# Impacts of reduced bird densities on pollination and dispersal mutualisms in New Zealand forests

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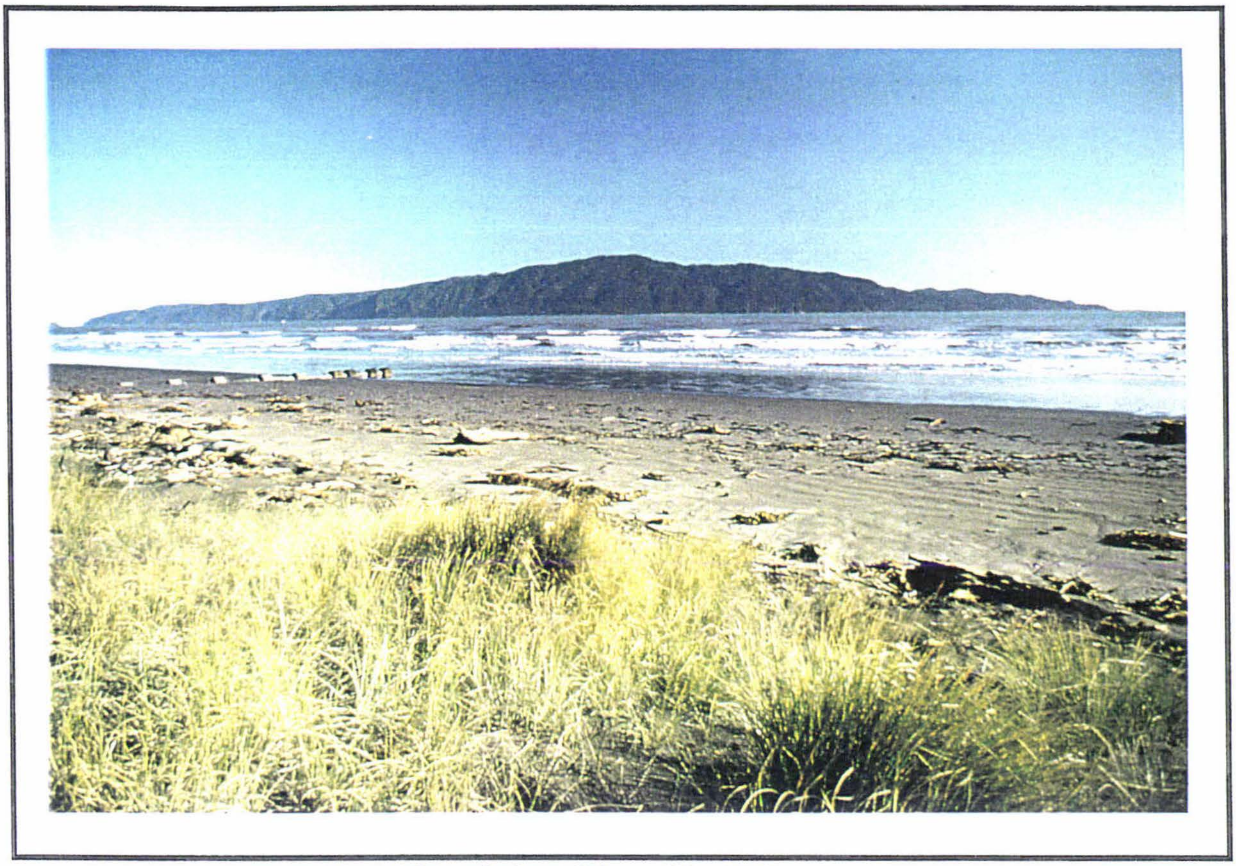

Kapiti Island viewed from Kapiti Coast

*Photo: Jeremy Rolfe*

"...Plant a new Truffula. Treat it with care.
Give it clean water. And feed it fresh air.
Grow a forest. Protect it from axes that hack.
Then the Lorax
and all of his friends
may come back."

*Dr. Seuss 1972*

# ABSTRACT

The arrival of humans in New Zealand has caused a severe decline in the numbers of endemic avian species and their densities. Consequently, there is concern that pollination and dispersal services which birds carry out in New Zealand forests are under threat because of continued bird decline. Studies were conducted to identify whether pollinator and/or dispersal limitation was occurring in New Zealand lowland forests. Mainland sites (located between Wellington and Palmerston North) were compared to Kapiti Island, an island sanctuary. Kapiti Island supports large densities of endemic bird species and is used here as a "benchmark" to measure changes in pollinator and dispersal mutualisms on the mainland.

Exclosure cages were constructed to determine how important birds were as pollinators and whether pollination limitation was occurring in two ornithophilous (bird-pollinated) species (*Metrosideros fulgens*, *Fuchsia excorticata*) and two entomphilous (insect-pollinated) species (*Dysoxylum spectabile*, *Geniostoma ligustrifolium*). Some cages prevented all floral visitors, others excluded birds only, while control branches allowed all bird and insect visitation. Data was collected on bird visitation rates, nectar depletion, number of pollen grains deposited, pollen tube growth and fruit set. Birds and insects were important visitors to *M. fulgens* on Kapiti Island and at Kahuterawa Rd. Birds and insects also pollinated *F. excorticata* but bird pollination was reduced at Gladstone Rd and Akatarawa Rd compared with Kapiti Island. Birds were the main visitors to *D. spectabile* at both Kapiti Island and Wilton Bush. Birds were also important important pollinators of *G. ligustrifolium*, especially so at Lake Papaitonga. Overall, there was strong evidence for pollination limitation of *F. excorticata* on the mainland. Additionally, there was some evidence for pollination limitation of *G. ligustrifolium* as fruit set was low at all sites. Floral morphology was not able to predict whether birds or insects were the most imporant floral visitors. Birds are therefore, probably involved in the pollination of species which do not display ornithophilous flowers.

The potential effects which pollinator limitation could have on the breeding systems of sexually dimorphic species was investigated. Some secondary sex characteristics (standing crop of nectar, the number of pollen grains on stigmas, pollen tubes in styles, flowering periods and fruit set) differed between the sexes of *F. excorticata* and *G. ligustrifolium*. It is suggested the plasticity of fruit set in male *F. excorticata*, *G. ligustrifolium* and *D. spectabile* would enable them to respond to pollinator limitation. Pollinator limitation has apparently not yet led to sex ratio differences between populations. Most populations demonstrated a male bias which may have resulted from varying environmental conditions.

Possible dispersal limitation of *F. excorticata* was tested at Kapiti Island, Gladstone Rd and Akatarawa Rd using caged branches which prevented bird dispersal and uncaged branches. On Kapiti Island, palms retained proportionally less ripe fruit compared to the mainland study sites and fruits were dispersed at a faster rate. The proportion of dispersed and undispersed *Rhopalostylis sapida* fruit was determined on Kapiti Island, Nikau Reserve and Manawatu Gorge. Again, a greater proportion of fruit was dispersed and at a faster rate on Kapiti Island. The fruit there suffered less pre-dispersal predation from the endemic caterpillar *Doxophyrtis hydrocosma*. Although *R. sapida* seedling transects showed seedlings were common, there was strong evidence for dispersal limitation of *R. sapida* as well as *F. excorticata* on the mainland. Dispersal limitation could thus, be adversely affecting plant-disperser mutualisms by reducing the ability of species to disperse to new sites and reducing the efficiency of forest regeneration.

The pollination and dispersal services which are carried out by endemic birds suggests their continued decline could be causing pollination and/or dispersal limitation. It is essential to address the problems of declining bird densities to ensure the perpetuation of New Zealand forest ecosystems.

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Tui on Northern Rata

# 1.1. POLLINATION

## 1.1.1. FLORAL CHARACTERISTICS OF NEW ZEALAND PLANTS

New Zealand flowers appear to be adapted for a wide range of unspecialized insect pollinators (entomophily) (Primack 1978, Lloyd 1985). The majority of plants have simple, small, clustered flowers, usually white, short-tubed with a prominence of unisexual flowers (Heine 1938, Godley 1979, Lloyd 1985, Webb and Kelly 1993). The oceanic isolation of New Zealand may have selected breeding systems which reduce inbreeding depression, and may explain the high proportion of dioecious species in New Zealand because females produce obligatory outcrossed progeny (Lloyd 1975, Lloyd 1985). New Zealand lacks specialised pollinators such as long tongued bees and hawkmoths which are important pollinators in other plant communities in Chile and North America (Heine 1938, Godley 1979, Primack 1983, Lloyd 1985). Diptera and short tongued Hymenoptera are thought to be important pollinators of New Zealand flowers (Thomson 1927, Heine 1938). Pollination in New Zealand has been reviewed by Thomson (1927), Heine (1938), Godley (1979), Lloyd (1985) while the pollination of *Parahebe* (Garnock-Jones 1976), *Melicytus* (Powlesland 1984), *Geniostoma ligustrifolium* (Rattenbury 1980), New Zealand grasses (Connor 1965, 1984), *Hebe subalpina* (Delph and Lloyd 1991, Delph 1993), *Pseudowintera colorata* (Lloyd and Wells 1992), *Pimelea* (Burrows 1960), alpine flora (Primack 1978, 1983), *Corokia contoneaster* (Webb 1994) and *Myosotis colenso* (Robertson 1989) have also been studied. Other authors have discussed the roles of lizards, thrips and bats in the pollination of some native plant species (Daniel 1976, Norton 1984, Whitaker 1987a, Whitaker 1987b, Ecroyd 1993).

In contrast, bird pollinated (ornithophilous) flowers are usually odourless, large, brightly coloured and have plentiful quantities of nectar (Faegri and van der Pijl 1979, Stiles 1978). Approximately 30 species of New Zealand plants (from 23 genera and 18 families) are known to be visited by birds (although this list has been expanded by Castro and Robertson 1997) and only half of these flowers have obvious adaptations for bird pollination (Godley 1979). Seven species of birds (excluding the recently self-introduced silvereye (*Zosterops lateralis*)), are known to visit flowers, but only tui

(*Prosthemadera novaezelandiae*) and bellbirds (*Anthornis melanura*) are common visitors (Godley 1979).

### 1.1.2. FLORAL REWARD

To ensure pollination, flowers usually offer a reward to visitors in the form of nectar or pollen. Most birds visit flowers to collect the sugar rich nectar (Simpson and Neff 1983). The benefits of producing nectar are the pollinating actions of these visits; therefore standing crops of nectar (the actual reward which pollinators encounter) are of greater significance to pollination studies than the rate of nectar production (Zimmerman 1988). Nectar is used to manipulate the behaviour of pollinators by modifying the reward to visitors (Pyke 1984, Zimmerman and Pyke 1986). As the standing crop increases for example, pollinators may spend more time on each flower, thus increasing pollen deposition and dispersal (Galen and Plowright 1985) or increase visitation frequency (Waddington 1981). The volume of nectar produced together with its concentration determines the sugar reward offered to foragers (Mitchell and Paton 1990). Plants with similar pollination syndromes (Faegri and van der Pijl 1979) produce similar concentrations of nectar, suggesting the concentration of a flower's nectar is a good indication of whether the plant is attracting insect or bird visitors (Mitchell and Paton 1990). Thus, the study of nectar can offer an insight into the coevolution between the plant and pollinator.

### 1.1.3. THE IMPORTANCE OF BIRD POLLINATION IN NEW ZEALAND

Birds have previously been thought to be relatively unimportant pollinators in New Zealand forests (Clout and Hay 1989, Lloyd 1985). This contrasts with the rest of Australasia where birds are important pollinators, particularly Australia where up to 1000 species of plants may rely on bird pollination (Ford *et al* 1979). Even though the majority of New Zealand plants appear to have few adaptations for bird pollination, the importance of birds should not be underestimated. Castro (1995) found nectar from small flowered species formed a large part of the diet for hihi (*Notiomystis cincta*) on Kapiti Island and bagged crops of flowers provided excess reward for the three honeyeaters (tui, bellbird, hihi). This combined with New Zealand's windy conditions (Coulter 1975), cool winter temperatures and greater potential for cross pollination via bird visitation, suggests that at times, plants may benefit significantly more from bird visitations than insect visitations (Castro and Robertson 1997). Collins *et al* (1984) suggest that flowers of the Australian plant *Calothamnus quadrifidus* appear suited for insect visitation yet honeyeaters are frequent visitors and significant pollen vectors. These studies suggest the most important vector for the pollination of a plant may not be accurately inferred from floral traits. Flowers may be visited incidentally without true ornithophily being involved (Godley 1979), however it is speculated that birds may play a greater role in pollination of New Zealand plants than has previously been thought (Castro 1995, Castro and Robertson 1997, Anderson 1997).

# 1.2. DISPERSAL

## 1.2.1. FRUITING CHARACTERISTICS OF NEW ZEALAND PLANTS

New Zealand has 250 species of plants which bear fleshy fruit and a high proportion (70%) appear adapted for vertebrate dispersal (Clout and Hay 1989, Lee *et al* 1991). Most species of lowland podocarp-broadleaved forests are fleshy fruited, (Lee *et al* 1991) and half the genera with separate sexes have fleshy disseminules (Wardle 1991). Bird dispersed fruits are usually brightly coloured (red, black, blue, orange) (Janson 1983). The majority of New Zealand fruits are small (less than 4mm diameter) and red but many other species have orange, black, purple, white or blue fruit (Godley 1975, Whitaker 1987a, Willson *et al* 1989, Lee *et al* 1991, Williams and Karl 1996). There are also a few large fruited species such as *Beilschmiedia* spp. and *Corynocarpus laevigatus* (Willson *et al* 1989).

## 1.2.2. THE IMPORTANCE OF BIRD DISPERSAL IN NEW ZEALAND

Relatively little is known about the history of New Zealand fruit dispersal mechanisms but New Zealand's isolation and high endemism is considered to have been a strong influence on their evolution (Lee *et al* 1991, Webb and Kelly 1993). New Zealand's high proportion of fleshy fruits is in contrast to other places (such as Australia) and may have evolved in part because of an overall lack of nectar in New Zealand forests (Craig *et al* 1981, Clout and Hay 1989, Lee *et al* 1991). Furthermore, mast seedling is a common phenomenon in the New Zealand flora and could have evolved in part to concentrate feeding by birds (Norton and Kelly 1988, also see Bawa 1980).

Flowering plants of New Zealand have coevolved with a relatively depauperate avian fauna (Fleming 1975, but see Norton 1982). However, like pollination, the importance of birds as fruit dispersers should not be underestimated (Clout and Hay 1989). Most forest birds are frugivorous (Clout and Hay 1989) and 12 species are regular frugivores (Lee *et al* 1991). Ground dwelling birds (eg weka *Gallirallus australis*, kiwi *Apteryx* spp.) and insectivores (eg robin *Petroica australis*) are opportunist fruit feeders whilst parrot species (eg kea *Nestor notabilis*, kaka *Nestor meridonalis*, red and yellow crowned kakariki (*Cyanoramphus* spp.) are seed predators (Clout and Hay 1989, Lee *et al* 1991). Until recently, New Zealand fleshy fruits were assumed to be bird dispersed but there is increasing evidence that lizards and the short tailed bat (*Mystacina tuberculata*) can disperse a wide variety of fruit (Daniel 1976, Whitaker 1987a, Whitaker 1987b, Webb and Kelly 1993).

These characteristics of New Zealand fruits have a great impact on the ecology and behaviour of New Zealand frugivores. New Zealand frugivores have a broad diet, are resident not migrant, and thus rely on food to be available throughout the year in one area (Lee *et al* 1991, Williams and Karl 1996). For example, kokako (*Callaeas cinerea*) eat fruit from at least 35 species and remain resident in an area of about 11 hectares (Hay unpublished data cited in Clout and Hay 1989, Kokako Recovery Plan 1992), while kereru, kokako and kakapo (*Strigops habroptilus*) are reproductively dependent on fruit (*Lee et al* 1991).

## 1.3. THE DECLINE OF NEW ZEALAND BIRD SPECIES AND DENSITIES

There are many accounts of how the New Zealand forest has been degraded. A good example is the Orongorongo Valley near Wellington where native bird densities, native bird species, plant species and forest health have all declined since the 1800's (Brockie 1992). In particular, honeyeater populations have declined on mainland New Zealand since the arrival of humans due to habitat destruction, hunting and introduced mammalian predators (Diamond and Veitch 1981, King 1984, Holdaway 1989, Gill and Martinson 1991). Many avian fruit dispersers are now extinct including the huia (*Heteralocha acutirostris*) and piopio (*Turnagra capensis*) or severely reduced in abundance and distribution such as the little spotted kiwi (*Apteryx oweni*), saddleback (*Philesturnus carunculatus*) and hihi *(Notiomystis cincta*) (Buller 1888, Simpson 1971, Diamond and Veitch 1981, Lee *et al* 1988, Clout and Hay 1989). The influence of moas on the evolution of New Zealand flora is unclear (Greenwood and Atkinson 1977, Clout and Hay 1989) but Keogh (1989) suggests the ecology and structure of New Zealand fruits may have been influenced by moa because they were probably important as fruit dispersers (but see Burrows 1994a).

# 1.4. POLLINATION AND DISPERSAL: TWO MUTUALISTIC PROCESSES

## 1.4.1. POLLINATION AND DISPERSAL MUTUALISMS ARE ANALOGOUS; OR ARE THEY?

Pollination and dispersal systems are thought to be analogous with each other because both are the result of a mutual coevolution between plants and animals (Wheelwright and Orians 1982). However, the two have many aspects which are fundamentally different.

It has been postulated the seed of *Calvaria major* (a fleshy fruited plant on the island of Mauritius) required passage through a dodo (*Raphus cucullatus*) gut before it could germinate, and consequently a new seedling of *Calvaria major* has not established since the extinction of the dodo 300 years ago (Temple 1977 but see Owadally 1979 and Witmer 1991 for alternative explanations). There is only one other known example which demonstrates a similar obligate dispersal relationship between plant and animal, that being between tomatoes and tortoises on the Galapagos islands (Rick and Bowman 1961). Examples of extreme coevolution between a plant and animal dispersal are the exception rather the rule and dispersal systems are now thought to be non-obligate, variable, loose and inefficient (Bawa 1980, Wheelwright and Orians 1982, Herrera 1985, Wheelwright 1988). New Zealand plants support this paradigm because they lack specialist frugivory relationships and rely on generalist frugivores to disperse their fruit (Clout and Hay 1989).

Pollination systems on the other hand, are often specialised and it is not unusual for a plant to rely upon an individual vector or a limited range of vectors for pollination. The mutualism between figs and their pollinating wasps was one of the first examples studied (eg Galil and Eistikowitch 1968). Almost all figs (*Ficus*) are pollinated by a single species of chalcidoid wasp which in turn relies on the fig for reproduction (Kerdelhue and Rasplus 1996). Other examples where specialised pollinators have evolved include orchids (Dressler 1968 cited in Wheelwright and Orians 1982) and

*Dactylanthus taylorii* (Ecroyd 1993). But, research is now suggesting specialist pollination relationships are also the exception rather than the rule. Waser *et al* (1996) argue there is a strong selection for generalised pollination systems where a single pollinator species uses several plant species or a single plant uses several pollinator species.

However, pollination and dispersal systems cannot be viewed completely separately. Both are indicators of the coevolution between plant and animal. Just as floral biology gives an insight into a plant's pollination syndrome, a plant's dispersal syndrome can be inferred from fruit size, shape and colour (eg Snow 1970, Janson 1983). Moreover, pollination and dispersal systems must interact to achieve efficient reproduction because there may be a tradeoff between flowering, fruiting and seedling establishment (Primack 1987).

### 1.4.2. EFFECTS OF THE LOSS OF MUTUALISMS

The extinction of the dodo on the island of Mauritius was one of the first studies which identified the vulnerablity of mutualistic relationships between plants and birds. There are strong parallels between New Zealand and Mauritius: both are isolated island archipelagos, lack native mammals, have flightless native birds and a high degree of endemism (Keogh 1989). These parallels suggest any perturbations to mutualistic relationships between New Zealand plants and animals could have strong adverse effects as any disruption to an ecosystem can affect its long term viability (Norton 1992, Aizen and Feinsinger 1994). Lord (1991) states decreased densities and abundances of animals in isolated islands such as New Zealand, provide a natural experiment on the specificity of ecosystem interactions. Reproductive mutualisms are part of a complex web of ecosytem interactions which could cause a cascade of extinctions if broken (Janzen 1974, Kevan 1975, Bond 1994). With a loss of biodiversity world wide, there is an increasing need to discover more about how mutualisms such as plant-bird interactions are being affected (Clout and Hay 1989, Lee *et al* 1991, Lord 1991, Castro and Robertson 1997). The extent to which native pollinators have been decimated remains unknown and their effects of their decline largely unstudied (Kevan 1975).

Little is known about frugivory of birds in temperate areas of Australasia (French *et al* 1992).

The continued extinction of ecological interactions is a process which may occur unnoticed because the complexity of interactions makes it difficult to pin point the cause of any disruption (Janzen 1974). Kearns and Inouye (1997) state habitat alteration, fragmentation, grazing, pesticides and introduction of foreign pollinators are some of the main threats to plant-pollinator relationships. Few studies have concentrated on determining the potential effects on ecosytems if mutualistic relationships are interrupted and to date, the effects from the loss or decline of mutualistic partners have only been studied at a basic level.

Plant reproduction could be threatened if the behaviour of pollinators is altered. Honey bees (*Apis mellifera*) for example, compete and displace some native birds (the natural pollinators) from nectar sources in Australia (Paton 1993) and native insects in New Zealand (Murphy 1996). Honey bees are less efficient at cross pollination and set less seed than birds on some species (Paton 1993). Pollinators can limit the reproductive output of a plant (Bierzychudek 1981) and therefore if pollinators are absent, the production of seed or fruit could be reduced (Kevan 1975, Snow 1982). This is termed as pollinator limitation and is caused by a limited number of pollinators visiting flowers and/or by a limiting availability of compatible pollen which causes low fruit:flower ratios (Garwood and Horvitz 1985, Horvitz and Schemske 1988). A rare fynbos shrub on the African Cape for example, has lost its specialist bee pollinator which has become locally extinct. These plants now have remarkably low seed sets and although the plant is not heading towards immediate extinction, it now primarily relies on vegetative propogation for reproduction (Steiner 1993). Similarly, the ieie vine in Hawai'i *(Freycinetia arborea)* was primarily pollinated by three bird species, of which two are now extinct and one endangered. Cox (1983) believes the vine relied on clonal reproduction until the introduction of the Japanese white eye (*Zosterops japonica*) which now is its principle pollinator. Pollination limitation has been investigated by many studies (eg Copland and Whelan 1989, Motten *et al* 1981, Ågren 1996) but relatively few have considered the importance of conservation for the species they have studied.

The loss of pollinators could cause inbreeding depression, which has genetic consequences especially in small populations (Kearns and Inouye 1997). Additionally, pollen competition could decrease so that selection for the most vigorous pollen tubes may no longer occur (Kearns and Inouye 1997) which could result in a reduction in the quality of offspring. Once a plant's natural abundance has been reduced it becomes prone to stochastic events which further threaten its survival. Consequently, plants most at risk from pollinator decline are dioecious, self incompatible, have a single pollinator and only propogate by seed (Bond 1994, Kearns and Inouye 1997).

Studies on pollination limitation in New Zealand have so far concentrated on mistletoes *(Peraxilla colensoi, P. tetrapetala)* and have discovered a relationship between mistletoes and honeyeaters which ensures pollination (Ladley and Kelly 1995a, 1995b). These studies suggests mistletoe regeneration could be threatened with the continuing decline of bird pollinators and possibly dispersers (Ladley and Kelly 1995a, 1995b, Ladley and Kelly 1996, Robertson *et al* unpublished manuscript). Another plant, *Freycinetia baueriana*, was thought to rely on pollination by the native bat (*Mystacina tuberculata*) which is locally rare but the plant still manages to set seed despite a requirement for cross pollination (Lord 1991). Anderson (1997) has also suggested pollination by New Zealand native birds is being limited in modified fragmented habitats.

Only a few studies have investigated the effects from losing indigenous frugivores. Clark and Clark's (1981) study on *Bursera gaveolens* on Santa Fe Island in the Galapagos demonstrated the importance of animal dispersers for the recovery of the plant from grazing. To date in New Zealand, there is no clear indication that forest ecosystems are suffering because of the lack of avian dispersers (Lee *et al* 1991, Clout and Tilley 1992), although disperser limitation has been suggested by Ladley and Kelly (1996) and Anderson (1997). Potential threats to forest regeneration due to reduced disperser abundances could be overstated (Webb and Kelly 1993). However, these effects could be difficult to detect especially with long lived plant species (Lee *et al* 1991). The keruru is the only abundant species which can consume fruit larger than 10mm in diameter. It has been suggested species regeneration could suffer if kereru numbers continue to decline, especially for those species which produce larger fruit (Clout and Hay 1989, Lee *et al* 1991).

Disturbances play a major part in the interactions between temperate fruits, birds and the communities in which they live (Thompson and Willson 1978). For example, studies are beginning to show that fragmentation of forest systems can potentially upset pollination and dispersal interactions which in turn reduces the "community health" of fragments (Aizen and Feinsinger 1994). Fruits on the edge of fragments and in light gaps created by forest disturbance may be removed faster and discovered earlier by frugivores than fruits under closed canopy (Thompson and Willson 1978). Fruits which are ignored and left to ripen are more prone to invertebrate damage and individual plants growing on the forest edge and in light gaps can contribute disproportionally to the next generation (Thompson and Willson 1978). Increasing levels of fragmentation can reduce the number of pollen tubes per style, fruit set and seed set. This in turn could be related to changes to pollinator service which affects pollen quality or quantity (Jennersten 1988, Aizen and Feinsinger 1994).

There could be genetic consequences for a plant population if pollinator and/or disperser services are reduced or altered. Seed dispersal influences geographical and demographic phenomena and thus, shapes the genetic structure of a plant population (Howe 1989). Avian dispersal patterns are instrumental in structuring the genetic population of *Ocotea tenera* (Gibson and Wheelwright 1995) and *Pinus albicaulis* (Furnier *et al* 1987). Finally, the viability of small populations is reduced disproportionally with their size, as shown by small populations of *Banksia goodii* (Lamont *et al* 1993). Reduced pollinator services encourages pollen to be transferred between closely related neighbours and small populations may set virtually no seed as a result of the Allee Effect (Lamont *et al* 1993).

### 1.4.3. POLLINATION SERVICES AND POLLINATOR EFFECTIVENESS

The importance of a pollinator to a plant's reproduction depends on many factors. These include their relative abundances (Olsen 1997), rate of visitation (Primack and Silander 1975, Schmitt 1983, Schemske and Horvitz 1984, Vaughton 1992), pollen removal and deposition (Collins *et al* 1984, Wilson and Thomson 1991, Vaughton 1992) and pollinator effectiveness (Primack and Silander 1975). Quantifying pollination effectiveness is critical to questions about pollination biology (Fishbein and Venable 1996). Pollinator effectiveness can be defined as the number of compatible pollen grains deposited on a stigma from a single pollinator visit to a flower (Dieringer 1992) and can be measured by the percentage of receptive florets in an inflorescence setting seed (Olsen 1997). Pollinators will vary in their effectiveness and the best pollinator will transfer pollen to produce the maximum seed set over an entire season (Stiles 1978).

Most pollination studies in New Zealand have studied the service which pollinators provide and few have investigated their effectivess. Mistletoes are primarily pollinated by birds yet native bees are also capable of pollination (although do not enable the same fruit set as achieved by birds) (Kelly *et al* 1996). Primack (1979) and Webb (1985) concluded flowers of *Discaria toumatou* are visited by generalised insect pollinators that vary in their effectivess. Anderson (1997) concluded birds were more effective pollinators than insects for a wide variety of native plants. *Corokia contoneaster* is another native plant whose pollination sydromes have been studied. Webb (1994) has determined *C. contoneaster* has generalised insect pollinators whose effectiveness and visitation frequencies differ. Studies on the introduced *Feijoa sellowiana* confirmed large birds were superior pollinators to small birds or insects (Stewart and Craig 1989). Overseas research has also demonstrated the variability in the ability of pollinators to set seed or fruit (eg Schemske and Horvitz 1984, Wilson and Thomson 1991, Vaughton 1992, Fishbein and Venable 1996). Generally, fruits pollinated by light pollen loads have lower probabilities of maturation than those with heavy loads (Bertin 1982, McDade and Davidar 1984), although it is necessary to consider pollen quality as well as quantity when assessing a pollinator's effectiveness (eg Kunin 1993, Lamont *et al* 1993).

### 1.4.4. COMPENSATORY MECHANISMS

It seems logical to assume plants with close specialist mutualistic relationships will be more vulnerable to decline than those with lose relationships because once a specialist pollinator or disperser is removed plants which depend on this obligate specialist pollinator will fail in their reproduction (Rathcke and Jules 1993). But in practise, how vulnerable are mutualisms? Can ecosystems somehow compensate for their loss? The specificity, reproductive dependence on the mutualism and demographic dependence on seeds will determine whether compensatory mechanisms allow the plant to avoid extinction (Bond 1994). New Zealand mistletoes are still able to reproduce even when their floral adaptations can limit the effectiveness of some pollination vectors (Kelly *et al* 1996, Ladley and Kelly 1995a, 1995b). The natural bat pollinator of the parasitic plant *Dactylanthus taylorii* is now severely reduced in abundance (Daniel 1990) yet the introduced ship rat (*Rattus rattus*) is probably a substitute pollinator (Ecroyd 1993). Inoue (1993) has shown plants which rely on bumblebee pollination on the Japanese mainland have compensated for the lack of pollinators on the Izu Islands by changing their flowering phenology, breeding system and fruiting strategy. Today, kereru, tui and bellbird are the only remaining indigenous frugivoures which are widespread (Webb and Kelly 1993). The decline of New Zealand endemic frugivores has been partially offset by the introduction of other bird species which are known to consume fruit from native plants. These bird species included blackbirds (*Turdus merula*), starlings (*Sturnus vulgaris*), indian mynahs (*Acridotheres tristis*) and song thrushes (*Turdus philomelos*) (Beveridge 1964, Beveridge 1975, Norton 1982, Baylis 1986, Webb and Kelly 1993, Williams and Karl 1996).

The majority of plants have multiple pollinators and most pollinators pollinate a range of species (Kearns and Inouye 1997). In addition, the failure of dispersers will only cause plant extinctions when populations are seed limited (Bond 1994). Indeed, the prevalence of compensatory mechanisms suggest plants are extremely resilient to mutualism failures (Bond 1994). So why worry about the loss of mutualisms? Bird-plant interactions have had to cope with change for millions of years during which some have become extinct and others have not. The problem with recent change is probably its rate; it could be occurring too fast for plants and animals to alter the nature of their interactions to ensure their survival.

# 1.5. THE USE OF KAPITI ISLAND

Located 5kms offshore from Paraparaumu and 50km north of the southern most point of the North Island, Kapiti Island is New Zealand's second largest offshore reserve. It is 1965 ha in area, 9km long, 2.3 km wide and reaches 542m at its highest point. Kapiti Island is one of the most intact wildlife reserves present in New Zealand because all introduced mammals (cattle, goats, sheep, pigs, cats, possums (*Trichosurus vulpecula*) have been eradicated (Esler 1967, Cowan 1992) and an eradication programme for the remaining norway rats (*Rattus norvegicus*) and kiore (*Rattus exulans*) was carried out in September-Octomber 1996.

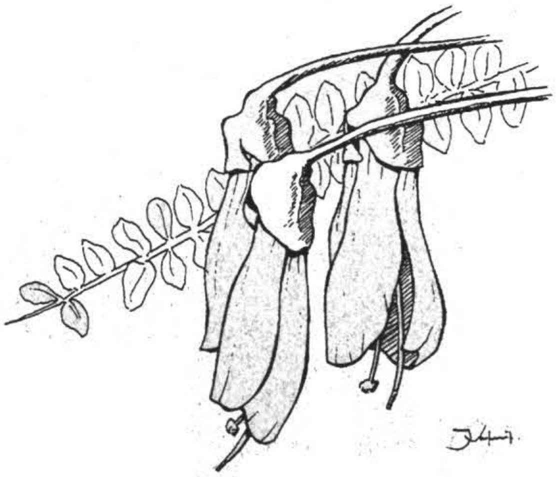
Predator-free and predator-reduced island sanctuaries now probably support higher densities of avian species than the mainland (Diamond and Veitch 1981, Brockie 1992, Castro 1995) and consequently they can be used as a benchmark to detect changes on mainland New Zealand (Diamond and Veitch 1981, Cowan 1992). The few overseas studies which have compared island and mainland pollination have been conducted on the premise that islands support a subset of mainland pollinators (Linhart and Feinsinger 1980, Spears 1987, Inoue 1993). However, New Zealand island-mainland comparisons would assume the opposite because the mainland now has a subset of the pollinators present on offshore islands. Only one New Zealand study to date has compared an intact island ecosystem (Tiritiri Matangi Island) with a degraded mainland site (Wenderholm Regional Park) (Anderson 1997).

In New Zealand, an island-mainland comparision is probably the only way to monitor and compare changes to pollination and dispersal processes that are occuring on the mainland. However, more than one mainland site needs to be used because no two sites will be affected in exactly the same way and any effects on pollination and dispersal will not be unifiorm throughout all forest systems. Consequently, two mainland sites are required to be compared with Kapiti Island to gain a better understanding of the changes on the mainland.

The primary aim of this thesis is to use Kapiti Island in an island-mainland comparision to identify pollinator and/or dispersal limitation in New Zealand lowland forests which may be resulting from the decline of endemic bird species. The possible occurrence of pollination limitation is investigated in Chapter Two using *Metrosideros fulgens*, *Fuchsia excorticata*, *Dysoxylum spectabile* and *Geniostoma ligustrifolium*. This chapter also assesses whether bird pollination should be more frequent in New Zealand than is currently assumed. Chapter Three presents the results from a study of dispersal limitation in two fleshy fruited species, *F. excorticata* and *Rhopalostylis sapida* and discusses how dispersal limitation could be affecting plant-disperser mutualisms. The secondary sex characteristics of *F. excorticata* and *G. ligustrifolium* are examined in Chapter Four. This chapter also investigates whether pollination limitation can be identified by the sex ratios of *F. excorticata*, *G. ligustrifolium* and *D. spectabile*.

# Chapter Two

# Reduced bird abundances and pollinator limitation in New Zealand forests



Kowhai

# 2.1. INTRODUCTION

The scarcity of advanced and specialised insect pollinators and nectar feeding birds in New Zealand has led to the belief that New Zealand's plants are reproductively dependent on the pollination services of generalised insect (entomophilous) pollinators, such as short tongued Hymenoptera and Diptera (Thomson 1927, Heine 1938, Primack 1983, Lloyd 1985). The floral morphology of the majority of New Zealand plants supports these conclusions as most are small in size, white or dull coloured, arranged in small clusters, short tubed and predominately unisexual (Heine 1938, Godley 1979, Primack 1983, Lloyd 1985, Webb and Kelly 1993). A large proportion of plant species are also dioecious (Godley 1979). Previous research on New Zealand insect pollinators has been limited and mostly restricted to anecdotes and observations. Thomson (1927) and Heine (1938) provide initial accounts of the pollination of some native species by birds and insects. Other exceptions are Primack (1978, 1983) who has described the insect assemblages for New Zealand's alpine and montane flora, Webb (1985, 1994) who studied the pollination of *Corokia contoneaster* and *Discaria toumatou*, Powlesland (1984) has described the pollination of *Melicytus* spp., and Robertson (1989) the pollination of *Myosotis colensoi.*

In contrast to insects, birds are thought to be relatively unimportant pollinators in New Zealand (Lloyd 1979, Clout and Hay 1989). Seven native bird species are known to visit flowers. However, only two honeyeaters (Meliphagidae), tui (*Prosthemadera novaezelandiae*) and bellbird (*Anthornis melanura*) are common visitors (Godley 1979). Bird pollinated (ornithophilous) flowers are often large and brightly coloured with plentiful quantities of nectar (Faegri and van der Pijl 1979, Stiles 1978, Godley 1979) although only approximately 13 New Zealand plants produce flowers which fit this description (Godley 1979, Castro and Robertson 1997). Thisl paucity of ornithophilous flowers is surprising (Craig *et al* 1981) when compared to the flora of close land masses such as Australia, where birds may pollinate up to 1000 species of plants (Ford *et al* 1979).

However, we should be cautious when ascribing pollination syndromes to plants based on their floral morphology and observed associations. The main vectors for a plant can only be crudely assessed from its floral morphology (Collins *et al* 1984, Bond 1994). Studies have shown plant-pollinator interactions can be subtle (Webb 1994), such as involving cryptically specialised or generalised pollinators (Lindsay and Bell 1985). *Dactylanthus taylorii* is a native plant with a specialised pollination system only recently discovered to involve the short tailed bat (*Mystacina tuberculata*) as its principle pollinator (Lord 1991, Ecroyd 1993). Other studies have investigated the roles of reptiles and thrips as pollinators (Norton 1984, Whitaker 1987a, Whitaker 1987b). Recent studies on New Zealand mistletoes (*Peraxilla tetrapetala, P. colensoi*) have revealed a specialist bird-plant relationship, where honeyeaters (tui and bellbird) are required to open special "twist top" flowers before pollination can take place (Ladley and Kelly 1995a, 1995b but see Kelly *et al* 1996). This, combined with Castro's (1995) observations of New Zealand's third honeyeater, hihi (*Notiomystis cincta*), feeding on a wide variety of ornithophilous and entomophilous flowers on Kapiti Island, has led to speculation that birds could be more involved in the pollination of New Zealand flowers than has previously been recognised (Castro and Robertson 1997). Currently, only basic information exists about New Zealand's pollination systems (Lloyd 1985).

Over the past 1000 years traditional pollinator assemblages have changed greatly in New Zealand. The number of New Zealand bird species and their abundances have declined dramatically, probably due to introduced mammalian predators and habitat fragmentation. Those remaining represent a small sample of what was present before the arrival of humans (Diamond and Veitch 1981, King 1984, Holdaway 1989). Currently, the implications of the loss of pollinators to plant-pollinator interactions remains largely unstudied (Bond 1995, Kevan 1975), but authors are beginning to warn of the potential threats to the long term functioning of ecosystems if mutualisms such as plant-pollinator relationships are interrupted (Clout and Hay 1989, Johnson and Bond 1992, Bond 1995, Kearns and Inouye 1997). New Zealand provides important opportunities to study how these mutualisms are being disrupted and diminished by bird extinctions (Clout and Hay 1989) and the pollinator limitation which may result (Schemske 1980, Ågren 1996)

Island sanctuaries are the best remaining examples of how New Zealand mutualistic relationships would have functioned prior to the arrival of humans. Many New Zealand islands lack introduced mammalian predators and have a greater diversity and abundance of bird species than the depauperate mainland (Diamond and Vietch 1981, Castro 1995). Island sanctuaries therefore, are a reference point which can be used to detect and measure changes on the mainland (Cowan 1992). This study uses Kapiti Island as a benchmark to identify changes in plant-pollinator interactions on the mainland which may be caused by reduced avian densities. These can be identified by several methods as follows.

1. Nectar is provided as a reward for pollinators and in doing so can manipulate their behaviour (Henrich and Raven 1972, Pyke 1984, Zimmerman and Pyke 1986). The plant must offer sufficient rewards to pollinators to ensure they return regularly (Heinrich and Raven 1972). Measuring standing crops of nectar is very important (Zimmerman 1988) as nectar depletion can give an indication of the relative abundances of pollinators (Collins *et al* 1984).
2. Pollen deposition can also help understand plant-pollinator interactions (Dieringer 1992) as it is the first requirement for successful pollination.
3. Fruit set is the ultimate measure of female reproductive success (Schemske and Horvitz 1984). More effective pollinators will generate the greatest fruit set (Stebbins 1970, Primack and Silander 1975, Thomson and Plowright 1980, Motton *et al* 1981, Schemske and Horvitz 1984).

Accordingly, this chapter investigates the pollination of four native lowland plant species, two of which display typical ornithophilous syndromes (*Metrosideros fulgens, Fuchsia excorticata*) and two which have entomophilous syndromes (*Dysoxylum spectabile, Geniostoma ligustrifolium*). Visitation rates, nectar removal, pollen deposition, pollen tube growth, and fruit set experiments and are used to determine:

1. whether birds or insects can pollinate ornithophilous and entomophilous plants.
2. whether the importance of birds or insect pollination varies with site.
3. whether sites are pollinator limited.
4. whether floral morphology can predict pollinator service.

# 2.2. METHODS

## 2.2.1. SPECIES AND SITE SELECTION

All four species are endemic to Kapiti Island and except for *M. fulgens*, were also present naturally at two mainland sites. Mainland sites were selected because they were geographically close to Kapiti Island. They were easily accessed by car and foot and were subject to ongoing possum control during the time of the study which was observed to improve the condition of flowering trees.

**Table 2.1. Summary table of sites, species and data collected**

| Species | #plants Kapiti | #plants mainland | breeding System | Flower type | visitation rates | caged/ uncaged treatments | nectar depletion | pollen deposition | pollen tube counts | fruit set |
|---|---|---|---|---|---|---|---|---|---|---|
| *Metrosideros fulgens* | 9 | Kahuterawa Rd 5 | hermaphroditic | ornithophilous | yes | yes | yes | no | no | no |
| *Fuchsia excorticata* (kotukutuku) | 6 (all hermaphrodite) | Akatarawa Rd 4 (hermaphrodite)<br>Gladstone Rd 4 (hermaphrodite) | gynodioecious | ornithophilous | yes | yes | yes | yes | yes | yes |
| *Dysoxylum spectabile* (kohekohe) | 7 (all male) | Raumati Reserve 5 (all male)<br>Wilton Bush 5 (all male) | [1, 2]dioecious | entomophilous | yes | yes | yes | no | no | no |
| *Geniostoma ligustrifolium* (hangehange) | 7 (all female) | Lake Papaitonga 4 (female)<br>Kahuterawa Rd 5 (female) | gynodioecious | entomophilous | yes | yes | yes | yes | yes | yes |

1. all trees studied were assumed to be male because no fruit was observed on any tree and all inflorescences abscised 2. suspected breeding system

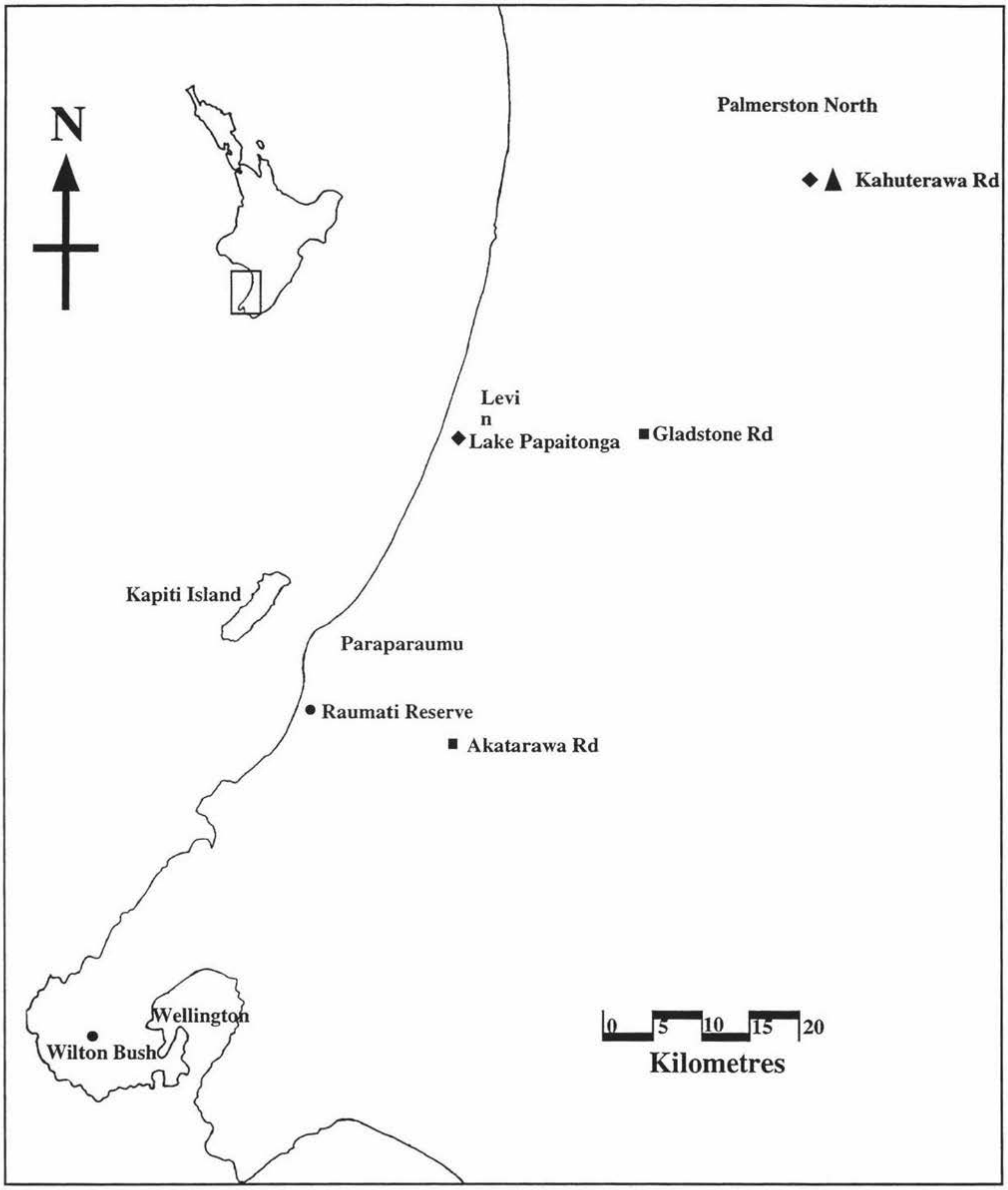


Figure 2.1. Map of mainland study sites. *M. fulgens* (triangles), *F. excorticata* (squares), *D. spectabile* (circles) and *G. ligustrifolium* (diamonds).

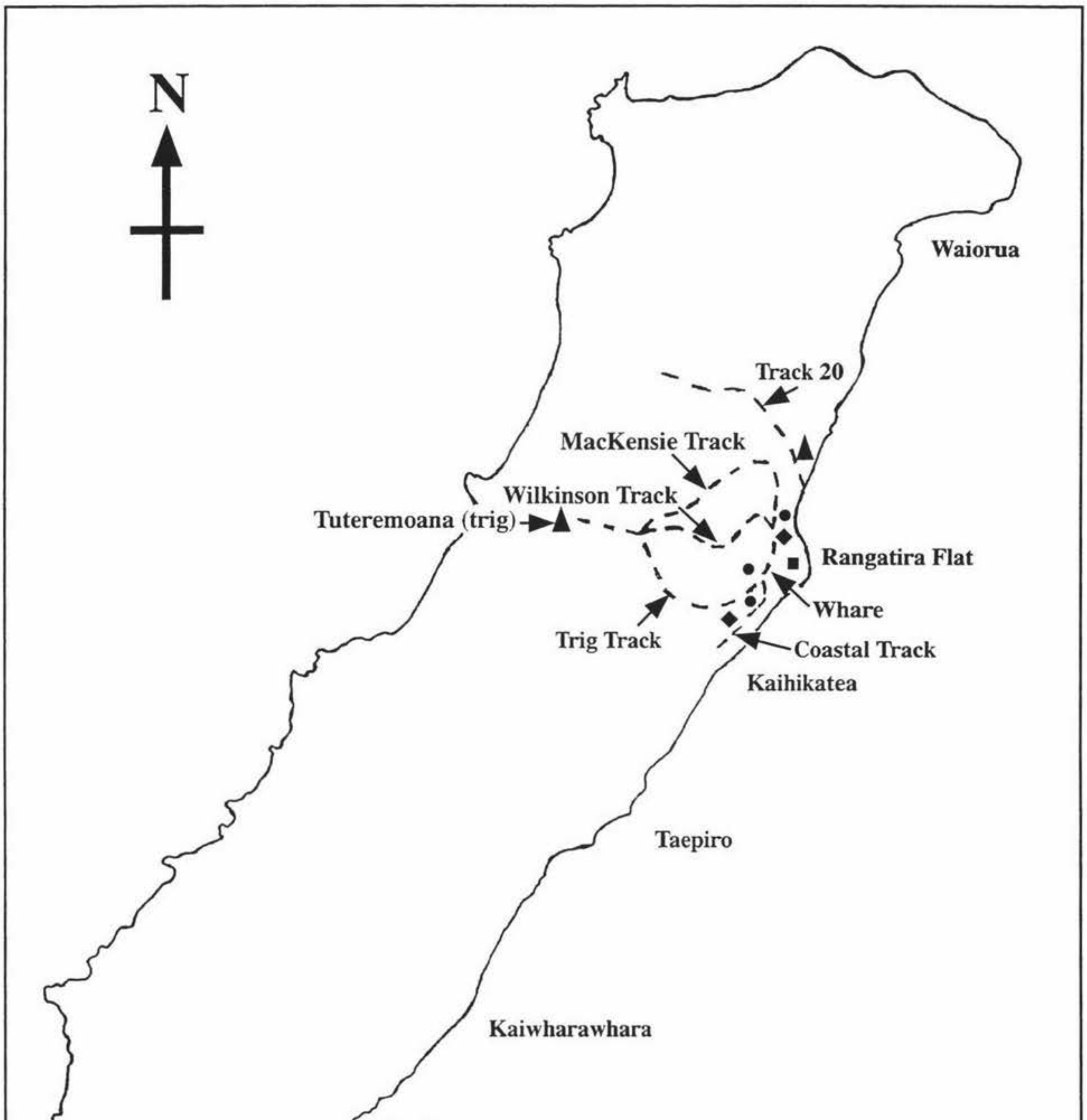


**Figure 2.2. Map of Kapiti Island study sites. *M. fulgens* (triangles), *F. excorticata* (squares), *D. spectabile* (circles) and *G. ligustrifolium* (diamonds).**

## 2.2.2. SPECIES DESCRIPTIONS

### 2.2.2.1. *Metrosideros fulgens* (aka kura, Myrtaceae)

One of 11 species of *Metrosideros* in New Zealand, this endemic liane produces large red ornithophilous flowers with conspicuous yellow pollen on the anthers (Salmon 1986). It is found throughout New Zealand in coastal and lowland forests except Stewart Island. The flowers develop at variable times but usually occur between February and October (Smith-Dodsworth 1991). Many seeds are enclosed in a capsule which dries and splits open. *Metrosideros* can probably self fertilise (Anderson 1997) but other *Metrosideros* spp. are thought to have some degree of self incompatibility (Carpenter 1976).

### 2.2.2.2. *Fuchsia excorticata* (kotukutuku, Onagraceae)

One of four *Fuchsia* representatives in New Zealand, this is the largest *Fuchsia* in the world growing up to 14 metres high (Salmon 1986). It is common throughout New Zealand from sea level to 1060 metres, as a dominant tree or second growth species often along roadsides and banks. *F. excorticata* is gynodioecious producing hermaphrodites which are self compatible but act principally as pollen donors, as well as females (Delph and Lively 1985). Only hermaphrodites were used in this study. Flowers are produced from August to January and are initially green but change to purple as they age. This species is primarily bird pollinated and the pollen is joined by sticky viscin threads (Delph and Lively 1989, Delph and Lively 1985). A study in the South Island New Zealand has shown flowers abscise when the pollen tubes have grown down the style and almost 100 percent of the flowers were pollinated by the end of the green phase (Delph and Lively 1989). Fleshy fruits form in late summer which each contain up to 400 tiny seeds and turn a dark purple when ripe and are eaten by birds (Godley 1955, Craig *et al* 1981) (Burrows 1995a). Seeds may remain viable for up to 20 years (Fountain and Outred 1991). Undispersed fruits tend to overripen and shrivel on the parent tree.

#### 2.2.2.3. *Dysoxylum spectabile* (kohekohe, Meliaceae)

This is the only species of the mainly tropical genus *Dysoxylum* found in New Zealand. In general Meliaceae produce entomophilous flowers (Styles 1972) but birds have been observed visiting *D. spectabile* flowers (Court 1985, Castro and Robertson 1997). Growing up to 15 metres, *D. spectabile* produces many flowers which are borne in clusters on panicles from April to August (Allan 1961, Salmon 1986). Recent studies have revealed *D. spectabile* is probably dioecious producing two plant forms, one a fruit bearing female which produces no pollen and the other a pollen producing male which rarely set fruit (Braggins and Large 1996). Fleshy fruits are enclosed in a capsule which breaks open to reveal bright red/orange fruits when ripe.

#### 2.2.2.4. *Geniostoma ligustrifolium* (hangehange, Geniostomaceae)

This endemic species is a bushy plant which commonly forms the understorey of coastal and lowland forest from Three Kings Island south to Golden Bay and Marlborough Sounds (Salmon 1986). Small green flowers are produced in early spring and insect pollinators are attracted to their strong scent (Rattenbury 1980). *G. ligustrifolium* is gynodioecious and produces two plant forms. A female form produces flowers with pollen free stigmas and reduced (sterile) anthers while the hermaphrodite (male) form presents sticky glue-like pollen on the stigma which sticks to floral visitors (Rattenbury 1980, Endress and Garnock-Jones in prep.). Flowers are thought to be self incompatible (Prof. Phil Garnock-Jones pers. comm). Females are thought to set large amounts of fruit while males only occasionally set fruit (Rattenbury 1980, Dr. Phil Garnock-Jones pers.comm.). Fruits are produced in capsules which darken and split open to release seed during the summer.

### 2.2.3. SITE DESCRIPTIONS

#### 2.2.3.1. *Kapiti Island (40° 51´S 174° 56´E)*

Kapiti Island is New Zealand's second largest offshore reserve. Nine kilometres long and over two kilometres wide, it covers 1965 hectares, reaches 542 metres at its highest point, averages 1050 millimeters of rain annually and 13.3°C. The island supports large populations of endemic birds and is a sanctuary for a number of bird species including hihi and saddleback (*Philesturnus carunculatus*). Large parts of the island were once grazed. During the 1800's the island supported populations of cattle, goats, sheep, pigs, feral cats, all of which have been removed. The possum (*Trichosurus vulpecula*) was eradicated in 1986 (Cowan 1992) and an eradication programme to remove the only remaining mammalian predators; kiore (*Rattus exulans*) and norway rats (*R. norvegicus*) was carried out during the time of this study (September-October 1996).

Toro (*Myrsine salicina*), hinau (*Elaeocarpus dentatus*), tawa (*Beilschmiedia tawa*), kamahi (*Weinmannia racemosa*) and mahoe (*Melicytus ramiflous*) dominate higher altitudes while vegetation at lower altitudes is predominantly karaka (*Corynocarpus laevigatus*) and kohekohe (*Dysoxylum spectabile*) forest with a five finger (*Pseudopanex arboreus*) and mahoe understorey. There are also emergent northern rata (*Metrosideros robusta*) and podocarps, miro (*Prumnopitys ferrunginea*) and matai (*P. taxifolia*). Kanuka (*Kunzea ericoides*) tends to persists at a late seral stage, while shrubs of manuka (*Leptospermum scoparium*), *Olearia paniculata*, heketara (*Olearia rani*), mapou (*Myrsine australis*) and puka (*Griselinia lucida*) are important understorey plants. Grasslands on ridges are dominated by mountain flax (*Phormium cookianum*), tauhinu (*Cassinia leptophylla*) and five finger, but these are gradually being replaced by shrubland species (Esler 1967).

Study species were dispersed throughout the middle of Kapiti Island. Two *M. fulgens* populations were used, one at Tuteremoana (the trig) and the other at the base of Track 20. All *F. excorticata* trees were located on Rangatira Flat. *D. spectabile* trees were dispersed along the MacKensie Track, behind the Whare and along the beginning of the Trig Track. *G. ligustrifolium* trees were situated at the lower MacKensie/Wilkinson junction and along the Coastal Track.

### 2.2.3.2. *Kahuterawa Road (40° 23'S 175° 37'E)*

This site was located on private land next to a road end bordering the Kahuterawa River. Approximately 200 metres in altitude, it receives an annual rainfall of approximately 906 millimetres, 1989 hours of sunshine and averages 12.9°C (New Zealand

Meterological Service 1983). Kamahi, *Metrosideros fulgens* and hangehange (*G. ligustrifolium*) dominate the understorey and there are a few emergent rewarewa (*Knightia excelsa*). Stock were able to graze under most trees and a poison operation was carried out to reduce possum numbers during the time of this study.

### 2.2.3.3. *Gladstone Road (40° 40´S 175° 20´E)*

This road winds east from Levin to the foot of the Tararua ranges at approximately 100 metres above sea level. It receives similar weather to nearby Levin, an average of 1120 millimetres rainfall each year, 1865 sunshine hours annually and averages 13°C (Wassilief *et al* 1986). Exotic plantations of *Eucalyptus* spp. cover parts of the northern side of the road. *F. excorticata* trees used for this study were growing in grazed or ungrazed paddocks, or in remnant road side bush patches which contain predominantly hangehange and kamahi. The northern side of the road receives ongoing poisoning to control possum populations.

### 2.2.3.4. *Akatarawa Road Saddle (40° 58´S 175° 10´E)*

The saddle road winds around the fringes of the Tararua ranges. *F. excorticata* trees were located in a boggy depression in a paddock on one side of the road located approximately 530 metres above sea level. The paddock is surrounded by pine plantations as well as bush remnants consisting of a hinau-kamahi-rimu (*Dacrydium cupressium*)-mahoe dominated canopy, which has supplejack, horopito (*Pseudowintera axillaris*), *Coprosma repens*, *C. foetodissima* and putputaweta (*Carpodetus serratus*) in the understorey. It has a high rainfall (3100 millimeters per year) and is buffeted by norwesterly winds (Park 1971 cited in Norton 1984). There is evidence of stock grazing around the study trees.

### 2.2.3.5. *Raumati Reserve (40° 54´S 174° 59´E)*

This reserve is located three kilometres south of Paraparaumu and covers 64 hectares with steep terrain rising to 202 metres above sea level. The coastal vegetation on lower slopes is similar to Kapiti Island being dominated by mature kohekohe, titoki (*Alectryon excelsa*) and karaka. These are bordered by remnants of *Olearia paniculata*, manuka, kawakawa (*Macropiper excelsum*), rangiora (*Brachyglottis repanda*), five finger, kaikomako (*Pennantia corymbosa*), hangehange, wharangi (*Melicope ternata*), poroporo (*Solanum aviculare*) and blackberry (*Rubus fruticosus*). Possums were controled in the reserve on 1 August 1995 but taller canopy trees had already suffered extensive possum browsing (Wassilief 1995, Wassilief *et al* 1986, Raumati Escarpment Reserve Draft Management Plan 1997). There appears to be little or no regeneration of kohekohe but karaka seedlings are abundant on the forest floor.

### 2.2.3.6. *Wilton Bush (41° 17´S 174° 44´E)*

This reserve is situated in Karori (a suburb of Wellington) and encompasses 80 hectares of near virgin rimu-tawa forest on the southern slopes with secondary podocarp-broadleaved (kohekohe) forest on the northern slopes. The reserve rises to approximately 152 metres above sea level, receives an average of 1586 millimetres of rain each year and a temperature of 11.7°C (New Zealand Meterological Service 1983). Patches of five finger, titoki and kotukutuku grow in the reserve. Intensive possum control since 1993 has improved the overall health of vegetation considerably (Pekelharing 1996).

### 2.2.3.7. *Lake Papaitonga Scenic Reserve (40° 39´S 175° 16´E)*

This 111 hectare reserve is situated five kilometres south of Levin and is the only intact sequence of wetland communities from swamp to terrace forests within the Wellington and Manawatu regions (Wassilief *et al* 1986). Over half of the reserve is either pond or lagoon. The reserve is 15-30 metres above sea level and receives similar weather and rainfall to Gladstone Rd. Mature tawa-titoki-kohekohe forest dominates the canopy and the understorey comprises nikau (*Rhopalostylis sapida*), mahoe, kawakawa and mamaku (*Cyathea medullaris*). The western end of the reserve is predominantly hinau, pigeonwood (*Hedycarya arborea*), ngaio (*Myoporum laetum*) and puka with a poorly developed understorey of kawakawa, hangehange and mahoe. Tall kahikatea (*Dacrycarpus dacrydioides*), pukatea (*Laurelia novae-zelandiae*), tawa, swamp maire (*Syzygium maire*), supplejack (*Rhypogonum scadens*), flax (*Phormium tenax*) and wheki (*Dicksonia squarrosa*) occur in gullies or swamp margins (Wassilief *et al* 1986). There is ongoing possum control in the reserve.

## 2.2.4. POLLINATION SERVICES

### 2.2.4.1. *Flower visitation rates*

Bird visitation rates were determined by videoing a known number of control flowers of each species on Kapiti Island and mainland sites. Control flowers had no treatments applied to them and could be accessed by bird and insect visitors. Videos ran for up to three hours at a time and were viewed at a later date to record the number and duration of visits. Data were converted into the number of visits per flower per hour. Any birds or insects seen visiting flowers during fieldwork were also noted. Visitation rates by birds per flower per hour were calculated for control flowers for all species except *M. fulgens* where visitation rates for birds were too infrequent to video and consequently, only visitation rates for insects were determined.

Close up videoing for insect visitors was carried out for *M. fulgens* to establish whether the bird exclusion cages were affecting insect visitation rates and therefore influencing pollination (see 2.2.4.2.). Consequently on Kapiti Island, insect visitation rates to bird excluded cages enclosing *M. fulgens* flowers were compared with insect visitation rates to control flowers.

### 2.2.4.2. *The treatments*

The following treatments were applied to each tree of each species at each site.

**No Vectors (bagged)**: This prevented all insects and birds from visiting the flowers and measured whether vectors were required to set fruit. Chicken wire (15mm mesh) was folded around a selected number of buds. Fine curtain netting was wrapped around the outside and secured to the chicken wire with small pieces of wire. The ends were tied with soft cord to encase the buds in a "cocoon" while the entire cage was secured to the plant by thin wire. The cage proved to be very effective although small crawling insects, spiders and thrips (order Thysandoptera) were occasionally found inside.

**Insect Only**: This cage allowed insects to visit flowers but prevented birds. Its construction was similiar to the no vectors cage, but the ends were wrapped in 12 millimetre diameter strawberry netting and secured with fine cord. The difference in fruit set between this treatment and the above treatment measured the importance of insect pollination.

**Birds and Insects Combined Access (control)**: This was a control treatment. These flowers were able to be freely visited by both birds and insects on the experimental branches. These were located as far away as practical from the cages on the tree to reduce any possible influence the cages may have had on bird and insect pollinators. The difference between this treatment and the above treatment measured the importance of bird pollination.

Any flowers and fruits which had already opened or formed prior to the establishment of the treatments were removed to eliminate them from the study.

### **2.2.4.3.** *Nectar Depletion*

The standing crop in the insects only and control treatments were compared to flowers in (bagged) treatments at each site to give an estimate of the rate of depletion. Nectar samples were collected at varying times between 0800 and 1600 hours. The methods used to collect nectar from the four species were species specific because of their differing floral morphologies as described below.

The amount of sugar produced by individual flowers of three species *(M. fulgens, F. excorticata, D. spectabile)* was measured using the capillary-refractometer method. Nectar volume was measured by removing all nectar from flowers using 50 or 10 microlitre capillary tubes and the concentration was read using a hand-held refractometer. These measurements were used to calculate the amount of sugar in a flower and this was converted into sucrose equivalents (Kearns and Inouye 1993).

### *Metrosideros fulgens*

Each site was sampled on seven to 14 occasions between mid-January and mid-March 1996. An attempt to sample flowers from each plant and treatment was made on each sample date but this was not always possible as there were not always open flowers available. Flowers were sampled only if their anthers were exposed with fresh pollen. On some occasions individuals were used to test cage designs and materials and had more than one replicate branch of the three treatments.

### *Dysoxylum spectabile*

Trees at each site were sampled on three to eight occasions between mid-May and September 1996. Flowers in the treatments could only be sampled if their flowers were open on the sample date. Tree climbing equipment was used to access flowers in the canopy. The number of replicates of each treatment differed between trees and additional cages were constructed to replace cages which had fallen off between sampling dates. Up to six flowers were removed from an exclusion cage on any one sample date and were categorised as "with pollen" or "without pollen". In addition, six to 14 control flowers which could be freely visited by birds and insects were selected at random and removed for sampling.

### *Fuchsia excorticata*

Nectar was sampled on two or three occasions at each site between August and November 1996. Only flowers which were green or purple-green in colour with fresh pollen were used, as nectar production ceases once flowers turn purple (Delph and Lively 1985). Up to five flowers were removed from a cage at any one time, and up to six control (bird and insects combined) flowers were randomly chosen from each tree.

### *Geniostoma ligustrifolium*

Flowers were sampled on two occasions at each site during October 1996. Only flowers with fresh and sticky stigmas were sampled. The above sampling method was unable to be used on this species because of the small size of the flowers. Therefore, a drop of distilled water was placed on each flower to dilute its nectar (Cresswell 1990). This solution was then absorbed using a wick cut from filter paper and each sample was redissolved and processed following the method of McKenna and Thompson (1988) and converted to sucrose equivilents (Kearns and Inouye 1993). Up to six flowers were sampled from each treatment and up to six control flowers were randomly sampled from each tree. Flowers were only removed if they had freshly exposed stigmas. Any flowers which were removed for nectar sampling from the exclusion treatments were eliminated from the fruit set counts (see 2.2.4.6.).

### 2.2.4.4. *Pollen Deposition*

Comparing the number of pollen grains deposited by pollinators can give an indication of which pollinators are carrying out the best pollination service. Styles from flowers which were removed for nectar analysis from *F. excorticata* and *G. ligustrifolium* were stored in a solution of 3 parts 75% ethanol to 1 part 45% acetic acid and used for the following analysis.

*Fuchsia excorticata*

In addition to analysing the flowers collected for the nectar analysis, up to six freshly abscissed flowers lying on the ground directly below the experimental tree were collected. These flowers were collected because flowers only abscise once pollen tube growth is complete and thus represent pollen accummulation over the life of the flower (Delph and Lively 1989). Styles were removed from flowers and stained in a solution of decolourised 0.1% aniline blue in 0.1 M $K_3HPO_4$ (Martin 1959). A histokinette washed each style in two solutions of distilled water then softened them in a 8N solution of NaOH. After washing them a further five times in distilled water they were stained for 12 hours in the aniline blue solution. The styles were mounted onto slides and viewed at X16 magnification using UV light and an epifluorescence microscope. As there were too many pollen grains to accurately count, the number of pollen grains deposited on a two dimensional area were counted at four sample areas on the stigma. The total number of pollen grains was extrapolated by multiplying the average number of pollen grains per unit area in the two dimensional areas by the total area of the stigma.

*Geniostoma ligustrifolium*

Flowers were washed three times in distilled water. The styles were dissected from the flowers and soaked in 0.1% decolourised aniline blue in 0.1 M $K_3HPO_4$ for at least 12 hours with no NaOH pre-treatment. Styles were mounted and viewed as for *F. excorticata* except exact counts of pollen grains and pollen tubes were made.

### 2.2.4.5. *Pollen tubes*

Pollen tubes were able to be counted and styles were mounted for pollen deposition counts. The large of number pollen tubes growing down the styles of *F. excorticata* flowers meant their numbers were categorised as zero, 10's, 100's or 1000's while the actual numbers of pollen tubes in *G. ligustrifolium* flowers were counted.

### 2.2.4.6. *Fruit set*

The relative importance of insects and birds as pollinators were compared by controlling their access to flowers and then counting the number of fruit they formed. *F. excorticata* and *G. ligustrifolium* were used in this experiment because female trees could be identified from their flowers, and fruits matured within a few weeks of fertilization.

*Fuchsia excorticata*

This species produced buds continuously throughout the flowering season which made it difficult to follow the development of individual buds. Consequently, by visiting each site every two to four weeks betweeen August to 1996 and January 1997, a peak number of buds and subsequent number of fruits was identifed in each treatment. This enabled a peak buds:fruit ratio to be calculated, which was used in the fruit set analysis. Flowers which had been removed from exclusion cages for the nectar analysis were assumed to have developed into mature fruit when fruit counts were carried out. The fruit set from the no vectors (bagged) cage on one tree at Akatarawa Road may have been underestimated because due to the fact the cage was found open between two visit dates. All fruits which had formed between these dates were eliminated from the analysis.

*Geniostoma ligustrifolium*

Experiments were conducted during September and October 1996. This species produced all its buds at the beginning of the season which made it possible to have a complete count of the number of buds produced in each treatment. The number of fertilized (swelled) and unfertilized (unswelled) fruits were counted four to six weeks after flowering had ceased. A tree at Kahuterawa Rd accidently had its insect only treatment placed on a male and consequently this replicate was removed from all analyses.

### 2.2.5. STATISTICAL METHODS

Results were analysed using SAS's general linear models procedure (SAS Institute 1988). Hypotheses for mixed model ANOVA's were tested for site, tree (nested in site), treatment and site by treatment effects. Flower type was used as another classification variable for the *D. spectabile* nectar analysis. The dependent variables (sugar per flower, pollen counts, pollen tubes, *Fuchsia excorticata* fruit set) were log transformed prior to analysis to standardise their distribution. Pollen tube counts for *F. excorticata* were estimated and assigned to frequency classes and an ANOVA was performed on these classifications as an approximation to a log scale. Type III sums of squares were used in all cases and were compared with type II sums of squares although little difference was found. Analyses for *F. excorticata* fruit set were conducted on the actual proportions of fruit formed.

The data on fruit set for *G. ligustrifolium* was binary where the number of successful pollinations and pollination failures were scored for each plant and each treatment. Fruit set data were therefore analysed using a generalised linear model with a binomial error distribution and logit link function using the S - PLUS statistical package (Mathsoft Inc. 1995). All significance was tested to 0.05.

# 2.3. RESULTS

In the analyses presented below, significant site and treatment effects indicate there were differences between sites or treatments. However, the most interesting effects are significant site by treatment interactions which suggest the effects caused by the treatments differed between the sites. The hypothesis that pollination service will be best in the control flowers at sites with high bird densities and poorest in the no vector (baggged) treatments would be supported by a significant site by treatment interaction.

## 2.3.1. METROSIDEROS FULGENS

### 2.3.1.1. *Visitation*

There was no significant difference in visitation rates between sites, possibly due to the limited time available and bad weather during the sample periods which prevented extensive videoing (Tables 2.2., 2.3.). Many bumblebees (*Bombus* spp.), wasps (*Vespula* sp.) and native bees were observed on flowers at Kahuterawa Rd. Honeybees (*Apis mellifera*), wasps and bellbirds were observed frequently visiting *M. fulgens* flowers on Kapiti Island. Visitation rates of insects between caged and uncaged flowers on Kapiti Island did differ but not significantly. Personal observations confirmed that cages could inhibit insect visitation but not to a large extent.

### 2.3.1.2. *Nectar*

The amount of nectar in the flowers varied significantly between treatments which explained a large proportion of the variation of the data (~55%) (Table 2.4., Fig 2.3.). Both insects and birds removed significant amounts of nectar at both sites but insects appeared to be removing the majority of nectar (an average of approximately 2 milligrams sucrose equivalent). An index of total nectar production per flower could be calculated from flowers in the no vectors (bagged) treatments. This was not significantly different between sites ($P = 0.9195$).

## 2.3.2. FUCHSIA EXCORTICATA

### 2.3.2.1. *Visitation*

Kapiti Island experienced the highest bird visitation rates but again, there was no significant difference in visitation rates between sites (tables 2.2., 2.3.). Tui and bellbirds were frequently observed visiting flowers on Kapiti Island as well as a single honeybee. Bellbirds, bumblebees and honeybees were seen on flowers at Gladstone Rd, and bellbirds and tui at Akatarawa Rd.

### 2.3.2.2. *Nectar*

Site, treatment and site*treatment all had significant effects on nectar removal. All explained a similar proportion of variation in the data (8.19%-17.54%) (Table 2.5., Fig 2.4.) . Trees at Akatarawa Rd produced more nectar in each flower than the other two sites, significantly so at Gladstone Rd ($P = 0.0497$). Insects removed some nectar from Kapiti Island and Akatarawa Rd but the difference between the insect only and no vector (bagged) treatments were not significant. Birds were significant nectar removers on Kapiti Island ($P = 0.0042$) while they removed minimal amounts of nectar from the mainland sites. Kapiti Island was notable for its virtual absence of sugar in control flowers which indicates a high depletion rate. Gladstone Rd demonstrates a strange anomaly in its nectar removal patterns as flowers in the no vectors (bagged) treatments contained less nectar than flowers which were insect visited, although this was not significant ($P = 0.2224$).

### 2.3.2.3. *Pollen Counts*

There was no clear pattern to the number of pollen counts on stigmas and there was no significant difference between the sites, treatment nor site*treatment interaction effects (Table 2.6., Fig 2.5.). However, there was a generally increasing number of pollen grains from the no vectors (bagged) treatments to insects only treatments, to flowers from the ground. This suggests insects and birds deposited large quantities of pollen on the stigma. The lack of conclusive results in comparison with nectar, pollen tubes (see below) and fruit set analyses (see below) suggests flowers were contaminated during their sampling by accidentally transferring pollen between them and few conclusions can be drawn about the pollinators.

#### 2.3.2.4. *Pollen tubes*

The number of pollen tubes significantly differed between sites and treatments. Treatment explained the largest proportion of the variation in the data (~32%) (Table 2.7., Fig 2.6.). The two mainland sites did not differ significantly ($P = 0.2157$), but Kapiti Island differed from Gladstone Rd ($P = 0.0095$). Control flowers (which included the ground treatment) had a significantly greater number of pollen tubes than flowers pollinated by insects only ($P = 0.0094$). Insects did not significantly increase the number of pollen tubes over when flowers had no vectors ($P = 0.5183$). In fact, both mainland sites had more pollen tubes grown in the no vectors treatment than from insect pollination. Kapiti Island control flowers had higher numbers of pollen tubes than both mainland sites but again, these were not significant.

#### 2.3.2.5. *Fruit set*

The treatments significantly affected the number of fruits formed and explained ~12% of the variation in the data (Table 2.8., Fig 2.7.). Pollination by insects only set some fruit at all sites. Kapiti Island was the only site where control treatments set more fruit than insects only ($P = 0.0042$) and was the highest overall, suggesting a significant site*treatment interaction but this effect fell just short of being significant. Flowers with no vectors at Akatarawa Rd set more fruit than insect only flowers, although this was not significant ($P = 0.4118$). One tree at this site appeared to produce more fruit in the no vectors cage in comparison to other trees. When this tree was removed from the analysis the overall treatment effect increased ($P = 0.0140$) but the site*treatment interaction did not become significant ($P = 0.0905$).

### 2.3.3. DYSOXYLUM SPECTABILE

#### 2.3.3.1. *Visitation*

There was no significant difference in visitation rates between sites (Tables 2.2., 2.3.). Flocks of silvereyes (*Zosterops lateralis*) were seen visiting flowers at both mainland

**Table 2.2. showing average visitation rate per flower per hour at each site. Visitation rates by birds were calculated for control flowers for all species except *M. fulgens* where visitation rates included birds and insects.**

| Species | *M. fulgens* | *D. spectabile* | *F. excorticata* | *G. ligustrifolium* |
|---|---|---|---|---|
| Minutes of videoing per site | Kapiti Control flowers -334<br>Kapiti Insect only-578<br>Kahuterawa Rd Control flowers-64 | Kapiti Control flowers -558<br>Wilton Bush Control flowers-185<br>Raumati Reserve Control flowers-299 | Kapiti Control flowers -873<br>Gladstone Rd Control flowers-87<br>Akatarawa Rd Control flowers-464 | Kapiti Control flowers -1349<br>Kahuterawa Rd Control flowers-782<br>Lake Papaitonga Control flowers-96 |
| Average visitation per flower per hour | Kapiti Control flowers -26.58<br>Kapiti Insect only flowers -6.69<br>Kahuterawa Rd Control flowers-31.01 | Kapiti Control flowers -8.37<br>Wilton Bush Control flowers-6.90<br>Raumati Reserve Control flowers-0 | Kapiti Control flowers -1.63<br>Gladstone Rd Control flowers-0.56<br>Akatarawa Rd Control flowers-0.46 | Kapiti Control flowers -0.05<br>Kahuterawa Rd Control flowers-0.07<br>Lake Papaitonga Control flowers-0.01 |

**Table 2.3. ANOVA showing insect visitation rates to *M. fulgens* and bird visitation rates to *F. excorticata, D. spectabile, G. ligustrifolium* between sites. This table also shows the comparision between visitation rates of *M. fulgens* flowers which could be visited by insects only and control (bird and insect combined) treatments.**

| Species | df | Sums of Squares | Pr (Chi) |
|---|---|---|---|
| *M. fulgens* | 1 | 29.8305 | 0.9021 |
| *F. excorticata* | 2 | 2.9341 | 0.3820 |
| *D. spectabile* | 2 | 94.9547 | 0.3820 |
| *G. ligustrifolium* | 2 | 0.0027 | 0.9325 |
| *M. fulgens* (between treatments) | 1 | 587.9878 | 0.3920 |

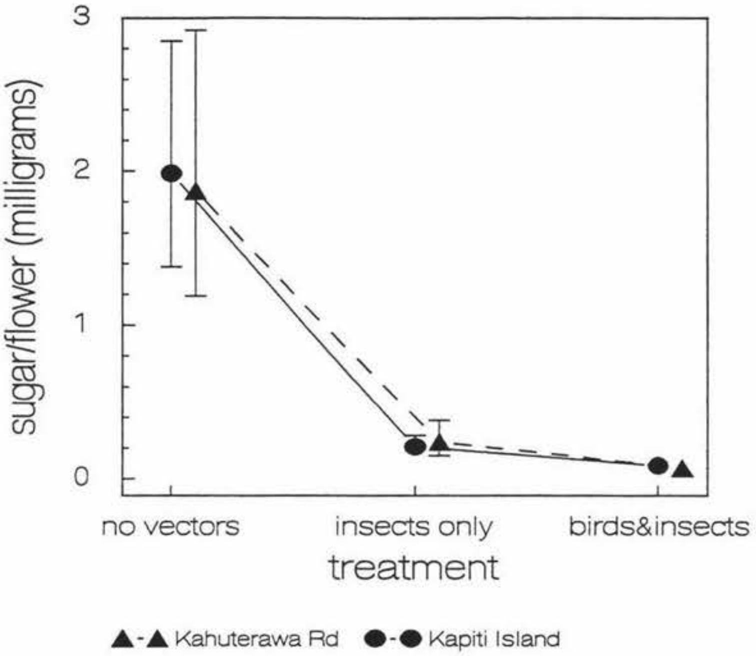


**Figure 2.3. showing the amount of sugar in the nectar of *M. fulgens* flowers according to the treatment and sites. Nectar was collected on 7 - 14 occasions at each site using the capillary-refractometer method and converted to sucrose equivalents.**

**Table 2.4. ANOVA table showing effects of site, tree, treatment and site*treatment interaction on the amount of sugar in the nectar of *M. fulgens* flowers. Raw data were log transformed prior to the SAS analysis**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 1 | 0.0104 | 0.02 | 0.9047 |
| Tree (site) | 13 | 0.7008 | 11.96 | 0.5142 |
| Treatment | 2 | 20.8521 | 54.75 | 0.0001 |
| Site * Treatment | 2 | 0.0564 | 0.14 | 0.9248 |
| Error | 14 | 0.7175 | | |

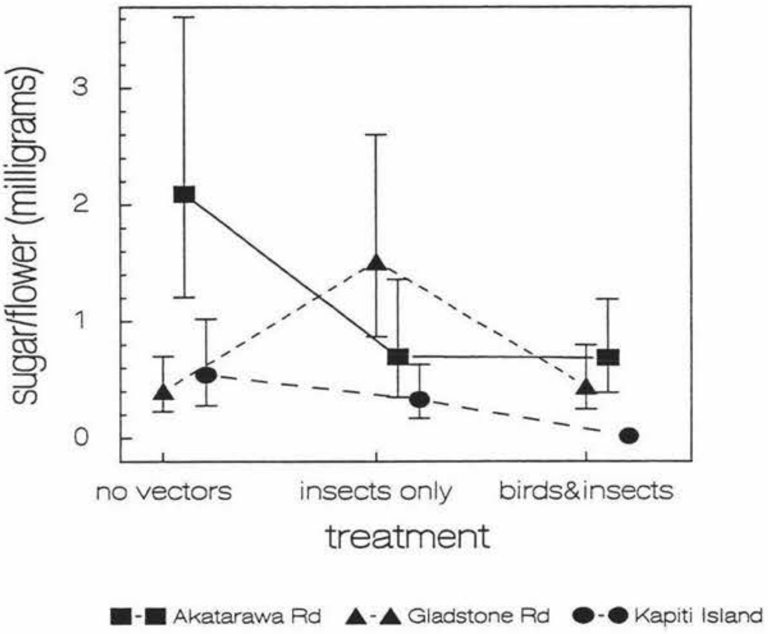


**Figure 2.4. showing the amount of sugar in the nectar of *F. excorticata* flowers according to the treatment and site. Nectar was collected on 2 occasions at each site using the capillary-refractometer method and converted to sucrose equivalents.**

**Table 2.5. ANOVA table showing the effects of site, tree, treatments and site*treatment interaction on the amount of sugar in the nectar of *F. excorticata* flowers. Raw data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 8.1914 | 17.54 | 0.0012 |
| Tree (site) | 11 | 0.6950 | 8.19 | 0.8169 |
| Treatment | 2 | 6.7010 | 14.34 | 0.0133 |
| Site * Treatment | 4 | 3.5324 | 15.13 | 0.0499 |
| Error | 17 | 1.1907 | | |

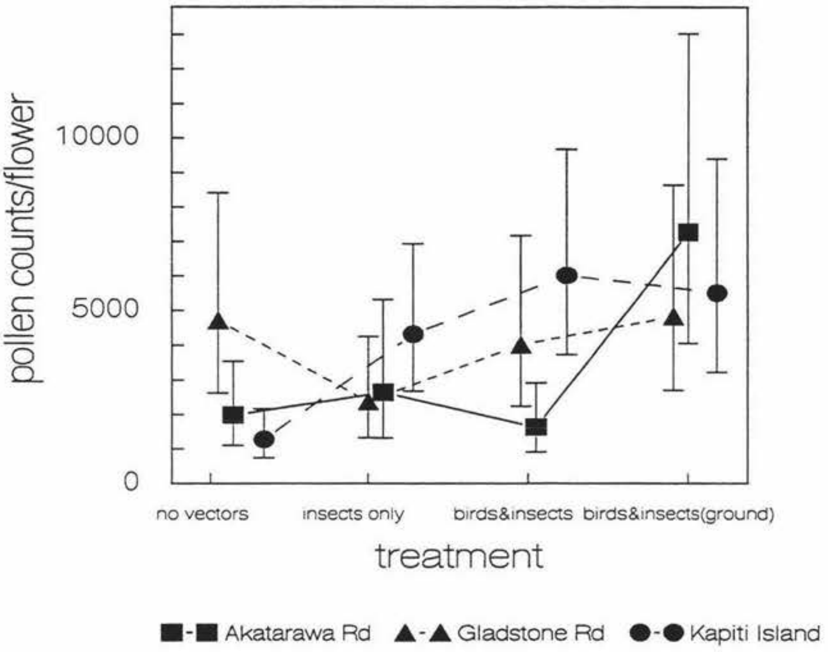


**Figure 2.5. showing the number of pollen grains deposited on the stigmas of *F. excorticata* flowers according to the treatment and sites. Flowers were collected on two occasions, stained in 0.1% declourised aniline blue and viewed using UV light and an epifluorescent microscope. The total number of pollen grains was determined by averaging the number of grains in four samples of a two dimensional area on the stigmata and multiplying this by the total area of the stigma.**

**Table 2.6. ANOVA table showing the effect of site, tree, treatment or site*treatment interaction on the number of pollen grains deposited on the stigmas of *F. excorticata* flowers. Raw data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 0.4400 | 1.12 | 0.7005 |
| Tree (site) | 11 | 1.1966 | 18.43 | 0.5666 |
| Treatment | 3 | 1.9181 | 8.06 | 0.2579 |
| Site * Treatment | 6 | 1.3748 | 11.55 | 0.4351 |
| Error | 30 | 1.3561 | | |

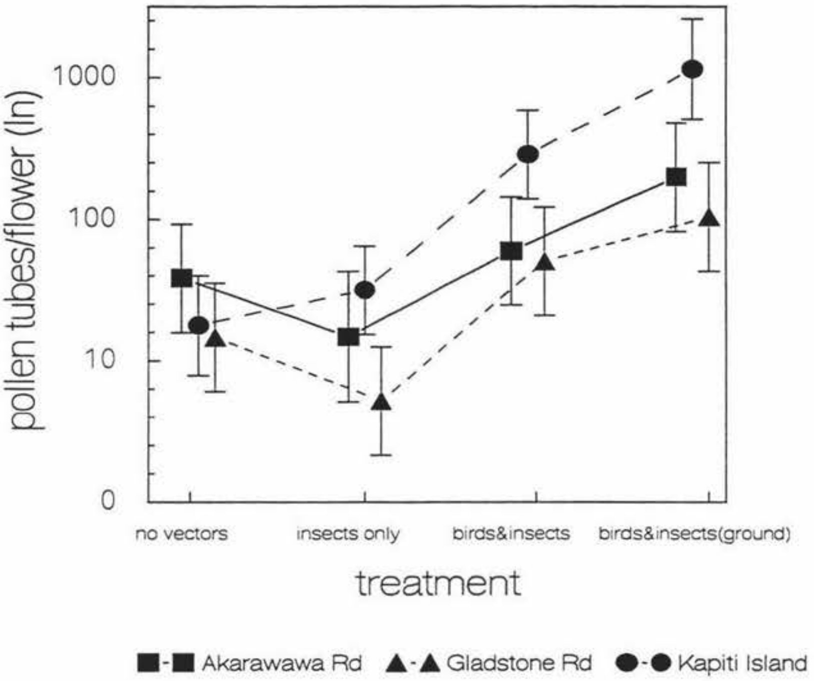


**Figure 2.6. showing the number of pollen tubes in *F. excorticata* flowers according to treatment and sites. Flowers were collected on two occasions, stained in 0.1% decolourised aniline blue and viewed using UV light under an epifluorescent microscope. The number of pollen tubes were assigned categories of 0, 10's, 100's, 1000's and plotted on a logarithmic scale.**

**Table 2.7. ANOVA table showing the effect of site, tree, treatment and site*treatment interaction on the number of pollen tubes in *F. excorticata*. Raw data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 2.0626 | 9.48 | 0.0287 |
| Tree (site) | 11 | 0.4135 | 10.45 | 0.7258 |
| Treatment | 3 | 4.5790 | 31.57 | 0.0005 |
| Site *Treatment | 6 | 0.0329 | 4.53 | 0.7593 |
| Error | 30 | 0.5882 | | |

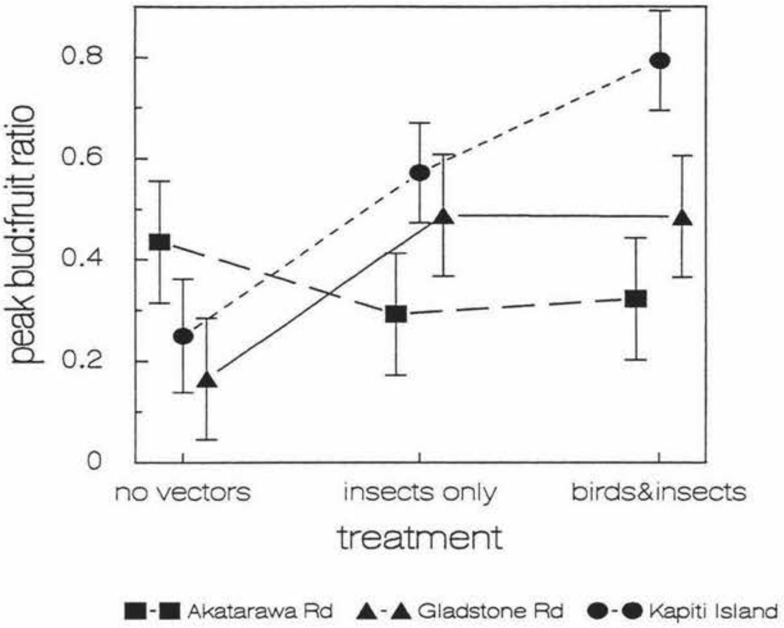


**Figure 2.7. showing the peak bud:fruit set of *F. excorticata* according to the treatment and sites. The peak number of buds were divided by the total number of fruits recorded during the flowering season in each treatment. These were converted into fruit set ratios which was used in the SAS analysis.**

**Table 2.8. ANOVA table showing the effects of site, tree, treatment and site*treatment interaction on the peak bud:fruit set in *F. excorticata* at three sites. The peak number of buds were divided by the total number of fruits recorded during the flowering season in each treatment. These were converted into fruit set ratios which was used in the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 0.149 | 8.33 | 0.2362 |
| Tree (site) | 11 | 0.090 | 27.72 | 0.1841 |
| Treatment | 2 | 0.210 | 11.76 | 0.0442 |
| Site * Treatment | 4 | 0.144 | 16.08 | 0.0748 |
| Error | 21 | 0.0579 | | |

sites and tui and bellbirds were observed feeding on flowers on Kapiti Island. A single honeybee and bumble bee at Raumati Reserve were the only insects seen visiting flowers.

### 2.3.3.2. *Nectar*

Site, treatment, and the site*treatment interactions all had significant effects on nectar removal (Table 2.9., Fig 2.8.). Site and site*treatment interaction each explained approximately the same proportion of the variation of the data (~13%). Flowers on Kapiti Island produced much larger quantities of nectar which was significantly different for the mainland sites (Raumati Reserve $P = 0.0001$, Wilton Bush $P = 0.0002$). Trees from Raumati Reserve offered virtually no nectar reward to potential pollinators. However, this also may have resulted from a sampling bias because only flowers at the very lower part of the canopy could be accessed.

Kapiti Island was the only site where there was evidence that insects removed any nectar at all ($P = 0.0354$). Overall, control flowers contained significantly less nectar than insect only flowers at Kapiti Island ($P = 0.0073$) and Wilton Bush ($P = 0.0032$). However, the results for Wilton Bush are confused by the fact that flowers visited by insects only had more nectar remaining in them than flowers which had no visitors ($P = 0.0032$). There was no significant difference in the amounts of nectar in flowers categorised as having "some pollen" and "no pollen". Consequently, site, treatment and site*treatment interactions all remained significant when flower type was removed from the analysis.

## 2.3.4. GENIOSTOMA LIGUSTRIFOLIUM

### 2.3.4.1. *Visitation*

There was no significant difference in visitation rates between sites (Tables 2.2., 2.3.). Several tui and bellbirds were seen feeding on flowers on Kapiti Island, as well as a honeybee and an unidentified fly. Honeybees were seen on *G. ligustrifolium* flowers at both Lake Papaitonga and Kahuterawa Rd. In addition, bumblebees, a native bee and an unidentified butterfly were seen on *G. ligustrifolium* flowers at Kahuterawa Rd.

### 2.3.4.2. *Nectar*

Site, tree, treatment, and the site*treatment interactions all had significant effects on nectar removal (Table 2.10., Fig 2.9.). Site and tree explained a large proportion of the variation of the data (25.02-32.81%). Kahuterawa Rd had significantly less nectar than both Kapiti Island and Lake Papaitonga (Kapiti $P$ = 0.0008, Lake Papaitonga p = 0.0041). Lake Papaitonga was the only site where control flowers contained significantly less nectar than flowers with just insect visitation ($P$ = 0.0001). In addition, control flowers at Lake Papaitonga had significantly less nectar than control flowers on Kapiti Island ($P$ = 0.0001) and Kahuterawa Rd ($P$ = 0.0398). Insects did remove some nectar from Lake Papaitonga but this was not siginificant here or at the other two sites.

### 2.3.4.3. *Pollen counts*

The site and treatment significantly affected the number of pollen grains deposited on flowers (Table 2.11., Fig 2.10.). Site explained over 50% of the variation in the data. The number of pollen grains deposited on flowers was generally very low but variable. Kapiti Island and Kahuterawa Rd had virtually no pollen grains deposited on control flowers. Control flowers at Lake Papaitonga had significantly more pollen grains than the other two sites (Kahuterawa Rd $P$ = 0.0181, Kapiti Island $P$ = 0.0014). Insects alone deposited some grains at Lake Papaitonga while they deposited almost none at Kapiti Island and Kahuterawa Rd.

### 2.3.4.4. *Pollen tubes*

The site, treatment and site*treatment interactions significantly affected the number of pollen grains deposited on flowers (Table 2.12., Fig 2.11.). Site explained the largest proportion of the variation of the data (~35%). The pattern of pollen tube growth was similar to the pattern of pollen counts. The number of pollen tubes found in *G. ligustrifolium* flowers was extremely low. Pollen tube numbers from insects only was very low except at Lake Papaitonga, which had significantly more pollen tubes than from insects only at the other sites (Kahuterawa Rd $P$ = 0.0100, Kapiti Island $P$ = 0.0002). Pollen tube growth in control flowers was also very poor, except at Lake

Papaitonga where pollen tube growth from this treatment was significantly higher (Kahuterawa Rd $P = 0.0022$ Kapiti Island $P = 0.0010$).

### 2.3.4.5. *Fruit set*

The proportion of fruits set significantly differed between both sites and treatments (Tables 2.13., 2.14., Fig 2.12.). Treatment explained the large proportion of the variation of the data in both SAS and S-PLUS analyses and the site*treatment interaction became significant in the S-PLUS analysis.. Insects only set moderate amounts of fruit at Lake Papaitonga while they set minimal fruit at Kahuterawa Rd and Kapiti Island. In comparison, fruit set increased by approximately the same proportion in the control treatments at Lake Papaitonga and Kahuterawa Rd, which were greater than the fruit set by control treatments on Kapiti Island

See Table 2.15. for summary of results for all four species.

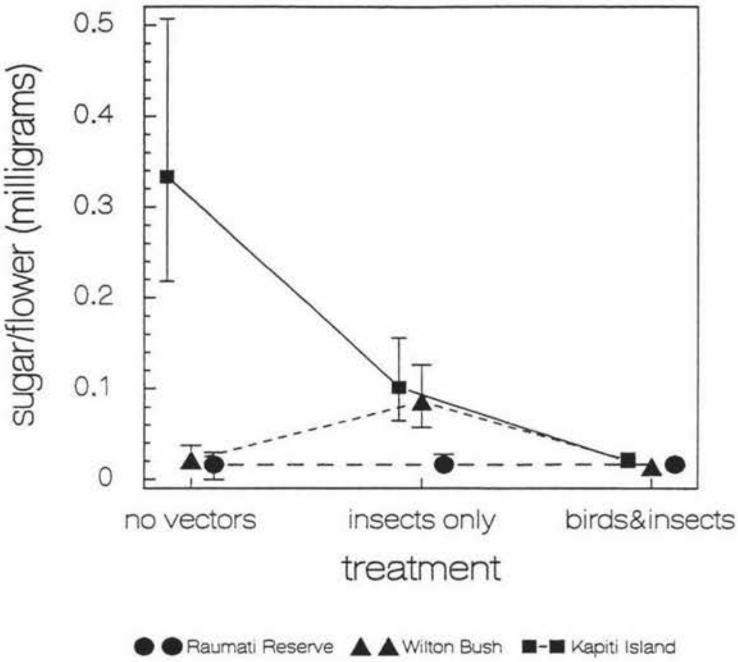


**Figure 2.8. showing the amount of sugar in the nectar of *D. spectabile* flowers according to the treatment and site. Nectar was collected on 3 to 8 occasions at each site using the capillary-refractometer method and converted to sucrose equivalents.**

**Table 2.9. ANOVA table showing the effect of site, tree, treatment, flower, site*treatment interaction and site*treatment*flower interaction on the amount of sugar in the nectar of *D. spectabile* flowers. Raw data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 9.2813 | 13.12 | 0.0014 |
| Tree (site) | 16 | 1.0971 | 12.41 | 0.3204 |
| Treatment | 2 | 6.9566 | 9.83 | 0.0015 |
| Flower stage | 1 | 0.0330 | 0.02 | 0.8516 |
| Treatment * Site | 4 | 4.7453 | 13.41 | 0.0017 |
| Treatment * Flower stage | 2 | 1.0887 | 1.54 | 0.3202 |
| Site * Treatment * Flower stage | 6 | 0.9909 | 4.20 | 0.3986 |
| Error | 49 | 0.9340 | | |

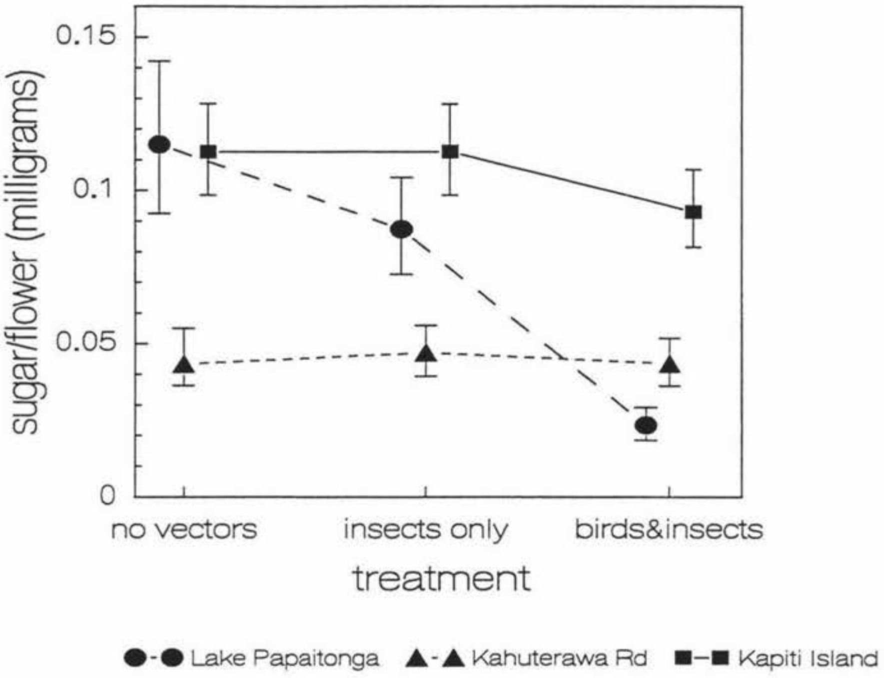


**Figure 2.9. showing the amount of sugar in the nectar of *G. ligustrifolium* flowers according to the treatment and site. Nectar was collected on 2 occasions by placing a drop of distilled water on the flower and soaking up the nectar using paper wicks. Nectar was processed following McKenna and Thompson (1988) and converted to sucrose equivalents.**

**Table 2.10. ANOVA table showing the effect of site, tree, treatment and site*treatment interaction on the amount of sugar in the nectar of *G. ligustrifolium* flowers. Raw data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 2.3532 | 32.81 | 0.0036 |
| Tree (site) | 13 | 0.2761 | 25.02 | 0.0184 |
| Treatment | 2 | 1.0606 | 14.79 | 0.0006 |
| Site * Treatment | 4 | 0.5528 | 15.41 | 0.0033 |
| Error | 24 | 0.1039 | | |

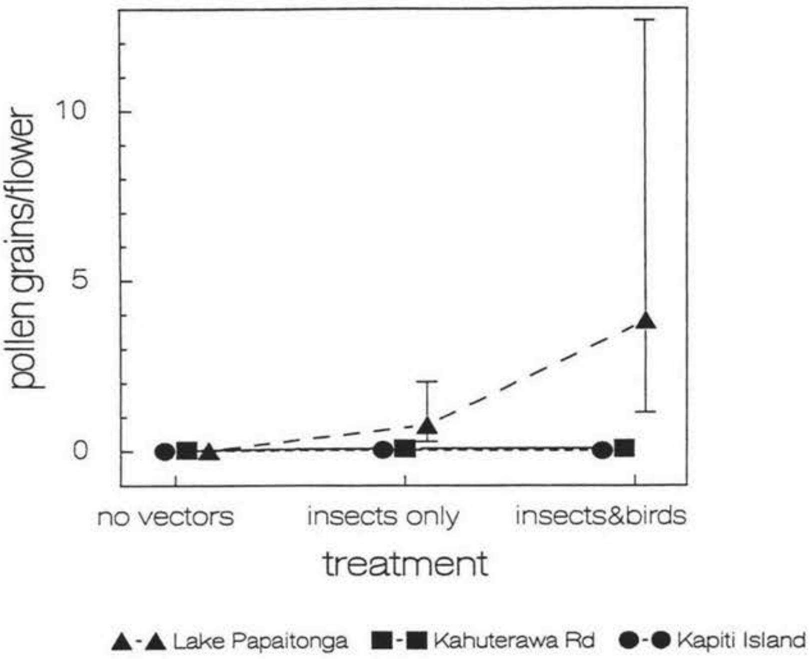


**Figure 2.10. showing the number of pollen grains deposited on the stigmas of *G. ligustrifolium* flowers according to site and treatment at each site. Styles were stained in 0.1% aniline blue and viewed using UV light and an epifluorescent microscope.**

**Table 2.11. ANOVA table showing the effect of site, tree, treatment and site*treatment interaction on the number of pollen grains deposited on the stigmas of *G. ligustrifolium* flowers. Raw data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 27.8278 | 52.01 | 0.0020 |
| Tree (site) | 13 | 2.7950 | 16.33 | 0.7172 |
| Treatment | 2 | 17.9943 | 16.17 | 0.0188 |
| Site * Treatment | 4 | 6.4903 | 11.67 | 0.1833 |
| Error | 24 | 3.8224 | | |

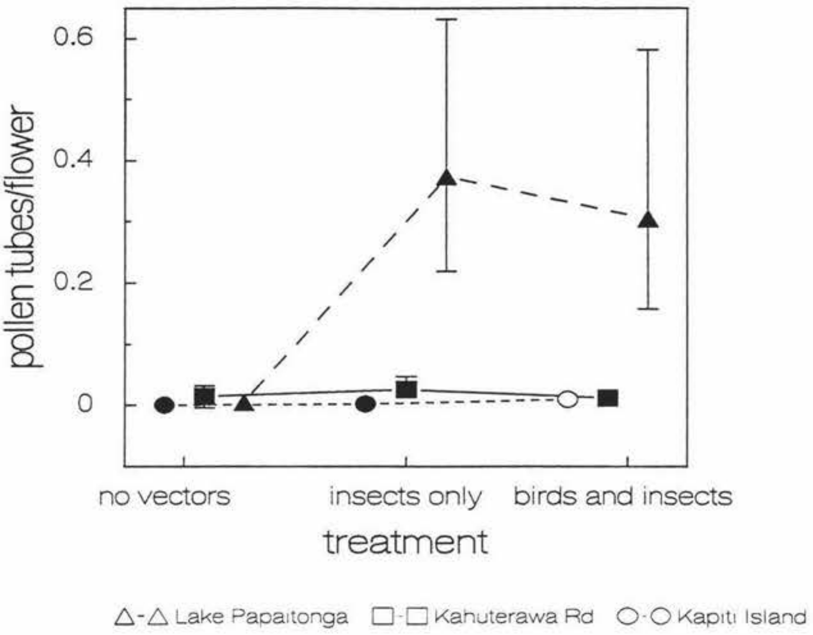


**Figure 2.11 showing the number of pollen tubes in *G. ligustrifolium* flowers according to treatment and site. Styles were stained in 0.1% aniline blue and viewed using UV light and an epifluorescent microscope.**

**Table 2.12. ANOVA table showing the effect of site, tree, treatment and site*treatment interaction on the number of pollen tubes in *G. ligustrifolium* flowers. Raw data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 16.8143 | 35.34 | 0.0004 |
| Tree (site) | 13 | 1.16170 | 15.87 | 0.4058 |
| Treatment | 2 | 7.10219 | 14.93 | 0.0048 |
| Site * Treatment | 4 | 4.21304 | 17.71 | 0.0129 |
| Error | 24 | 1.0582 | | |

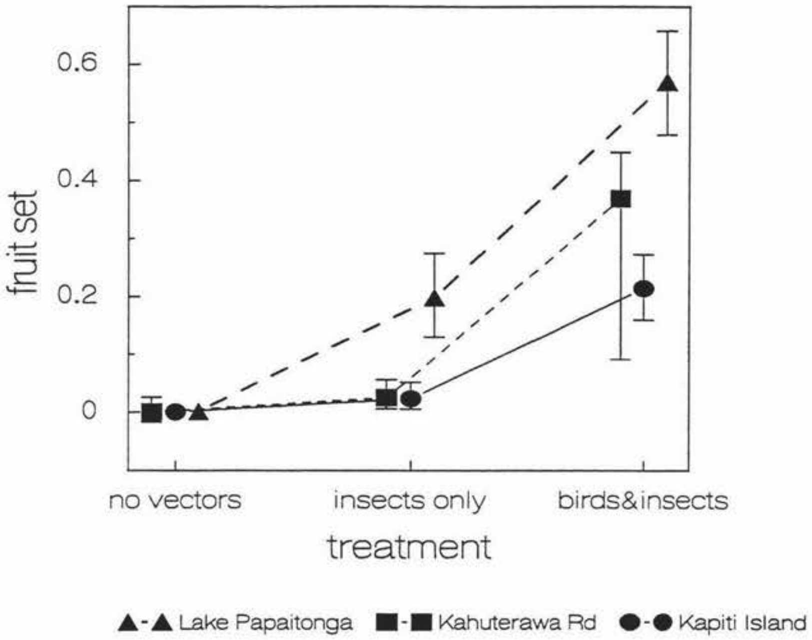


**Figure 2.12. showing the fruit set of *G. ligustrifolium* according to treatment and site. Fruit set was expressed as a ratio after counting the number of fruits formed from a known number of buds/flowers in each treatment. Analyses were perfromed on the arcsine and square root of the fruit set which was back transformed for this graph. All flowers removed for the nectar analysis were eliminated from the data.**

**Table 2.13. ANOVA table showing the effect of site, tree, treatment and site*treatment interaction on the fruit set of *G. ligustrifolium*. Fruit set was expressed as a proportion of fruits formed from a known number of buds/flowers in each treatment. The square root and arcsin of the proportions were used in the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 0.21142 | 8.84 | 0.0170 |
| Tree (site) | 13 | 0.03996 | 10.86 | 0.3384 |
| Treatment | 2 | 1.28335 | 53.65 | 0.0001 |
| Site * Treatment | 4 | 0.05165 | 4.32 | 0.2207 |
| Error | 22 | 0.0332 | | |

**Table 2.14 ANOVA table showing the effect of site, tree, treatment and site*treatment on the fruit set of *G. ligustrifolium*. The number of fruit which were formed from a known number of buds/flowers in each treatment was used in the GLM with a binomial error distribution and logit link function.**

| Model | df | Deviance | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 128.386 | 9.25 | <0.0001 |
| Tree (site) | 3 | 300.7631 | 21.68 | <0.0001 |
| Treatment | 3 | 855.7295 | 61.62 | <0.0001 |
| Site * Treatment | 4 | 14.9785 | 1.08 | 0.0475 |

**2.15. Summary table whether site and treatment significantly effected the results from the caged treatments on Kapiti Island and mainland sites for each species.**

| Species | Visitation rates | | | Nectar depletion | | | Pollen deposition | | | Pollen tubes | | | Fruit set | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | site | treat | site*treat | site | treat | site*treat | site | treat | site*treat | site | treat | site*treat | site | treat | site*treat |
| *M. fulgens* | N | [1]N | | N | Y | N | | | | | | | | | |
| *F. excorticata* | N | | | Y | Y | Y | N | N | N | Y | Y | N | N | Y | N |
| *D. spectabile* | N | | | Y | Y | N | | | | | | | | | |
| *G. ligustifolium* | N | | | Y | Y | Y | Y | Y | N | Y | Y | Y | Y | Y | [2]Y |

1 Difference between insect only and control flowers

2 Became significant under the GLM binomial error distribution and logit link function

# 2.4. DISCUSSION

Most published accounts of pollination of New Zealand plants would suggest that *F. excorticata* and *M. fulgens* are mostly pollinated by birds, whilst insects pollinate *G. ligustrifolium* and *D. spectabile* (Thomson 1927, Heine 1938, Godley 1979, Lloyd 1985). However, little attention has been given to the possibility that exclusive insect pollination may not be as prevalent as it is currently assumed in the New Zealand flora (Castro and Robertson 1997). This study suggests both birds and insects can be important visitors for both ornithophilous and entomophilous plants, an interaction which has not previously been recognised. Birds are probably important pollinators of a wide range of native plant species and their contribution to plant reproduction could differ betweeen sites because of their varying abundances and the availability of other resources.

## 2.4.1. WHAT CARRIES OUT POLLINATION SERVICES AND WHERE?

### 2.4.1.1. *"Ornithophilous" species*

Significant depletion of *M. fulgens* nectar between experiments indicated pollinator services were being carried out by both birds and insects. Due to size differences, individual insects presumably remove less nectar than birds (Collins *et al* 1984) yet the majority of nectar appeared to be removed by insects. Consequently, insect abundances and their visitation rate may have been greater than birds. Observations confirmed the majority of visitors were insects at both sites. Birds did remove some nectar, but their visits were much less frequent than insects suggesting insects may be just as, or even more important flower visitors to *M. fulgens*. *M. fulgens* was the only species which did not have site differences in the amount of nectar removed by birds and insects. This suggests Kapiti Island and Kahuterawa Rd may have similar bird and insect abundances, although this appears unlikely (see 2.4.2., 2.4.4.).

In *F. excorticata*, insects produce some pollen tubes and enhanced fruit set at all sites which indicated insects were pollinators. Insects on Kapiti Island were slightly more important than at the other sites but honeybee hives close to the study site may have increased their contribution to pollination. Birds were important pollinators on Kapiti Island but were not important at the mainland sites.

#### 2.4.1.2. *"Entomophilous" species*

Birds appeared to be the main visitors to *D. spectabile* flowers. Only on Kapiti Island was there evidence of insect visitation. Birds are thought to be potential pollinators of *D. spectabile* in forest around Auckland (Court 1985), and have been frequently observed on *D. spectabile* on Kapiti Island (Castro and Robertson 1997). Birds significantly depleted floral rewards at Kapiti Island and Wilton Bush where flocks of silvereyes were seen feeding on *D. spectabile* flowers. Raumati Reserve appeared to be offering very little reward for visitors. However, pollination must have occurred because fruit was observed maturing on trees during December 1996.

Results suggest birds were the most important pollinators of *G. ligustrifolium* at all sites as fruit set was poor when birds were excluded. Anderson (1997) also found fruit set significantly increased once birds were permitted access to flowers of a range of native species including *G. ligustrifolium*. *G. ligustrifolium* flowers are faintly scented which is supposedly a feature on entomophilous flowers (Faegri and van der Pijl 1979, Rattenbury 1980). However, fragrance is not always a reliable attractant (Montalvo and Ackerman 1986). A small range of insects were seen visiting *G. ligustrifolium* flowers and they did allow some fruit to be set at Lake Papaitonga but they removed virtually no nectar, deposited virtually no pollen grains, producing few pollen tubes which resulted in little fruit set at the other two sites. The results at Kahuterawa Rd seemed surprising because flowers were not offering any nectar reward for pollinators yet there was some fruit set in the control treatments.

### 2.4.2. BIRD DECLINE AND POLLINATOR LIMITATION

The number and nature of pollinators can limit the reproductive output of a plant (Bierzychudek 1981, Rathcke 1983). Pollinator limitation is caused by a limited number of pollinators visiting flowers and/or by a limiting availability of compatible pollen which causes low fruit:flower ratios (Garwood and Horvitz 1985, Horvitz and Schemske 1988). Several studies have cited pollination limitation as a major factor in plant population dynamics (Schemske 1980, Worthen and Stiles 1988, Ågren 1996) but it can be difficult to identify. Flowers may be well pollinated but still set low levels of fruits (Stephenson 1981, Snow 1982), or flowers may be used for pollen donation rather than fruit production (Willson and Rathcke 1974). For example, *D. spectabile* was observed to produce roughly ten times as many flowers as fruit per raceme. Pollinator limitation can be confirmed by hand-pollination experiments by applying supplemental pollen to see if fruit set can be increased (Bierzychudek 1981, Campbell 1987, Ågren 1996). Although no hand pollinations were performed in this study, there is evidence that *F. excorticata* and possibly *G. ligustrifolium* are pollinator limited and this is probably due to the lack of birds. This study confirmed female *G. ligustrifolium* plants required a vector to produce fruit, but *G. ligustrifolium* had very few pollen grains transferred to female plants and had extremely low fruit sets at two sites. When birds were permitted to visit *F. excorticata* flowers in addition to insects, the resultant fruit set and pollen tube numbers greatly increased on Kapiti Island. The enhanced pollination success from birds on Kapiti Island implied pollination of *F. excorticata* was not reaching its potential on the mainland. The fact that birds were prevalent and important visitors for *F. excorticata* was not unexpected given the morphological floral adaptations of *F. excorticata* for bird pollination (Delph and Lively 1985, Delph and Lively 1989). Moreover, there was evidence that birds may be less abundant at the mainland sites because cages which excluded birds contained similar quantities of nectar, pollen tubes and fruit set to open pollinated controls. However, it is possible the apparent low fruit set by insects in *F. excorticata* and *G. ligustrifolium* may have resulted because the cages which were meant to exclude birds inadvertedly excluded insects as well, thereby over emphasizing the importance of bird pollination.

Pollinator limitation can be caused by a varity of factors including unfavourable weather conditions for pollinators (Cruden 1972, Campbell 1987), habitat fragmentation (Jennersten 1988, Rathcke and Jules 1993, Buchmann and Nabhan 1996), changes in abundances of exclusive pollinators (Johnson and Bond 1992), or changes in the importance of pollinators between sites (Webb 1985). Overall, differences in pollination limitation between sites can be caused because pollination is dependent on local pollinator assemblages whose abundances and pollinating behaviour can vary between locations (Campbell 1987, Herrera 1988, Jennersten 1988, Johnson and Bond 1992, Kunin 1993). Although pollination limitation can be difficult to detect, it is probably more frequent than is recognised (Garwood and Horvitz 1985). Small plant populations are especially prone to pollinator limitation since they may support smaller pollinator abundances (Ingvarsson and Lunderberg 1995).

The decline of bird pollinators on mainland New Zealand is likely to be affecting the pollination of other species (Anderson 1997). Their decline has already been suggested as the cause of reduced seed set in mainland plant populations compared with offshore island reserves (Anderson 1997) as well as limiting the pollination of native mistletoes (Ladley and Kelly 1995b). Consequently, it is possible pollination limitation is decreasing the regeneration efficiency of lowland forests.

### 2.4.3. COMPENSATORY MECHANISMS

The high number of unisexual species in New Zealand (Lloyd 1985) could potentially render plants vulnerable to bird decline as vectors are required for successful pollination (excluding pollination by wind). Dioecious species are especially prone to changes in pollination effectiveness because half the population does not bear seeds (Faegri and van der Pijl 1979).

However, Bond (1994) states plants can be very resilient to the loss of their pollinators because they may possess mechanisms which can compenstate for reduced or absent pollinator services. If such mechanisms are possessed by New Zealand plants, the reduction of avian densities in New Zealand may not be a significant threat to forest regeneration. Clout and Hay (1989) suggest the pollination of bird visited plants are probably not being affected by the decline of birds, although recent studies question this (Ladley and Kelly 1995a, Ladley and Kelly 1995b, Kelly *et al* 1996, Robertson *et al* unpublished manuscript, Anderson 1997). Temperate regions often have generalised plant-bird interactions (Wheelwright 1988) and such generalised mutualisms may be at less risk from extinction in fragmented forests than specialist plant-pollinator relationships (Rathcke and Jules 1993). The vast majority of New Zealand plants probably do not depend on specialised pollination mechanisms (Godley 1979) and therefore, may be able to buffer a reduction in the abundance of their primary pollinators by utilising more generalised pollinators. It would be highly unlikely that common species such as *F. excorticata* and *G. ligustrifolium* would be threatened with immediate extinction because of low bird densities. However, replacement pollinators may not be complete substitutes. Pollinators are usually not completely interchangeable because they have their own pollinating characteristics (Herrera 1988). Silvereyes and bumblebees for example, may not pollinate *F. excorticata* effectively because they access the nectar by cutting the base of the flowers (Delph and Lively 1985)

The question of whether introduced species can compensate or replace native pollinators needs further research. For example, it is debatable whether the introduced honey bee (*Apis mellifera*) in Australia is beneficial or disruptive to native pollinator systems but they have been shown to effectively pollinate plants where native pollinators are lacking (Paton 1993). Butz Huryn (1995) has discussed whether honeybees are detrimental to pollination systems in New Zealand, considering the range of plant species visited is so wide. Competition with native pollinators could potentially lead to a disruption of pollination systems and threaten some plant abundances. Native bees are able to cause some fruit to be set in New Zealand mistletoes (Kelly *et al* 1996) and to some degree compensate for the decline of native bird pollinators. *Freycinetia arborea* in Hawai'i successfully reproduced vegetatively until introduced bird species replaced their original avian pollinators which had become extinct (Cox 1983).

At Akatarawa Rd, *F. excorticata* produced more nectar than at the other two sites and showed some potential for selfing. Similarly, *D. spectabile* on Kapiti Island produced more nectar per flower than other sites. Vectors may respond positively to increasing nectar rewards (Cresswell 1990) and plants which produce more nectar could experience higher levels of pollination (Paton and Ford 1983). A relatively small reward could make flowers less attractive to vectors, thereby decreasing their pollination potential. Although it can not be established whether these are compensatory mechanisms, it has been documented that plants can change their morphological characteristics, nectar production, and degree of self incompatibility according to the presence of pollinator assemblages (Feinsinger *et al* 1982, Inoue 1993).

### 2.4.4. AVAILABILITY OF RESOURCES

Declining bird abundances and species on the New Zealand mainland (Diamond and Vietch 1981, Holdaway 1989) implies bird pollination should be limited at mainland sites compared to island sanctuaries. However, this study indicates this may be not true in all cases because birds set the greatest amount of *G. ligustrifolium* fruit at Lake Papaitonga and Kahuterawa Rd, while Kapiti Island had the poorest fruit set. Additionally, the similarity in nectar depletion of *M. fulgens* by birds and insects on Kapiti Island and Kahuterawa Rd suggests they had similar bird abundances which seems unlikely. This apparent prominence of bird visitation at some mainland sites could be due to patterns of resource availability.

Nectar is the major source of energy for honeyeaters in Australia and New Zealand (Gravatt 1970, Gravatt 1971, Pyke 1980, Collins 1985). In Australia, honeyeaters can respond to changing sources of nectar to forage preferentially on plant species which offer the greatest nectar rewards (Collins and Briffa 1982, Ford and Paton 1982, Collins and Newland 1986). Kapiti Island has substantial populations of *Knightia exclesa* located at higher altitudes which flowered simultaneously with G. *ligustrifolium*. *K. excelsa* is an ornithophilous species with flowers more profitable to honeyeaters than *G. ligustrifolium* (Perrot 1997). Kapiti Island becomes noticeably devoid of birds at lower altitudes at that time as they move up the island to feed on *K. excelsa* (Peter Daniel pers. comm, pers. obs.). If honeyeaters moved up the island to feed on *K. exclesa* they may have ignored flowering *G. ligustrifolium* plants, even though they were available in high densities. If there were a lack of other nectar resources at the two mainland sites, G. *ligustrifolium* plants could have received more visits than plants on Kapiti Island and increased their fruit set. However, it should be noted that pollination has been positively correlated with plant density (Pyke 1982, Worthen and Stiles 1988, Ågren 1996).

Habitat fragmentation can decrease the flowering diversity in reserves (Jennersten 1988) and habitat loss and introduced mammals have destroyed important sources of nectar in Hawai'i (Pimm and Pimm 1982). Mainland sites may not have the diverse range of resources available for birds on Kapiti Island and only a fraction of the number of plants which could have caused honeyeaters to move in search for nectar between reserves. The evidence for bird visitation at Lake Papaitonga and Kahuterawa Rd could have resulted from birds concentrating their feeding on the few plants flowering at the time and even small numbers of birds could have become very effective pollinators. Additionally, pollinator services could have been temporarily upset by unfavourable conditions such as the rat eradication which occurred on Kapiti Island during the flowering of *G. ligustrifolium*. Plants with small flowers often have short flowering seasons (Primack 1985) and species such as *G. ligustrifolum* would be especially prone to changes in pollinator services because of their requirement for synchrony between plant and pollinator (Stiles 1978).

### 2.4.5. THE RELIABILITY OF BIRD POLLINATION

A plant's pollination may also be influenced by pollinator foraging behaviour and the presence of other competing species with similar pollinator affinities (Waser 1978, Uno 1982, Powlesland 1984). Consequently, some plants may flower during the cooler months to avoid competition for vectors with the majority of other flowering plants. Staggered flowering periods in New Zealand could have evolved to reduce interspecific competition for pollinators (Carpenter 1976). The general scarcity of resources during winter months may help ensure plants receive concentrated feeding by birds which may increase pollination success.

*G. ligustrifolium* and *D. spectabile* are two of the few species which flower during the coldest, wettest and windiest time of year in winter and early spring (Castro 1995, Castro and Robertson 1997, Perrot 1997). Insect abundances were apparently extremely low during the winter months of May to September 1996 judging from few observations of them and small amount of nectar they appeared to remove from *D. spectabile* and *G. ligustrifolium* flowers.

Species with relatively short flowering seasons such as *D. spectabile* and *G. ligustrifolium* need reliable pollinators whose pollination service is not interrupted by the range of environmental conditions present during their flowering period. Pollination by birds may be more successful than relying on insects because birds are more reliably available than insects (Ford *et al* 1979) as they maybe more active throughout a wider range of conditions and able to cope with variation in nectar availability (Stiles 1971, Cruden 1972, Paton and Ford 1977, Vaughton 1992).

## 2.4.6. FLORAL MORPHOLOGY AS A PREDICTOR OF POLLINATOR SERVICE

The fact that both birds and insects are servicing ornithophilous and entomophilous plants questions the validity of the effective pollinator principle. This principle states that floral traits which attract the best pollinator service will be selected (Stebbins 1970). Flowers have often been characterised according to their floral traits which have then been used to predict pollinator service (Faegri and van der Pijl 1979, Nobel and Whalley 1978). This study has shown this is not always wise as the floral morphology of all four species was not an absolute predictor of the most abundant or important visitor or pollinator. Honeyeaters have been shown to make contact with the stigma whilst feeding on small flowered species such as *D. spectabile* and *G. ligustrifolium*, and native bees frequently contact the stigma of *Metrosideros excelsa* (Anderson 1997). Studies on *Banksia* spp. in Australia have demonstrated they are effectively pollinated by honeybees yet their floral morphology would imply that birds should be their only pollinator (Whelan and Burbidge 1980, Collins *et al* 1984, Vaughton 1992). Likewise, ornithophilous flowered *Metrosideros* in Hawai'i are often visited and effectively pollinated by insects (Carlquist 1974, Carpenter 1976). Honeybees are known to visit all of the species used in this study (Butz Huryn 1995) and occasionally even supposedly anemophilous (wind pollinated) plants may be effectively pollinated by insect vectors (Stelleman 1978).

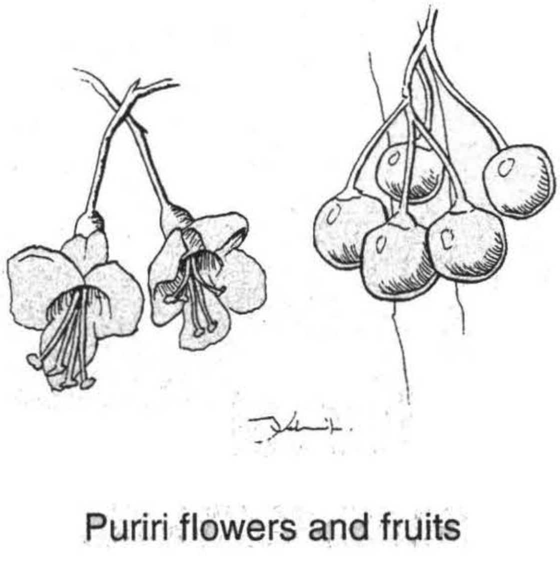
Species often have versatile pollination syndromes which can be subtle and difficult to predict (Carlquist 1974, Webb 1985). Conclusions about the effectiveness of pollinators based simply on casual observations and floral traits maybe suspect (Fishbein and Venable 1996). In New Zealand, visitation by birds to small flowered species which apparently offer small nectar rewards are probably more than incidental (Castro 1995, Castro and Robertson 1997). Anderson (1997) suggests small flowered native species can provide sufficient energy rewards for bellbirds (excluding *D. spectabile*), and similarly Castro and Robertson (1997) found small flowered species can sustain hihi and bellbirds. Honeyeaters are relatively unspecialised in their food resources (Ford and Paton 1977, Paton and Ford 1977) and so it seems reasonable to expect them to be quite widely involved in visiting and/or pollinating more native plant species than is currently acknowledged (Castro 1995, Castro and Robertson 1997, Perrot 1997).

### 2.4.7. THE VALUE OF ISLAND-MAINLAND COMPARISONS

Pollination success is variable in space and time (Grubb 1977). This study therefore, is acknowledged to be just one snapshot of pollination in New Zealand. However, each mainland site showed variation in their pollinator interactions and abundances, indicating the necessity of using at least two mainland sites to gain an accurate measure of pollination and dispersal limitation. Plant-pollinator interactions are critical to ecosystem functions, but the loss of ecosystem interactions can be a subtle process which often takes place unnoticed (Janzen 1974). Island-mainland comparisons are becoming increasingly used to identify and measure changes in plant-pollinator interactions in places which now suffer from depleted pollinator diversities (Feinsinger *et al* 1982, Spears 1987). Further island-mainland comparisons should be used to determine the extent to which birds are involved in the reproduction of New Zealand plants, how pollinator services vary between sites and whether compensatory mechanisms are operating. The relative importance of birds and insects as pollinator vectors should be further explored by directly comparing their effectiveness. Finally, the concept of an island should be broadened to included "mainland islands" which could be used to study changes in plant-pollinator relationships in response to research by management programmes.

## Chapter Three

# Secondary sex characteristics and pollinator limitation in sexually dimorphic plants



Puriri flowers and fruits

# 3.1. INTRODUCTION

Gynodioecy, a form of sexual dimorphism, was first recognised by Darwin (1877) who described two types of plants within the same species, one with female (male-sterile) flowers and one with hermaphrodite (pollen bearing male) flowers. Gynodioecy is a relatively rare condition (Lloyd 1975, Charlesworth and Charlesworth 1978a), but is more common in New Zealand and Hawai'i than anywhere else (Lloyd 1975, Sakai *et al* 1989).

The evolutionary forces driving gynodioecy have been reviewed and debated (Lewis 1942, Godley 1964, Godley 1979, Lloyd 1975, Lloyd 1979, Charlesworth and Charlesworth 1978a, Charlesworth and Charlesworth 1978b, Webb 1979, Connor 1984). Dioecy (complete separation of male and female individuals) could have evolved from a gynodioecious state (Lewis 1942, Charlesworth and Charlesworth 1978a, Lloyd 1973), through the reduction of female fertility in male (hermaphrodite) plants (Arroyo and Raven 1975). However, often there can be no absolute distinction between dioecy and gynodioecy (Arroyo and Raven 1975). Consequently, the term "male" is used here to describe the pollen bearing morph respectively.

Gynodioecy is often thought to be a breeding system which encourages outcrossing in an inbred species, and therefore high rates of selfing in males and inbreeding depression are probably major factors in establishing females in a population (Darwin 1877, Lewis 1941, Lewis 1942, Lloyd 1975, Charlesworth and Charlesworth 1978a). Indeed, there is a positive relationship between inbreeding and the frequency of gynodioecy (Maki 1992). The high number of gynodioecious and dioecious species in New Zealand (Lloyd 1975, Godley 1979) may have evolved to increase outbreeding and consequently reduce high rates of inbreeding on an oceanic island (Lloyd 1975). Females produce obligatory outcrossed progeny which may have more fitness than progeny from males (Lloyd 1975, Lloyd 1976, Ganders 1978, Cox 1988, Sakai *et al* 1989, Delph and Lloyd 1996).

The evolution of breeding systems are intimately linked with pollination biology and sexual selection (Burrows 1960, Godley 1979, see Baker 1983 and Wyatt 1983 for reviews). Secondary sex characteristics, the differences between males and females of sexually dimorphic seed plants in other characteristics besides the actual male and female components of a flower (Lloyd and Webb 1977), are probably selected to adapt each sex to their respective reproductive roles (Lloyd and Webb 1977). Sexual selection in sexually dimorphic plants can cause differences in the phenology, fruit set, floral rewards and pollination characteristics between males and females (Lloyd and Webb 1977, Stephenson and Bertin 1983) but these differences can often be inconspicuous (Lloyd and Webb 1977). Although having knowledge of the secondary sex characteristics is crucial to understandimg the pollination and breeding systems of plants, they have been understudied in more recent times (Lloyd and Webb 1977).

The pollination biology of a species can change with the nature of available pollinators (Handle 1983) and there is an increasing need to look at differences in pollination biology at the population level (Charlesworth and Charlesworth 1978b, Handel 1983). Pollinator limitation caused by changes to pollinator services could potentially affect the functions of males and females and alter their breeding systems (see Chapters One and Two for a summary of pollinator limitation in New Zealand). Male biased sex ratios could indicate pollinator limitation in gynodioecious species because pollinator limitation may alter the levels of inbreeding depression and influence the frequency of females in the population (Lloyd 1975, Charlesworth and Charlesworth 1978a, Lande and Schemske 1985, Delph and Lloyd 1996). The function of males may shift towards increased pollen production to compensate for a shortage of pollinators (Charlesworth and Charlesworth 1978a).

This study therefore, investigates:

1. The potential effects which pollination limitation may have on the breeding systems of two gynodioecious species (*Fuchsia excorticata, Geniostoma ligustrifolium*) and one dioecious species (*Dysoxylum spectabile*). This study compares a site with high densities of pollinators on Kapiti Island with sites with lower pollinator densities on the

mainland (see Chapters One and Two for detailed explanations of pollinator limitation and island-mainland comparisons).

2. To investigate secondary sex characteristics of male and female *F. excorticata* and *G. ligustrifolium* by assessing differences in phenology, nectar depletion, pollen counts, pollen tube growth and fruit production.

# 3.2. METHODS

## 3.2.1. SPECIES AND SITE SELECTION

**Table 3.1. Summary table of sites, species and data collected.**

| Species | # Male plants | # Female plants | Breeding system | Were sex ratio determined? | Were nectar depletion between sexes compared? | Were pollen counts between sexes compared? | Were pollen tubes between sexes compared? | Was fruit set between sexes compared? |
|---|---|---|---|---|---|---|---|---|
| *Fuchsia excorticata* (kotukutuku) | Gladstone Rd 4<br>Akatarawa Rd 4 | Gladstone Rd 3<br>Akatarawa Rd 1 | gynodioecious | no | yes | yes | yes | yes |
| *Geniostoma ligustrifolium* (hangehange) | Kapiti Island 2 - 6<br>Kahuterawa Rd 0 - 9<br>Lake Papaitonga 0 - 7 | Kapiti Island 7<br>Kahuterawa Rd 6<br>Lake Papaitonga 4 | gynodioecious | yes | yes | yes | yes | yes |
| *Dysoxylum spectabile* (kohekohe) | Kapiti Island 7<br>Raumati Reserve 5<br>Wilton Bush 5 | | [1] dioecious | yes | no | no | no | yes |

[1] suspected breeding system

See Chapter Two (2.2.2. and 2.2.3) and Figs 2.1., 2.2. for species and sites descriptions.

### 3.2.2. SEX RATIOS

An uneven sex ratio may indicate pollinator limitation. A male bias may eventually evolve with pollinator limitation because males are selected to increase pollen production to compensate for a shortage of pollinators.

#### 3.2.2.1. *Fuchsia excorticata*

No direct measure of the sex ratio was made because of the low number of trees at Gladstone Rd or Akatarawa Rd.

#### 3.2.2.2. *Geniostoma ligustrifolium*

The sex ratio for 100 *G. ligustrifolium* plants was measured at each site (Kapiti Island, Lake Papaitonga, Kahuterawa Rd) in October 1996. The methods differed between the sites because of the spatial distribution of the plants. *G. ligustrifolium* grew densely in some areas on Kapiti Island and consequently, 100 flowering trees were randomly chosen within a 50 x 50 metre plot. Density of *G. ligustrifolium* trees was lower at both mainland sites, and access to some areas was difficult because of dense supplejack (*Ripogonum scandens*) growth and steep banks. Consequently, the first 100 accessible trees were sampled.

#### 3.2.2.3. *Dysoxylum spectabile*

The sex ratio for 50 adult *D. spectabile* trees was measured at each site (Kapiti Island, Raumati Reserve, Wilton Bush) in December 1996. All trees which grew on or near a 50-100m transect were sexed at each site. Female trees were identified from their mature fruit capsules which were not present on males.

### 3.2.3. FLOWERING PERIODS

The flowering period of male and female *F. excorticata* were compared by counting the number of buds and open flowers on a defined segment of a branch on one to three female, and four male trees at Gladstone Rd and Akatarawa Rd. They were counted every two to four weeks from August 1996 to January 1997, or until the branch had ceased flowering.

### 3.2.4. NECTAR DEPLETION

#### 3.2.4.1. *Fuchsia excorticata*

Four male trees at Gladstone Rd and Akatarawa Rd, and three females at Gladstone Rd and one from Akatarawa Rd were sampled. One to six flowers were removed on two or three occasions from each tree between August and November 1996. Only flowers which were green or purple-green in colour with fresh pollen were used as nectar production ceases once the flowers turn purple (Delph and Lively 1985). Nectar was removed and converted to sucrose equivalents as outlined in the methods in Chapter Two (2.2.4.3.).

#### 3.2.4.2. *Geniostoma ligustrifolium*

Nectar was sampled from five to six randomly selected male plants, and four to six randomly selected female plants on Kapiti Island on two occasions during October 1996. Similarly, nine randomly selected males were sampled on two occasions at Kahuterawa Rd, and six female trees were sampled twice because of the lack of other flowering females. Only flowers with fresh and sticky stigmas were sampled. Nectar samples were taken from three to six flowers on each tree. Nectar was processed and converted to sucrose equivalents as outlined in the methods in Chapter Two (2.2.4.3.).

### 3.2.5. POLLEN COUNTS

#### 3.2.5.1. *Fuchsia excorticata*

The number of pollen grains on the stigmas of male and female flowers at Gladstone Rd and Akatarawa Rd were counted to determine whether they varied between the sexes. Four male trees at Gladstone Rd and Akatarawa Rd, and three females at Gladstone Rd and one from Akatarawa Rd were sampled. One to six flowers were removed on one to three occasions from flowers between August and November 1996. See Chapter Two for method details (2.2.4.4.).

### 3.2.5.2. *Geniostoma ligustrifolium*

The number of pollen grains on male and female stigmas at Kapiti Island and Kahuterawa Rd were counted to determine whether they varied between the sexes. A total of seven male trees on Kapiti Island, and nine male trees at Kahuterawa Rd were sampled over two occasions at each site. Seven female trees on Kapiti Island and five at Kahuterawa Rd were sampled twice on the same dates as the males. One to six flowers were removed between August and November 1996. See Chapter Two for method details (2.2.4.5.).

## 3.2.6. POLLEN TUBES

### 3.2.6.1. *Fuchsia excorticata*

The number of pollen tubes in male and female flowers at Gladstone Rd and Akatarawa Rd were counted to determine whether they varied between the sexes. Four male trees at Gladstone Rd and Akatarawa Rd and three females at Gladstone Rd and one from Akatarawa Rd were sampled. One to six flowers were removed on one to three occasions between August and November 1996. See Chapter Two for method details (2.2.4.5.).

### 3.2.6.2. *Geniostoma ligustrifolium*

The number of pollen tubes in male and female flowers at Kapiti Island and Kahuterawa Rd were counted to determine whether they varied between the sexes. A total of seven male trees at Kapiti Island and nine male trees at Kahuterawa Rd were sampled over two occasions at each site. Seven female trees on Kapiti Island and five at Kahuterawa Rd were sampled twice on the same dates as the males. One to six control flowers were removed between August and November 1996. See Chapter Two for method details (2.2.4.3.).

### 3.2.7. FRUIT SET

#### 3.2.7.1. *Fuchsia excorticata*

The fruit set on male and female trees at Gladstone Rd and Akatarawa Rd was counted to determine whether it varied between the sexes. Four male trees at Gladstone Rd and Akatarawa Rd, and two females at Gladstone Rd and one from Akatarawa Rd were sampled. The number of buds on one or two branches were counted every two to four weeks between August 1996 and January 1997. Fruit set was expressed as a ratio of the peak number of buds to the total number of fruits formed. See Chapter Two for method details (2.2.4.6.).

#### 3.2.7.2. *Geniostoma ligustrifolium*

The fruit set on two male and seven female trees at Kapiti Island was counted to determine whether it varied between the sexes. This species produced all its buds at the beginning of the season which made it possible to have a complete count of the number of buds produced on the branch. See Chapter Two for method details (2.2.4.6.).

### 3.2.8. STATISTICAL METHODS

Differences in the sex ratio between sites were determined using R x C *G*-tests of independence with Williams correction (Sokal and Rohlf 1981). Differences in the sex ratio within sites were determined using a *z*-score binomial approximation to normal distributions. Nectar, pollen counts, pollen tubes and fruit set for *F. excorticata* and *G. ligustrifolium* were analysed using SAS's general linear models procedure (SAS Institute 1988) (see Chapter Two 2.2.5.). For *G. ligustrifolium*, nectar samples on each date at Kahuterawa Rd were analysed separately because female trees (not males) were sampled twice. All raw nectar data were log transformed to standardise their distribution. Type III sums of squares were used in all cases and compared with type II sums of squares showed little difference. Significance was analysed to the 0.05 level.

# 3.3. RESULTS

## 3.3.1. FUCHSIA EXCORTICATA

### 3.3.1.1. *Sex ratio*

Although no direct measure of sex ratio was made because of the small sample size, there were substantially more males than females amongst the few trees present at both sites. In fact, only one female was present at Akatarawa Rd.

### 3.3.1.2. *Flowering period*

*F. excorticata* had a long flowering period, lasting betweeen 130-170 days. Both males and females began flowering at approximately the same time at each site (Fig 3.1.). Flowering periods for males and females were considerably longer at Akatarawa Rd than at Gladstone Rd. Both sexes peaked at about 120 days at Gladstone Rd. At Akatarawa Rd, males peaked at 136 days which was slightly later than females at 120 days.

### 3.3.1.3. *Nectar depletion*

The sex of the trees explained a significant percentage (~ 47%) of the variation in the amount of sugar in the flowers with less sucrose in females (Table 3.2., Fig 3.2.), despite the fact that few trees at each site were available. Females averaged 0.0783 and males 1.778 milligrams of sugar per flower.

### 3.3.1.4. *Pollen counts*

Sex explained a significant proportion of the variation in the number of pollen grains on *F. excorticata* stigmas (~ 57%) (Table 3.3., Fig 3.3.). Males had significantly more pollen than females at both sites particuarly at Akatarawa Rd. However, these results should be regarded with caution because of the possible contamination of the sample flowers (see Chapter Two, pollen counts 2.3.2.).

### 3.3.1.5. *Pollen tubes*

At Akatarawa Rd, females had fewer tubes than males while at Gladstone Rd the difference was small and reversed, hence the significant site*sex interaction (Table 3.4., Fig 3.4.).

### 3.3.1.6. *Fruit set*

Only a small percentage of the data was explained by this model and only 0.11% was explained by the sex of the tree which was not significant (Table 3.5., Fig 3.5.). However, females tended to have higher peak bud:fruit ratios than males. Consistent with the pollen tubes, Akatarawa females produced the least fruit and Gladstone Rd females produced the most fruit.

## 3.3.2. GENIOSTOMA LIGUSTRIFOLIUM

### 3.3.2.1. *Sex ratio*

There was no significant difference in the sex ratio between sites ($G = 0.8529$ $P > 0.05$ df = 2) although there was a significant male bias at both mainland sites (Lake Papaitonga $z = 2.37$ $P = 0.0178$ 2 tailed test, Kahuterawa Rd $z = 3.72$ $P = 0.0002$ 2 tailed test) but not on Kapiti Island ($z = 1.52$ $P = 0.1286$ 2 tailed test) (Table 3.6.).

### 3.3.2.2. *Nectar depletion*

Overall, sex explained less than 11% of the variation of nectar in female and male flowers at both sites and consequently, sex was not a significant factor (Tables 3.7., 3.8., 3.9., Fig 3.6.). The date and date*sex interaction also failed to explain a significant proportion of the variation in the nectar on Kapiti Island. However, there was a general trend for females to have less nectar per flower than males at both sites.

### 3.3.2.3. *Pollen counts*

The sex of the tree was the cause of a significant amount of variation in the number of pollen grains on *G. ligustrifolium* stigmas (59%) (Table 3.10., Fig 3.7.) Females had

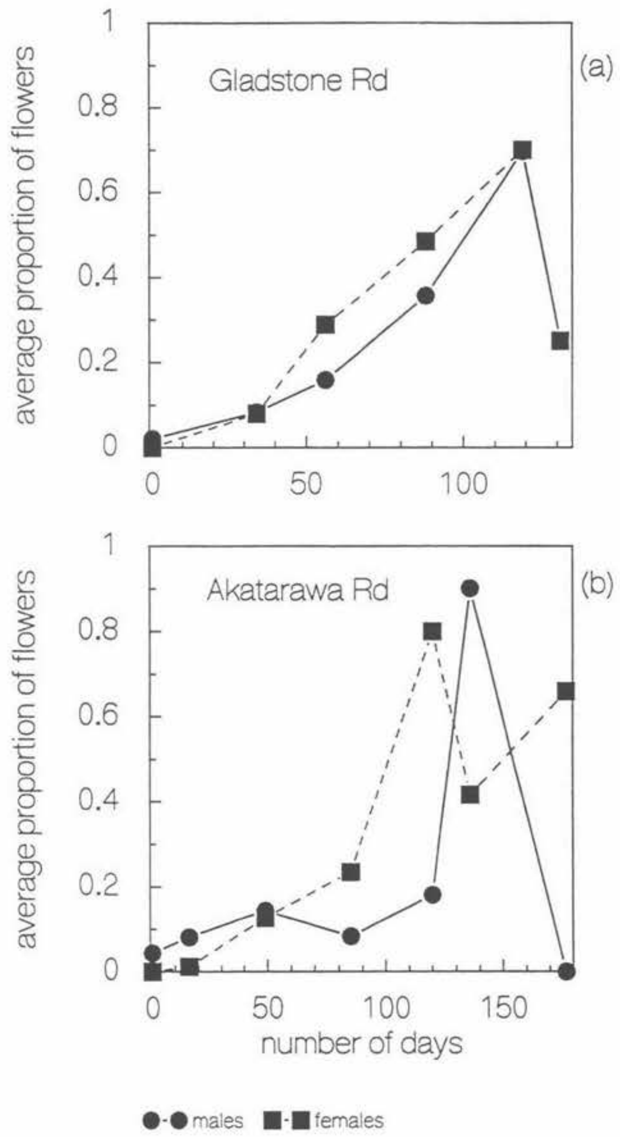


**Figure 3.1. showing the average number of open flowers as a proportion of buds and flowers during the flowering period of male and female *F. excorticata* at (a) Gladstone Rd (b) Akatarawa Rd. The number of flowers and buds on branches were counted and converted to a proportion and averaged over the number of trees sampled on each sampling date.**

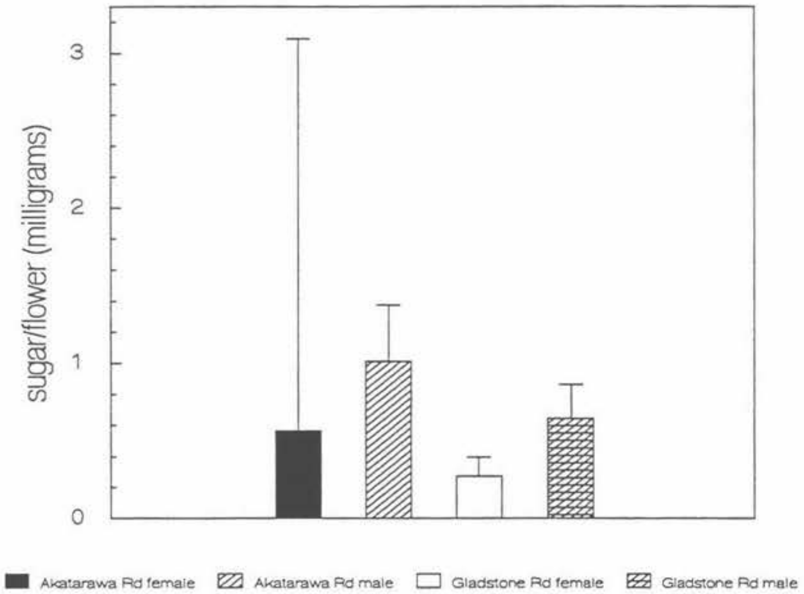


**Figure 3.2. showing differences in the amount of sugar in the nectar in male and female *F. excorticata* flowers at two sites. Nectar was collected on 2-3 occasions at each site using the capillary-refractometer method and converted to sucrose equivalents.**

**Table 3.2. ANOVA table showing the effects of site, sex, and site*sex interaction on the amount of sugar in the nectar of male and female *F. excorticata* at two sites. Raw data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 1 | 0.9450 | 7.64 | 0.1065 |
| Sex | 1 | 5.7761 | 46.85 | 0.0020 |
| Site* Sex | 1 | 0.1052 | 0.85 | 0.5602 |
| Error | 8 | 2.2789 | | |

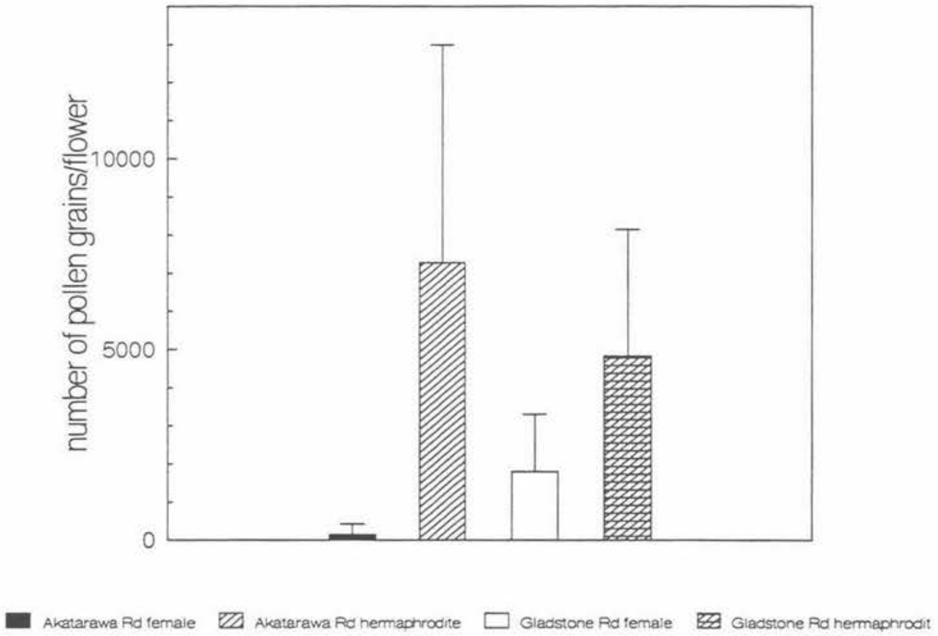


**Figure 3.3. showing the number of pollen grains on the stigmas of male and female *F. excorticata* flowers at two sites. Flowers were collcted on 2 occasions, stained in 0.1% decolourised aniline blue and viewed using UV light and an epifluorescent microscope. The total number of pollen grains was determined by averaging the number of grains in four samples of a two dimensional area on the stigmata and multiplying this by the total area of the stigmata.**

**Table 3.3. ANOVA table showing the effects of site, sex and site*sex interaction on the number of pollen grains on male and female the stigmas of *F. excorticata* flowers at two sites. Data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 1 | 2.3750 | 10.51 | 0.1799 |
| Sex | 1 | 12.9808 | 57.45 | 0.0089 |
| Site * Sex | 1 | 4.6084 | 20.40 | 0.0749 |
| Error | 8 | 8.8002 | | |

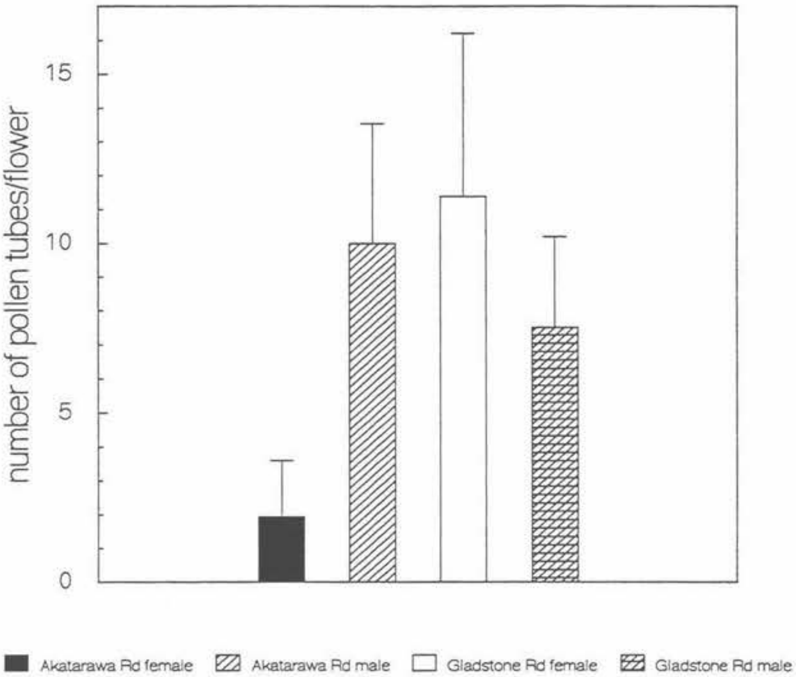


**Figure 3.4. showing the number of pollen tubes in male and female *F. excorticata* flowers at two sites. Flowers were collected on two occasions, stained in 0.1% decolourised aniline blue and viewed using UV light and an epifluorescent microscope. The number of pollen tubes were assigned categories of 0, 10's, 100's, 1000's and plotted on a logorithmic scale.**

**Table 3.4. ANOVA table showing the effects of site, sex, treatment and site*sex interaction on the number of pollen tubes in *F. excorticata* flowers at two sites. The number of pollen tubes were assigned frequency categories as 0's, 10's, 100's or 1000's.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 1 | 1.1961 | 21.51 | 0.1116 |
| Sex | 1 | 0.8041 | 14.46 | 0.1809 |
| Site * Sex | 1 | 2.2830 | 41.06 | 0.0387 |
| Error | 8 | 2.9943 | | |

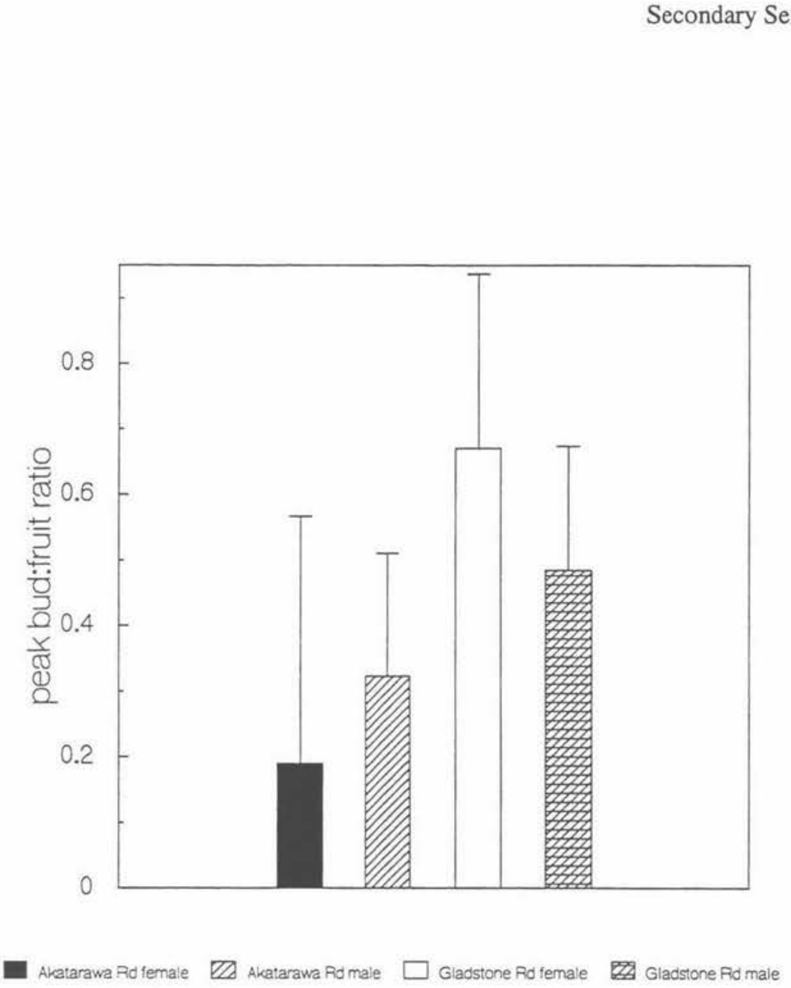


**Figure 3.5. showing peak bud:fruit ratio in male and female *F. excorticata***

**Table 3.5. ANOVA table showing the effects of site, sex, treatment and site*sex on the peak bud:fruit ratio of *F. excorticata*. The peak number of buds were divided by the total number of fruits recorded during the flowering season. These were converted to fruit set ratios which were used in the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 1 | 0.2064 | 18.64 | 0.2672 |
| Sex | 1 | 0.0014 | 0.11 | 0.9243 |
| Site* Sex | 1 | 0.0504 | 4.11 | 0.5701 |
| Error | 7 | 0.9944 | | |

**Table 3.6. sex ratios of *G. ligustrifolium* plants.**

| Site | Females | Males | Total |
|---|---|---|---|
| Lake Papaitonga | 38 | 62 | 100 |
| Kahuterawa Rd | 33 | 67 | 100 |
| Kapiti Island | 42 | 58 | 100 |

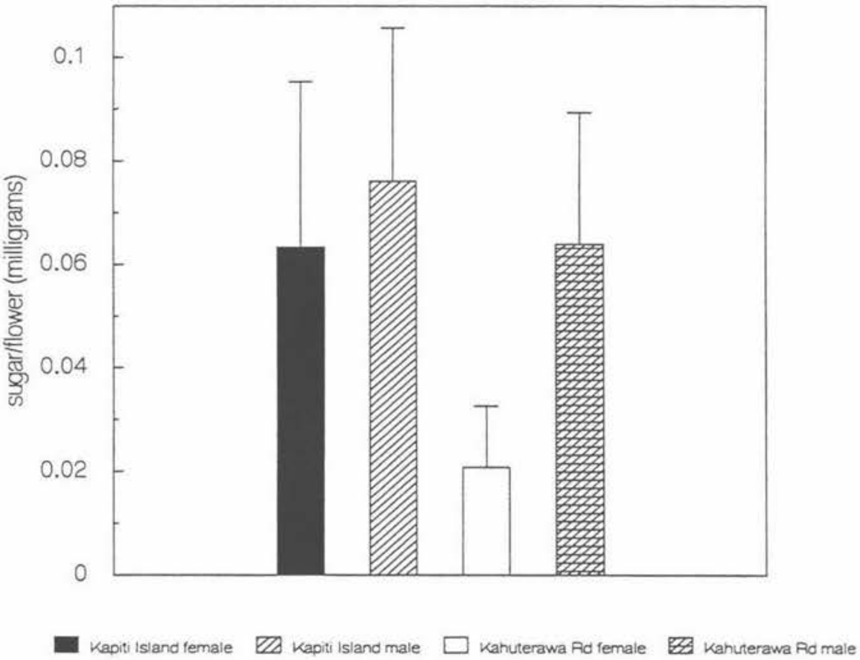


**Figure 3.6. showing the amount of sugar in the nectar of male and female *G. ligustrifolium* flowers at two sites. Nectar was collected on 2 occasions by placing a drop of distilled water on the flower and soaking up the nectar using paper wicks. Nectar was processed following McKenna and Thompson (1988) and converted to sucrose equivalents.**

**Table 3.7. ANOVA table showing the effects of date, sex and date*sex interaction on the amount of sugar in nectar of male and female *G. ligustrifolium* flowers at Kapiti Island. The amount of nectar was converted to sucrose equivalents and log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Date | 1 | 1.3303 | 10.82 | 0.1295 |
| Sex | 1 | 1.3967 | 11.13 | 0.1243 |
| Date * Sex | 1 | 0.6511 | 5.29 | 0.2804 |
| Error | 17 | 8.9065 | | |

**Table 3.8. ANOVA table showing the effects of sex on the amount of sugar in the nectar of male and female *G. ligustrifolium* flowers at Kahuterawa Rd on the first sample date. Nectar had to be analysed separately for the two sample dates because the same female trees were sampled twice, where different male trees were sampled. The amount of nectar was converted to sucrose equivalents and log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Sex | 1 | 0.2672 | 9.12 | 0.3667 |
| Error | 9 | 2.6614 | | |

**Table 3.9. ANOVA table showing the effects of sex on the amount of sugar in the nectar of *G. ligustrifolium* flowers at Kahuterawa Rd on the second sample date. The amount of nectar was converted to sucrose equivalents and log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Sex | 1 | 0.0096 | 0.11 | 0.9181 |
| Error | 10 | 8.6554 | | |

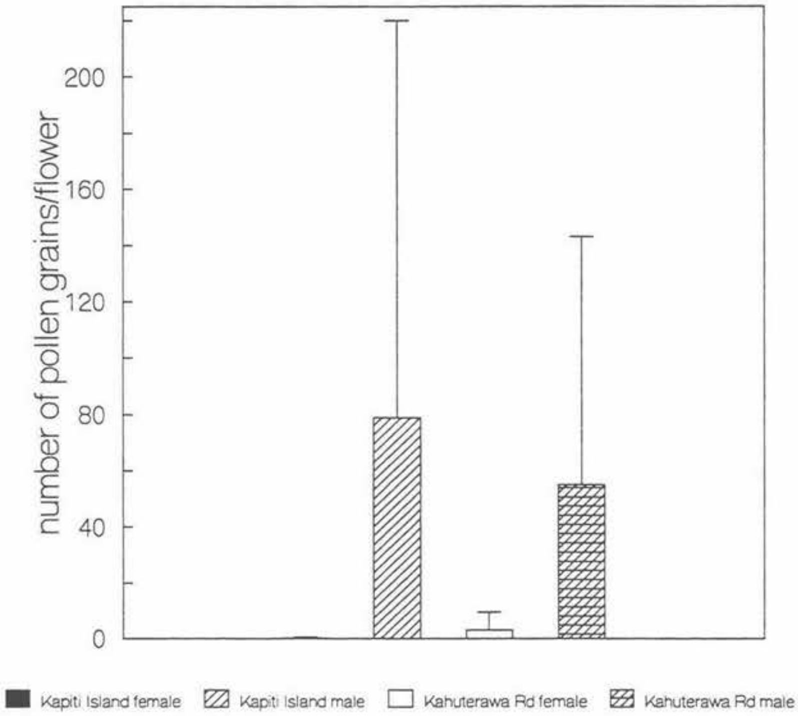


**Figure 3.7. showing the number of pollen grains on the stigmas of male and female *G. ligustrifolium* flowers at two sites. Styles were stained in 0.1% aniline blue and viewed using UV light and an epifluorescent microscope**

**Table 3.10. ANOVA table showing the effects of site, sex, site*sex interaction on the number of pollen grains the stigmas of male and female *G. ligustrifolium* flowers at two sites. Data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 1 | 8.7769 | 1.71 | 0.2853 |
| Sex | 1 | 304.2938 | 59.31 | 0.0001 |
| Site * Sex | 1 | 15.2854 | 3.00 | 0.1622 |
| Error | 24 | 176.4011 | | |

significantly fewer pollen grains than males. Site and site*sex interaction were not significant effects.

### 3.3.2.4. *Pollen tubes*

A strong sex effect suggests a large percentage of the variation in the number of pollen tubes was caused by the sex of the tree (74%) (Table 3.11., Fig 3.8.). Females had significantly fewer pollen tubes than males, and this difference was particularly prevalent on Kapiti Island. The lack of a significant site or site*sex interaction indicates that the number of pollen tubes were not affected by site.

### 3.3.2.5. *Fruit set*

No fruit was set by male *G. ligustrifolium* on Kapiti Island. Female fruit set varied between 9.62 to 36.81%.

## 3.3.3. DYSOXYLUM SPECTABILE

### 3.3.3.1. *Sex ratio*

There was no significant difference in the sex ratios between sites ($G = 1.42$ $P > 0.05$ df = 2) (Table 3.12.) There was a significant male bias on Kapiti Island ($z = 2.74$ $P = 0.0064$ 2 tailed test) and Raumati Reserve ($z = 2.24$ $P = 0.0064$ 2 tailed test) but not Wilton Bush ($z = 1.00$ $P = 0.3174$ 2 tailed test).

### 3.3.3.2. *Fruit set*

Trees which were selected for nectar samples were chosen because they produced large quantities of flowers and were relatively easy to access because of the branch architecture. All trees lacked fruit capsules from the previous year and did not bear any fruit at the end of the flowering season. Consequently, all trees were assumed to be male.

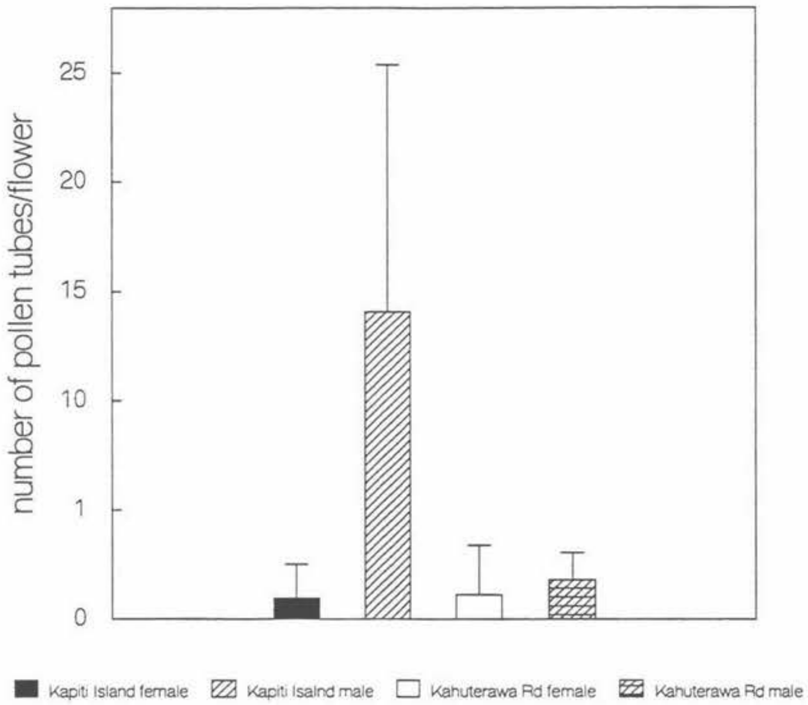


**Figure 3.8. showing the number of pollen tubes in male and female *G. ligustrifolium* flowers at two sites. Styles were stained in 0.1% aniline blue and viewed using UV light and an epifluorescent microscope**

**Table 3.11. ANOVA table showing the effects of site, sex and site*sex interaction on the number of pollen tubes in male and female *G. ligustrifolium* flowers at two sites. Data were log transformed prior to the SAS analysis.**

| Model | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 1 | 6.2650 | 2.29 | 0.1222 |
| Sex | 1 | 202.8459 | 74.09 | 0.0001 |
| Site * Sex | 1 | 7.7965 | 2.847 | 0.0865 |
| Error | 24 | 58.5666 | | |

**Table 3.12. sex ratios of *D. spectabile* trees.**

| Site | Females | Males | Total |
|---|---|---|---|
| Kapiti Island | 13 | 37 | 50 |
| Raumati Reserve | 17 | 33 | 50 |
| Wilton Bush | 21 | 29 | 50 |

# 3.4. DISCUSSION

## 3.4.1. GYNODIOECY AND SECONDARY SEX CHARACTERISTICS

The male morph in a gynodioecious species differs from a true hermaphrodite because they usually have reduced fruit production and they contribute their genes predominantly by donating pollen (Lloyd 1976, Sutherland and Delph 1984). However, gynodioecy can occur on a wide-ranging spectrum because the sex function of males can vary (Webb 1979). Males can approach the hermaphrodite end of the spectrum and produce considerable amounts of fruit, or alternatively verge upon the dioecy end and produce low levels of fruit (Lloyd 1976). The sex function of males can also vary between populations (Burrows 1960, Webb 1979, Webb 1981). Many studies have confirmed that fruit set is more variable in males than females (Shore 1969, Lloyd 1973, Shore 1978, Webb 1979, Webb 1981, Delph 1990, Delph and Lloyd 1991, Delph 1993) including other species of *Fuchsia* (Arroyo and Raven 1975, Atsatt and Rundel 1982). As discussed below, based on fruit production, *F. excorticata*, *G. ligustrifolium* and *D. spectabile* are species whose male functions lie at different ends of the gynodioecy spectrum.

Male *F. excorticata* can produce large quantities of fruit (Godley 1955, Godley 1979) and indeed, this study did not detect a significant difference in fruit set between males and females. Consequently, this suggests males are functioning more as a hermaphrodite than as a complete pollen donor. This contrasts with the conclusions of Delph and Lively (1985) who have suggested male *F. excorticata* act principally as pollen donors as do males in other *Fuchsia* species (Arroyo and Raven 1975, Atsatt and Rundel 1982). Fruit set in males has been used frequently to distinguish gynodioecious and dioecious breeding systems (Lloyd 1976). However, Lloyd (1976) cautions against assessing the function of males based solely on the presence or absence of fruit. It can cause misconceptions because gynodioecy is a form of sexual dimorphism which does not have distinct boundaries. Indeed, Rattenbury (1980) initially classified *G. ligustrifolium* as dioecious not gynodioecious.

Male *G. ligustrifolium* probably function primarily as pollen donors because they set little or no fruit, and have secondary presentation of pollen on their stigmas which explains why males had substantially more pollen grains than females. Males may require this pollen to be removed before the stigma can become receptive (Prof. Phil Garnock-Jones pers. comm.). The significantly larger number of pollen tubes in male *G. ligustifolium* was probably misleading as the tubes did not extend down the length of the style, as they often did in female flowers. Unfortunately, the length of the pollen tubes were unable to be observed consistently under the epifluorescent microscope because parts of the style were often unable to be viewed due to the large area of the stigma. However, these findings support speculation that male *G. ligustrifolium* are self incompatible (Rattenbury 1980, Prof. Phil Garnock-Jones pers. comm).

The dioecious nature of *D. spectabile* has only recently been described (Braggins and Large 1996) before which there had been no speculation that it was even subdioecious in previous reviews (Godley 1979). This study suggests the male function of *D. spectabile* is located at the dioecy end of the gynodioecey spectrum. It is not surprising that *D. spectabile* is dioecious considering other species of Meliaceae are cryptically dioecious (Styles 1972). Cryptic dioecy is when male and female flowers are functionally dioecious but they are difficult to identify because they both appear to be hermaphroditic (Kevan and Lack 1985, Kevan *et al* 1990).

The timing of flowering and relative rates of nectar production by males and females may have been selected to enhance fruit production. Males and females of gynodioecious species often have flowering periods which coincides more closely than dioecious species (Webb 1976). Males and female *F. excorticata* did flower more-or-less synchronously, but females peaked slightly earlier and flowered for longer than males at Akatarawa Rd. Male and female *G. ligustrifolium* flowered synchronously (pers. obsv) but this does not always occur for all gynodioecious species. Males generally have been found to flower earlier in the season than females, reach their peak flowering later, and flower for longer (Webb 1976, Lloyd and Webb 1977, Uno 1982, Delph and Lively 1989). Different flowering patterns may have been selected to ensure females finish fruit maturation before seasonal changes (Webb 1976, Mulcahy 1968, Uno 1982). Females maybe pollinated by the end of the season (Webb 1976, Mulcahy 1968) to gain a competitive advantage for pollinators over males (Burrows 1960), or to permit cross fertilisation for females and self fertilisation by males throughout the flowering period (Uno 1982).

Nectar may be used to manipulate the behaviour of pollinators to achieve pollination (Stephenson and Bertin 1983). Female *F. excorticata* and *G. ligustrifolium* had smaller standing crops than males which could be because they produced less nectar than males or because nectar was depleted though higher visitation rates. This study did not measure nectar production, but measured the amount of nectar remaining after pollinator visitation. However, it has already been established that male *F. excorticata* produce significantly more nectar than females (Delph and Lively 1985, Delph and Lively 1989). The few studies which have investigated nectar production differences in females and males of gynodioecious species have concluded that males generally produce more nectar than females (Ponomarev and Dem'Yanova 1975 cited Uno 1982, Uno 1982). For example, males of the subdioecious *Fuchsia lycioides* produced up to six times more nectar than females (Atsatt and Rundel 1982). Reduced nectar production by females could relate to the generally smaller size of female flowers (Godley 1955, Burrows 1960, Lloyd and Webb 1977, Atsatt and Rundel 1982) which could restrict the amount of nectar they could produce (Ponomarev and Dem'Yanova 1975 cited Uno 1982). On the other hand, females in tropical dioecious species may produce more nectar than males in order to ensure pollinators move between the sexes (Bawa and Opler 1975). Greater nectar production has been documented to encourage pollinators to visit in unfavourable environmental conditions (Atsatt and Rundel 1982), increase pollination levels (Paton and Ford 1983), increase visitation frequency (Waddington 1981, Bell 1985), and restrict pollinator movements to increase self pollination (Stephenson and Bertin 1983).

## 3.4.2. SEX RATIOS

### 3.4.2.1. *Pollinator limitation*

Sex ratio theory was first proposed by Fisher (1930) who suggested sex ratios should be 1:1 if the cost of producing a male was the same as producing a female. However, most plant populations with unequal sex ratios show a male bias (Webb 1992), as shown by many New Zealand examples (Gordon 1959, Godley 1964, Shore 1969, Lloyd 1973, Lloyd and Webb 1977, Webb 1979, Webb 1981, Powesland 1984, Delph 1990). A male bias was shown in two out of three populations of *G. ligustrifolium* and *D. spectabile*, and in both populations of *F. excorticata* in this study. The sex ratios of *G. ligustrifolium*, except on Kapiti Island, did not differ largely from Rattenbury (1980) who found five *G. ligustrifolium* males (62.5%) to every three females (37.5). On Kapiti Island the sex ratio was closer to 1:1. Although the sex ratio for *F. excorticata* was not accurately measured for females, females were less frequent than males at the two sites. Godley (1955) has reported the frequency of *F. excorticata* females to be variable and ranged between four and 40%. However, other species of *Fuchsia* have sex ratios closer to 1:1 (Godley 1963, Arroyo and Raven 1975). Female frequencies did not exceed 50% which has been suggested as the upper theoretical limit for females in gynodioecious species (Lewis 1941). The male bias in two out of three populations of *D. spectabile* differs from other authors findings who have suggested females form 50% of New Zealand populations (Braggins and Large 1996), but supports suggestions there is a general male bias in Meliaceae (Styles 1972).

Theoretical models have predicted that levels of inbreeding depression decrease with increased selfing rates (Lande and Schemske 1985). However, gynodioecious populations probably have naturally high rates of selfing in males and inbreeding depression otherwise gynodiocey would be unlikely to have evolved (Lloyd 1975, Charlesworth and Charlesworth 1978a, Maki 1992). Therefore, inbreeding is thought to influence the frequency of females in a population (Charlesworth and Charlesworth 1978a, Charlesworth and Charlesworth 1978b, Ganders 1978, Sun and Ganders 1986, Delph and Lloyd 1996). Inbreeding depression could decrease male fitness (Connor 1965, Maki 1992) which could select for an increase in the frequency of females and an increase in their seed output (Lloyd 1975, Charlesworth and Charlesworth 1978a, Delph and Lloyd 1996). Indeed, populations with high rates of self fertilisation and inbreeding do have higher frequencies of females (Sun and Ganders 1986, Delph and Lloyd 1996).

Self incompatibility may be rare in New Zealand plants (Webb and Kelly 1993) and therefore, pollinators may be required to reduce inbreeding depression caused by self fertilisation (Garnock-Jones and Molloy 1982). Changes to the amount or quality of pollen through pollinator limitation could affect the selfing rate of self-compatible gynodioecious species (Charlesworth and Charlesworth 1978b), or cause inbreeding depression in an outcrossed species (Lande and Schemske 1985). If seed production in males was reduced, males would be selected to donate more pollen (Charlesworth and Charlesworth 1978a). Indeed, theoretical models predict that maximum seed set occurs when females predominate but pollinators are required to visit each flower more than once and male fruit set must be low (Lloyd 1974).

If populations have differences in their pollinator services, inbreeding could explain differences in sex ratios (Delph and Lloyd 1996) by creating an oscillating cycle driven by levels of inbreeding and fruit production. It has been suggested excess number of male *Melandrium album* plants, a dioecious species, could have arisen to compensate for poor pollination (Godley 1964). The absence of pollinators from populations could select for increased self fertilisation and self compatibility (Ganders 1978, Inoue 1993, Puterbaugh *et al* 1997). Lack of pollinators may increase self pollination of male *G. ligustrifolium* in the southern areas of New Zealand (Prof. Phil Garnock-Jones pers. comm.) and shifted the male function toward maleness in gynodioecious *Bidens* spp. in Hawai'i in order to increase seed set in females (Sun and Ganders 1986). Sparse pollination in *Rumex acetosa* (a dioecious perennial herb) reduced pollen competition and increased the frequency of males (Correns 1928 cited Korpelainen 1991, Lewis 1942). A reduction of pollinator services could also increase the time for pollen to be removed and deposited. Delayed cross pollination has been shown to increase the male bias in the offspring of the trioecious (male, female and hermaphrodite individuals)

*Spinacea oleracea* to increase the quantity of available pollen (Miglia and Freeman 1996).

The response to pollination limitation could be quite species specific. For example, the small numbers of pollen grains and tubes in female *G. ligustrifolium* indicate they could be sensitive to changes in pollinator services and pollinator limitation. The single *F. excorticata* female at Akatarawa Rd had substantially fewer pollen tubes and lower bud:fruit ratio than the other males or females which may indicate some pollen limitation as many ovules in the flowers may not have been fertilised. Alternatively, being a gynodioecious species (with probably high levels of inbreeding already) could indicate the self-compatibility of male *F. excorticata* would make them more vulnerable to further inbreeding depression than self-incompatible *G. ligustrifolium*.

Lower nectar production by females could make them less attractive to pollinators (Uno 1982), and reduce their visitation rates compared to males (Bell 1985). This suggests females are probably at greater risk from pollinator limitation than males. Consequently, males in sexually dimorphic species which rarely set fruit could particularly suffer from reduced reproductive output because females are the primary fruit producing morph.

Pollination biology and secondary sex characteristics may alter over time to maintain a species reproductive potential in response to changes in pollinator services. The plasticity of breeding systems suggests that species would be able to modify their breeding systems and secondary sex characteristics in response to pollination limitation to increase their reproductive output. However, coevolution between plants and their pollinators takes place over large time periods. Species are likely to suffer a time lag between the reduction of pollination services and alteration to characteristics of their breeding systems. The rapid decline of bird species in New Zealand has occurred relatively recently (Diamond and Veitch 1981, King 1984, Holdaway 1989) and may have been too rapid for plants to make successful adjustments to pollination limitation. Processes of forest regeneration may not be occurring efficiently if plants are not reaching their reproductive potential.

Sex ratios can be estimates of the relative contributions of females and males to the plant's reproduction in the absence of knowledge of the quality of the offspring (Lloyd 1976). The significant male bias in the sex ratio of *G. ligustrifolium* at both mainland sites and male bias for *D. spectabile* on Kapiti Island imply pollinator limitation of females may have been occurring. However, the sex ratios are probably unreliable evidence for pollination limitation on their own. The relatively long life of *D. spectabile* imply few or no generations would have elapsed during the short time pollinator limitation may have been occurring on the mainland. A large number of generations may be required before the sex ratio could be altered significantly. The sex ratio of *D. spectabile* could have biased males if there were frequent non-fruiting females as this species can sometimes have a biannual flowering cycle. In addition, juvenile *D. spectabile* are thought to be mostly male and change sex when their branch architecture changes (Dr. Mark Large pers. comm). Moreover, other closely related families of Meliaceae can change the sex of their flowers at different times of the year (Styles 1972). *D. spectabile* trees sexed on Kapiti Island were noticeable straighter and less branched than trees at the mainland sites which may have limited Kapiti Island trees changing their sex from male to female.

### 3.4.2.2. *Environmental conditions*

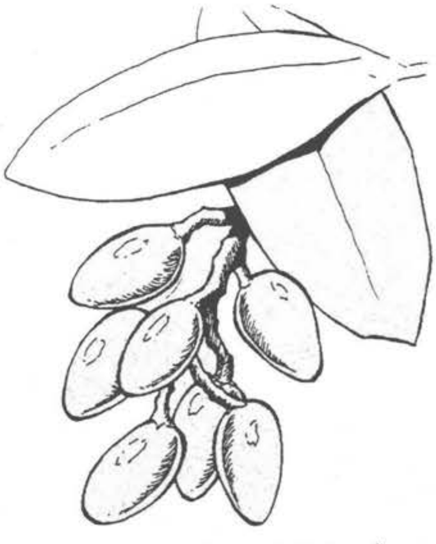
External environmental conditions can also influence the sex ratios of sexually dimorphic species by favouring one sex. Females are thought to incur greater metabolic costs than males because they have to produce seeds and fruits in addition to flowers (Korpelainen 1991). Consequently, a female bias has been found in more productive environments where females appear to respond more to favourable growth conditions than males (Korpelainen 1991, Houssard *et al* 1994). Environmental conditions have been suggested as a factor influencing the frequency of females in New Zealand species such as the gynodioecious *Gingidia flabellata* (Webb 1981). Harris (1968) attributed a male bias in dioecious *Rumex acetosella* to the ability of males to cope and be more competitive under environmental stress than females. Male *Hebe subalpina* were able to alter fruit production in response to environmental thresholds (Delph and Lloyd 1991). Additionally, whether trees of Meliaceae tend toward maleness or femaleness is likely to be affected by nutrition and other environmental factors (Styles 1972). Consequently, differences in environmental variables may have explained sex biases in *F. excorticata*, *G. ligustrifolium* and *D. spectabile* between sites.

This study has confirmed that *G. ligustrifolium* males set little fruit compared to females (Prof. Phil Garnock-Jones pers. comm), as found in other gynodioecious populations (Burrows 1960, Shore 1969, Webb 1981, Shore 1978, Delph 1990). The greater plasticity of male fruit set may increase male fitness over a range of environments and populations (Delph 1990, Delph and Lloyd 1991). Males may adjust investment in reproduction by altering the number of flowers which produce fruit, whereas females commit themselves to fruit production and sacrifice growth instead (Delph 1993). Male fruit set has been found to be negatively correlated with the frequency of females in populations (Webb 1979, Delph 1990) and thus, the plasticity of fruit set on males may partially control the sex ratio of gynodioecious species (Delph 1990). The frequency of females may increase under stressful environmental conditions because the more plastic males may decrease their fecundity which would select for females, as demonstrated for the two gynodiocious species *Hebe strictissima* (Delph 1990) and *Eritrichum aretioides* (Puterbaugh *et al* 1997).

The secondary sex characteristics of sexually dimorphic plants in New Zealand remains a largely unstudied area in pollination biology. It is important to understand the breeding system of a plant to assess its dependence on pollinators (Bond 1994). The classification of the breeding systems of many New Zealand species and recognition that breeding systems are a continuum have also been neglected. Further research into these two areas would give insights into the evolutionary forces involving pollinators and plants which have occurred in New Zealand. Further knowledge would also enable predictions to be made about how breeding systems could alter in the absence of native pollinators and/or in the presence of introduced ones.

# Chapter Four

# Evidence for dispersal limitation in Fuchsia excorticata and Rhopalostylis sapida: are dispersal mutualisms being hindered by reduced bird densities?



Karaka fruits

# 4.1. INTRODUCTION

A plant's reproductive success and fitness is enhanced by dispersing its seeds (Snow 1970, Howe and Smallwood 1982). In New Zealand, fleshy fruits predominate in over 50 families and 70 percent of all fruiting species have adaptations for vertebrate dispersal (Clout and Hay 1989, Lee *et al* 1991, Burrows 1994a) and in temperate regions, most fruit dispersal is by birds (van der Pijl 1982). Most New Zealand fruits display features typical of a syndrome of bird dispersal (van der Pijl 1982, Janson 1983). They are predominantly red, white, or black in colour and small in size (<10 millimetres diameter) (Willson *et al* 1989, Lee *et al* 1991, Burrows 1994b) although there are also a few large fruited species such as *Beilschmiedia* sp. and *Corynocarpus laevigatus* (Willson *et al* 1989). The high number of fleshy fruiting species in New Zealand is surprising considering the paucity of bird species and the fact that most forest birds are only partially frugivorous (Bull and Whitaker 1975, Clout and Hay 1989). However, lizards (Whitaker 1987a, Webb and Kelly 1993) and bats (Daniel 1976, Lord 1991) probably disperse some fruit as well.

Half of New Zealand's endemic frugivorous bird species have become extinct since the arrival of humans (Lee *et al* 1991). Predation pressure from introduced mammals, hunting and habitat destruction (King 1984, Holdaway 1989, Gill and Martinson 1991) have forced the extinction of species such as the piopio (*Turnagra carpensis*), huia (*Heteroclocha acutirostris*) and moa (Dinornithidae) (Clout and Hay 1989, Lee *et al* 1991). Other frugivorous bird species that once were common such as the kokako (*Callaeas cinerea*) kakapo (*Strigops habroptilus*) and saddleback (*Philesturnus carunculatus*) are now severely restricted in range and/or confined to offshore islands (Clout and Hay 1989, Lee *et al* 1991). On the mainland, kereru (*Hemiphaga novaeseelandiae*) and two honeyeater (Meliphagidae) species, the tui (*Prosthemadera novaeseelandiae*) and bellbird (*Anthornis melanura*), are the only remaining endemic fruit dispersers which are relatively abundant and widespread. Some introduced bird species are also known to consume native plant fruits (Baylis 1986, Webb and Kelly 1993, Burrows 1994b, 1994c, Williams and Karl 1996). Kereru are the only species able to disperse large sized fruits (Clout and Hay 1989, Webb and Kelly 1993).

Ecosystem processes of forest regeneration are intimately linked with the interaction between frugivorous birds and the fruit which they feed on (Burrows 1994b). Even though dispersal mutualisms in temperate regions are generally loose and non specific (Herrera 1985, Wheelwright 1988, Burrows 1994b), there are increasing concerns about the ability of New Zealand forests to compensate for the decline of endemic avian dispersers (Clout and Hay 1989, Lee *et al* 1991, Bond 1994, Burrows 1994b, 1994c, Ladley and Kelly 1996). Results of two recent studies may indicate fruit dispersal limitation was due to the reduced availability of dispersers on the New Zealand mainland (Ladley and Kelly 1996, Anderson 1997).

Offshore islands may support avian denisites approaching those once present on mainland New Zealand (Diamond and Veitch 1991, Castro 1995), thus they are able to be used as "benchmarks" by which to measure changes on the mainland (Diamond and Vietch 1991). Kapiti Island, located northwest of Wellington provides an opportunity to compare bird dispersal in a bird rich island sanctuary to dispersal in bird-depauperate forest on the mainland (Brockie 1992, Castro 1995). This study uses an island to mainland comparsion to determine whether fruit dispersal of Kapiti Island differs from the mainland using *Fuchsia excorticata* and *Rhopalostylis sapida*.

# 4.2. METHODS

## 4.2.1 SPECIES AND SITE SELECTION

Mainland sites containing *F. excorticata* and *R. sapida* were selected because they were geographically close to Kapiti Island, were accessible and received possum control which improved the overall condition of the trees (see Cowan 1991, Esler 1969, Enright 1985). Individual *R. sapida* palms were selected because their fruits occurred at a height where treatments could be easily carried out.

**Table 4.1. sites and number of *F. excorticata* and *R. sapida* trees sampled at each site**

| Species | Kapiti | Mainland |
|---|---|---|
| *Fuchsia excorticata* | 5 trees<br>(all hermaphrodites) | Akatarawa Rd (Waikanae): 5 trees<br>(1 female, 4 hermaphrodites)<br>Gladstone Rd (Levin): 5 trees<br>(1 female, 4 hermaphrodites) |
| *Rhopalostylis sapida* | [1] 3 palms | Manawatu Gorge:<br>5 palms<br>Nikau Reserve (Paraparaumu):<br>5 palms<br>Lake Papaitonga (Levin):<br>4 palms |

[1] a further three *R. sapida* were sampled but because they failed to ripen during the season they were removed from all analyses.

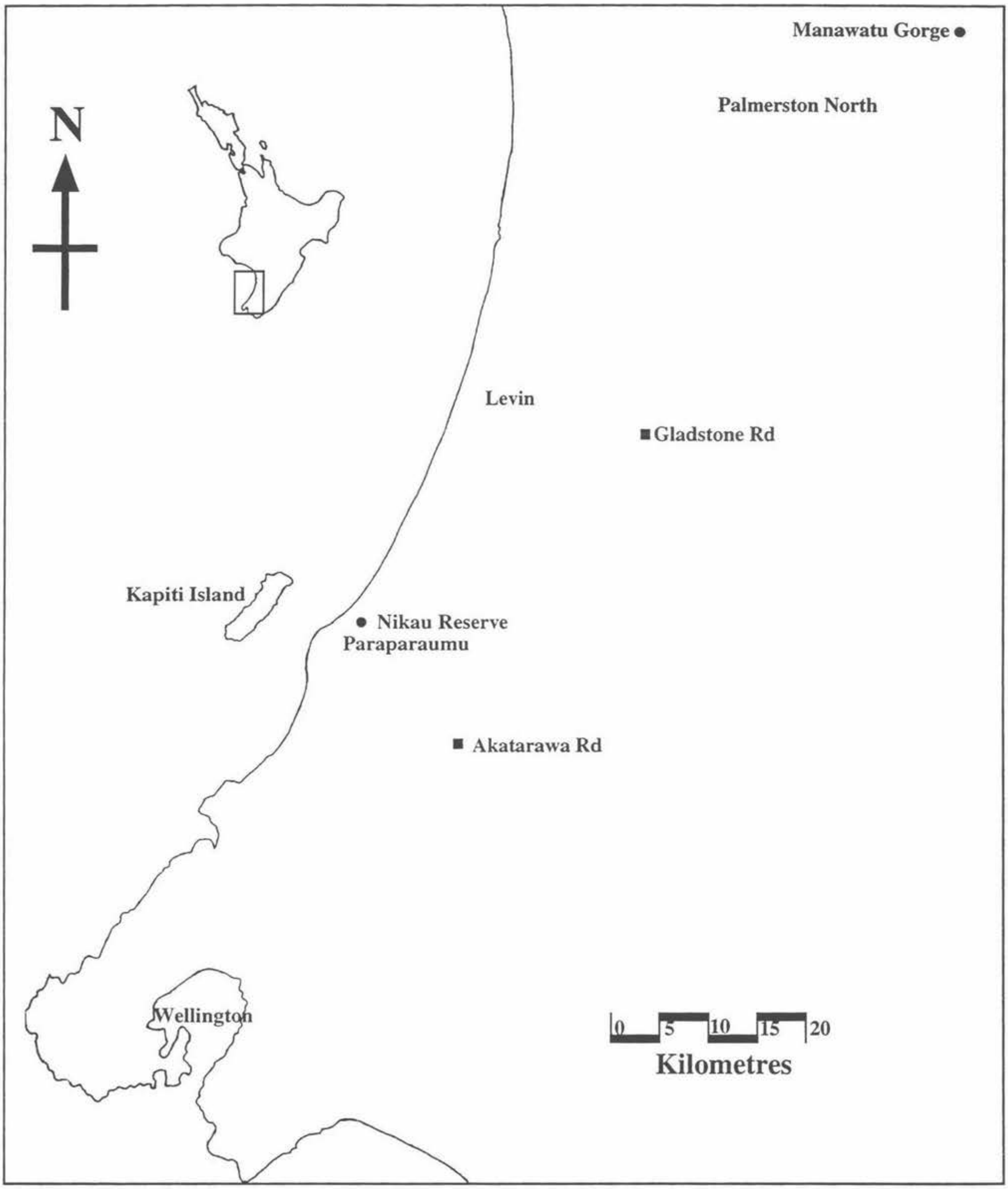


Figure 4.1. Map of mainland study sites. *F. excorticata* (squares) and *R. sapida* (circles).

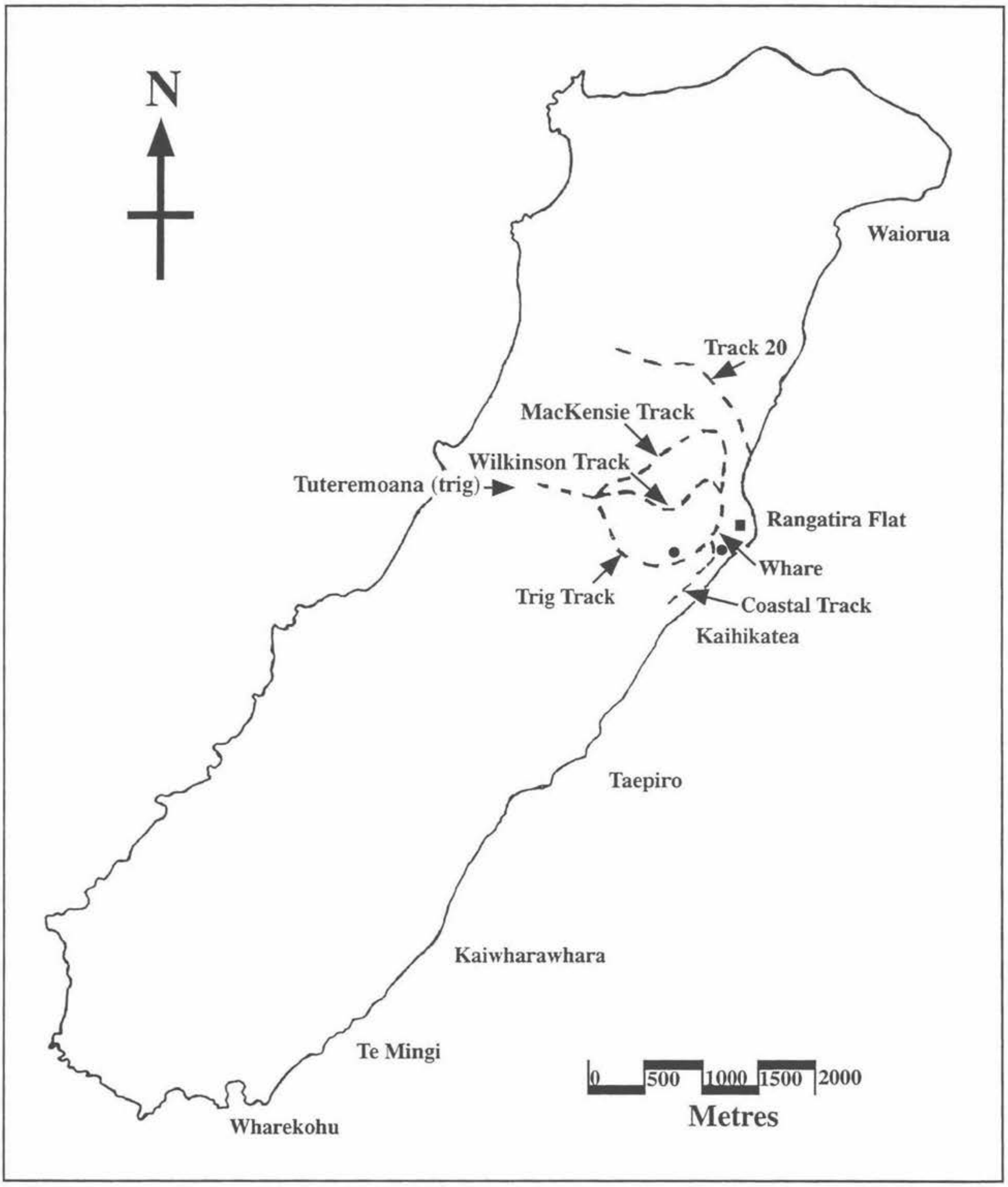


**Figure 4.2. Map of Kapiti Island study sites. *F. excorticata* (squares) and *R. sapida* (circles).**

## 4.2.2. SITE DESCRIPTION

### 4.2.2.1. *Kapiti Island (40° 51´S, 174° 56´E)*

For a full site description, see Chapter Two (2.2.3.).

### 4.2.2.2. *Gladstone Road (40° 40´S, 175° 20´E)*

For a full site description, see Chapter Two (2.2.3.).

### 4.2.2.3. *Akatarawa Road Saddle (40° 58´S, 175° 10´E)*

For a full site description, see Chapter Two (2.2.3.).

### 4.2.2.4. *Nikau Scenic Reserve (40° 54´S 174° 59´E)*

Covering 11 ha, Nikau Scenic Reserve is located on the mainland adjacent to Kapiti Island. The reserve reaches 160 metres above sea level at its highest point. Rainfall averages 1054 mm per year, mean temperature is 12.9°C and averages 2043 sunshine hours. *R. sapida* dominates the lower slopes and the forest floor is thick with its seedlings. Elsewhere, a dense understorey of supplejack (*Ripogonum scandens*), mahoe (*Melicytus ramiflorus*), kawakawa (*Macropiper excelsum*) and hangehange (*Geniostoma ligustrifolium*) ocurrs under a kohekohe (*Dysoxylum spectabile*)-tawa (*Beilschmiedia tawa*) canopy with occasional emergent pukatea (*Laurelia novae-zelandiae*) and rewarewa (*Knightia excelsa*). The reserve is bounded by pasture, State Highway 1, and a cement factory (Wassilief *et al* 1986). There is an ongoing possum control programme.

### 4.2.2.5. *Manawatu Gorge (40° 23´S, 175° 37´E)*

Covering 597 ha, the Manawatu Gorge Scenic Reserve is located 12 km northeast from Palmerston North and 5 km west of Woodville. One of the prime reserves in the Manawatu it reaches 400m in altitude at its highest level. Rainfall average is 1002 millimetres per annum, 13°C and averages 1826 sunshine hours. The reserve is dominated by tall tawa-rewarewa forest with a mahoe, pigeonwood (*Hedycarya arborea*), tarata (*Pittosporum eugenioides*) and hinau understorey. Bush rice-grass

(*Microlaena avenacea*) and hook grass (*Unicinia uncinata*) grow where the canopy is open. Shrub species include sapling tawa, kawakawa, rangiora (*Brachyglottis repanda*), pate (*Schefflera digitata*), five finger (*Pseudopanex arboreus*), karamu (*Coprosma robusta*) and hangehange while supplejack, nikau, tree ferns (*Cyathea* spp., *Dicksonia* spp.) and kiekie (*Freycinetia baueriana*) grow in gullies. There is ongoing possum control however, deer, rats, sheep, cattle and possibly goats roam the reserve (Manawatu Scenic Gorge Draft Management Plan 1986).

#### 4.2.2.6. *Lake Papaitonga Scenic Reserve (40° 39´S, 175° 16´E)*

For a full site description, see Chapter Two (2.2.3.).

### 4.2.3. FUCHSIA EXORTICATA

#### 4.2.3.1. *The species*

For a full species description, see Chapter Two (2.2.2.). Trees were located on Rangatira flat on Kapiti Island.

#### 4.2.3.2. *Estimated fruit crop*

The total fruit crop available for dispersal on each tree was estimated by counting the number of ripe and unripe fruits on an estimated ten percent portion of the tree between January and February 1997. This figure was multiplied by ten to estimate tree totals. This was carried out on at least three occasions over a total duration of 31 days at Gladstone Rd 22 days, at Akatarawa Rd, and 31 days on Kapiti Island.

#### 4.2.3.3. *Proportion of ripe and unripe fruits*

Dispersal services were assessed by determining the ratio of ripe to unripe fruits. Sites with poorer dispersal services should have a greater proportion of undispersed ripe fruits than sites with good dispersal services. To test this, samples of one hundred fruits were counted on three to four occassions throughout the fruiting season (January to February

1997) and each fruit was classified as either ripe or unripe. As fruits were quite scarce towards the end of the season less than one hundred fruits were counted at times.

#### 4.2.3.4. *Bird accessible and bird excluded fruits*

This experiment explored the fate of ripe and unripe fruits which were unable to be dispersed by birds (caged) in comparison to the fate of ripe and unripe fruits which were available for bird dispersal (uncaged). Each tree had two treatments:

**Caged Fruits**: Single branches with up to 73 fruits were surrounded by chicken wire (15 mm mesh) and a diagram was drawn to identify the position of each fruit on the branch. The entire cage was wrapped in curtain netting and secured at both ends with with soft cord, covering the branch like a "cocoon". The rest of the cage was secured to the tree with thin wire. Once a fruit became ripe, it was tagged with coloured electrical wire to be identified. The cage also caught any fruit falling from the selected branch.

**Uncaged Fruits**: These fruits were open to bird dispersal. Up to 51 fruits were identified and mapped on up to two branches. Ripe fruits were tagged using coloured electrical wire.

Fruits were recorded as ripe once more than 50% of their surface darkened. Each site was visited up to six times between mid January and late February 1997 until most fruit had disappeared from the branches. Some fruit was still present on the sample branches at the end of the sample period. Each fruit was recorded as either being ripe, unripe or fallen off on each recording date. Overripe fruit were no longer counted once they had completely shrivelled and deflated.

### 4.2.4. RHOPALOSTYLIS SAPIDA (ARECACEAE)

#### 4.2.4.1. *The species*

New Zealand's only endemic palm, *R. sapida* grows from the extreme north of New Zealand to Hokitika and Banks Peninsula in the south (Enright and Watson 1992, Marshall 1995). The palms can remain in their juvenile stage for up to 50 years (Enright 1985) and can become reproductively mature when the stem reaches two metres in height (Enright 1992). Approximately 40 branched spadices are usually produced between November and May (Esler 1969, Enright and Watson 1992, Marshall 1995). Typical of New Zealand's many endemic plants, inflorescences are unisexual and produce thousands of male or female flowers which can set up to 2000 fruits per spathe (Enright 1992, Marshall 1995). Fruits are 8mm by 12mm (Marshall 1995) and take 12 months to mature, turning brick red when ripe. A single-seeded fruit is surrounded by three thin layers of pericarp and a smooth exocarp covers a fibrous mesocarp and thin endocarp (Marshall 1995). Trees were located near the Whare and the beginning of the Trig Track on Kapiti Island.

The obligate seed predator *Doxophrytis hydrocosma* (Lepidoptera, Yponomeutidae) burrows into the spadices and attacks the fruit (Esler 1969, Sullivan *et al* 1995). It is monophagous (completely restricted) to *R. sapida.* Apart from its habit of feeding on developing mature fruits and the basal sheath of the frond, little else is known about the ecology of *D. hydrocosma* (Dugdale 1975).

#### 4.2.4.2. *Fruit caught*

Experiments to determine how important birds were as dispersers of *R. sapida* fruit were conducted on Kapiti Island, Manawatu Gorge and Nikau Reserve. It was expected that if birds were less prevalent on the mainland than on Kapiti Island, a larger proportion of the total fruit crop should drop to the ground there than on Kapiti Island. Additionally, the fruit crop might be expected to be removed at a faster rate and fewer ripe fruit should be caught on Kapiti Island.

At the beginning of the experiment, fruit crops were estimated by counting the total number of spathes on a tree. The average number of fruit on each spathe was estimated by averaging the number of fruit on up to 14 representative spathes which was multiplied by the total number of spathes. Binoculars were used for some of the taller palms.

A fruit-catching hoop constructed from number eight wire and shade cloth was secured to the trunk of each palm (figure 3.3.). The ends of the shade cloth were tied with cord to form a "basket". Hoops were mounted as close as possible to within 0.50m below the fruiting spathes. Catchers were emptied every two to six weeks between January and September 1997, or until the entire fruit crop on every palm had disappeared.

**Figure 4.3. Diagram of *R. sapida* fruit-catching hoop**

### 4.2.4.3. *Fruit categories*

To determine the proportion of fruit attacked by *Doxophrytis hydrocosma*, all fruit in the hoops were counted and categorised as being unripe (green), ripe (red), unripe with insect damage or ripe with insect damage. Fruit with the pericarp removed were categorised as either attacked by mice or rats (*Rattus rattus, R. norvegicus, R. exulans, M. musculus*) (Daniel 1973, Marshall 1995), or with the entire outer flesh removed ("seeds only").

### 4.2.4.4. *Seedling distribution*

If there are reduced dispersal services on the mainland, seedlings may be expected to be confined to a small area at the base of parent palms, whereas seedlings may be found at large distances from parent palms on Kapiti Island.

To investigate this question, four isolated parent *R. sapida* palms were selected at Kapiti Island and the Manawatu Gorge. No isolated palms could be found at Nikau Reserve and so Lake Papaitonga was used as the second mainland site. Isolated palms were ideally 50 metres from a neighbouring palm, but Kapiti Island was the only site where palms met this criteria. Transects of 50 metres were established north, south, east and west from each adult palm. The number of seedlings in a one $m^2$ quadrat were counted at one metres, two metres and subsequently every two metres from each adult palm along each transect. Seedlings were counted if they had fronds less than two metres in length and no visible stem. Areas of swamp and *R. scandens* thickets prevented complete sampling of some transects.

## 4.2.5. FRUIT DISPERSERS

Video recording aimed to identify bird dispersers of *F. excorticata* and *R. sapida* fruits and whether their visitation rates varied between Kapiti Island, Nikau Reserve and Manawatu Gorge. On each occasion, a known number of unripe and ripe fruits were videoed by a camera for up to three hours at a time. These were later viewed to record the number and duration of visits. Data were converted into the number of visits per fruit per hour. Any other bird visitors seen consuming fruits during the course of fieldwork were also noted.

### 4.2.6. STATISTICAL ANALYSES

Visitation results were analysied using SAS's general linear models procedure (SAS Institute 1988). Hypotheses for mixed model ANOVA's were tested for site effects. Type III sums of squares were used in all cases and were compared with type II sums of squares although little difference was found. *R. sapida* fruits were binary data where the number of ripe and unripe, insect damaged and undamaged and caught and dispersed fruit were scored for each palm. Similary, the number of *F. excorticata* fruits in the caged and uncaged treatments and the number of ripe and unripe fruits were binary. Data were therefore analysed using a generalised linear model with a binomial error distribution and logit link function in S-PLUS statistical package (Mathsoft Inc. 1995). Analyses were performed for site effects for *R. sapida* and site, treatment, date and site*treatment effects for *F. excorticata*. In the case of *F. excorticata*, the numerator for the binomial on each sample date was the number of fruit which disappeared (either shrivelled or dispersed) since the previous sample, and the denominator was the number ripened. Thus, each sample date was independent and assesses the likelihood of new ripe fruits to disappear within the sampling period. Thus, it avoids the necessity of a repeated measures ANOVA. All significance was analysed to the 0.05 level.

# 4.3. RESULTS

## 4.3.1. FUCHSIA EXORTICATA

### 4.3.1.1. *Fruit dispersers*

Kapiti Island tended to have greater visitation rates than both mainland sites, but this difference was not significant ($P = 0.4706$) (Tables 4.2., 4.3.). Tui and kereru were observed consuming fruit on Kapiti Island and red and yellow-crowned kakariki (*Cyanoramphus* sp.) were observed in *F. excorticata* trees and may have been feeding on fruit. Tui consumed fruits at Akatarawa Rd. Bellbirds visited fruiting *F. excorticata* trees at Akatarawa Rd and Gladstone Rd but it could not be confirmed whether they were feeding specifically on fruit. Keruru were present at Akatarawa Rd but none were seen feeding on *F. excorticata* fruit.

### 4.3.1.2. *Estimated fruit crop.*

Gladstone Rd produced the greatest number of fruits, followed by Kapiti Island then Akatarawa Rd (Figs 4.4 (a), 4.5 (a), 4.6 (a)). Over time, ripe fruits consistently formed only a small part of the total fruit crop on Kapiti Island but made up a greater part of the total fruit crop at the mainland sites thoughout the sampling period. The number of ripe fruits at all sites was reasonably constant throughout the fruiting season, but numbers decreased at both mainland sites over the final sampling dates. Virtually all fruits had disappeared by the final sampling date on Kapiti Island by day 31 (240 remained) while both mainland sites still had many fruits remaining on the trees (Gladstone Rd 1250 fruits day 31, Akatarawa Rd 1050 fruits day 22). There was only a small decline in the fruit crop during the final 10 days of sampling at Akatarawa Rd which may have been due to a slower ripening rate at this site.

### 4.3.1.3. *Hundred fruit counts*

Ripe fruits were at their lowest proportion on Kapiti Island, averaging 3% to 30% of the hundred fruit sampled on each sample date (Figs 4.4 (b)). Their proportional increase during the last few days of sampling can be attributed to the low numbers of fruit remaining on each tree (36 fruits or less) which tended to overestimate the relative prominence of ripe fruit. In comparision, the proportion of ripe fruits at both mainland sites was generally much higher, averaging 16% to 49%. The average proportion of ripe fruits was more consistent at Akatarawa Rd than Gladstone Road (~30%) where the proportion tended to fluctuate to a greater extent (Figs 4.5. (b), 4.6 (b)).

#### **4.3.1.4.** *Bird accessible and bird excluded fruits*

The proportion of ripe fruit in the caged branches was initially low at all sites (Figs 4.4 (c), 4.5. (c), 4.6. (c)). This proportion increased quickly over a short period of time to remain roughly constant as the ripening rate more or less equalled the overripening and disappearance of fruit. Kapiti Island was the only site where there was a marked decrease in the proportion of ripe fruits on the final day of sampling because most fruits had either fallen off and/or become overripe, probably because sampling occurred over a greater number of days on Kapiti Island. Once fruits ripened, they varied in how long they remained attached to the plant, taking up to 16 days to shrivel from the time they were first recorded as being ripe. In contrast, on Kapiti Island ripe fruit was consistently very scarce in the uncaged treatments, forming an extremely small proportion of the fruits (Fig 4.4 (d)). In comparison, the proportion of ripe fruits was consistently larger at both mainland sites (Figs 4.5 (d), 4.6. (d)).

The treatment (caged versus non-caged) accounted for 37% of the variation in the data of fruit disappearance (Table 4.4.). The effect of the cages significantly reduced the number of fruits dispersed. A significant sample date*treatment interaction suggests that the proportion of fruits dispersed by birds was different on each sample date. Moreover, a significant site*treatment interaction suggested the proportion fruits dispersed by birds was dependent on site.

**Table 4.2. showing average bird visitation rates of *F. excorticata* per fruit per hour at each site.**

| Site | Minutes of videoing | Average visitation per hour per fruit | bird species seen consuming fruit |
|---|---|---|---|
| Kapiti | 630 | 0.52 | tui, kereru, [1]kakariki |
| Gladstone Rd | 286 | 0.11 | [2]bellbird, [2]tui |
| Akatarawa Rd | 278 | 0.00 | tui |

1 red and yellow-crowned kakariki were observed in *F. excorticata* trees and may have been feeding on fruit

2 were observed in *F. excorticata* trees and may have been feeding on fruit

**Table 4.3. ANOVA showing bird visitation rates to *F. excorticata* at Kapiti Island, Gladstone Rd and Akatarawa Rd.**

| Species | df | Sums of Squares | Pr(Chi) |
|---|---|---|---|
| Site | 2 | 0.5210 | 0.4706 |

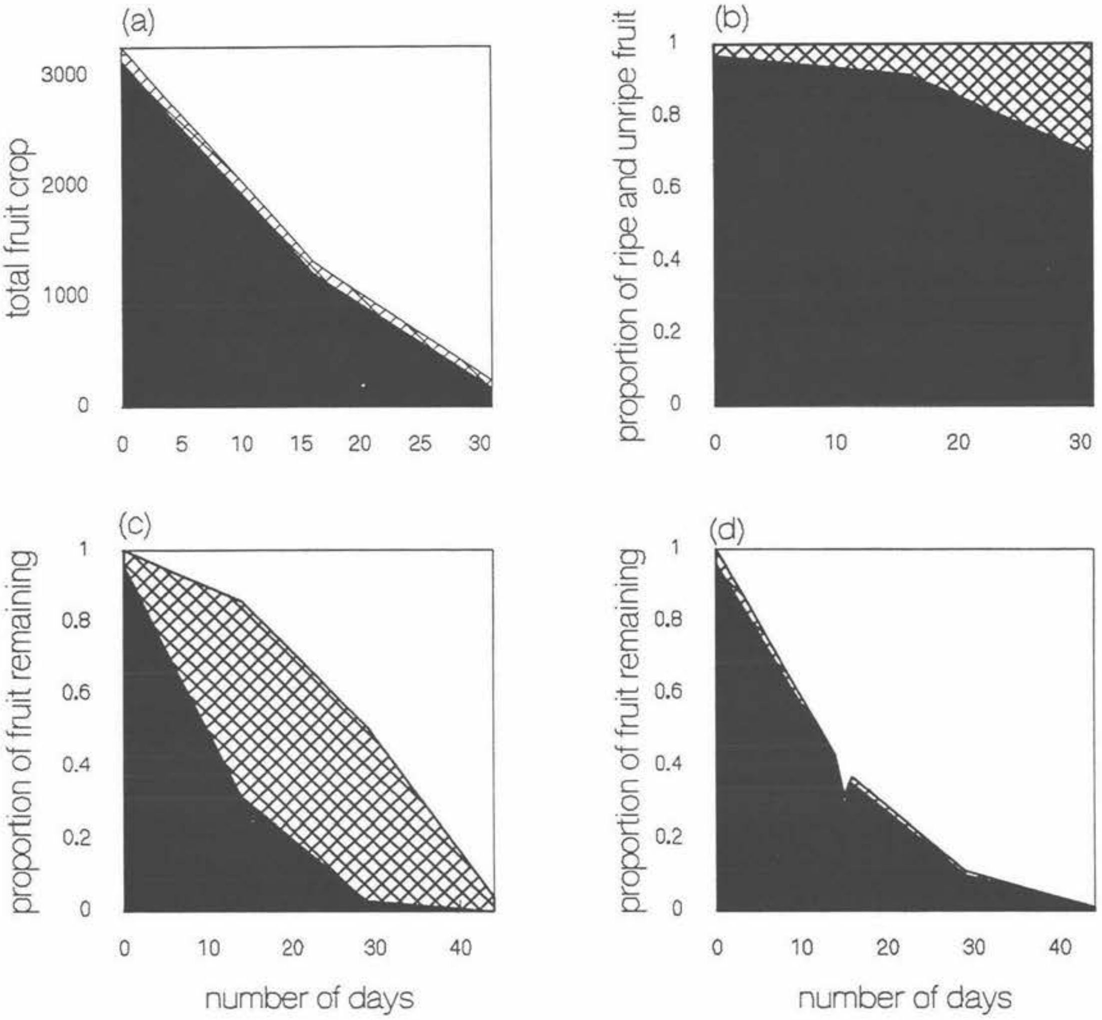


**Figure 4.4. showing bird dispersal of *Fuchsia excorticata* on Kapiti Island**

**Ripe fruit=hatched Unripe fruit=solid**

**(a) actual numbers of ripe and unripe fruits out of the total fruit crop of all 5 trees**

**(b) proportion of fruits which were ripe and unripe out of one hundred fruits**

**(c) proportion of fruits which were ripe and unripe when birds were excluded from dispersing fruits**

**(d) proportion of fruits which were ripe and unripe when birds were permitted to disperse the fruits**

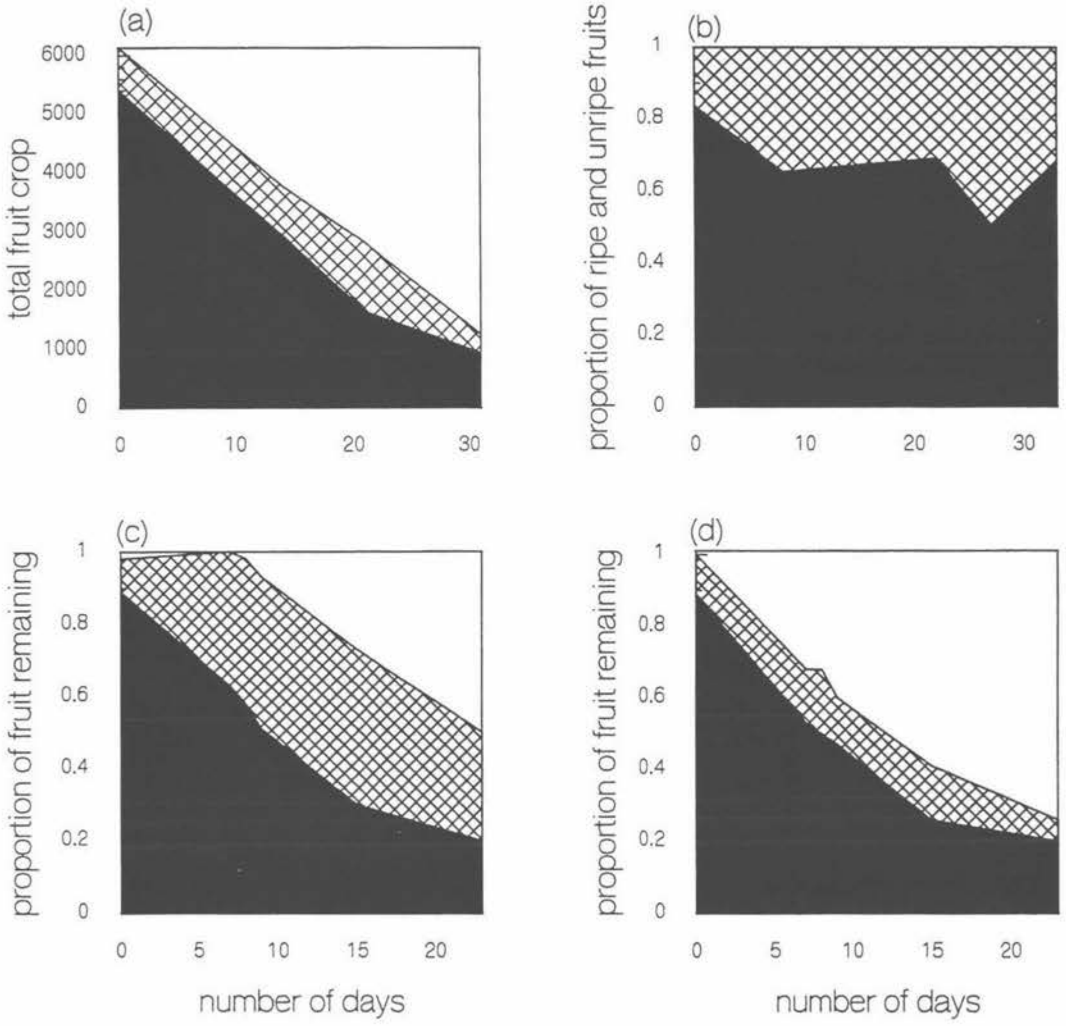


**Figure 4.5. showing bird dispersal of *F. excorticata* at Gladstone Rd**

**Ripe fruit=hatched Unripe fruit=solid**

**(a) actual numbers of ripe and unripe fruits out of the total fruit crop of all 5 trees**

**(b) proportion of fruits which were ripe and unripe out of one hundred fruits**

**(c) proportion of fruits which were ripe and unripe when birds were excluded from dispersing fruits**

**(d) proportion of fruits which were ripe and unripe when birds were permitted to disperse the fruits**

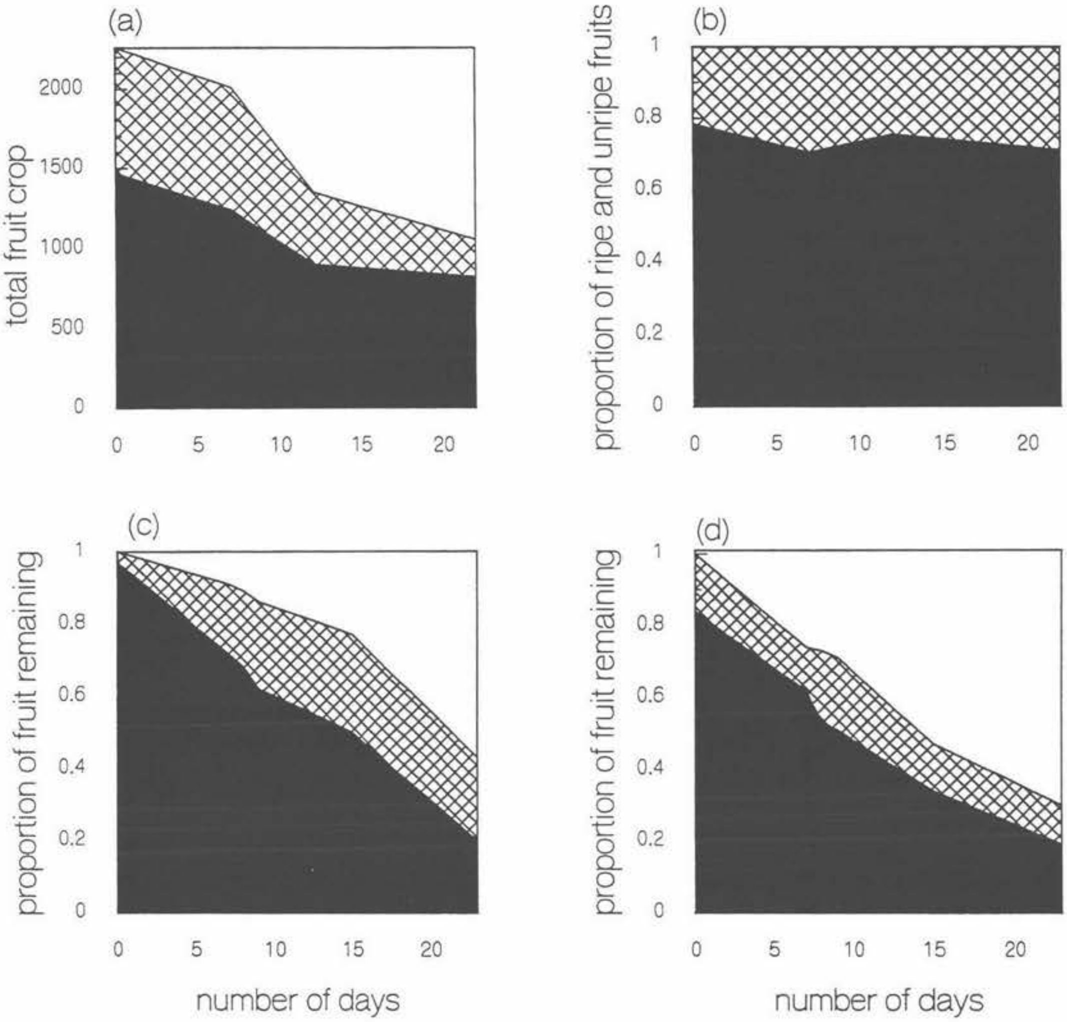


**Figure 4.6. showing bird dispersal of *F. excorticata* at Akatarawa Rd**

**Ripe fruit=hatched Unripe fruit=solid**

**(a) actual numbers of ripe and unripe fruits out of the total fruit crop of all 5 trees**

**(b) proportion of fruits which were ripe and unripe out of one hundred fruits**

**(c) proportion of fruits which were ripe and unripe when birds were excluded from dispersing fruits**

**(d) proportion of fruits which were ripe and unripe when birds were permitted to disperse the fruits**

**Table 4.4. ANOVA showing overall significance tests for the effect on the number of ripe and unripe fruits in two treatments (when birds were permitted and prevented from dispersing fruit) at three sites. These were sampled on 3 or 4 occasions. Data was pooled if there were two bird accessed branches on a tree. Data were analysed using a GLM with a binomial distibution and logit link function, using the number of fruits which had ripened and dispersed between sample dates. Analyses were performed for site, tree, sample date, treatment, site*treatment and sample date*treatment interaction.**

| | df | deviance | % explained | Pr (Chi) |
|---|---|---|---|---|
| Site | 2 | 1.1977 | 0.44 | 0.5494 |
| Tree(site) | 12 | 31.4458 | 11.59 | 0.0017 |
| Sample date | 2 | 8.2191 | 3.03 | 0.0164 |
| Treatment | 1 | 100.5214 | 37.06 | <0.0001 |
| Site*treatment | 2 | 14.2874 | 5.27 | 0.0008 |
| Sample date*treatment | 2 | 7.3644 | 2.7148 | 0.0252 |

## 4.3.2. RHOPALOSTYLIS SAPIDA

### 4.3.2.1. *Fruit dispersers*

The only record of a bird consuming *R. sapida* fruit, was a blackbird (*Turdus merula*) at Nikau Reserve (Table 4.5.), which was included in the birds visitation rates. A North Island robin (*Petroica australis*) was observed perching on the fruiting spathes at Kapiti Island and may have been drawn to the palms to feed on insects which had been attracted to the new season's flowers. Bellbirds were also seen pecking around the spathes of a palm on Kapiti Island but neither species appeared to consume any fruit.

### 4.3.2.2. *Dispersal*

A significantly greater proportion of fruit were dispersed on Kapiti Island than at both mainland sites (Table 4.6., Fig 4.7.). Close to 90% of the variation in the data was explained by the differences between sites, as shown by the highly significant site effect.

Overall, there was a significant difference in the ratio of ripe to unripe fruit caught at each site (after pooling all classes of damage together by ripeness) which explained a large proportion of the variation in the data (~ 37%) (Table 4.6., Fig 4.7.). Manawatu Gorge had proportionally the most ripe fruit caught while Kapiti Island and Nikau Reserve had approximately the same. However, the actual numbers of fruit caught on Kapiti Island were extremely low.

Both mainland sites had a significantly greater proportion of ripe and unripe fruit which were insect damaged than Kapiti Island (Table 4.6., Table 4.7.), although this explained less of the variation in the data (~ 16%). All fruit was caught within 64 days on Kapiti Island compared with 250 days at Manawatu Gorge, and 157 days at Nikau Reserve (Table 4.8., Figs 4.8 (a), (b), (c)). Thus, Kapiti Island removal rates were three to five times faster than at the mainland sites.

All sites had one or two peak periods where a large proportion of their fruits fell (Fig 4.8. (d)). The peak fruit fall at Kapiti Island occurred at 12 days and consisted mostly of unripe fruit. Nikau Reserve's fruit fall peaked at 98 days and consisted mostly of fruit with their pericarp removed. The Manawatu Gorge peaked around 150 days with many fruits with their pericarp removed and moderate amounts of insect damaged fruits. It was difficult to accurately determine how ripe fruits were when their pericarp had been removed. Consequently, the high proportion of the pericarp-removed fruits (especially at Nikau Reserve) may have caused the number of fruit in the other categories to be underestimated. However, the presence of many shavings of red pericarp and exocarp in the catching hoops, the fact pericarp removed fruits were only found after fruits had become ripe on the palm and the absence of outer signs of insect damage would suggest pericarp removed fruits were probably originally ripe and undamaged.

#### 4.3.2.3. *Fruiting synchrony*

When fruits ripened, they did so more or less simultaneously on each palm. Although the sites were visited too infrequently to get an accurate time of ripening, there appeared to be differences betwen sites. Most Kapiti Island palms ripened in early January, those at Nikau Reserve in early February to mid-March and those in the Manawatu Gorge mid March to mid April.

#### 4.3.2.4. *Seedling distribution*

*Manawatu Gorge*

At the Manawatu Gorge site, the occurrence of other adult palms within the 50 metre radius of the sampled parent palm hampered the interpretation of the seedling diagrams because it was not possible to unambiguously assign some seedlings to the parent palms (Figs 4.9.(a),(b),(c),(d), Fig 4.12.(a)). There was a higher occurrence of seedlings along the transects at this site than Kapiti Island but fewer than at Lake Papaitonga. Quadrats with four or more seedlings mostly occurred close to the parent palms except for one palm (Fig 4.9.(a)) where high densities occurred up to 50 metres from the parent palm. Fig 4.9.(c) was the only palm which had virtually no seedlings around it.

### *Lake Papaitonga*

Again, the seedling diagrams at Lake Papaitonga were interpreted with difficulty because of other adult palms within 50m of the sampled adult (Figs 4.10. (a), (b), (c), (d), Fig 4.12.(b)). Quadrats with four or more seedlings were common around all plams. Overall seedling densities were higher than Manawatu Gorge and Kapiti Island and often continued up to 50 metres. Several large clumps of up to 20 seedlings per quadrat were found.

### *Kapiti Island*

Kapiti Island tended to have the least number of seedlings compared with the other two sites (Figs 4.11. (a), (b),(c),(d), Fig 4.12. (c)). Most seedlings were distributed within a 30m radius around the parent palm. Most of the quadrats with over three seedlings were close to the parent palm. The direction of the slopes at all sites showed no particular relationship with the distribution or number of seedlings along the transect lines.

**Table 4.5. showing average visitation rate of *R. sapida* per fruit per hour at each site.**

| Site | Minutes of videoing | Average visitation per hour per fruit |
|---|---|---|
| Kapiti | 1140 | 0.00 |
| Nikau Reserve | 464 | 0.00 [1] |
| Lake Papaitonga | 172 | 0.00 |

[1] a single blackbird was observed feeding on *R. sapida* fruit at Nikau Reserve

**Table 4.6. ANOVA showing overall significant tests for the dispersal of *R. sapida* fruits between sites. Ripe and unripe fruits included all insect damaged fruits. Ripe fruits included pericarp removed fruits and seed only fruits were ignored. Data were analysed using a GLM with a binomial distibution and logit link function. Analyses were performed at the site level only.**

| Analysis | df | Sums of Squares | % explained | Pr (Chi) |
|---|---|---|---|---|
| Caught:Dispersed | 2 | 6329.205 | 89.53 | <0.000001 |
| Ripe:Unripe | 2 | 945.0297 | 37.47 | <0.000001 |
| Uninsect damaged : insect damaged | 2 | 328.3897 | 15.75 | <0.000001 |

**Table 4.7. showing the proportion of *R. sapida* fruits attacked by the endemic catepillar *Doxophrytis hydrocosma* at three study sites, Nikau Reserve, the Manawatu Gorge and Kapiti Island.**

| Site | Nikau Reserve | Manawatu Gorge | Kapiti Island |
|---|---|---|---|
| % fruits with *D. hydrocosma* predation | 59.4 | 55.1 | 27.2 |

**Table 4.8. showing the proportion of total dispersed fruit removed per day at each site. Removal rates per day were estimated for both mainland sites by determining the proportion removed per day from the sample date in which all palms at each site had ripe fruit found in their fruit catcher. Removal rates for Kapiti Island were calculated from the initial date which fruit catchers were set up because fruit was dispersed while it was unripe.**

| Site | Kapiti Island | Manawatu Gorge | Nikau Reserve |
|---|---|---|---|
| Total Fruit Removed | 5254 | 15967 | 17330 |
| Total Number of Days | 64 | 165 | 111 |
| Proportion of Fruit Dispersed | 0.94259 | 0.68942 | 0.3664 |
| Proportion of Dispersed Fruit Removed/Day | 0.01473 | 0.00418 | 0.0033 |

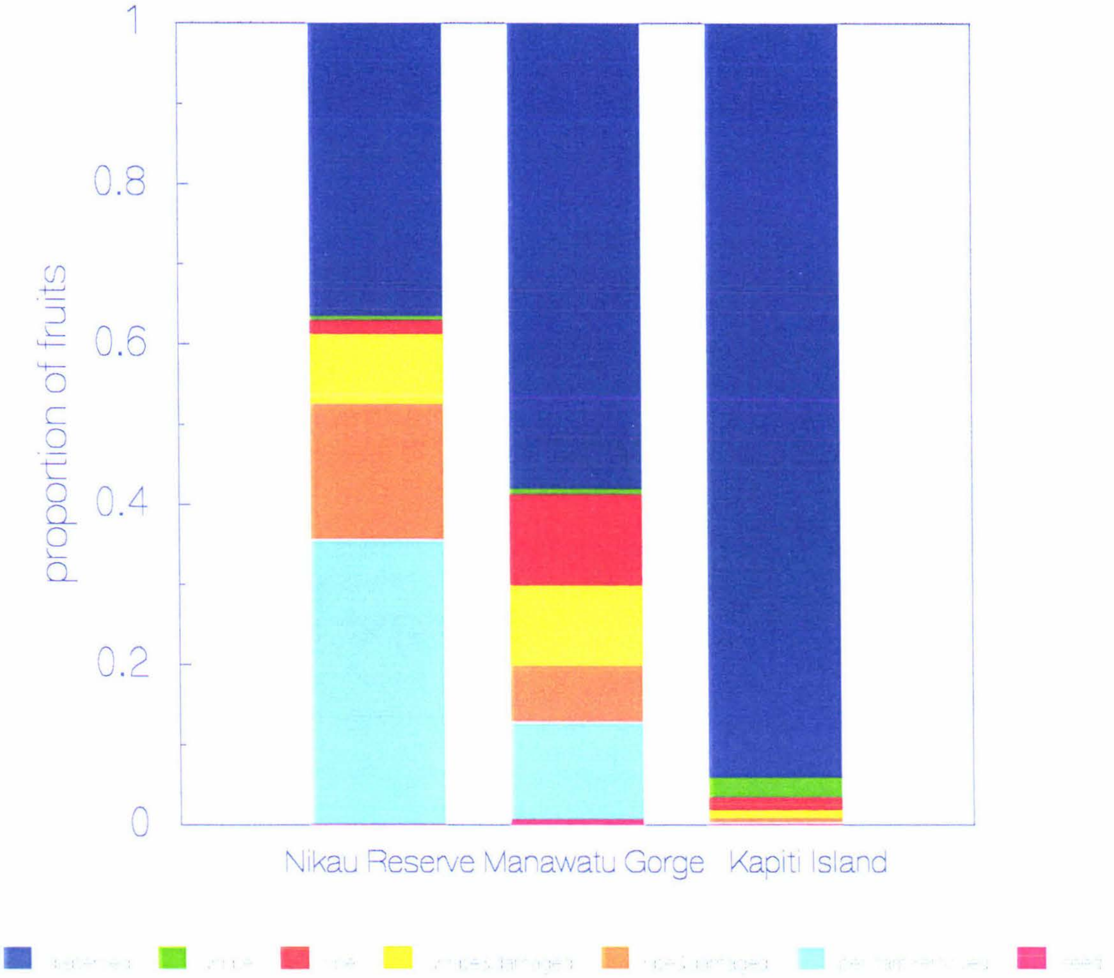


**Figure 4.7. showing proportion of *R. sapida* fruits caught categories (relating to ripening and pre-dispersal damage) and dispersed at Nikau Reserve, Manawatu Gorge and Kapiti Island. Insect damaged fruits were affected by *Doxophrytis hydrocosma* and pericarp removed fruits had probably been gnawed by rats or mice.**

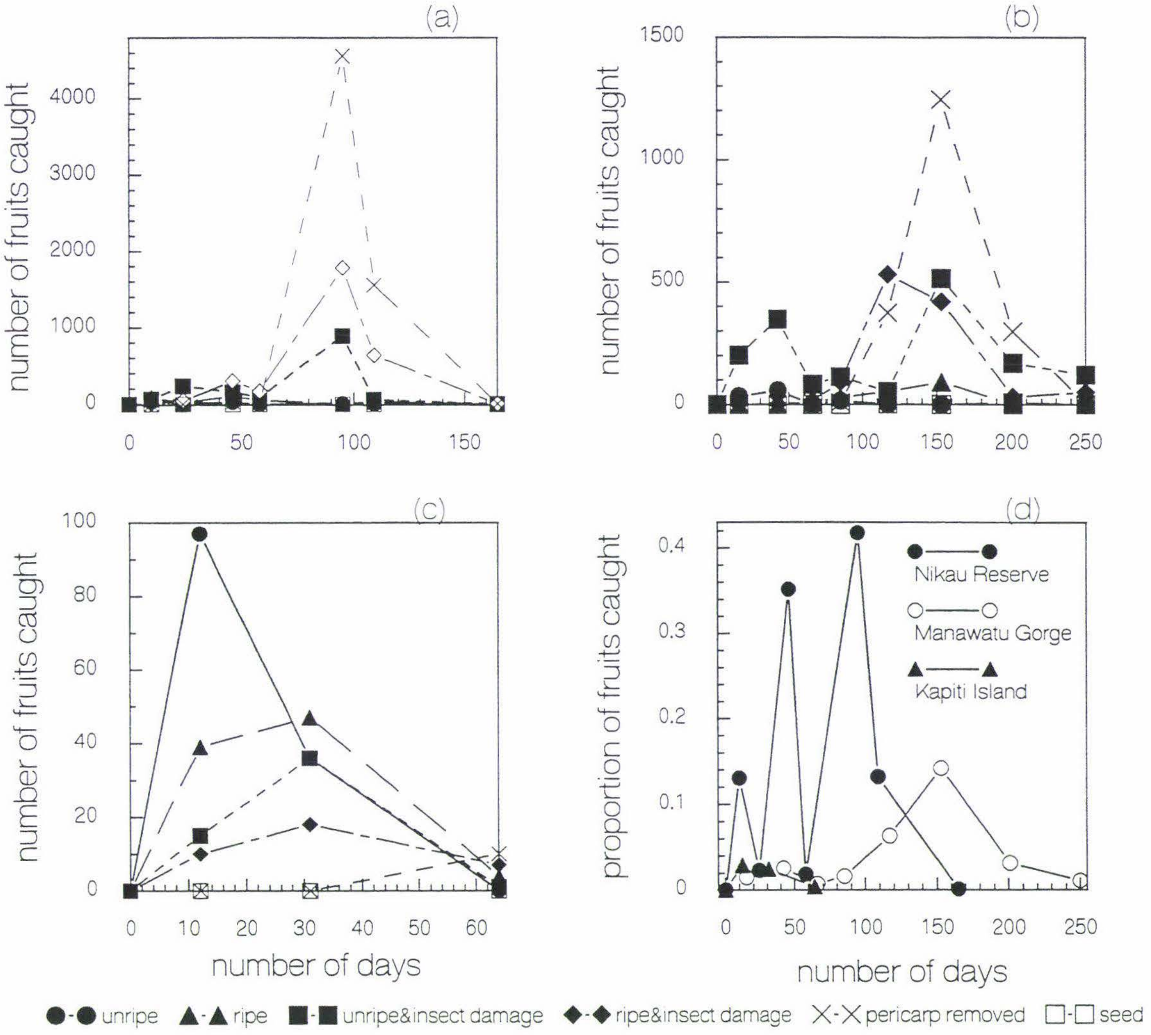


**Figure 4.8. showing the numbers of *R. sapida* of fruits caught over time at (a) Nikau Reserve (b) Manawatu Gorge (c) Kapiti Island (d) proportions of *R. sapida* fruits caught at the three sites over time.**

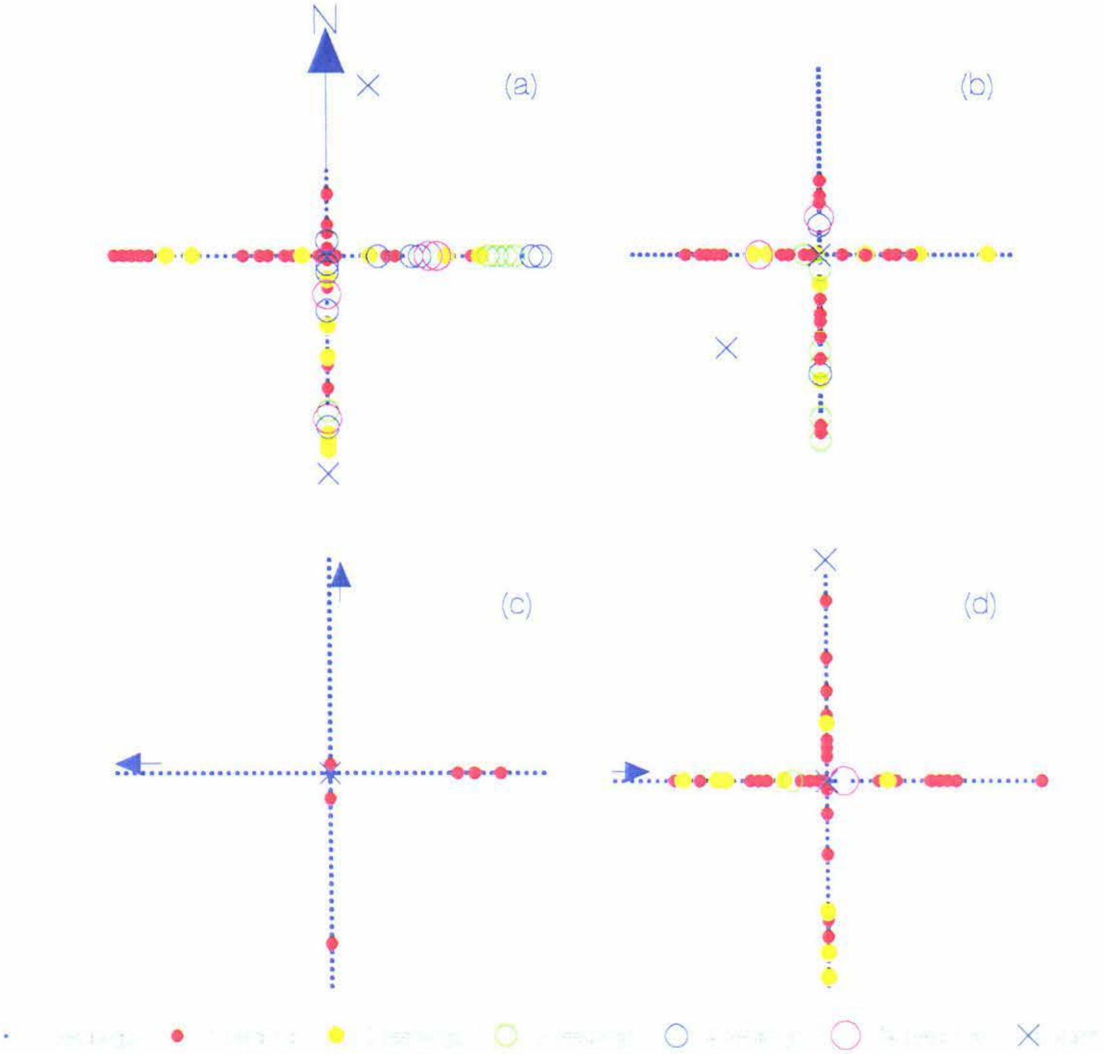


**Figure 4.9. showing distribution of *R. sapida* seedlings at Manawatu Gorge around parent palms along 50m transects. The number of seedlings per quadrat is indicated by the symbol. Arrows point down slopes. Straight lines indicate quadrats which were unable to be sampled.**

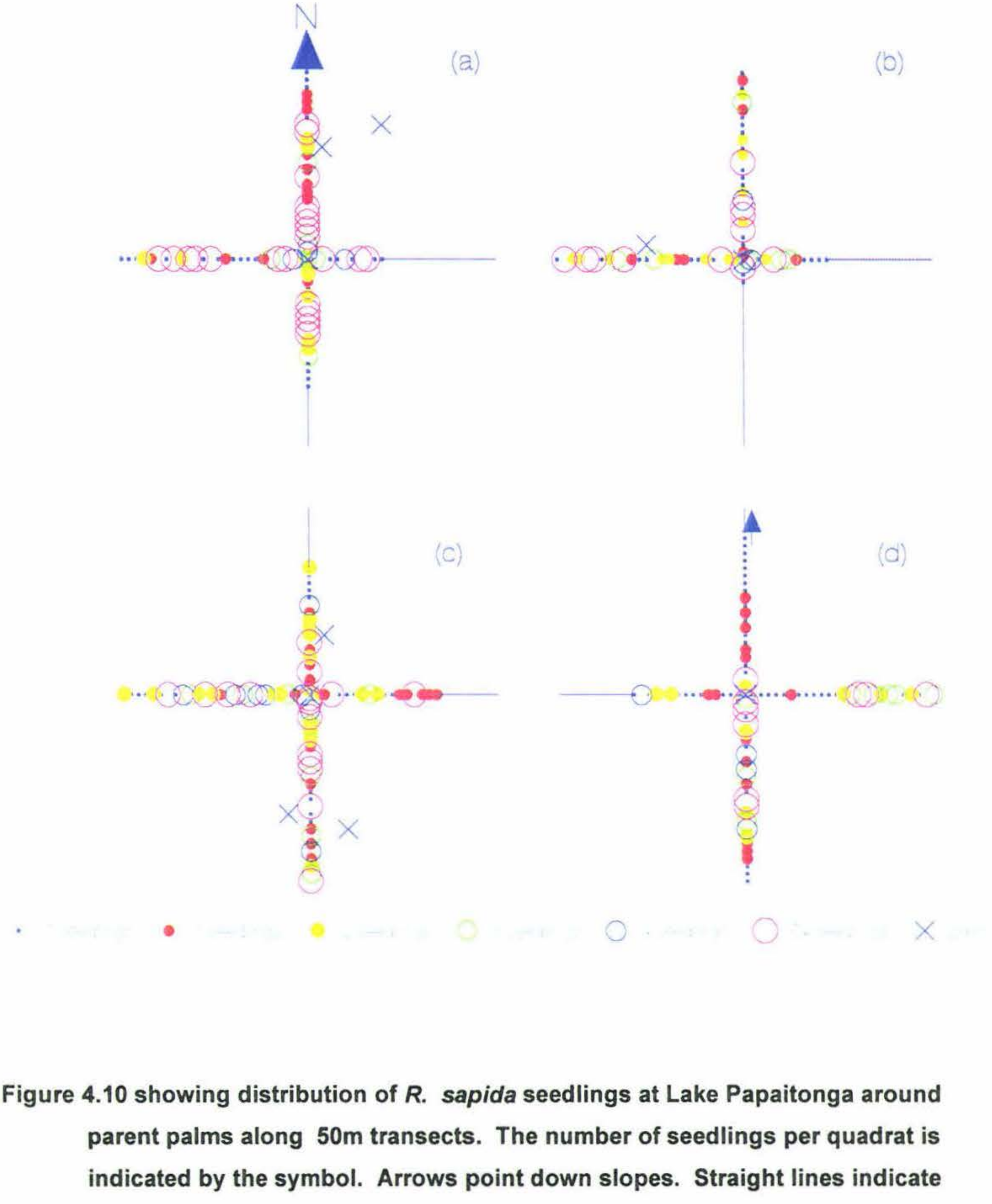


Figure 4.10 showing distribution of *R. sapida* seedlings at Lake Papaitonga around parent palms along 50m transects. The number of seedlings per quadrat is indicated by the symbol. Arrows point down slopes. Straight lines indicate quadrats which were unable to be sampled.

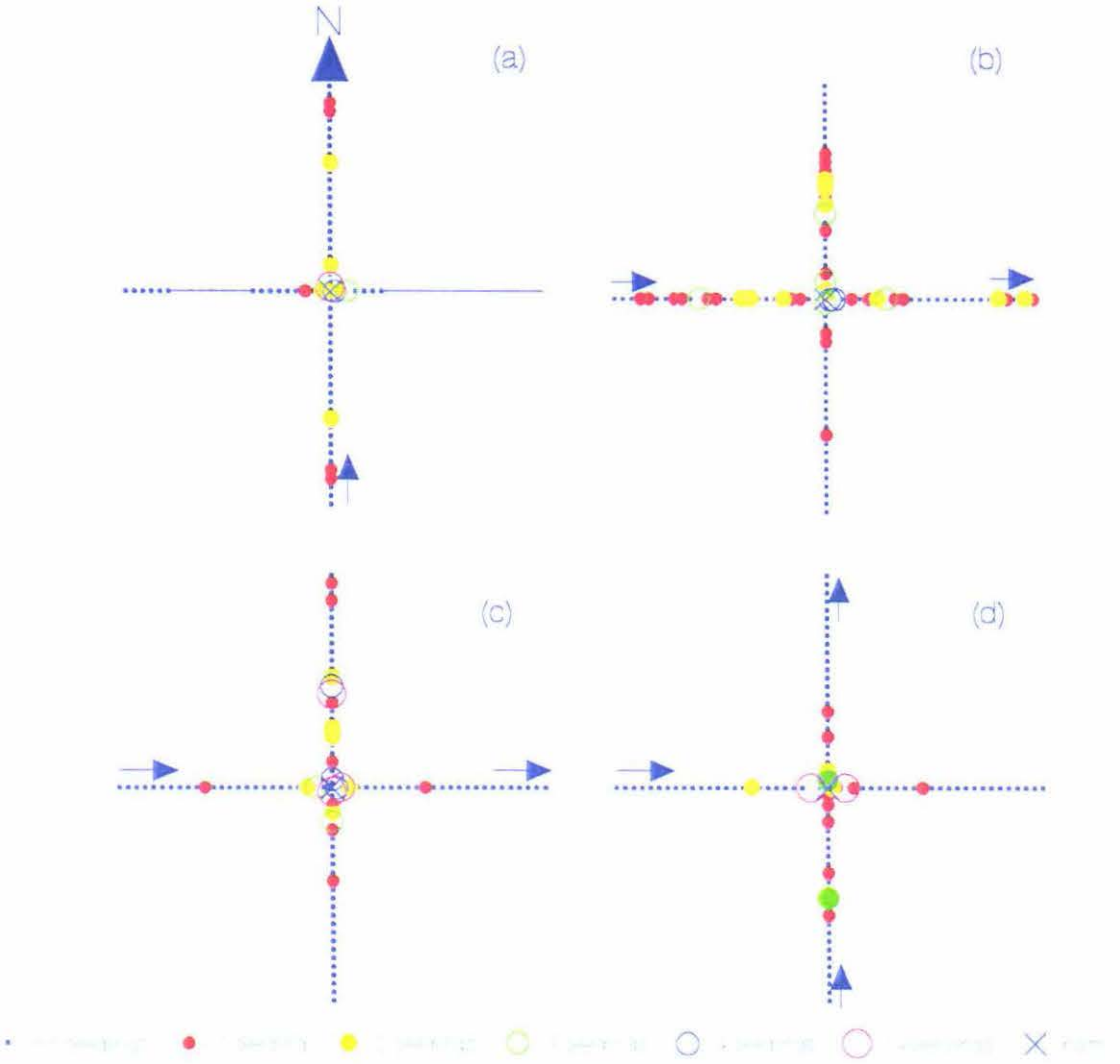


**Figure 4.11 showing distribution of *R. sapida* seedlings at Kapiti Island around parent palms along 50m transects. The number of seedlings per quadrat is indicated by the symbol. Arrows point down slopes. Straight lines indicate quadrats which were unable to be sampled.**

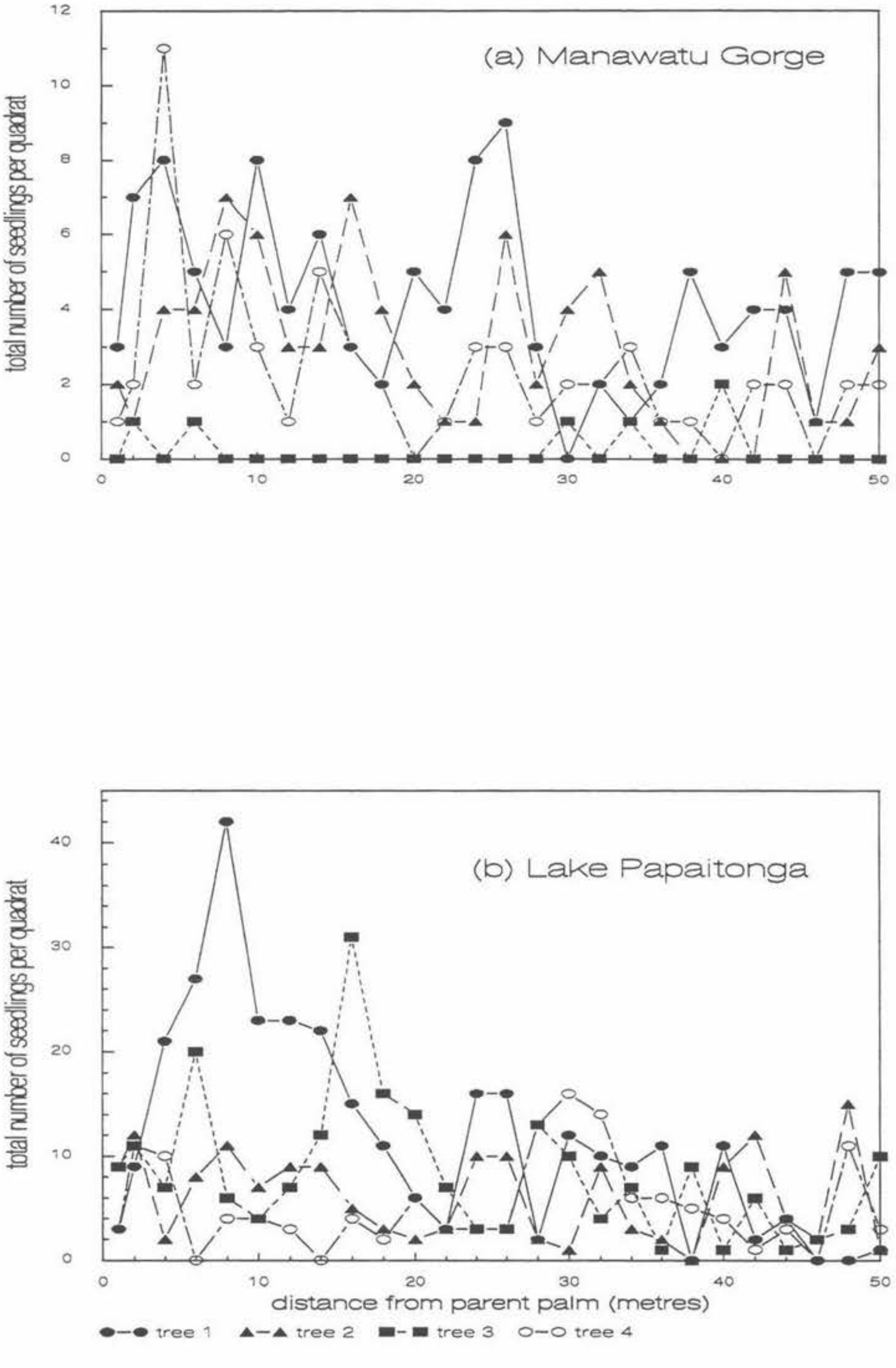


**Figure 4.12. Showing the total numbers of seedlings per quadrat for 4x50m transects from parent *R. sapida* palms (a) Manawatu Gorge (b) Lake Papaitonga. Quadrats which were within 20m from other adult palms were not included. Some parts of transects were unable to be sampled due to the terrain (see Figs 4.9., 4.10.)**

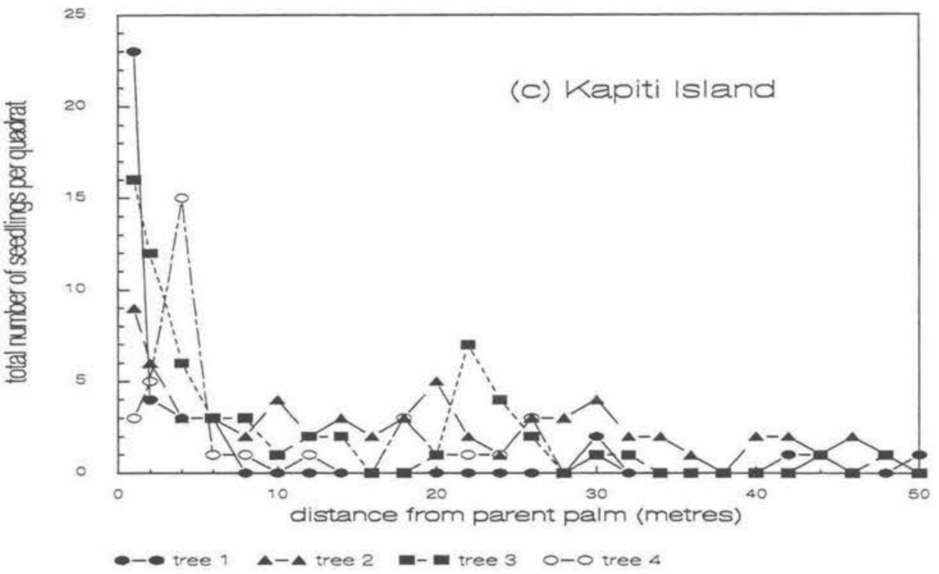


**Figure 4.12. Showing the total number of seedlings per quadrat for 4x50m transects from parent *R. sapida* palms. (c) Kapiti Island. All parts of the transects were able to be sampled and no other adult palms were present.**

# 4.4. DISCUSSION

This is one of only a handful of studies quantifying avian dispersal in New Zealand forests. It has shown that dispersal of *F. excorticata* and *R. sapida* is limited at mainland sites compared with Kapiti Island. This is probably a direct consequence of the decline in abundances of fruit-dispersing birds on mainland New Zealand.

## 4.4.1. DISPERSAL LIMITATION OF *FUCHSIA EXCORTICATA* FRUIT

As *F. excorticata* seed is probably resistant to a bird's digestive tract (Burrows 1995b), the removal of *F. exorticata* fruit by birds is likely to be an accurate measurement of their dispersal. Additionally, the cage experiments demonstrated that very few fruits fell off before they were ripe or overripe. Thus, the disappearance of fruit was a reliable indicator of dispersal rates. *F. excorticata* fruits are known to be dispersed by kereru, bellbirds and tui (Wilkinson 1952 cited in Godley and Berry 1995, McEwen 1978), and this study found tui and bellbird were the main dispersers for *F. excorticata.* This is not surprising given fruit is an important constituent of honeyeater diet (Gravatt 1971, Lee *et al* 1991) and honeyeaters are probably biased towards non-red fruit (Lee *et al* 1988).

Possums feed on a wide variety of fruits (Manson 1958) but are considered to be seed predators rather than dispersers (Beveridge 1964, Brockie 1992, Burrows 1994c but see Lord 1991). Rats are known to eat *F. excorticata* fruit (Allen *et al* 1994) so their potential to remove fruit cannot be ignored. However, active poisoning programmes and the overripening of fruit at the mainland sites suggested possum (*Trichosurus vulpecula*) and rat fruit consumption was negligible and therefore fruit dispersal was most probably by birds.

Dispersal appeared to be limited on both mainland sites as judged by the greater proportion of ripe fruits found there compared with Kapiti Island throughout the entire sampling period. The greater differences between the proportion of ripe fruits in bird accessed (uncaged), and bird excluded (caged) treatments on Kapiti Island was evidence that fruit was being dispersed at a faster rate here. In fact, fruit was dispersed so quickly on Kapiti Island, it was being removed before it was even ripe, which was similarily observed by Wilkinson (1952 cited in Godley and Berry 1995). This compared starkly with the abundance of overripe and rotting fruits at the mainland sites. Rotting fruits on parent trees is a definite sign there is a shortage of dispersal agents (McKey 1975). Of the two mainland sites, Gladstone Rd appeared to be receiving better dispersal services than Akatarawa Rd. This may have been due to the different habitats at these sites. Several of the *F. excorticata* trees at Gladstone Rd are somewhat isolated from small bush remnants that exist on the edge of the roads, while at Akatarawa Rd trees are situated on the fringes of the Tararua Ranges. Other studies have found that dispersal rates were faster where trees were isolated (Denslow 1987) or located on the edge of forest gaps (Thompson and Willson 1978).

### 4.4.2. DISPERSAL LIMIATATION OF *RHOAPLOSTYLIS SAPIDA* FRUIT

One aspect of disperser efficiency is the quantity of fruits removed from fruiting trees (Chavez-Ramirez and Slack 1994). The removal of *R. sapida* fruit on the mainland was not as rapid as on Kapiti Island as less fruit disappeared and a smaller proportion of fruit disappeared per day than on Kapiti Island. As with *F. excorticata* fruits, feeding pressure was so intense on Kapiti Island that most fruit disappeared before it was ripe, whilst ripe fruit was present for approximately six months at Manawatu Gorge and four months at Nikau Reserve. Ripe *R. sapida* fruit have been observed on parent trees for up to nine months in Canterbury (Burrows 1995a).

The Manawatu Gorge had proportionally more fruit dispersed than Nikau Reserve, even though it took longer for the fruit to be dispersed. This may have been related to the ratio of the number of fruiting *R. sapida* adults to the number of available dispersers. Being small in size, Nikau Reserve is likely to support lower numbers of dispersing birds than the much larger Manawatu Gorge reserve (see MacArthur and Wilson 1967). Additonally, the total fruit crop would have been much higher in Nikau Reserve because of the very high density of fruiting individuals, whilst Manawatu Gorge had only scattered individuals. Other studies have found fruit removal can increase with the crop size on an individual tree (Denslow 1987) or be unrelated to crop size (Davidar and Morton 1986, Laska and Stiles 1994), but it is debated whether the absolute number or the proportion of fruits removed is the more appropriate measure of dispersal efficiency (Carr 1992).

The lack of sightings of bird dispersers at the mainland sites was not unexpected, but it was surprising that no dispersal events were recorded on video on Kapiti Island especially as the island supports large populations of kereru. There can be little doubt that birds were the only dispersal agents on Kapiti Island because it lacks introduced mammals. However, fruit removal may not have directly equated to fruit dispersal. There were substantial populations of kaka *(Nestor meridionalis)* and red and yellow-crowned kakariki (*Cyanoramphus* sp.) on Kapiti Island which are known to include fruit in their diet (Gravatt 1971). Red and yellow crowned kakariki on Kapiti Island have been observed feeding on *R. sapida* fruit (Peter Daniels pers comm). Some fruits were observed to have their pericarp partially removed or have "slice" marks down their sides which could have resulted from kaka or red or yellow-crowned parakeets biting them. True *R. sapida* fruit dispersal could have been overestimated if these birds were regular feeders because parrots are often seed predators rather than dispersers (Clout and Hay 1989, Lee *et al* 1991). Kakariki may also be present in the Manawatu Gorge but it is unlikely their small numbers would have influenced estimates of fruit dispersal.

Temperate fruiting species may suffer from lack of dispersal if their fruiting ocurrs during the breeding season of their frugivores because breeding birds may change their dietary needs away from fruits to invertebrates at this time (Morton 1973). Even though *R. sapida* fruits appear to lack some characteristics of fleshy fruits (van der Pijl 1982, Janson 1983), they are high in calcium (Astrid Dijkstraaf pers comm). Birds are known to actively seek high calcium food during breeding (Jones 1976, Houston 1978) as calcium is required by nesting birds to form eggs (Taylor and Moore 1954). Insufficient calcium can lead to eggshell defects (Houston 1978, Graveland and Drent 1997) and decreased hatching success (St Louis and Barlow 1993, Graveland and Drent 1997). Keruru breed irregularly and are reproductively dependent on the availability of fleshy fruits (Lee *et al* 1991), but generally breeding peaks between November and January (Clout *et al* 1995). *R. sapida* fruits may have been favoured on Kapiti Island because they became available (but not necessarily ripe) during the kereru breeding season and thus, were targeted by breeding kereru. Kereru are known to consume green *R. sapida* fruit (Rachael Bell pers. comm.). Mainland fruit dispersal therefore, could have suffered not only because keruru were less abundant, but because fruits became available and/or ripened after the kereru breeding season.

Fruits of *F. excorticata* and *R. sapida* became ripe over a short period of time within each site, which implied fruits had to be dispersed by a limited number of bird dispersal agents quickly (see McKey 1975). Avian dispersers differ in local abundances (Jordano 1982, Herrera 1984) and, like any resource, dispersal agents can be in short supply (McKey 1975). The proportion of fruit retained by *R. sapida* adults maybe related to the abundance of fruit eating birds, especially kereru (Burrows 1995a). Overseas studies have shown the amount and rate of fruit removal can be directly related to the size and abundance of frugivore populations (Thompson and Willson 1978, Jordano 1987, Chavez-Ramirez and Slack 1994). Evidence for dispersal limitation in New Zealand has been suggested for the mistletoe *Peraxilla tetrapetala* during one fruiting season at Craigieburn Forest Park (Ladley and Kelly 1996). However, subsequent mistletoe fruiting seasons showed no signs of dispersal limitation (Robertson *et al* unpublished manuscript).

#### 4.4.2.1. Doxophrytis hydrocomsa *fruit predation*

The number of fruits available for dispersal may be reduced by seed predation in the pre-dispersal phase (Jordano 1987). In this study, there was evidence that the ability of *R. sapida* to disperse its fruit was inhibited by three main fruit predators: *D. hydrocomsa*, and rats and mice. All four rodent species present in New Zealand are known to include *R. sapida* fruits in their diet (Daniel 1973, Campbell 1978, Marshall 1995). Possums are also known to feed on *R. sapida* fruit (Mason 1958, Cowan 1991, Marshall 1995) but there were no signs of possum damage to fruit at any of the three study sites.

The endemic caterpillar *D. hydrocomsa* occurred in both ripe and unripe fruits, especially at the mainland sites. The percentage of affected fruit at the three sites (27.2 to 59.4%) was higher than other studies which have reported between 14 and 23 percent

(Esler 1969, Enright and Watson 1992, Marshall 1995, Sullivan *et al* 1995). In this study Kapiti Island had lower proportions of infested fruit than the two mainland sites This may have been due to faster fruit removal rates which reduced the time for caterpillars to infest fruit. Invertebrate damage and removal rates are two processes which are often antagonistic (Jordano 1987). Rapid removal of ripe fruits may be necessary in temperate regions to reduce the probability of fruit destruction by invertebrates (Thompson and Willson 1978, 1979, Jordano 1987). Thus, it maybe advantageous for *R. sapida* to have its fruits removed quickly so that a greater proportion of fruit is dispersed rather than predated. Invertebrate predation can alter the foraging behaviour of dispersers (Manzur and Courtney 1984) for example by making fruit less palatable to birds (Janzen 1977). As *R. sapida* fruits can remain ripe for many months (Burrows 1995a, pers. obs.) they suffer an increased risk from *D. hydrocomsa* predation throughout this period (Sullivan *et al* 1995). Other, studies have found invertebrate damage can increase throughout the fruiting season (Manzur and Coutney 1984) and can be positively correlated with the size of the fruit crop (Jordano 1987).

Rodent predation only occurred on ripe fruit at the mainland sites. The pericarp of *R. sapida* fruits must be removed before the seed can germinate (Burrows 1995a). Thus, rodents may not be true fruit predators in this case because they can remove the pericarp with no obvious damage to the seed (Daniel 1973, Marshall 1995, pers. obs.) which might actually aid *R. sapida* gemination. Rat or mouse predation may have also led to an overestimation of bird dispersal on the mainland because they probably removed some fallen fruit from the catchers to hoard in their caches (see Campbell 1978).

#### 4.4.2.2. **Rhopalostylis sapida** *seedlings transects*

The number of seedlings recruited from each palm is a measure of female fitness (Bond 1995). Palm fitness on Kapiti Island appeared to be less than the mainland sites because there were fewer quadrats with seedlings in them and seedlings did not occur as far from the parent palm as at mainland sites. However, any conclusions drawn from the seedling transects should be regarded with caution, especially because of the presence of additional palms within 50m of the parent palms and the longevity of both seedlings and the seed bank for this species. Although there was no obvious relationship between seedling density and the direction of the slopes, it is likely the steep gradient of Kapiti Island would roll fruits further away from the parent palm. Moreover, seedlings may be an inaccurate measure of dispersal because seed germination depends on a combination of factors including microsites (Crawley 1990), habitats (Willson and Whelan 1990) and the behaviour of dispersers (Jordano 1992, Chavez-Ramirez and Slack 1994, Ladley and Kelly 1996). Seedling distribution patterns may reflect historical dispersal patterns. Marshall (1995) found that decreases in *R. sapida* seed and seedling numbers more than 20 metres from the parent palm corresponded to historical events of bush clearing. Kapiti Island's seedling patterns are probably still reflecting grazing and predation pressure from introduced mammals, the last of which were only finally eradicated in September-October 1996. These historical events may be long-lasting because *R. sapida* seeds are slow and staggered in their germination compared to other New Zealand species (Burrows 1995a). They are not shade tolerant, and can remain as small seedlings for up to 50 years (Esler 1969, Enright and Watson 1992).

The clumps of seedlings found at Lake Papaitonga may result from kereru roosting sites. Lake Papaitonga had the lowest canopy and therefore roost sites would concentrate deposited seeds in a small area. Clumped dispersal patterns have similarly been found by Marshall (1995) and Burrows (1994c).

### 4.4.4. THE EFFECT OF DISPERSER LIMITATION ON NEW ZEALAND DISPERSAL MUTUALISMS

The fragmentation of landscapes in temperate regions has caused losses of avian dispersers which is threatening the survival of remnant stands (Willson 1993). This may affect the structure of vegetation and influence local plant species survival (Willson 1992). Fragmentation has already been directly linked with decline in avian dispersers and decreased dispersal efficiency and regeneration in central Spain (Santos and Tellería 1994). The risk of plant extinctions depends in part on the specificity and degree to which reproduction relies on the mutualism, and also the plant's dependence on seed for reproduction (Bond 1994). Forest regeneration may be limited by the means to transfer seed to colonise habitats. Most New Zealand woody species germinate quickly and seed banks are short-lived (Burrows 1994a). Both *F. excorticata* and *R.*

*sapida* for example, rely on dispersal to colonise disturbed or secondary growth areas (Burrows 1995a, Burrows 1995b). Similarly, without dispersal, it is unlikey podocarp-broadleaved forests in New Zealand would regenerate and widely and uniformly as they would have prior to the decline of avian dispersers (Lee *et al* 1991). However, evidence for dispersal may be difficult to detect because it may not become apparent for decades in such long lived plants.

Birds also maybe essential to ensure quick germination and establishment because New Zealand plants often have germination-inhibiting pericarps (Burrows 1995a) which are probably removed by a bird's digestive processes. However, Anderson (1997) found that seeds from many New Zealand plants did not gain any germination advantage after they had been voided from a bird. The size of a bird's gape sets the upper limit to the size of the fruits it can swallow (Herrera 1984, Wheelwright 1985) although this is not absolute because birds can occasionally swallow fruits larger than their gape size (Ladley and Kelly 1996). In New Zealand, it has been suggested keruru densities are especially critical because they are the only widespread frugivore which can consume fruits greater than 10 to 12 millimetres in diameter (Clout and Hay 1989, Lee *et al* 1991, Burrows 1994b). But concerns should also be raised about the declining abundances of honeyeaters because tui have gape sizes between 11.0 and 12.2 millimetres (Gravatt 1971, Anderson 1997) enabling them to disperse relatively large-fruited species. Most New Zealand fruits match the gape sizes of bellbird and tui (Burrows 1994b) which is alarming when the importance of honeyeaters as fruit dispersers is not widely appreciated (Dr. Dave Kelly pers. comm).

The occurrence of a tight mutualistic relationship between a plant and its disperser is the exception rather than the rule (eg. Temple 1977 but see Owadally 1979 and Witmer 1991). The usually generalised nature of dispersal mutualisms in New Zealand and elsewhere (Wheelwright 1988, Herrera 1985, Willson and Whelan 1993, Burrows 1994a, 1994b) suggests widespread plant extinctions from the loss of dispersers are unlikely because other mechanisms may compensate for the loss of mutualistic partners (Bond 1994). Burrows (1994c) suggests bird dispersal at Ahuriri Scenic Reserve in Canterbury was inefficient and involved extreme wastage of fruits which was probably related to the loose mutualistic relationships between birds and fleshy fruits. Yet forest regeneration did not appear to be severely inhibited. The extent to which introduced frugivorous birds are replacing extinct native dispersers is currently debated. Burrows (1994b) states that if not for the introduction of European birds, dispersal mutualisms and processes of forest regeneration would be tenuous as introduced birds have partially offset the decline of endemic frugivores (Baylis 1986, Lee *et al* 1991, Anderson 1997). The self-introduced silvereye (*Zosterops lateralis*) for example is now an important disperser in New Zealand (McEwen 1978, Burrows 1994b, 1994c, Anderson 1997) but it may be less efficient than native dispersers (Burrrows 1994b). Additionally, introduced birds can spread weed species through forest remanants (Williams and Karl 1996).

Introduced mammals may also be performing minor dispersal roles (Lord 1991). However, dispersal limitation will still probably occur even with the presence of introduced species. Introduced birds may not be able to completely replace an absent fruit disperser for some plant species (Ladley and Kelly 1996, Anderson 1997). No introduced frugivore can disperse fruits greater than 12 millimeters diameter (Clout and Hay 1989) which could adversely effect the regeneration of larger-fruited species, compounding the effects of disperser limitation in New Zealand.

Further studies are necessary to quantify dispersal limitation in New Zealand. Studies are needed to identify whether the composition of New Zealand forests is being altered in favour of species which do not require bird dispersal. Additionally, studies should explore the extent to which introduced birds are compensating for extinct endemic dispersers and how pre- and post-dispersal seed predation is affecting forest regeneration.

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