seedlings occurred in some of the darkest plots. However, there were a few exceptions. Naturally occurring manuka seedlings generally survived better in the broom habitat than in lower light conditions under a native forest canopy. This may be because manuka is a light demanding species and cannot tolerate heavy shading (Ogle-Mannering 1995).

Seedlings are dependent on the availability of sufficient soil moisture for establishment and survival (Davis *et al.* 1999, Weltzin & McPherson 1999). The year in which the study was carried out was drier on average than previous years (section 1.2.2) and may not reflect previous or future recruitment patterns. Ultimately, environmental factors that reduce soil water availability may reduce seedling survival by intensifying competition with herbaceous neighbours, whereas factors that increase water availability may increase seedling success by decreasing competition with neighbouring plants (Davis *et al.* 1998).

4.4.6 Effect of frosts

As already mentioned, the establishment of native woody species was favoured by greater canopy cover. One of the other effects of a more complete canopy is that seedlings growing underneath are more protected from the damaging effects of frost (Evans 1983). Indeed, many seedlings in the grass and broom habitats appeared to have been damaged by frost as they showed signs of blackened leaves and stems (personal observation). In fact, frost damage was probably one of the main causes of death in these habitats. Reitsma (1994) suggested that the frost hardiness of different species could be related to successional patterns after disturbance. Not only the maximum level of frost resistance is important, but also the time and magnitude of hardening and dehardening in spring and autumn (Levitt 1980). Some of the native species found in the broom habitat such as *Dracophyllum filifolium*, *Phyllocladus aspleniifolius* var. *alpinus*, and manuka (*Leptospermum scoparium*) have a high resistance to frosts in mid-winter (Reitsma 1994). This could help explain the greater survival of manuka seedlings in the broom habitat, compared with other native species. However, manuka dehardens quickly in spring and is thus prone to damage by infrequent summer frosts (Reitsma 1994). Other species listed in order of decreasing resistance to frosts include: *Pittosporum tenuifolium* (Bannister *et al.* 1995). *Griselinia littoralis* (Bannister 1985, Neuner & Bannister 1995), *Coprosma* species (Bannister & Lee 1989), and *Pseudopanax arboreus* (Reitsma 1994) which is closely related to *P. colensoi*. Broom seedlings also have a high frost resistance (Timmins & McKenzie 1995). Although the frost resistance of *Coprosma* 'taylorii' is not known, it seems likely that this species is fairly resistant given the comparative abundance of its seedlings and saplings in weedy areas.

Furthermore, frost resistance and drought resistance are related, so that many plants that are resistant to frost are also resistant to drought (Levitt 1980). Both manuka (*Leptospermum scoparium*) and broom (*Cytisus scoparius*) are known to be relatively drought tolerant and able to survive low water potentials without showing obvious signs of stress (Bannister 1986, Timmins & McKenzie 1995). In comparison, other native species, such as those examined in this study, are more prone to water stress in dry conditions (Bannister 1986, Timmins & McKenzie 1995).

4.4.7 Nutrient availability

Minerals necessary for plant survival and growth can often be limiting. Due to its low mobility in the soil, phosphorous is especially important for determining early seedling growth (Fenner & Lee 1989). Nutrients may be limiting seedling survival in the study area, especially in broom and grassy habitats where competition is probably greater. Soil nutrient accumulation has been found to be two or three times higher beneath adult trees than in adjacent grassland (McPherson *et al.* 1993, Scholes & Archer 1998, Weltzin & McPherson 1999). However, experimental addition of nutrients by Weltzin and McPherson (1999) indicated that soil nutrients did not limit seedling growth in their study. Similarly, nitrogen is unlikely to be limiting under a canopy of broom as this shrub has an association with nitrogen-fixing bacteria (Peterson & Prasad 1998). However, a pilot study by Waterhouse (1986) was unable to demonstrate nutrient enrichment of soil by broom in Australia.

Linked with nutrient availability is the association of plants with mycorrhizal fungi. These symbionts can increase the survival and growth rate of seedlings by increasing their ability to uptake limiting nutrients such as phosphorous (Hartnett *et al.* 1994). Seedlings growing under a canopy of native forest or near forest margins are probably more likely to come into contact with their symbionts than those growing in non-forest areas. Therefore, a lack of mycorrhizal symbionts may be limiting native woody seedling survival in non-forest areas. Johnson (1985) found that the soil concentration of phosphorus required for growth without mycorrhiza was greater for species with coarse root systems than for those with fine root systems. For instance, when grown without their associated mycorrhizae, *Griselinia littoralis* (a species with thick roots)

required more phosphorous than *Coprosma robusta*, which has fine roots (Johnson 1985).

4.4.8 Limitations

Unfortunately, it was only possible to investigate the very early stages of seedling establishment and survival in this study. Short time-scales are also a problem with many of the examples in the literature (Clark *et al.* 1999). Few studies continue monitoring for long enough to determine whether or not self-sustaining populations were successfully established (Turnbull *et al.* 2000). However, as all of my plots are permanently marked, it will be possible to remeasure seedling survival in the future and the Department of Conservation has expressed an interest in further monitoring.

4.4.9 Conclusions

In this study, the establishment of most native woody species was increased by a greater canopy cover, protection from most seed and seedling predators, and removal of vegetative ground cover and/or litter. Experimental addition of seeds also increased seedling establishment for two of the three species studied. Thus, most species were found to be both seed and microsite limited for the establishment of seedlings. However, the effects of seed addition and other experimental factors on seedling survival were generally less apparent. This may be due to smaller sample sizes with the result that there is less statistical power for detecting significant differences. Results from this chapter are discussed in relation to differential species invasion and succession in Chapter 5.

Chapter 5

GENERAL DISCUSSION

*"The ultimate test of the value of our work is whether we
really can make predictions about the real world"*

Paul Keddy, 1991.

GENERAL DISCUSSION

The purpose of the current chapter is to synthesise and discuss the findings of previous chapters in order to provide an overall picture of vegetation change in the study areas. Likely scenarios for successional pathways are presented and management options aimed at accelerating succession are also discussed.

5.1 Factors limiting succession in weedy areas

A number of factors are probably limiting the rate of succession in the weedy areas studied, including both the availability of seed and suitable microsites. Very few native seeds are being dispersed into weedy areas, with the exception of some wind dispersed species such as manuka (*Leptospermum scoparium*). Seed densities of most native species decline dramatically with increasing distance from the forest edge in the broom habitat (section 2.3.3). In most cases, less seed input will lead to less establishment of seedlings. Two of the three species used in sowing experiments were shown to be seed limited (*Griselinia littoralis* and *Coprosma* 'taylorii') (section 4.3.1). Very low establishment of the third species (*Pittosporum tenuifolium* var. *colensoi*) made it difficult to detect any statistically significant differences between sown and unsown plots. This species may have been limited by post-dispersal seed predation by invertebrates (4.4.3) and/or the necessity of bird passage for germination (3.4.1).

Sowing seed into the exotic grass sward that dominates the non-forest vegetation at both sites, largely failed to produce significant numbers of seedlings. However, all species showed increased establishment in plots that were cleared of this ground cover. Thus, in the absence of disturbance, a lack of suitable microsites in weedy areas is also limiting succession to native vegetation. In non-forest habitats, seedlings have to cope with competition from the dense layer of exotic grasses, less protection from frosts, greater temperature extremes, and an increased risk of drying out (4.4.4). Even in the cleared plots, seedling establishment was often low suggesting that disturbance alone might not allow those seedlings to persist. Recruitment of native seedlings may also be limited by a lack of suitable mycorrhizal fungi, or by higher levels of predation and herbivory in weedy areas (4.4.3). Experimental treatments had less significant effects on seedling survival compared with establishment. This may be due to lower sample sizes, or a

narrower window of establishment compared with survival. Since succession in weedy areas depends on both establishment and survival of native woody species, it is likely that a combination of these factors is limiting the rate of succession.

5.2 Differential species invasion

The species studied differed in seed availability, germination responses and seedling survival in this study. These differences can form the basis for predictions as to which species are most likely to invade weedy areas. Although *Griselinia littoralis* had the best establishment and survival of the three species used in the planting experiments (section 4.3.1), very few seeds of this species were dispersed into weedy areas (2.3.2.4). Because this species appears to be limited by a lack of dispersal, very few seedlings are likely to successfully establish naturally in weedy areas. Low seedling and sapling densities of *G. littoralis* in weedy areas confirms this (1.4.2, 1.4.3). *Coprosma* 'taylorii' had the next highest densities of seedlings establish from the seed sowing experiments. It also had a greater seed availability (2.3.2.4), which might help explain the relatively higher proportion of seedlings and saplings of this species in weedy areas (1.4.2, 1.4.3). *C.* 'taylorii' was also the only native species to have reasonable densities of seedlings and saplings in the grassy habitat at Raetihi hill, even though this microsite appears to be the least suitable for seedling establishment and survival (1.4.2.3). Thus, of all the bird dispersed species, *C.* 'taylorii' is probably the most likely to invade the weedy areas. *Pittosporum tenuifolium* var. *colensoi* had the poorest performance in terms of dispersal, establishment, and survival, and would not be expected to be a major invader. However, seedlings of this species that did establish from sown seed grew much faster than other species (personal observation). Thus it may be a better competitor once it has reached a certain size. Of all the fleshy fruited species, lancewood (*Pseudopanax crassifolius*) had the greatest dispersal into weedy areas both in terms of abundance and distance from the forest edge. However, seedling establishment and survival for this species was very low in weedy areas. Lancewood appears to be limited by a lack of suitable microsites, even when the ground cover is disturbed. Indeed, although seedlings and saplings of this species were common in forest habitats (especially at Raetihi hill), none were found in weedy areas (1.4.3). Manuka had by far the greatest seed densities dispersed into weedy areas. However, establishment of this species is also apparently limited by a lack of suitable microsites. In this case, seedlings appear to require disturbance to successfully establish (4.3.2). Once established, manuka appears to have a greater ability to tolerate the

more exposed conditions in weedy areas than most other native species (4.4.6). Although very low seed densities of *Phyllocladus aspleniifolius* var. *alpinus* were caught in non-forested areas, seedlings of this species were quite commonly found under a canopy of heather (1.4.2.2). Indeed, this species has often been found in heather-dominated vegetation and may be a good invader of such weedy areas (Rogers 1996). Since dispersal and recruitment of most other native species was negligible, it can be assumed that they are unlikely to rapidly invade and persist in weedy areas.

During the course of this study, rooting by feral pigs caused considerable disturbance in some broom habitats. In doing so, these animals may possibly encourage succession to native forest by making more suitable microsites for recruitment of native seedlings. However, native shrubs were also found uprooted by pigs in weedy areas on several occasions (personal observation). Pigs in the area also had a short return period every 2-3 months. So any seedlings that might establish since the last pig rooting may be uprooted in the next episode. Given their other effects on native vegetation, feral pigs probably do more harm than good.

5.3 Seed banks

Seedlings can establish from two sources; the recent seed rain, or the more persistent seed bank. Seed rain has already been discussed in Chapter 2, and because seed banks were not directly measured in this study, it is useful to review knowledge of them here. Many native species have transient seed banks, as most seeds are only viable for less than a year (Partridge 1989, Ogle-Mannering 1995, Sem & Enright 1996). Sem & Enright (1996) estimated that only 10% of the annual seed rain entered the persistent soil bank in a forest remnant near Auckland. They also note that most of the seeds entering the seed bank were from exotic species. In fact, it has often been stated that there is little relationship between the composition of the soil seed bank and current vegetation in forested areas (Hopkins & Graham 1984, Enright & Cameron 1988, Partridge 1989, Sem & Enright 1996).

In contrast, seed banks in weedy areas are likely to be more similar to their current vegetation. For example, mature broom stands in New Zealand and overseas generally have a large and deeply buried bank of broom seeds ranging from 400 to 5000 per square metre (Smith & Harlen 1991, Partridge 1992, Rees & Paynter 1997, Gorman 1998).

There appears to be a trend towards accumulation of larger seed banks under more mature stands. For example, Williams (1998) found an average of 3300 broom seeds per square metre in the seed bank under mature broom in the South Island. In comparison, Gorman (1998) found only 112 to 365 broom seeds per m^2 in relatively young broom patches in Tongariro National Park. Williams (1998) found the highest numbers of broom seeds under patches of dead broom and grass swards.

Broom seeds can stay viable in the seed bank for up to 60 years (Parker *et al.* 1994), and usually only a small proportion of the seed bank germinates each year (Williams 1981). However, at Barrington Tops in Australia, A Sheppard and P. Hodge (unpublished data) found that in the absence of seed rain, the seed bank declined by about 50% over one year (Hosking *et al.* 1996). In contrast, Williams (1998) found no measurable decline in the broom seed bank over four years despite the emergence of seedlings after spraying adult plants in the South Island of New Zealand.

In my study, more broom seedlings established where disturbance had occurred (section 4.3.2). For example, the number of broom seedlings was much higher in areas cleared of exotic grasses (213 per m^2) than in undisturbed grassy areas (35 per m^2). Most of these released seedlings probably came from the seed bank. Disturbance also increased the establishment of some native species (where seed was available). However, because broom has a much larger seed bank, there is a high probability that it would dominate following disturbance. Even if all the adult broom plants were removed it seems likely that broom is capable of persisting for many generations in the study area as long as conditions remain suitable. Thus, attempting to control broom by chemical or mechanical means in these areas is likely to be ineffective in the short term as well as cost prohibitive in the long term.

5.4 Likely scenarios for successional pathways at Mangatepopo

The future vegetation of the study areas depends on the presence or absence of seedlings and saplings of other species in the understorey, the ability of seed to invade the community, and the suitability of conditions for establishment and survival. There were few native saplings and seedlings found in the broom habitat at the Mangatepopo sites. The exceptions were manuka saplings (*Leptospermum scoparium*) which were found in reasonably high densities at transect B, and *Coprosma* 'taylorii' seedlings and saplings

found at transect A. The area sampled by transect B (opposite Mangatepopo school camp, Fig. 1.2) appears to be further along in the succession to native forest than the apparently older senescent broom stands sampled by transects A and C. However, the successional sequence around transect B may in fact be older because there was evidence of a previous generation of broom existing before the current population (1.4.1.4). This apparent anomaly could also be explained if manuka established at the same time as the current broom population, probably after a reasonably large disturbance. This area also had a slightly higher availability of native seeds in the seed rain than the other study sites (2.3.3). The greater canopy cover provided by younger broom stands in this area may also provide more suitable conditions for recruitment of native seedlings. In fact, some species had significantly more seedlings establish and survive at this transect than any other (4.3.2).

Observations of broom stands of different ages leads to the conclusion that broom goes through cycles in the study area. The overall picture is of an initially dense population of young broom plants progressively thinning out as they age. As senescent plants collapse, canopy cover of broom becomes increasingly patchy. The increase in light levels following senescence is usually followed by rapid establishment and growth of broom seedlings, especially in disturbed areas (section 1.4.4). In the absence of disturbance, as the broom canopy breaks down, there is an increase in growth of exotic grasses and/or heather, which as a result generally suppress the establishment of native species. Thus, rather than conditions becoming easier for the succession of woody species into broom stands with time, the reverse appears to be true as the exotic grasses increase in dominance.

On the basis of seed availability, and the establishment and survival responses of all species examined, broom would be expected to remain dominant at least in the short term (probably for several more generations) in most places. Broom stands opposite Mangatepopo school camp may succeed to native forest in a relatively shorter time, as they already have reasonable densities of manuka saplings scattered in amongst the broom. Since later-successional species generally have a longer lifespan and a taller maximum height (Huston & Smith 1987), some native species can be expected to eventually over-top broom. However this process could be very slow, as the species currently present and most capable of invading weedy areas such as manuka, *Coprosma*

'taylorii', flax (*Phormium tenax*) and toetoe (*Cortaderia toetoe*) do not normally grow taller than broom. However, conversion of broom-dominated vegetation to native shrubland by these pioneer species would probably encourage succession of other native species. Both manuka and flax have been shown to be good nurse species elsewhere (Porteous 1993, Reay & Norton 1999), and based on observations from this study, *Coprosma* 'taylorii' and toetoe probably are too.

Another possible scenario is that heather could invade grassland to a greater extent (currently it only dominates small patches under broom). This would probably increase the probability of native seedlings establishing as observations suggest that native seedlings are more common under heather than in grass as long as there is an available seed source.

If for some reason adult broom plants were removed from these areas, the most likely scenario would be thick swards of grasses, heather, and a new generation of broom seedlings. However, native seedlings are more likely to establish and survive under a canopy of broom (especially in the denser stages) than in open grassland with no canopy. Thus in a way, broom may facilitate recruitment of native species by first acting as a perching place for bird dispersers, secondly by ameliorating conditions beneath its canopy, and thirdly by inhibiting the growth of exotic grasses to some extent (especially in younger denser stages). However, as there was no experimental removal of broom in this study, it is difficult to know for certain its effect on other species.

5.5 Likely scenarios for successional pathways at Raetihi hill

Even though this area has been retired from farming for 40 years, thick swards of exotic grasses still dominate the landscape on the flats. Native woody seedlings are mostly found under a canopy of forest or on logs where conditions are apparently more suitable. Dispersal of native seeds into open grassland is very low and probably limited by a lack of perches for bird-dispersed species. Even with the addition of seed and clearing of exotic grasses, very few native seedlings established and survived in grassy habitats. Thus, suitable microsites appear to be limiting recruitment. In comparison, seedling recruitment was much better at Mangatepopo under a canopy of broom than in grassy areas at Raetihi hill. Possible reasons for this include the damaging effects of frosts and greater moisture stress on seedlings establishing in the open, or increased competition

from the relatively thicker grass swards at this site. Raetihi hill also had less rainfall than at Mangatepopo during the study period. In addition, browsers such as hares may have caused more damage at Raetihi hill (4.4.3). Given all these limiting factors, succession will probably only occur by slow spread from the margins of existing patches of woody vegetation (nucleation).

The comparative abundance of *C.* 'taylorii' saplings in grassy areas (1.4.3) suggests that this species is sometimes able to establish and survive in this habitat, despite the results of seed sowing experiments which showed very low recruitment (4.3.1.4). This species will probably also act as a 'nucleation' site for other native species. In some places, bracken is invading the exotic grasses (personal observation). Given enough seed dispersal, some woody native species may be able to invade and overtop the bracken. However, other authors have stated that areas of bracken can persist for generations in certain situations without succession (Partridge 1992, Porteous 1993, Reay & Norton 1999).

5.6 Management options

The first major decision when considering the future of weedy areas is whether active management is required to encourage a succession to native forest. One of the major factors in determining whether weedy areas will revert to native forest without active management is whether seed is present at the site. The general absence of most native woody species from the standing vegetation, short dispersal distances, and the transient nature of the seed bank, means that the availability of native seeds is likely to be limiting the rate of succession in weedy areas. Conditions in weedy areas also seem to be unsuitable for the establishment of native species, hence the availability of suitable microsites is also limiting.

Active management may be desirable to accelerate succession to native forest. Active management can also be useful in establishing species that have become locally extinct. There are several management options that may be appropriate, including addition of native seed, improving conditions for native seed germination and establishment, and transplanting native seedlings. Adding seed will probably not be very effective by itself, as most native seedlings did not establish well in the exotic grasses dominating most areas. Succession from weedy areas to native forest could be hastened by disturbance (or spraying) of the ground cover to provide more suitable microsites for natural

establishment of well-dispersed species such as manuka. Spraying grass around the margins of forest patches with a grass selective herbicide would reduce competition from exotic grasses at the margins where dispersal and recruitment of native seedlings are more likely. Dense sowing of native seed on newly cleared sites would also increase the probability of seedling establishment. For example, laying down branches of manuka bearing ripe seed capsules over disturbed soil is one option (Porteous 1993). As the branches dry out, the capsules split open and release large quantities of seed. Even though broom seedlings will still germinate from the seed bank at the Mangatepopo sites, manuka is likely to be able to compete with broom and provide a more suitable microhabitat for other native species to establish under (Evans 1983).

Another option is to transplant seedlings or saplings. This would bypass the high mortality risks involved with germination and early establishment. However, transplanted seedlings are often at risk from herbivory. Nevertheless, in this study, although herbivory appears to have claimed some seedlings, it does not seem to be the most important factor affecting seedling survival. Instead, the effects of type of habitat, especially canopy cover seems to be most important. Thus, seedlings planted under younger broom stands with greater canopy cover are more likely to survive. It may be advisable to wait until the next generation of broom is in a denser phase (probably around 5 years from now) before transplanting seedlings. However, obviously if these seedlings are already being grown there will also be an optimal time to plant them before they grow too large. Choice of species for transplanting is also important. For example, fleshy-fruited native shrubs that are attractive to frugivorous birds will increase the food supply for native dispersers. They will also encourage nucleation at the same time by promoting the addition of seed and amelioration of conditions under their canopy. However, many of the bird dispersed species have lower tolerance to frost and drought than wind dispersed species such as manuka and *Dracophyllum* species (4.4.6). Therefore, transplant losses may be less for these latter species. Although the frost resistance of *Coprosma* 'taylorii' is not known, it seems likely that this species is relatively hardy given its persistence in weedy areas. Thus, C. 'taylorii' could be another good candidate for transplantation.

5.7 Further research

There were clear differences between forest and non-forest habitats in terms of seedling establishment and survival (4.4.4). As I only directly tested the influence of two factors on seedling establishment and survival (disturbance and predation), further research on other factors would be recommended. For example, experiments using shadecloth to simulate canopy cover, or removal of different densities of broom plants, could test the importance of canopy cover (for frost protection etc) on native seedlings. Lower recruitment of native seedlings in weedy areas may also be due to lower moisture, or nutrient levels, greater temperature extremes, or absence of symbiotic mycorrhizae. Experiments designed to test each of these hypotheses would help to tease these mechanisms apart. The planting experiments presented in chapter 4 were limited to areas dominated by exotic grasses. Although initial observations suggest that native seedlings can establish under a canopy of heather, similar planting experiments would be useful in testing the specific effects of heather on seedlings. If heather continues to invade the grassland under broom then the question of whether or not seedlings can establish in exotic grasses may become irrelevant at the Mangatepopo sites. Since this study was constrained by the length of a Masters project, it was only possible to investigate the very early stages of seedling establishment and survival. Given that it is difficult to study successional processes in such a short time-scale, I highly recommended that the plots be remeasured in the future. Monitoring changes over time would provide a better picture of the rate of succession in weedy areas.

5.8 Conclusions

Results from this study indicate that recruitment of native woody plants within weedy areas (broom and grassy habitats) is relatively low. Recruitment of natives was constrained by low rates of seed dispersal for most species, coupled with a low probability of seedling establishment and survival in areas without disturbance. Broom would appear to be capable of replacing itself at the Mangatepopo sites. It can establish in undisturbed areas, although increased establishment was observed when ground cover was disturbed. On the basis of seed availability, establishment, and survival of woody species, a relatively stable broom community with only the occasional occurrence of native trees would be predicted for most areas. Eventually these natives will grow up and overtop the broom, but it is likely to be a slow process. With active management however, the rate of succession to native forest can almost certainly be accelerated.

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APPENDIX 1

Table 1.1 Weather data collected at Whakapapa field station located at Latitude 39° 11.8'
S and Longitude 175° 23.7' E.

Month	Total rainfall (mm)	Mean daily minimum grass temperature (°C)	Mean soil temperature (°C at 10 cm depth)	Mean minimum air temp. (°C)	Mean maximum air temp. (°C)
May 1999	472.9	0.8	5.9	2.6	11.2
June 1999	199.3	-2.3	4.0	-0.1	7.7
July 1999	254.5	-2.5	3.1	-0.5	7.2
August 1999	282.4	-3.6	2.5	-1.3	7.4
September 1999	128.0	-4.1	4.6	3.5	10.5
October 1999	106.0	0.8	7.5	2.6	12.5
November 1999	330.1	3.7	9.5	4.7	13.5
December 1999	181.5	2.3	10.0	3.8	14.6
January 2000	170.9	5.6	11.8	6.8	16.3
February 2000	17.4	4.9	12.8	6.6	20.1
March 2000	70.8	3.0	11.4	5.5	16.6
April 2000	118.2	2.7	8.7	3.9	13.4
TOTAL	2332.0				

Table 1.2 Weather data collected at Ohakune field station located at Latitude 39° 24.5' S
and Longitude 175° 25.1' E.

Month	Total rainfall (mm)	Mean daily minimum grass temperature (°C)	Mean minimum air temperature (°C)	Mean maximum air temperature (°C)
May 1999	169.5	0.2	3.8	13.6
June 1999	111.0	0.4	1.9	10.3
July 1999	141.1	0.1	1.3	8.0
August 1999	125.2	-0.7	0.4	10.8
September 1999	84.2	0.9	2.4	13.5
October 1999	38.3	4.5	5.6	15.9
November 1999	218.6	6.7	8.3	17.3
December 1999	65.1	6.3	7.6	17.3
January 2000	208.2	8.7	9.7	19.7
February 2000	125.0	6.8	7.7	21.4
March 2000	356.0	5.1	6.5	19.6
April 2000	146.8	7.0	7.9	16.3
TOTAL	1789.0			

Table 1.3 Matrix of pairwise mean differences of species richness between habitats. *
indicates those that are significantly different at the 1% level (Bonferroni's test)

SITE	Mangetepopo		Raetihi hill	
Habitat	**ForestA**	**Broom**	**ForestB**	**Grass**
ForestA	-	-	-	-
Broom	-13.33*	-	-	-
ForestB	0.60	13.93*	-	-
Grass	-14.78*	-1.44	15.38*	-
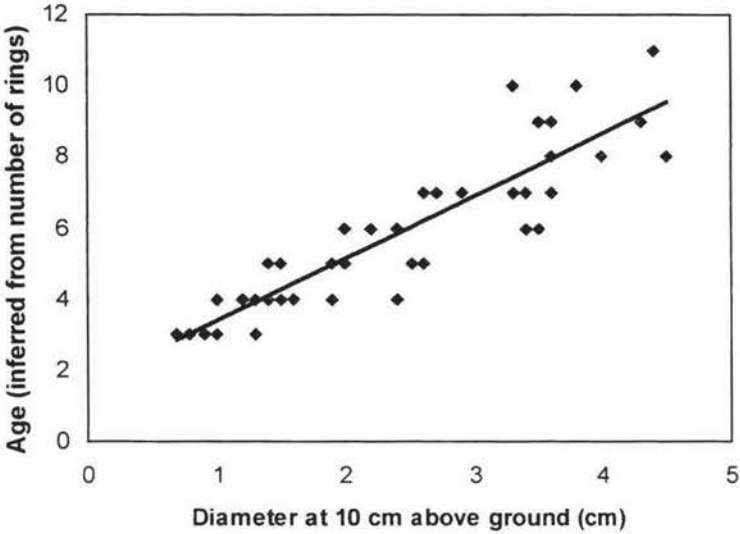
Fig. 1.1 Linear regression of diameter and age of harvested broom plants.
$(y=1.76x + 1.65, N = 47, P<0.001, R^2=0.79)$

Table 1.4 Environmental characteristics of 21 5x5 m plots located at Mangatepopo. NB:
m.a.s.l = metres above sea level, * denotes naturalised exotic species, *Gri lit = Griselinia
littoralis, Phy asp = Phyllocladus aspleniifolius* var. *alpinus, Lep sco = Leptospermum
scoparium* (manuka), *Heb str = Hebe stricta, Cyt sco = Cytisus scoparius* (broom), *Pte esc
= Pteridium esculentum* (bracken), *Cal vul = Calluna vulgaris* (heather), *Cor toe =
Cortaderia toetoe, Pho ten = Phormium tenax* (flax).

Habitat	Plot	Altitude (m.a.s.l)	Aspect (°)	Slope (°)	Mean litter depth (cm) n= 8 per plot	Main canopy species
Forest	A7	735	28	6	2.25	*Gri lit, Phy asp*
Forest	B1	758	62	22	4.25	*Lep sco, Phy asp*
Forest	B2	760	238	2	6.00	*Lep sco, Cyt sco**
Forest	C1	690	90	3	5.25	*Lep sco, Phy asp*
Forest	C2	690	20	4	2.88	*Lep sco, Heb str*
Broom	A1	735	100	2	7.50	*Cyt sco*, His inc*
Broom	A2	735	243	3	2.88	*Cyt sco*, Pte esc*
Broom	A3	733	295	4	6.75	*Cyt sco*, Pho ten*
Broom	A4	733	0	0.5	5.00	*Cyt sco**
Broom	A5	732	21	2	3.13	*Cyt sco*, Pho ten*
Broom	A6	732	288	4	12.25	*Cyt sco*, Cal vul**
Broom	B3	760	100	4	9.88	*Cyt sco*, Cal vul**
Broom	B4	758	40	1	5.75	*Cyt sco**
Broom	B5	758	342	7	7.25	*Cyt sco*, Cal vul**
Broom	B6	757	340	3	6.13	*Cyt sco*, Cal vul**
Broom	B7	757	65	3	9.50	*Cyt sco*, Cal vul*
Broom	C3	689	90	2	4.13	*Cyt sco*, Cal vul**
Broom	C4	688	330	5	2.50	*Cyt sco*, Cor toe*
Broom	C5	687	300	2	2.75	*Cyt sco**
Broom	C6	686	330	2	3.00	*Cyt sco**
Broom	C7	686	325	2	2.25	*Cyt sco**

Table 1.5 Environmental characteristics of 14 5x5 m plots located at Raetihi hill. NB: *Gri lit = Griselinia littoralis, Cop gra = Coprosma grandifolia, Cop tay = Coprosma* 'taylorii', *Pen cor = Pennantia corymbosa* (ducksfoot), *Car ser = Carpodetus serratus* (putaputaweta), *Nes cun = Nestegis cunninghamii* (black maire), *Dac dac = Dacrydium dacrydioides* (kahikatea), *Heb str = Hebe stricta, Pse cra = Pseudopanax crassifolius* (lancewood).

Habitat	Plot	Altitude (m.a.s.l)	Aspect (°)	Slope (°)	Mean litter depth (cm) n= 8	Main canopy species
Forest	D1	740	46	14	10.00	*Gri lit, Cop gra*
Forest	D3	735	24	8	11.75	*Pen cor, Gri lit*
Forest	D5	728	340	18	5.50	*Car ser, Cop tay*
Forest	D7	726	330	18	5.75	*Heb str, Gri lit*
Forest	E1	735	210	30	7.20	*Nes cun, Gri lit*
Forest	E5	724	32	2	5.00	*Dac dac, Cop tay*
Grass	D2	739	350	12	8.50	None
Grass	D4	739	18	9	10.00	None
Grass	D6	727	102	5	9.88	None
Grass	E2	735	30	10	4.50	*Heb str*
Grass	E3	730	30	20	3.50	*Cop tay, Pte esc*
Grass	E4	725	30	3	5.38	None
Grass	E6	724	90	5	5.00	*Lep sco*
Grass	E7	723	35	1	7.34	*Lep sco, Pse cra*

Table 1.6 Summary of stand characteristics in 21 5x5 m plots at Mangatepopo. Ages are predicted from diameter/age regression (see Fig. 1.1 previous page).

Habitat	Plot	Total basal area (m²)	Total density (stems/m²)	Canopy cover (%)	Maximum height (m)	Maximum broom age (yrs)	Mean broom age (yrs)
Forest	A7	0.17	0.60	72	7.8	-	-
Forest	B1	0.14	2.76	90	7.0	-	-
Forest	B2	0.05	2.60	30	3.1	25	6
Forest	C1	0.04	2.00	54	3.9	-	-
Forest	C2	0.10	1.84	92	3.8	8	7
Broom	A1	0.02	0.36	20	3.5	18	12
Broom	A2	0.02	0.40	12	3.8	15	10
Broom	A3	0.03	0.64	30	3.9	20	10
Broom	A4	0.03	1.20	24	4.2	13	8
Broom	A5	0.04	0.80	35	3.9	16	9
Broom	A6	0.01	1.36	26	2.9	13	7
Broom	B3	0.01	2.04	24	2.3	8	4
Broom	B4	0.04	5.44	35	3.7	11	5
Broom	B5	0.02	0.56	23	3.1	12	8
Broom	B6	0.03	9.88	50	2.7	9	4
Broom	B7	0.001	1.72	10	2.8	10	5
Broom	C3	0.03	1.08	22	4.0	13	8
Broom	C4	0.04	3.56	45	3.6	13	5
Broom	C5	0.02	0.76	12	3.6	18	8
Broom	C6	0.001	0.16	1	1.7	8	4
Broom	C7	0.03	0.52	26	4.0	16	11

Table 1.7 Summary of stand characteristics in 14 5x5 m plots at Raetihi Hill

Habitat	Plot	Total live basal area (m^2)	Total density $(stems/m^2)$	Canopy cover $(\%)$	Maximum height (m)
Forest	D1	0.42	1.04	95	4.0
Forest	D3	0.35	0.56	80	6.7
Forest	D5	0.05	0.68	44	3.9
Forest	D7	0.20	0.60	95	3.9
Forest	E1	0.28	1.04	96	6.5
Forest	E5	0.15	0.88	48	6.5
Grass	D2	0.01	0.12	4	2.3
Grass	D4	0	0	0	0.9
Grass	D6	0	0	0	0.7
Grass	E2	0.01	0.16	46	2.1
Grass	E3	0.01	0.40	16	1.7
Grass	E4	0	0	0	0.6
Grass	E6	0.002	0.04	16	2.2
Grass	E7	0.01	0.12	4	3.5

Table 1.8 Results from a loglinear analysis on three species of seedlings found in different microsites, % = percentage of deviance explained by each source, % cover = percent cover of each microsite in each plot (log base 10 transformed).

		Cytisus scoparius		*Griselinia littoralis*		*Coprosma* 'taylorii'	
Source	DF	%	P	%	P	%	P
Site	1	-	-	0.65	0.0002	9.6	0.0001
Habitat	2	0.56	0.0001	32.44	0.0001	16.53	0.0001
Transect	3	24.35	0.0001	4.13	0.0001	17.04	0.0001
% cover	1	42.40	0.0001	27.56	0.0001	28.84	0.0001
Microsite	4	1.52	0.0001	9.84	0.0001	6.95	0.0001
Habitat*microsite	12	1.74	0.0001	4.05	0.0001	5.67	0.0001
Total		70.57		78.67		84.63	0.0001

Table 1.9 Species list for Raetihi hill

SCIENTIFIC NAME   **COMMON NAME**

Trees and shrubs:

Aristotelia serrata   wineberry, makomako
Brachyglottis repanda   bushman's toilet paper, rangiora
Carpodetus serratus   putaputaweta, marbleleaf
Coprosma foetidissima
Coprosma grandifolia
Coprosma robusta   karamu
Coprosma rotundifolia
Coprosma 'taylorii'   NB: species 27 in Wilson & Galloway (1993)
Coprosma tenuifolium
Coriaria arborea   tutu
Cyathodes juniperina   prickly mingimingi
Dacrydium cuppressinum   rimu, red pine
Dacrycarpus dacrydioides   kahikatea, white pine
Elaeocarpus dentatus   hinau
Elaeocarpus hookerianus   pokaka
Fuchsia excorticata   kotukutuku, tree fuchsia
Griselinia littoralis   kapuka, broadleaf
Hebe stricta   koromiko
Leptospermum scoparium   manuka, teatree
Leucopogon fasiculata   mingimingi
Melicytus lanceolatus   mahoe wao
Melicytus ramiflorus   mahoe
Nestegis cunninghami   black maire
Nestegis lanceolatus   white maire
Nothofagus solandri var. *cliffortioides* mountain beech, tawhai rauriki
Pennantia corymbosa   ducksfoot, kaikomako
Pittosporum tenuifolium var. *colensoi*   kohuhu
Podocarpus hallii   mountain totara, Hall's totara
Prumnopitys ferruginea   miro, brown pine
Prumnopitys taxifolia   matai, black pine
Pseudopanax crassifolius   lancewood, horoeka
Pseudopanax colensoi   five-finger, whauwhaupaku
Pseudowintera colorata   horopito, peppertree
Schefflera digitata   pate, seven-finger
Weinmannia racemosa   kamahi

Climbers/lianes:

Clematis foetida   clematis, puawananga
Clematis forsterii   clematis
Metrosideros diffusa   climbing rata
Muehlenbeckia complexa   pohuehue
Parsonsia capsularis var. *tenuis*   native jasmine, aka kiore
Parsonsia heterophylla   native jasmine, kaiwhiria
Rubus cissoides   bush lawyer, tataramoa
*Rubus fruticosa**   blackberry

Rubus schmidelioides	bush laywer

Ferns:

Asplenium bulbiferum	hen and chicken's fern, mouku
Asplenium flaccidum	hanging spleenwort, makawe
Asplenium polyodon	sickle spleenwort, petako
Blechnum discolor	crown fern, piupiu
Bechnum fluviatile	creek fern, kiwikiwi
Blechnum pennamarina	
Bechnum sp (Kiokio)	palm-leaf fern, kiokio
Cyathea smithii	soft tree fern, katote
Dicksonia fibrosa	wheki-ponga
Histiopteris incisa	waterfern, matata
Hymenophyllum species	filmy fern, mauku
Leptopteris hymenophylloides	single crape fern, heruheru
Paesia scaberula	ring fern, matata
Phymatosorus diversifolius	hound's tongue fern, kowaowao
Polystichum richardii	common shield fern, pikopiko
Polystichum vestitum	prickly sheild fern, puniu
Pteridium esculentum	bracken, rarahu
Tmesipteris sp	

Monocotyledons:

Agrostis capillaris*	browntop
Anthoxanthum odoratum*	sweet vernal
Carex germinata	bush sedge
Cortaderia toetoe	toetoe, cutty grass
Dactylis glomerata*	cocksfoot
Festuca rubra*	chewings fescue, red fescue
Holcus lanatus*	yorkshire fog
Juncus articulatus	sedge
Phleum pratense*	timothy
Uncinia uncinata	hookgrass, kamu
Vulpia bromoides*	vulpia hair grass

Herbaceous dicotyledons:

Acaena sp	bidibid, piripiri
Achillea millefolium*	yarrow
Calluna vulgaris*	heather
Cirsium arvense*	californian thistle
Digitalis purpurea*	foxglove
Hypochaeris radicata*	catsear
Lotus pedunculatus*	lotus
Senecio jacobaea*	ragwort
Trifolium repens*	white clover

Table 1.10 Species list for Mangatepopo sites

SCIENTIFIC NAME   **COMMON NAME**

Trees and shrubs:

Aristotelia fruticosa
Carmichaelia ensyii var. *orbiculata*   native broom
Carpodetus serratus   putaputaweta, marbleleaf
Coprosma foetidissima
Coprosma propinqua   mingimingi, mikimiki, black scrub
Coprosma propinqua x robusta
Coprosma rhamnoides   twiggy coprosma
Coprosma robusta   karamu
Coprosma 'taylorii'   NB: species 27 in Wilson & Galloway (1993)
Coprosma tenuifolia
Cordyline australis   cabbage tree, ti kouka
*Cotoneaster franchesii**
*Cotoneaster simonsii**
Cyathodes juniperina   prickly mingimingi
Dracophyllum filifolium   grass tree
Dracophyllum longifolium   grass tree
Griselinia littoralis   broadleaf
Hebe stricta   koromiko
Leptospermum scoparium   manuka, teatree
Melicytus lanceolatus   mahoe wao
Myrsine divaricata
Phyllocladus aspleniifolius var. *alpinus* tanekaha
*Pinus contorta**   lodgepole pine
Pittosporum tenuifolium var. *colensoi* kohuhu
Podocarpus hallii   mountain totara, Hall's totara
Prumnopitys ferruginea   miro, brown pine
Prumnopitys taxifolia   matai, black pine
Pseudopanax colensoi   fivefinger
Pseudopanax crassifolius   lancewood, horoeka
Pseudowintera colorata   horopito, peppertree
Olearia arborescens

Climbers/lianes:

Clematis forsterii   clematis, puawananga
Parsonsia heterophylla   native jasmine, kaiwhiria
Rubus cissoides   bush lawyer, tataramoa
*Rubus fruticosa**   blackberry
Rubus schmidelioides   bush lawyer, tataramoa

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Ferns:

Asplenium flaccidum	hanging spleenwort,
Blechnum fluviatile	creek fern, kiwikiwi
Blechnum pennamarina	
Blechnum sp ('kiokio')	palm-leaf fern, kiokio
Grammitis sp	strap fern, paretao
Histiopteris incisa	waterfern, matata
Paesia scaberula	ring fern, matata
Phymatosorus diversifolius	hound's tongue fern, kowaowao
Polystichum vestitum	prickly shield fern, puniu
Pteridium esculentum	bracken, rarahu
Sticherus cunninghamii	umbrella fern, waekura

Monocotyledons:

*Aira caryophyllea**	silvery hair grass
*Agrostis capillaris**	browntop
*Agrostis stolonifera**	creeping bent
*Anthoxanthum odoratum**	sweet vernal
Astelia fragans	
Carex comans	
Cortaderia toetoe	toetoe, cutty grass
*Dactylis glomerata**	cocksfoot
Heirochloe redolens	holy grass
*Holcus lanatus**	yorkshire fog
Phormium tenax	flax, harakeke
*Poa pratensis**	kentucky bluegrass
*Poa trivialis**	rough-stalked meadow grass
Uncinia rubra	hookgrass

Other dicotyledons:

*Calluna vulgaris**	heather
*Cardamine debilis**	bitter cress
Celmisia glandulosa	
Celmisia gracilenta	
*Cerastium glomeratum**	annual mouse-ear chickweed
Chiloglottis cornuta	
*Cirsium arvense**	californian thistle
Coprosma cheesemanii	
Coriaria pteridioides	
Corybas trilobus	spider orchid
Gaultheria antipoda	snowberry, tawiniwini
Gaultheria colensoi	snowberry
Gaultheria depressa	snowberry
Gaultheria paniculata	
*Lotus pedunculatus**	lotus
Melicope simplex	wharangi
Pterostylis sp	hooded orchid, tutukiwi
Ranunculus repens	buttercup

APPENDIX 2

Table 2.1 Results of a loglinear analysis comparing number of species of different dispersal modes caught per trap in different habitats.

a) Likelihood ratio statistics

Source	Percentage of deviance explained	DF	P
Site	1.84	1	0.2151
Habitat	38.60	2	0.0001
Transect	2.80	3	0.5041
Dispersal mode	8.26	1	0.0086
Site*dispersal mode	0.66	1	0.4561
Habitat*dispersal mode	20.85	2	0.0002

b) Analysis of parameter estimates (only significant results from Table 2.1a presented). Where an estimate is significantly less than (negative) other estimates less species are caught. When an estimate is significantly greater than (positive) other estimates, more species are caught.

Source		Estimate	DF	P
Site	Mangatepopo	-1.52	1	0.0002
	Raetihi hill	0.00		-
Habitat	ForestA	1.12	1	0.0001
	Broom	0.00		-
	Grass	-2.43		0.0001
	ForestB	0.00		-
Dispersal mode	Wind	-0.93	1	0.0044
	Bird	0.00		-
Site*dispersal mode	Mangatepopo*wind	1.47	1	0.0017
	Mangatepopo*bird	0.00	-	-
	Raetihi*wind	0.00	-	-
	Raetihi*bird	0.00	-	-
Habitat*dispersal mode	ForestA*wind	-1.42	1	0.0010
	Broom*wind	0.00		-
	ForestA*bird	0.00		-
	Broom*bird	0.00		-
	Grass*wind	1.78	1	0.0199
	ForestB*wind	0.00		-
	Grass*bird	0.00		-
	Forest*bird	0.00		-

APPENDIX 3

Table 3.1 Results of log linear analyses on final germination percentages (with binomial error distribution) for four native species: a) *Griselinia littoralis,* b) *Coprosma robusta* (Feilding), c) *Coprosma robusta* (Mt Bruce) d) *Pittosporum tenuifolium* var. *colensoi,* and e) lancewood (*Pseudopanax crassifolius*). Treatments are seeds left in-fruit, cleaned by hand, and bird-voided.

a) *Griselinia littoralis*

Source	Percentage of deviance explained	DF	*P*
Place	0.14	1	0.3224
Treatment	99.13	3	0.0001
Place*treatment	0.35	2	0.3050
Individual bird	-	0	-
TOTAL	**99.62**		

b) *Coprosma robusta* (Feilding)

Source	Percentage of deviance explained	DF	P
Place	0.02	1	0.7387
Treatment	95.30	3	0.0001
Place*treatment	2.52	3	0.0069
Individual bird	0.05	2	0.8958
TOTAL	**97.83**		

c) *Coprosma robusta* (Mount Bruce)

Source	Percentage of deviance explained	DF	P
Place	0.001	1	0.9239
Treatment	97.40	2	0.0001
Place*treatment	0.96	2	0.0884
Individual bird	-	1	-
TOTAL	**98.36**		

d) *Pittosporum tenuifolium* var. *colensoi*

Source	Percentage of deviance explained	DF	P
Place	27.66	1	0.0001
Treatment	72.29	3	0.0001
Place*treatment	0.00	2	-
Individual bird	0.00	0	-
TOTAL	**99.95**		

e) Pseudopanax crassifolius

Source	Percentage of deviance explained	DF	P
Place	44.30	1	0.0001
Treatment	52.90	3	0.0001
Place*treatment	0.00	2	-
Individual bird	0.00	0	-
TOTAL	**97.20**		

Table 3.2 Results of ANOVAs on median time to 50% germination (in days) for different treatments (seeds left in-fruit, cleaned by hand, and bird-voided).

a) *Griselinia littoralis*

SOURCE	SS	DF	MS	F	P
Place	6.09	1	6.09	5.34	0.0820
Treatment	40.12	2	20.06	17.57	0.0104
Place*treatment	0.00	0	-	-	-
Individual	5.92	2	2.96	2.59	0.1896

b) *Coprosma robusta* **(Fielding)**

SOURCE	SS	DF	MS	F	P
Place	57.80	1	57.80	59.68	0.0001
Treatment	0.01	1	0.01	0.01	0.9208
Place*treatment	12.62	2	6.31	6.52	0.0085
Individual	11.09	2	5.54	5.73	0.0133

c) *Coprosma robusta* **(Mount Bruce)**

SOURCE	SS	DF	MS	F	P
Place	0.00	1	0.00	0.05	0.8267
Treatment	0.92	1	0.92	10.24	0.0085
Place*treatment	0.17	1	0.17	1.88	0.1972
Individual	0.01	1	0.01	0.06	0.8098

d) *Pittosporum tenuifolium* **var.** *colensoi*

SOURCE	SS	DF	MS	F	P
Place	-	-	-	-	-
Treatment	10.80	1	10.80	0.61	0.4932
Place*treatment	-	-	-	-	-
Individual	-	-	-	-	-

e) *Pseudopanax crassifolius*

SOURCE	SS	DF	MS	F	P
Place	-	-	-	-	-
Treatment	17.16	1	17.16	88.86	0.0001
Place*treatment	-	-	-	-	-
Individual	-	-	-	-	-
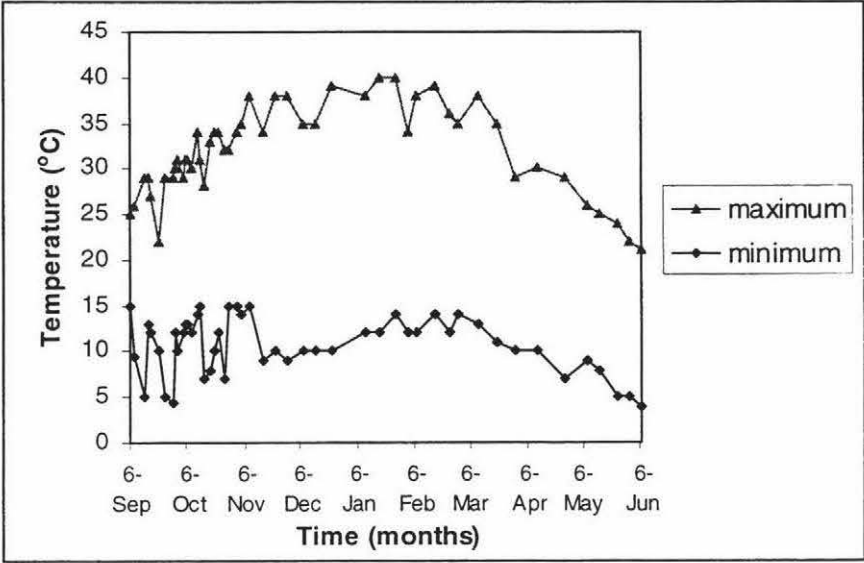
Fig. 3.1 Maximum/minimum temperatures in the unheated glasshouse in which germination experiments were carried out at Massey University, Palmerston North.

APPENDIX 4

SOWN SPECIES

Table 4.1 Results of a log linear analysis comparing establishment (with poisson error distribution) and survival (binomial error distribution) in sown areas and unsown areas for three native species. a) *Griselinia littoralis,* b) *Coprosma* 'taylorii' and c) *Pittosporum tenuifolium* var. *colensoi.* Where area=area of the sown and unsown sections, position=position of the section relative to the other squares, i.e: sown section, unsown sections adjacent to the sown section, unsown section diagonally opposite the sown section (See Chapter 4 methods for further information). E=established, S=survived to the last recording episode (survived for at least 2 months).

a) *Griselinia littoralis*

Source	Percentage of deviance explained		DF	P	
	E	S		E	S
Site	0.95	0.23	1	0.4199	0.2550
Habitat nested within site	12.73	22.15	2	0.0128	0.0001
Transect	4.30	3.06	3	0.3999	0.0006
Area	11.49	1.88	1	0.0050	0.0011
Position	39.17	0.85	1	0.0001	0.0283
TOTAL	**68.64**	**28.17**			

b) *Coprosma* 'taylorii'

Source	Percentage of deviance explained		DF	P	
	E	S		E	S
Site	1.39	1.82	1	0.4301	0.0172
Habitat nested within site	21.44	1.80	2	0.0081	0.0613
Transect	2.84	15.16	3	0.7357	0.0001
Area	6.90	4.43	1	0.0785	0.0002
Position	32.01	0.47	1	0.0002	0.2291
TOTAL	**64.58**	**23.68**			

b) *Pittosporum tenuifolium* var. *colensoi*

Source	Percentage of deviance explained		DF	P	
	E	S		E	S
Site	0.08	6.87	1	0.9286	0.0436
Habitat nested within site	6.62	7.09	2	0.7058	0.1224
Transect	0.66	8.85	3	0.9953	0.1551
Area	6.77	24.53	1	0.3986	0.0001
Position	22.08	-	1	0.1274	-
TOTAL	**36.21**	**47.34**			

Table 4.2 Effect of experimental treatments and other factors on establishment and survival of seedlings arising from sown seed. E=established, S=survived to the last recording episode (survived for at least 2 months).

a) *Griselinia littoralis*

Source	Percentage of deviance explained		DF	P	
	E	S		E	S
Site	3.34	0.04	1	0.0001	0.6864
Habitat nested within site	29.03	33.61	2	0.0001	0.0001
Transect	6.73	1.36	3	0.0001	0.1109
Cleared	11.66	3.76	1	0.0001	0.0001
Caged	1.17	7.07	1	0.0036	0.0001
Cleared*caged	0.00	1.04	1	0.9062	0.0317
Site*cleared	0.39	0.21	1	0.0922	0.3417
Site*caged	0.95	0.75	1	0.0090	0.0677
Site*cleared*caged	1.53	0.05	1	0.0009	0.6426
Habitat*cleared	6.52	0.86	2	0.0001	0.1480
Habitat*caged	0.77	2.67	2	0.0622	0.0027
Habitat*cleared*caged	2.64	0.33	2	0.0001	0.4860
TOTAL	**64.73**	**51.75**			

Table 4.2 b) *Coprosma* 'taylorii'

Source	Percentage of deviance explained		DF	P	
	E	S		E	S
Site	1.59	2.81	1	0.0003	0.0091
Habitat nested within site	53.33	1.96	2	0.0001	0.0933
Transect	3.17	15.12	3	0.0001	0.0001
Cleared	8.44	8.37	1	0.0001	0.0001
Caged	0.30	9.55	1	0.1107	0.0001
Cleared*caged	0.01	0.31	1	0.7619	0.3891
Site*cleared	1.66	0.95	1	0.0002	0.1294
Site*caged	0.43	8.70	1	0.0572	0.0001
Site*cleared*caged	0.23	1.50	1	0.1638	0.0571
Habitat*cleared	6.46	1.78	2	0.0001	0.0378
Habitat*caged	0.20	4.06	2	0.4323	0.0074
Habitat*cleared*caged	0.08	0.82	2	0.7089	0.1599
TOTAL	**75.90**	**55.93**			

Table 4.2 c) *Pittosporum tenuifolium* **var.** *colensoi*

Source	Percentage of deviance explained		DF	P	
	E	S		E	S
Site	0.55	5.96	1	0.2484	0.0787
Habitat nested within site	22.51	16.07	2	0.0001	0.0155
Transect	1.61	17.87	3	0.2741	0.0259
Cleared	5.39	7.26	1	0.0003	0.0523
Caged	6.69	3.37	1	0.0001	0.1857
Cleared*caged	2.11	6.22	1	0.0242	0.0725
Site*cleared	0.04	0.02	1	0.7420	0.9220
Site*caged	3.47	0.01	1	0.0038	0.9375
Site*cleared*caged	4.52	7.03	1	0.0010	0.0561
Habitat*cleared	2.73	2.09	2	0.0374	0.4707
Habitat*caged	1.98	-	2	0.0923	-
Habitat*cleared*caged	0.66	-	2	0.4526	-
TOTAL	**52.26**	**66.71**			

UNSOWN SPECIES

Table 4.3 Effect of experimental treatments and other factors on establishment and survival of seedlings arising from naturally dispersed seed. E=established, S=survived to the last recording episode (survived for at least 2 months).

a) *Pseudopanax crassifolius*

Source	Percentage of deviance explained		DF	P	
	E	S		E	S
Site	7.58	20.48	1	0.0001	0.0001
Habitat nested within site	45.48	1.73	2	0.0001	0.1976
Transect	9.84	6.67	3	0.0001	0.0936
Cleared	3.49	2.29	1	0.0001	0.1385
Caged	2.40	0.18	1	0.0001	0.6736
Cleared*caged	2.12	13.53	1	0.0001	0.0003
Site*cleared	2.66	2.38	1	0.0001	0.1336
Site*caged	0.33	2.80	1	0.0730	0.1011
Site*cleared*caged	5.64	-	1	0.0001	-
Habitat*cleared	1.06	0.32	2	0.0027	0.5789
Habitat*caged	0.20	1.26	2	0.1934	0.2707
Habitat*cleared*caged	0.04	-	2	0.5794	-
TOTAL	**73.90**	**50.06**			

Table 4.3 b) Establishment and survival of seedlings of the genus *Coprosma* arising from naturally dispersed seed. Includes *C. grandifolia, C. robusta, C. tenuifolia,* and *C. foetidissima,* but not *C.* 'taylorii'.

Source	Percentage of deviance explained		DF	P	
	E	S		E	S
Site	10.78	0.00	1	0.0001	1.0000
Habitat nested within site	42.93	0.00	2	0.0001	-
Transect	3.75	25.14	3	0.0722	0.0387
Cleared	0.04	7.98	1	0.7815	0.1027
Caged	3.41	0.01	1	0.0117	0.9653
Cleared*caged	0.13	45.12	1	0.6247	0.0001
Site*cleared	4.13	7.10	1	0.0055	0.1239
Site*caged	0.49	-	1	0.3401	-
Site*cleared*caged	0.00	0.00	1	0.9562	1.0000
TOTAL	**65.66**	**85.35**			

Table 4.3 c) *Leptospermum scoparium* NB: Seedlings of this species were only found at the Mangatepopo sites.

Source	Percentage of deviance explained		DF	P	
	E	S		E	S
Habitat nested within site	10.15	54.72	2	0.0001	0.0001
Transect	19.21	0.42	3	0.0001	0.8326
Cleared	30.12	0.76	1	0.0001	0.4234
Caged	6.09	0.16	1	0.0001	0.7124
Cleared*caged	0.23	-	1	0.1262	-
Habitat*cleared	0.81	-	1	0.0043	-
Habitat*caged	0.47	20.78	1	0.0295	0.0010
Habitat*cleared*caged	-	-	1	-	-
TOTAL	**67.08**	**76.84**			

Table 4.3 d) Establishment of broom (*Cytisus scoparius*) seedlings from naturally dispersed seed. NB: Analysis on survival of broom seedlings was not possible as they were removed from the soil each month. This species was only found at the Mangatepopo sites.

Source	Percentage of deviance explained	DF	P
Habitat	5.23	1	0.0001
Transect	7.73	2	0.0001
Cleared	18.19	1	0.0001
Caged	1.32	1	0.0001
Cleared*caged	0.06	1	0.3235
Habitat*cleared	3.73	1	0.0001
Habitat*caged	3.83	1	0.0001
Habitat*cleared*caged	0.24	1	0.0471
TOTAL	**40.33**		

LIGHT LEVELS

Table 4.4 Results of a log linear model on the total number of native seedlings established (poisson error distribution) and survived (binomial error distribution). E=established, S=survived to the last recording episode (survived for at least 2 months).

| Source	Percentage of deviance explained		DF	P	
	E	S		E	S
Site	3.55	0.00	1	0.0001	0.9576
Transect	12.95	10.90	3	0.0001	0.0001
Light	65.48	35.10	1	0.0001	0.0001
Habitat nested within site	2.58	16.69	2	0.0001	0.0001
TOTAL	**84.56**	**62.69**			
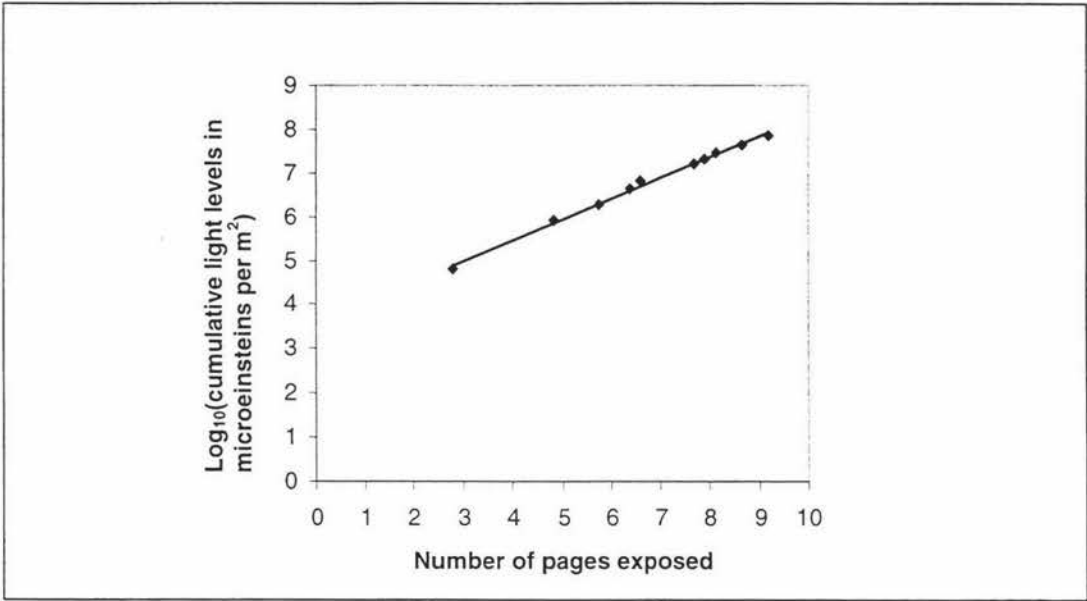
Fig 4.1 Calibration curve for diazo paper booklets exposed to sunlight for one week ($y=0.47x + 3.56$, $R^2=0.99$). Each point is a mean of two replicate booklets.

TRANSPLANTED SEEDLINGS

Table 4.5 Effect of experimental treatments and other factors on survival of transplanted *Griselinia littoralis* seedlings. NB: L=larger size class, S=smaller size class of transplanted seedlings.

Source	Percentage of deviance explained		DF	P	
	L	S		L	S
Site	0.90	0.80	1	0.2818	0.3236
Habitat nested within site	42.15	40.45	2	0.0001	0.0001
Transect	9.40	5.23	3	0.0082	0.0938
Cleared	4.73	0.08	1	0.0149	0.7564
Caged	2.56	0.08	1	0.0732	0.7563
Cleared*caged	0.14	4.02	1	0.6757	0.0267
Site*cleared	1.65	1.33	1	0.1500	0.2020
Site*caged	0.96	1.57	1	0.2733	0.1655
Site*cleared*caged	0.08	0.28	1	0.7508	0.5573
Habitat*cleared	2.40	0.03	2	0.2216	0.9815
Habitat*caged	2.65	0.03	2	0.1894	0.9799
Habitat*cleared*caged	0.00	3.57	2	1.0000	0.1129
TOTAL	**67.62**	**57.47**			

Table 4.6 Effect of experimental treatments and other factors on final number of leaves of transplanted *Griselinia littoralis* seedlings. NB: L=larger size class, S=smaller size class of transplanted seedlings.

Source	Percentage of deviance explained		DF	P	
	L	S		L	S
Site	4.52	4.07	1	0.0001	0.0010
Habitat nested within site	22.34	36.51	2	0.0001	0.0001
Transect	4.53	6.10	3	0.0014	0.0010
Cleared	5.65	1.69	1	0.0001	0.0344
Caged	0.40	0.08	1	0.2412	0.6467
Cleared*caged	0.12	1.91	1	0.5264	0.0242
Site*cleared	2.77	0.07	1	0.0020	0.6753
Site*caged	0.87	0.05	1	0.0842	0.7178
Site*cleared*caged	0.00	1.92	1	0.9613	0.0242
Habitat*cleared	4.59	0.27	3	0.0004	0.9633
Habitat*caged	0.00	0.39	3	-	0.5984
Habitat*cleared*caged	0.00	6.73	3	-	0.0001
TOTAL	**45.79**	**59.79**			

Table 4.7 Effect of experimental treatments and other factors on relative height growth of transplanted *Griselinia littoralis* in a) the larger size class, and b) the smaller size class.

a) larger size class of transplants

Source	SS (Type 1)	DF	F	P
Site	0.0101	1	0.06	0.8038
Habitat nested within site	1.0462	1	6.50	0.0152
Transect	0.4407	3	0.91	0.4442
Cleared	0.0334	1	0.21	0.6514
Caged	0.0136	1	0.08	0.7729
Cleared*caged	0.0551	1	0.34	0.5622
Site*cleared	0.0151	1	0.09	0.7610
Site*caged	0.0296	1	0.18	0.6706
Site*cleared*caged	0.0649	1	0.40	0.5294
Habitat*cleared	0.0304	1	0.19	0.6664
Habitat*caged	0.0376	1	0.23	0.6318
Habitat*cleared*caged	0.1380	1	0.86	0.3605

b) smaller size class of transplants

Source	SS (Type 1)	DF	F	P
Site	0.3823	1	3.60	0.0710
Habitat nested within site	0.0107	1	0.10	0.7538
Transect	0.1686	3	0.53	0.6670
Cleared	0.0004	1	0.00	0.9492
Caged	0.6094	1	5.74	0.0256
Cleared*caged	0.1126	1	1.06	0.3144
Site*cleared	0.7721	1	0.73	0.4031
Site*caged	0.0768	1	0.72	0.4043
Site*cleared*caged	0.0254	1	0.24	0.6295
Habitat*cleared	0.1285	1	1.21	0.2833