An experimental evaluation of resource allocation in island plants with respect to their invertebrate herbivores.

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M.K. (Nod) Kay

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Abstract of a thesis submitted in partial fulfilment of the requirements for the Degree of Doctor of Philosophy

An experimental evaluation of resource allocation in island plants with respect to their invertebrate herbivores

by M.K. Kay

Abstract

New Zealand's isolation and periods of marine transgression have limited its biota to an extent which can be considered depauperate, even by island standards. Endemic vertebrates are rare and prominent invertebrate families, such as the renowned forest defoliators of the Lymantriidae, are absent. The proven vulnerability of the flora to introduced vertebrates reaffirms a belief in the invasiveness of islands and fuels the contingency plans aimed at averting similar devastation from further alien invertebrate defoliators.

Nothofagus is a dominant element of the climax forests of New Zealand and the larger landmasses bordering the South Pacific Ocean. Assessments of the resistance to defoliation of continental and New Zealand species of *Nothofagus,* and a range of other forest genera endemic to New Zealand, was undertaken using bioassays of naïve polyphagous defoliators. The bioassays were undertaken in Europe, utilising gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae) and the fall webworm, *Hyphantria cunea* (Lepidoptera: Arctiidae) as defoliators, fed foliage plants growing in European arboreta. In New Zealand, bioassays utilised Australian painted apple moth, *Teia anartoides* (Lepidoptera: Lymantriidae) and tree species from local arboreta, gardens and natural populations.

Larval growth rate was the primary parameter recorded to assess plant resistance. The relevance of growth rate was investigated by comparison with other recorded parameters and resistance to a surrogate pathogen, in the form of commercially available bio-insecticide. Larval growth rate was positively correlated with survivorship, potential fecundity, mating success and resistance to disease. The growth rate of larvae fed *Nothofagus* was positively correlated to the species-specific leaf nitrogen content.

The results of the bioassays showed that despite the accepted paradigms, New Zealand's flora was largely resistant to exotic defoliators. As an explanation of this apparent anomaly, the Island Resource Allocation (***IRA***) hypothesis was developed and posits that 'the palatability of a plant to invertebrate herbivores is proportional to the geographic range of the plant'. The basis for the ***IRA*** hypothesis proposes a redefinition of the fundamental ecological principle of the species: area relationship. Islands, or similarly geographically constrained ecosystems, which support lower biodiversity, have impoverished trophic levels and consequently have weaker top-down regulation of herbivores by natural enemies. The ***IRA*** hypothesis argues that island ecosystem stability is achieved through the bottom-up process of plant defence.

The ***IRA*** hypothesis was tested intra-specifically using bioassays using painted apple moth in which larvae were offered foliage of specimens from naturally discontinuous populations of *Nothofagus truncata*. The results supported the hypothesis in that the smallest populations of *N. truncata* exhibited the greatest resistance to the defoliator. The ***IRA*** hypothesis and a demonstrated mechanism for a differential resistance in *Nothofagus* species could resolve a number of enduring debates in ecology. Habitat area appears to explain the relative strengths of top-down and bottom-up regulation of herbivores. It also predicts the strengths of reciprocal evolution within the geographic mosaic of co-evolution and highlights the influence of biodiversity in invasive ecology. It may also help to resolve the contentious and extremely relevant debate of the role of biodiversity in ecosystem function.

Keywords

Plant defence, *Nothofagus,* insect: plant interaction, leaf nitrogen, co-evolution, biodiversity, resource allocation, island biogeography, ecosystem function.

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Chapter 1

Island plants and their invertebrate defoliators: red-shift ecology

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" *..predictive calculations are exponentially hard. The best that one can do is to watch and see how they [complex systems] evolve*" Davies 2005

Introduction

Islands, as spatially constrained ecosystems, are profoundly interesting places in which to examine evolutionary patterns and community processes (Spiller and Schoener 1995, Whittaker 1998, Brown and Lomolino 2000). Their isolation and simplicity provide natural 'Ecotrons' in which to seek an understanding of the role of biological diversity in the functioning of ecosystems. The entrenched theory of island ecology (Macarthur and Wilson 1967) suggests that the continuous immigration and extinction of species on islands results in a dynamic equilibrium of constant species turnover. Not surprisingly it has become axiomatic to represent the simple island ecosystems as particularly susceptible to the loss of endemic biodiversity following invasion by continental biota (Williamson 1981, Paulay 1994, Primack 2002). However, the reality may be somewhat different (Mueller-Dombois 1975, D'Antonio and Dudley 1995, Brown and Lomolino 2000)) and unfortunately, the complexity of even simple island ecosystems defies predictions for new species' interactions.

The complexity of ecological systems is considered virtually incalculable (Fretwell 1987, Polis and Strong 1996, Davies 2005) and can produce widely divergent outcomes from very similar starting points. While ecology has advanced to a stage where it can provide plausible explanations for the divergence, it is woefully inadequate in predicting them. This led to an admission (Lawton 1999), that despite 150 years of deductive studies of population and community ecology, very few 'rules' have been identified that allow predictions of ecological scenarios to be made. May (1997) also lamented our lack of understanding of the way the biosphere operates, but noted that spatial considerations may be important in understanding multi-trophic processes and the way ecosystems function.

Spatial considerations support one enduring 'rule', which is possibly the strongest empirical generalization in community ecology (Holt et al. 1999). Biodiversity (considered here as the number of species) can be expected to increase with habitat area. This species-area relationship (SAR) was first noted in 1854, and first realised as a theory of island ecology by Munroe in 1948 (Brown and Lomolino 2000). SAR has been reviewed by Strong et al. (1984) and Price (1997), who concluded that the confounding components of time, isolation, regionalism, habitat complexity and population size, often bedevilled its explanation. These issues have been delightfully teased out by Rosenzweig (1995) who considered that species are niches for other species - along the lines of the ‘frequency of exposure’ hypothesis, developed by Southwood (1961), to explain the larger number of insect species on more widespread trees. Species assemblages, such as trees and their associate insects, define communities and the complex and complementary interactions between their species describe how communities function (Fukami and Morin 2003).

Plants and their associated insects represent two of the most diverse lineages of the Earth’s eukaryotic biota (Agrawal and Fishbein 2006). This suggests that they must be involved in pivotal ecosystem processes. Despite initial scepticism (Hairston et al 1960, Strong et al. 1984, Crawley 1989, Jermy 1993) insects have been shown to be the most influential of plant herbivores (Bigger and Marvier 1998) and capable of affecting plant diversity and ecosystem function (Marquis 1992, Mulder et al. 1999, Frost and Hunter 2004). The influence of insects is now considered to be at least as great as that of competition between plants (Buckland and Grime 2000). Just how insects and plants interact has been a very productive line of research. However, even at a species-to-species level, current predictions of insect-plant interactions are plagued by exceptions (Stamp 2003), which is not helpful when we try to understand interactions within multi-species assemblages of the genetically variable populations which make up communities.

Traditionally, food webs have been used to describe communities. The garnering and allocation of resources for growth, reproduction and defence are the primary occupation of all living organisms (Charnov 1991, Herms and Mattson 1992, Hunter et al. 1992, Silby 1997). Eating and being eaten are major evolutionary pressures and food webs of various qualitative and quantitative designs have been used as a method of describing complex community processes (Hairston, Smith and Slobodkin1960 (hereafter-HSS), Fretwell 1987). Understandably there is a dearth of empirical food web data that can be used to realistically model the complexity of actual multi-trophic interactions (Grange & Brown 1997, Polis and Strong 1996). However, a broad regulatory role has been ascribed to food webs in complex communities to explain why the bulk of plant biomass is not consumed by insect herbivores. The HSS ‘Green World’ hypothesis proposed that in tri-trophic communities, plant biomass was maintained through the top-down regulation of the populations of herbivores by their natural enemies. HSS implied that all plants had the potential to be grazed to extinction and that plant defences did not account for the persistence of vegetation. The success of biological control programmes that release parasites, parasitoids, predators and pathogens to control pestiferous plant feeders is often cited as an example of the regulatory top-down process. However, the Green World hypothesis ignored the demonstrable ‘greening’ effects of plant defences, which are assumed to have evolved as a bottom-up food-limiting reaction to the depredations of herbivores (White 1978, 2005).

It was recognized that both top-down and bottom-up processes occur in nature, but that the relative importance of each varied from habitat to habitat (Power 1992, White 1993). The Fretwell-Oksanen solution to resolve variations in trophic dynamics (Fretwell 1977, 1987, Oksanen et al. 1981, Oksanen 1990) stated that the strength of top-down regulation increased with habitat productivity. However, exceptions are apparent (Fretwell 1987, Schädler et al. 2003) and Walker and Jones (2001) acknowledged the lack of consensus and the dearth of empirical analyses of the relative strengths of top-down and bottom-up forces in terrestrial ecosystems. Unfortunately, both processes are extremely relevant to, if not the crux of the current debate of the role of biodiversity in ecosystem function (BD/EF) (Fraser and Grime 1997, Schmitz et al. 2000, Cameron 2002, Duffy, 2002).

Both top-down and bottom-up processes are considered to regulate herbivore abundance. Regulation implies negative feed-back mechanisms, and while relatively rapid density dependent mechanisms may drive the top-down regulation of herbivore populations, bottom-up processes work by exclusion and often involve a slow co-evolutionary response. Co-evolution is the reciprocal evolutionary interaction between organisms. Both top-down and bottom-up processes undoubtedly invoke some degree of co-evolution, but the co-evolution between plants and insects is by far the most recognized example.

In the interaction between plants and insects, the selection imposed by foliage loss caused by phytophagous insects results in the evolution of plant defences. This development of plant resistance results in a reduced herbivore fitness and the generation of counter-resistance in the herbivore, which consequently leads to another co-evolutionary cycle. Although it has often been argued that phytophagous insects are too rare in natural systems to evoke any evolutionary response (Strong et al. 1984, Bernays and Graham 1988), the empirical evidence supporting the counter-evolution by insects to plant resistance is overwhelming (Rausher 2001) and there is a belief that the co-evolutionary process, which can also be applied to plant pollination and seed dispersal, has generated much of the Earth's biodiversity (Erlich & Raven 1964, Thompson 1994).

However, there is considerable evidence to show that the co-evolution of species' interactions is geographically variable (Gomulkiewicz et al. 2000, Thompson and Cunningham 2002). This variability has been conceptualised as a geographic mosaic of co-evolutionary 'hot spots' and 'cold spots'. Hot spots are said to occur where close reciprocal evolution takes place between two species, whereas cold spots reflect areas of neutral or ambivalent co-evolution. Thompson (1994, 1997, 2005) argues that the dynamics of species interactions are driven by selection mosaics. However, although complex patterns of phenotypic selection among habitats have been recorded, he acknowledges that predictions of the distribution of co-evolutionary selection are unknown.

The exposition of plant defences against insect herbivores has been an extremely interesting field of research for the last 50 years. However, and possibly as a result of the reductionist principles that have served other sciences so well, predictions for the occurrence of plant defence have resulted in a 'quagmire' of hypotheses (Stamp 2003). It is recognized that evolutionary changes can occur in stable abiotic environments as a result of the dynamic interactions between organisms within a community –the Red Queen effect (reviewed in Via 2001), but Stamp (2003) argues that for the development of a reliable theory of the co-evolution of plant defence, we need an explanation that takes all biotic and abiotic interactions into account.

Understandably, given the primacy of insect-plant interaction in terrestrial food webs, most hypotheses view the plant as the principal player and a 'phytocentric' view prevails among the most prominent hypotheses (Price et al. 1980). The Optimal Defence Hypothesis (ODH) holds that plants produce and allocate defences to maximize fitness. There is an assumed metabolic cost for that defence and the evolution of the defence should be a compromise between the risk of herbivory and its metabolic cost. The ODH requires that 1.there is genotypic variation in defence within a plant population; 2.that herbivory is the primary selective force for the defence; 3. that the defence reduces herbivory and 4. the plant fitness is increased. The defence in question may be qualitative, quantitative, constitutive, induced, or any combination of these, and overall there is a wealth of data to support the above ODH contentions (Stamp 2003). Key issues in testing the hypothesis are the estimation of the probability of herbivory and understanding how plants evolve a balance of defence against numerous herbivores while optimizing their own growth and reproduction.

Feeny's (1976) Apparency Hypothesis (AH) offers a solution to the issue of probability by proposing that long-lived, 'apparent', plants would need to allocate quantitative broad-spectrum defences against the multitude of insect herbivores they would encounter across their geographic range. Southwood's (1961) illustration of the positive correlation between tree species geographic range and their herbivore load gave credence to the hypothesis, which also gained some experimental support from the bioassays of (Edwards et al.1984) and the demonstration of many quantitatively defensive plant compounds (Harborne1977). Although there are many contradictory examples to the AH (Fox 1981, Coley et al. 1985, Stamp 2003) it has gained considerable acceptance, especially with respect to plant phenolics (Forkner et al. 2004).

The Environmental Constraint Hypothesis (ECH) attempted to explain the second issue of the balance of plants' resources between growth, reproduction and defence, through the availability of photosynthates (carbon) and soil nutrients, or plant nutrient reserves (Bryant et al. 1983, Toumi et al. 1988). An excess of photosynthates and nutrients necessary for growth and reproduction was assumed to allow some allocation to defence. As nitrogen is usually the limiting nutrient, the C: N balance of a plant was thought to determine the production of non-nitrogen- (e.g. saponins, quinones, terpenes etc) or nitrogen- (alkaloids, peptides etc) based defences (Tuomi et al. 1988). However although the hypothesis highlighted the potential influence of resources, it was awash with exceptions and complications and was superceded by a similar, but more pragmatic growth hypothesis. The Coley et al. (1985) Growth Rate Hypothesis (GRH) suggested that there was a negative correlation between inherent plant growth and the plant's allocation to defence; *.i.e.* slow-growing plants should be better defended than fast growers. It assumed that plant growth rate was determined by the availability of resources in the plant's preferred habitat and those slow-growing plants should have lower levels of herbivory because they invest more in defence to protect their meagre resources. Latterly this line of thinking has been modified to include ECH in a Latitudinal

Defence Gradient (LDG) (Dyer and Coley 2002) to explain an apparent increase in defence allocation in fast-growing tropical plants.

There are variations on the growth-resource-defence theme (e.g. Herms and Mattson 1992, Wise and Abrahamson 2007), but these and the GRH, ODH, ECH and LDG are all riddled with exceptions and, despite the obvious potential to unravelling the way ecosystems function (not to mention the benefits to primary industries and biosecurity agencies), it has been suggested that the development of an over-arching predictive theory of plant defence is an unrealistic expectation (Berenbaum 1995, Stamp 2003).

In summary, we have a hugely complex biosphere in which interactions between the main players, plants and insects, occur. We can elucidate some of these, but other than basic fundamentals, accurate predictions for these biological interactions are likely to be exponentially hard. As an added factor, we know that the biosphere may be entering a phase of unprecedented change which will undoubtedly decrease the biodiversity responsible for these interactions (Eldrige 1998, Purvis et al. 2000). We know something about the causes of extinction but we know very little about the consequences. There is a vague suspicion that, despite models to the contrary (May 1973, Pimm and Lawton 1978), ecosystems with more biodiversity are more stable and more efficient, but we are unable to predict outcomes for even the simplest systems. The current biodiversity-ecosystem function (BEF) debate highlights the urgent need to understand the contribution of biodiversity to ecosystem stability.

It is possible that we have over-stressed the role of plants in the functioning of ecosystems. Although plants are the primary producers, and the phytocentric view that pervades plant defence hypotheses is understandable; plants do reside in communities, each with different physical constraints and biological complexity. Many radically different communities exist and appear stable. There may be community ‘quantum’ laws that are bent to reflect the relative strengths of their inhabitants.

The anathema of the reductionist approach to investigation is to accept that additional laws or organizational ‘principles’ may emerge from complexity. Macroecology (Brown and Maurer 1989) has emerged in recognition of the inertia that ecosystem complexity has inflicted on ecological research. In almost Darwinian fashion, it attempts to identify patterns in the allocation of food and space among species in complex assemblages that have accrued over geographical and evolutionary scales. It recognizes that communities assemble according to the individual properties of their component species. The species assemblages may be almost random (Hubbell 2000), but their interactions, structure and define communities.

Interactions within communities are not necessarily stable over time. Invasion and habitat fragmentation can result in the variation of species diversity and could significantly alter species interactions despite their common origin (Leach & Givinish 1996, Didham et al. 1998). However, the possible effect of evolution on food web structure has not been greatly explored since Pimm (1982) stated 'How evolution affects the functions of multi-species systems and further restricts their possible food web shapes is uncertain. It is likely to remain that way for some time' (p193)

The study reported here primarily investigates the interaction between the climax forest species of *Nothofagus* and naïve insect folivores. *Nothofagus* is the dominant cool-temperate forest tree genus of the Southern Hemisphere, circum-Pacific, landmasses. The trees are long-lived, with notoriously poor dispersal abilities (Preest 1963- but see Knapp et al. 2005), and typically form virtually mono-specific, even aged stands in cool montane habitats. From a common east-Gondwana locale, the genus has been fragmented, by continental drift and/or long-distance dispersal, over the last 80MY and now comprises some 35 species endemic to the landmasses of Australia, New Zealand, South America, Papua New Guinea and New Caledonia. Paleopollen data indicate that the subgenera of *Nothofagus* were widespread and diversified before the relevant landmasses became separated and that the current distribution of species represents the result of substantial sympatric extinction and speciation (Linder & Crisp 1995). The extant forests are in comparatively pristine condition and, as an iconic example of biogeography, the ecology and associate insect fauna of *Nothofagus* is reasonably well known (Veblen et al.1996, McQuillan 1993, Quiroz et al. 1998, Russell et al. 2000).

Nothofagus could be considered the foundation species (*sensu* Dayton 1972) of a common community that was naturally geographically fragmented over evolutionary time. Whether by vicariance or long-distance dispersal (Trewick et al. 2007), the resulting extant fragments developed with varying degrees of complexity that were dictated by differences in the spatial dimensions and the isolation of their respective habitats. Almost serendipitously the study investigates the role of biodiversity in ecosystem function, while avoiding the criticism levelled at the Biodepth-type manipulations of contrived communities that have been enlisted to resolve the BD/EF debate (Tilman 1996, 1999, Grime 1997, Tilman et al. 1997, Wardle et al. 2000, Loreau et al. 2001). The approach is pretentiously analogous to Hubble's red-shift investigation, in avoiding the reductionist approach to an unfathomable complexity [of ecosystems] by demonstrating a consequential pattern of ecosystem function across spatially distinct communities.

Thesis aims

The initial aims of this research were to assess the risk alien invertebrate defoliators could pose to the New Zealand flora, and to provide a plausible explanation of the results. The study uses bioassays of polyphagous defoliators which are naïve the NZ flora to assess the degree of plant defence, primarily in species of *Nothofagus* endemic to different landmasses. Foliage for the bioassays was taken from trees growing in common garden situations. An explanation for the results is proposed, and then tested, using a single species of *Nothofagus*. A possible mechanism of the resistance within *Nothofagus* is investigated and the research conclusions, which remarkably are at odds with accepted plant defence and biogeographic theory, offer a testable hypothesis for the ecography of plant defence and the role of biodiversity in the functioning of ecosystems.

Thesis outline

There are seven chapters to the thesis. The first provides background in an attempt to provide some cohesion for the diversity of the others.

Chapter two describes and reports on the numerous bioassays which were undertaken as risk assessment studies of invasive alien defoliators which are perceived threat to the NZ flora. The bioassays were conducted in France and New Zealand over the period 2002-2004. The relevance of larval growth rate, the main parameter utilized to measure plant defence in these bioassays, is expounded in the third chapter. Chapter four records the research undertaken in 2006 in which foliage of a selection of the plants used in the original bioassays, was analysed to identify a potential explanatory variable of larval growth rate.

The conceptual model described in chapter five is an expansion of a publication to explain the bioassay results of chapter two. The model is then tested using a species specific example in chapter six.

The final chapter takes on the task of discussing the results in terms of current ecological theory, while offering a testable explanation of the role of herbivory in the biosphere.

Chapter 2

The Resistance of the New Zealand Flora to Alien Invasive Defoliators

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"*You can observe a lot just by watching*." Yogi Berra

Abstract

Invasion ecology is an inexact science supported by largely untested hypotheses. Not surprisingly it lacks predictive reliability as to the identity of invasive species and/or the vulnerability of ecosystems to those species. Island ecosystems are often perceived as vulnerable to invasion, but in bioassays, the flora of New Zealand proved to be resistant to recognised invasive, polyphagous, continental lepidopteran species. Furthermore this resistance could not be convincingly attributed to the high endemicity of the flora.

Introduction

The invasion of indigenous habitats by alien species is a global phenomenon with potentially serious ecological consequences (Vitousek et al. 1996, Fritts and Rodda 1998, Pimental et al. 2000). Various 'biosecurity' agencies and protocols have been created to mitigate the risk, yet despite decades of research, few reliable generalisations regarding the predictability of the establishment of alien species have emerged to support these agencies (Williamson 1996, Davis et al. 2001, Kennedy et al. 2002). The most commonly cited predictors of invasive species are a proven history of invasion and/or propagule pressure (Kolar and Lodge 2001). A generalisation for the invasive process is the ineloquent statistical '10s' rule; 10% of dispersing alien species will survive, 10% of those will establish in the new environment and 10% of the establishing species may achieve naturalisation. This rule offers no prediction as to the identity of successful colonisers, or the habitats that are most likely to be susceptible to their establishment.

It has become axiomatic to represent oceanic islands as simple, fragile ecosystems, which because of their evolution in isolation, are particularly susceptible to the loss of endemic biodiversity following invasion by continental biota (Whittaker 1998, Primack 2002). This premise is based in part, on Elton's (1958) seminal work on invasion ecology, which stressed the vulnerability of simple ecosystems to invasion, and partly on the over-emphasis of species turnover within the equilibrium theory of island biogeography developed by MacArthur and Wilson (1967). The appealing logic of both theories is not well supported in practice (Strong 1979, Davis et al. 2001, Wilson 2001). More often than not anthropogenic disturbance is a major cause of species invasions and indigenous species extinctions and D'Antonio and Dudley (1995) conclude that island habitats are not inherently more easily invaded than their continental counterparts.

New Zealand is continually bombarded by exotic invertebrate defoliators riding cyclonic meteorological events; particularly northwest storms originating in Australia (Harding 1971, Ramsay 1971, Fox 1978, Kay 1980). Typically these events deposit insects along the western coastal prominences (Northland, Taranaki, Nelson and Fiordland) of New Zealand within 48 hours of leaving Queensland. The flow of migrants along this flight path to New Zealand has been demonstrated by Holloway (1996) who recorded 38 non-resident Macrolepidopteran species over a 12 year period of light trapping on Norfolk Island. On arrival in New Zealand migrant Lepidoptera may flourish for a few seasons but usually disappear following inclement weather. Others may be more persistent (e.g. *Spodoptera litura*, the tropical armyworm) and, because adults of vagile species rarely carry parasitoids, they may require management through chemical or biological control programmes. Natural enemies that do arrive co-incidentally with migrants may fail to establish through a lack of alternate hosts and/or Allee effects that drive small founding populations to extinction.

The natural influx of arthropods is compounded by others – principally from the Northern Hemisphere – whose dispersal is assisted by trade. The estimated 2000 alien invertebrate species that have naturalised in New Zealand (Anon 1997) comprise 90% of the country's invertebrate pest species – largely because they are associated with primary production industries that are based on Northern Hemisphere plant and animal species. Of the 216 introduced forest and timber insects, only about 12% have been recorded from living indigenous forest trees and shrubs (Bain 2003). None, with the exception of the two *Eriococcus* species, have caused significant damage to indigenous host plants. The two species that did were Australian eriococcids that were essentially attacking their natural hosts, *Leptospermum scoparium* and *Kunzea ericoides* (both occur naturally in Australia), in temporarily enemy-free space.

It is possible that the unexpected resistance of the New Zealand flora to alien invertebrate defoliators may be a reflection of its high endemism. Not only is the Southern Hemisphere flora is distinctly different from that of the Northern Hemisphere, but insular floras are also characterised by high rates of endemism (Whittaker 1998). Insects, even polyphagous species, have host preferences, usually for phylogenetically related plants (Erlich and Raven 1964, Jaenike 1990, Mitter et al. 1991, Futumya et al. 1995, Kopf et al. 1998, Pogue and Schaefer 2007). The very high endemicity of the New Zealand flora (Allen 1982) may provide a significant taxonomic hurdle for invasive alien species.

In the past, the pace of trade and a seasonal asynchrony may have limited the arrival and establishment of Northern Hemisphere exophytic insects in New Zealand. More recently the containerisation of cargoes and a greater emphasis on more regional SE Asian trading partnerships has coincided with the establishment of a number of Lepidopteran forest defoliators (Table 1). These insects are principally polyphagous Macrolepidoptera – typical super-tramp *r*-selected generalists (Diamond 1974). They are recognised invasive forest pests (Stamp and Casey 1993, Price 2003) and would be expected to devastate a naïve insular flora.

Three invasive Macrolepioptera, the gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae), the fall web-worm, *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae) and the painted apple moth *Teia anartoides* Walker (Lepidoptera: Lymantriidae) have recently been the targets of eradication programmes in New Zealand. gypsy moth and fall web worm probably have the widest recorded host ranges of any defoliating insect species. The larvae of both species feed on over 600 species of plant world-wide and they have common hosts in a number of plant families. Although the number of recorded host plant families for the gypsy moth is larger than that of fall web-worm it is possible that gypsy moth is more demanding in the quality of its hosts. The gypsy moth is univoltine and the deleterious effect of aged host foliage is well documented (Feeny 1970). The fall web-worm, on the other hand, being multivoltine, may be less constrained, or better adapted to feed on a wider range of physiologically less salubrious diets. The painted apple moth, *Teia anartoides* is also polyphagous and multivoltine, but less catholic in its host range (Kay 2003).

The natural distribution of the gypsy moth includes most of temperate Eurasia and north-west Africa, while that of fall web worm includes most of temperate North America. In reciprocal moves, gypsy moth was accidentally released into N. America in the late 1860's, while the fall web-worm was accidentally introduced into Eurasia in the 1940's. The painted apple moth is of Australian origin. It had not established outside Australia prior to its establishment in Auckland, New Zealand in the late 1990's. All three polyphagous forest Macrolepidoptera caused considerable defoliation to forests following their establishment in novel environments.

The importance of the availability of suitable host plants is illustrated in the guidelines for assessing the susceptibility of forests to gypsy moth defoliation in the US. Evaluations are based upon the percentage basal area of oaks and other preferred host plants (Campbell 1979, Gottschalk 1993, Davidson et al. 1998). Similarly fall web worm became a pest of its favoured natural host genera, mulberry, *Morus*, maple, *Acer*, and *Prunus* in Eurasia (Ito and Miyashita 1968, Anon 1980). Painted apple moth has a preference for hosts within the Papillioneacae, but is also a pest of apple, *Malus*, and pine, *Pinus,* introduced from the Northern Hemisphere.

The endemic populations of these defoliators are capable of outbreaks but are usually regulated by competitors and suites of natural enemies, including pathogens, parasitoids and vertebrate and invertebrate predators. The depauperate biota of New Zealand lacks many equivalent natural enemies or competitors (Valentine and Walker 1991, Dugdale 1975). Lymantriids and arboreal Arctiids are conspicuously absent from the New Zealand invertebrate fauna. New Zealand's flora, although distinct, does have some plants taxonomically related to the hosts of these defoliators. If the New Zealand flora could provide adequate hosts for them, outbreaks would inevitably ensue.

The perceived threat that continental defoliators pose to the New Zealand flora evoke extensive eradication programmes whenever they are discovered here. Gypsy moth, fall web worm and painted apple moth were the targets of successful eradication programmes following their detection in New Zealand. Typically these eradication programmes are supported by cost benefit analyses, which include the experimental assessment of the risk the invader poses to the New Zealand endemic forest flora.

Although all elements of the New Zealand flora are equally valued there is particular concern for the ecologically dominant *Nothofagus* (Fagales: Nothofagaceae) because of its phylogenetic relatedness to hosts of the Northern Hemisphere defoliators. *Nothofagus* is the foundation genus of the temperate Southern Hemisphere forests. The southern beeches are the taxonomic and ecological equivalent of the beech/oak, *Fagus*/*Quercus* (Fagales: Fagaceae), forests of the Northern Hemisphere. To put the assessment of the New Zealand flora into some ecological context, the New Zealand species of *Nothofagus* were compared with those from Australia and S. America.

There are three temperate subgenera (*Nothofagus, Lophozonia* and *Fuscospora*), with the subgenus *Nothofagus* restricted to S. America. The leaf character of the Southern beech species varies considerably. Approximately half of the species are deciduous but deciduousness occurs in all three subgenera. Leaf size, thickness and texture varies from small tough coriaceous persistent leaves through to large delicate or trichomatose and deciduous.

The results of these assessments of *Nothofagus* and other elements of the New Zealand flora to gypsy moth, fall web worm and painted apple moth are recorded here.

Methods

The host risk assessments followed similar principles to those used to assess the risk of weed biological control agents destined for release in novel habitats. The geographic range of *Nothofagus* does not extend into the Northern Hemisphere and those of gypsy moth and fall web worm do not extend into the Southern Hemisphere. In effect the assessments of *Nothofagus* utilising these insect species are double-blind bioassays.

The bioassays for gypsy moth, fall web worm and painted apple moth were mechanically identical to the methods of Matsuki et al. (2001). Those of gypsy moth and fall web worm were undertaken in the same quarantine facility and conditions, at CSIRO-Europe, Montpellier, France, while the painted apple moth bioassays were undertaken in the quarantine facility at NZFRI, Rotorua, New Zealand.

The bioassays took the form of no-choice larval feeding trials. No-choice feeding trials with naïve larvae are a recommended method of risk assessment of potential host plant species, although they have a tendency to over- estimate host acceptance (Hill 1999). The method was particularly relevant for the two Lymantriids as both have apterous females and host plant choice is made by dispersing first instar larvae. Females of the fall web worm normally oviposit large egg masses on the larval host plant (Yearian et al. 1966).

Newly eclosed first instar larvae were caged with cut foliage of one plant species in a two-chamber containment system. This system kept the stem of the plant specimen in a lower (595 ml) water-filled container, while allowing a dry enclosed upper (395 ml) arena around the foliage for the test larvae.

Ten larvae were released into the upper arena and when the majority were in the fourth instar they were equally divided into two identical arenas to avoid overcrowding. Five replicates were run for each plant used and the whole trial was arranged as five randomised blocks within a quarantine facility.

Foliage was sourced from gardens and arboreta. Foliage samples were taken from a sunny quarter of the canopy at about 1-3m above ground level. Foliage was placed in Ziplok® bags with damp paper towels and couriered, usually over-night, in insulated Eskies® with ice packs. (The DHL invoices were in excess of $14000 for the 2002 trials.) At the laboratory foliage was fed to insects as required and surplus foliage was held at 4º C.

Gypsy moth bioassays - 2002

Because of the uncertainty as to the integrity of the species (Roy *et al* 1995), gypsy moth is considered a biosecurity risk throughout the world and so, despite its occurrence in France, the trials reported here were undertaken in a quarantine glasshouse at the CSIRO European laboratory, Montpellier, France, utilising natural lighting, day-length, and minimum temperatures, but with a controlled maximum temperature of 22 ±2°C.

Foliage of a mature oak tree, *Quercus petraea*, close to the laboratory, was used as a control. It was cut at 7-10 day intervals and treated in the same manner as the test foliage.

The Insects

For the principal gypsy moth trial larvae were reared from egg batches of the ‘New Jersey’ strain, obtained from the USDA/APHIS Otis Methods Development Centre gypsy moth artificial rearing facility, Massachusetts, USA. *i.e.* a European strain of gypsy moth reared on artificial diet and commonly referred to as the New Jersey strain (Tanner *pers. comm.*). To limit viral infection, eggs were separated from their individual masses, combined, soaked for one hour in 10% formalin, and then rinsed with water for two hours. The eggs were then caged on filter paper at 20ºC till eclosion.

Field collected strains were sourced from Poland and Austria. Egg batches from Poland were supplied by Iwona Skrzecz, Warsaw University. Larvae had already started to emerge from these egg masses by the time they arrived at the CSIRO laboratory, so it was not possible to sterilise them to rid them of viral contamination. These eggs had been collected from the forest near Warsaw, which had recently had an epidemic of gypsy moth. The likelihood of viral infection of these egg batches was considered to be high.

The foliage

The foliage for the bioassays was sourced from the private gardens and arboreta listed in Tables 1, 2 and 3. *Nothofagus* is relatively common large arboreta held 8 -12 species. A total of 15 of the 17 taxa from the three temperate subgenera of *Nothofagus* were available (Two specimens *N. nitida* proved to be *N. dombeyi*, and the previously used specimen at Hilliers (Matsuki et al 2001) had died. The first successful planting of *N. gunnii* in Europe took place at Wakehurst in 2005 – it was stolen two days later!). All trees sampled were mature specimens. Foliage samples were taken by the curator or staff, as requested, from a common set of instructions. Herbarium specimens of the plants used were taken back to Forest Research, Rotorua, for verification by C. Ecroyd.

The bioassays

Trials of plant species other than *Nothofagus* were started on the 19th May for the Polish strain of gypsy moth and on the 6th June for the New Jersey strain. The two trials ran until all but the larvae on the oak control foliage had died; 16 and 20 days respectively.

There were insufficient numbers of Polish larvae to include in a trial with the full complement of *Nothofagus* species. An extensive trial of *Nothofagus* species using the ‘New Jersey’ strain of gypsy moth started on the 23rd May and ran until early August. For this trial 106 site: species combinations of foliage were run with over 5000 larvae. A maximum of twelve site-specific replicates used for some species. Occasionally, as late instar larvae consumed large amounts of foliage, logistical problems with foliage supplies meant that a few site: species combinations were compromised. The affected larvae were fed only one species, but the foliage came from a number of sites. However the vast majority of foliage fed to those larvae came from the named site.

For all trials larval mortality, development time, pupal weight (3 days after pupation) and sex were recorded for each treatment.

Miscellaneous Observations

Other observations made during the course of the trials included the determination pupal weight loss recorded for one early cohort of female pupae to determine the best time to record this parameter.

The potential fecundity was recorded by egg counts from the dissection of a number of emerging females throughout the trial.

Statistical Analysis

Simple linear regression analyses were used to identify correlations between male and female growth rates, potential fecundity and female pupal mass and larval survivorship and larval growth rate. ANOVA followed by LSD test was used to identify species differences in the growth rate of larvae supported by *Nothofagus* species.

TABLE 2.1

New Zealand indigenous under-story plants trialled and their origin in Europe

Locality and acronyms are: Scotland, The Royal Botanic Garden Edinburgh, (RBGE); England, Wakehurst Place – Kew Gardens Arboretum, (WK), Hilliers Arboretum (HA); Ireland, Mount Congreve Estate (MC), Mount Stewart (MS), Mount Usher Garden (MU), Fota Estate (F), Ilnacullin (Ilc), Earlscliffe (Ecl), Dublin Botanic Garden (DBG), John F Kennedy Arboretum (JFK), Rowallane Garden (RW), Castlewellan (CW), Talbot Garden Malahide, (Mal); France, Arboretum National de Barres (ANB), La Roche Fauconniere (AlF), Antibes Jardin Botanique (Ant)

Plant species	**European source**
Pseudopanax laetus	CW
P. arboreus	MS
Pittosporum eugenoides	MS, Ant, Ant
P. eugenoides 'varigatum'	CW
P. revolutum	DBG
P.tenuifolium	Ecl, Mal, CW
P.tenuifolium ssp. colensoi	Ant, Mal
P.tenuifolium 'Garnettii'	Mal
P. bicolor	Mal
P. ralphii	Ant
Olearia cheesemanii	MS
O. lineata	DBG
O. paniculata	Ecl
Fuchsia exortica	MS
Pseudowintera colorata	CW
Grisilinia littoralis	MS, Ecl
Sophora tetraptera	DBG
Metrosideros umbellata	Ilc
M. robusta	Ecl
Myoporum laetum	Ecl
Hebe venustala	DBG
Hoheria sexstylosa	CW

TABLE 2.2

New Zealand indigenous gymnosperms trialled in bioassays, and their originin Europe

(Locality and acronyms as for Table 2.1)

Plant species	**European source**
Dacrydium cupressinum	Ilc
Dacrycarpus dacrydioides	CW
Agathis australis	Ilc

TABLE 2.3

The 13 taxa of Nothofagus used in bioassays; their origin and their source of supply in Europe

(Locality and acronyms as for Table 2.1)

***Nothofagus* species**	**Origin**	**European source**
alessandri	S. America	MC, AlF
alpina	S. America	MS,Ilc,WK,ANB,RBGE,JFK,MU,HA,AlF,RW
antarctica	S. America	MS,Ilc,WK,DBG,ANB,Ecl,Rbge,JFK,MU,HA,AlF,RW
betuloides	S. America	MS,Ilc,WK,RBGE,JFK,MU,HA,AlF
dombeyi	S. America	MS,Ilc,MC,WK,F,DBG,JFK,MU,HA,AlF,RW
glauca	S. America	WK,AlF,HA
obliqua	S. America	MS,MC,WK,F,DBG,ANB,RBGE,JFK,MU,HA,AlF,RW
pumilio	S. America	MC,WK,RBGE,MU,RW
cunninghamii	Australia	MS,Ilc,MC,WK,F,DBG,JFK,MU,HA,AlF,RW
moorei	Australia	Ilc,MU
fusca	New Zealand	MS,Ilc,MC,WK,CW,RBGE,JFK,MU,HA,AlF,RW
menziesii	New Zealand	MS,Ilc,MC,WK,F,RBGE,JFK,MU,AlF
solandri var. *solandri*	New Zealand	F,MU,HA,AlF,RW
solandri var. *cliffortioides*	New Zealand	MC,WK,RBGE,RW
truncata	New Zealand	MU

The fall web-worm bioassays - 2004

No laboratory colonies of fall web worm could be located. Egg masses of fall web worm are difficult to locate in the field and the larval webbing of host foliage is usually the first prominent indicator of a population. The lack of a collectable spring generation in Europe meant that although trials were mechanically identical to the gypsy moth trials above the trials for the fall web worm were more constrained temporally, so that they formed a collage of a number of different instars of different provenance.

The fall web worm is not dimorphic and the pupae are considerably smaller than those of gypsy moth and weight loss during pupation is assumed to be minimal. Therefore pupae of the fall web-worm were weighed on the day they pupated.

The insects

Fall web worm for the bioassays were received as field collections of early instar larval colonies and laboratory-reared pupae. Larvae of fall web-worm were sourced from Hungary, Slovakia and USA (West Virginia).

Early instar larvae of fall web-worm are small and gregarious. The susceptible to high mortality if they are not transferred to host plants in sufficient numbers and with webbing. When dealing with these instars, groups of approximately 20 larvae were transferred with webbing to the host plant. Trials with later instars utilised five larvae/host plant replicate.

The foliage

Arboreta in UK and Ireland, and plants from a commercial botanical supplier in France, provided the foliage used in the trials (Table 2.4). The ecological integrity of commercially available species was in doubt and it was presumed they had been subjected to considerable anthropogenic selection. When specific *Nothofagus* foliage supplies were interrupted, foliage from Wakehurst (WK) was used as the default foliage. The identification of plants not used previously, was verified by the staff of the Forest Research herbarium.

Mulberry, *Morus* sp. sourced from local trees (Ville de Clapiers) was used as the control. (For the sake of simplicity the identity of the host plants in Tables and Figures is often presented as the first syllable of each Latin binomial).

The bioassays

a. The Hungarian larval collection arrived at the laboratory on 28th June. The late instar larvae were reared to adults on *Morus*. F1 neonates from these adults were used in an unreplicated, four-day, no-choice feeding trial. The trial was curtailed because of the pre-determined contractual time-table.

b. The US larval collection on black cherry, *Prunus serotinia*, arrived 1st July. First/second instar larvae were used in a limited no-choice New Zealand indigenous plant feeding trial which ran for 30 days. Third/forth instar larvae were used in a broader host plant feeding trials as five larvae/host plant replicates. The frass produced in these trials was oven dried to a constant weight at 70°C and weighed, to provide a quantitative measure of feeding.

c. The Serbian larvae arrived on 6th July, collected from mulberry, *Morus*. Third/forth instar larvae were used in replicated New Zealand indigenous plant, no-choice feeding trials and expanded *Nothofagus* trials of five larvae/host plant replicate. Frass from these trials was treated as above.

Statistical Analysis

Simple linear regression analyses were used to identify correlations between male and female growth rates.

TABLE 2.4

The contributing arboreta and the plant list of foliage received for trials

(RBGE- The Royal Botanic Garden Edinburgh; WK -Wakehurst Place; MTS- Mount Stewart; ROB- Earlscliffe; JFK- John F Kennedy Arboretum; ROW- Rowallane Garden; CW- Castlewellan;Bot- Botanic Centre de Jardin)

Species	**RBGE**	**WK**	**JFK**	**ROW**	**MTS**	**Bot**	**ROB**	**CW**
Nothofagus alpina	✓	✓	✓					
N. antarctica	✓	✓	✓	✓			✓	
N. betuloides	✓	✓	✓		✓			
N. cunninghamii		✓	✓		✓			
N. dombeyi	✓	✓	✓	✓				
N. fusca	✓	✓	✓	✓	✓			✓
N. glauca		✓						
N. menziesii	✓	✓	✓					
N. moorei		✓						
N. obliqua	✓	✓	✓	✓	✓			
N. pumilio	✓	✓		✓				
N. solandri var. *solandri*	✓	✓		✓				
N. solandri var. *cliffortioides*		✓		✓				
Brachyglottis greyi						✓		
Coprosma rham			✓					
Corokia buddleoides							✓	
Dodonea visocsa						✓		
Griselinia littoralis			✓		✓		✓	
Hebe venustala								
Hebe traversii						✓		
Hoheria sexstylosa								
Fuchsia exorticata					✓			
Leptospermum scoparium						✓		
Metrosideros kermadecensis						✓		
Metrosideros robusta							✓	
Olearia hectori			✓					
O. albida			✓					
O. macrodonta			✓					
O. panniculata							✓	
O. ranni					✓			
Pittosporum eugenoides					✓			✓
P. tenuifolium			✓				✓	✓
P. ralphi			✓					
Pseudowintera colorata								✓
Pseudopanax arboreus								✓
Sophora microphylla		✓						
Dacrycarpus dacrydium								✓
Podocarpus totara			✓					
P. totara halli			✓					

The painted apple moth bioassays - 2002-2005

As with the gypsy moth trials the bioassays consisted of 'no-choice' tests, where newly eclosed first instar larvae were caged with cut foliage of one plant species in a two-chamber containment system. At about the fourth instar larvae were 'thinned' to a maximum of five/pot to avoid overcrowding. Five replicates of each tree's foliage were run as five randomised blocks within the invertebrate quarantine facility at NZFRI, Rotorua, New Zealand. Trials were run at a constant 22 ± 1°C and 14 hour photoperiod.

Mortality, developmental time and pupal weight and sex, were recorded. Pupae were weighed and sexed three days after cocoon construction began and a sub-sample of weighed females was dissected to record their potential fecundity.

The insects

Larvae were supplied from a colony reared on artificial diet within the invertebrate quarantine facility at NZFRI. The colony of painted apple moth was established in quarantine at NZFRI, Rotorua, from the population in Auckland and reared on the standard gypsy moth artificial diet.

The foliage

The assays utilised foliage of local indigenous and naturalised plants. Black wattle, *Acacia mearnsii*, (Leguminales: Papillionaceae) from the Forest Research campus was the control host plant. Bioassays took place over the spring /summer so that control host quality varied. Unfortunately artificial diet, which would have provided a stable control, gave considerable variation in larval mortality when used in a non-sterile environment.

Foliage from plants grown in gardens and arboreta outside Rotorua was couriered overnight to the Forest Research quarantine facility in Rotorua. Excess foliage was stored at 4°C and remained in good condition for up to 10 days.

The bioassays

The bioassays were carried out as bench space and foliage came to hand.

- Indigenous species trials

- Indigenous Papillionaceae species trials utilised foliage from the living collection at LandcareResearch, Lincoln. The *Carmichaelia* trial was only run for the period of foliage availability. At day 13 the larvae were killed in ethanol, air dried and weighed to obtain a larval growth rate.

Nothofagus trials utilised foliage from a limited number of exotic specimens in Christchurch Botanic Garden, John Wardle's private collection, Oxford, Canterbury, Banks Peninsular provenance trial, FRI grounds, Tiniroto and Eastwoodhill arboreta, Hawkes Bay and specimens within natural forests of the Bay of Plenty. The number of specimens within New Zealand was limited but the trials did allow further testing of species under-represented in the gypsy moth trials of 2002.

Statistical Analysis

Simple linear regression analyses were used to identify correlations between male and female growth rates, potential fecundity and female pupal mass and larval survivorship and larval growth rate.

Results

The plant species assessed in the trials of each moth represented examples from about a third of the endemic shrub and tree families within the New Zealand flora. Nearly all of the New Zealand indigenous forest plants trialled failed to support larval growth of all three polyphagous continental defoliators. The growth rates for the majority of larvae that did survive on New Zealand indigenous plants were lower than those for larvae fed the control hosts and some other continental host plants. *N. menziesii* was consistently a poor host, but one specimen, from the JFK arboretum, was an acceptable host for both the gypsy moth and the fall web worm. There was a similar acceptance of S. American *Nothofagus* species for all three insects, with *N. antarctica* and *N. obliqua* consistently proving to be adequate hosts.

Gypsy moth

The New Zealand indigenous plants proved to be poor hosts for gypsy moth larvae of either strain (Tables 2.5 and 2.6), although the natural Polish population appeared more capable of feeding on the novel hosts. Only *Sophora tetraptera* and *Myoporum laetum* supported some larvae to the second instar and the larvae on *M. laetum* appeared to have eaten only the flowers of this species. All larvae placed on non-Fagales hosts were dead within 20 days.

New Zealand species of *Nothofagus* were also poor hosts for gypsy moth when compared with oak (Table 2.7). No survival was recorded for larvae fed *N. truncata* and only one out of eight *N. menziesii* specimens trialled supported some larval development through to pupation. Three out of ten *N. fusca* specimens also failed to produce pupae. By comparison, a number of the South American species were the equal or better hosts than the oak control (Fig.2.1), although larvae placed on *N. alessandri* died in the first instar. The Australian *N. cunninghamii* supported larval development to pupation but larvae on *N. moorei* also failed to progress passed the first instar.

Larval growth rates varied considerably between *Nothofagus* species, but for this dimorphic species, female larval growth rates were consistently almost twice that of male larvae (Figure 1). In subsequent analyses extrapolations from male larval growth rates were made for the two species replicates that failed to produce female pupae. Female growth rates are used in most subsequent analyses, for although males are important (Ranlin and Kokko 2007), the majority of population dynamics models place more biological relevance on female growth and survival.

Larval growth rates varied within and among *Nothofagus* species. There was an obvious species effect and the mean growth rate of surviving larvae on a species was taken as the ‘potential’ larval growth rate of gypsy moth on that species. Larval survival also varied within and among species, with some species producing very few pupae. There was a strong positive correlation ($P< 0.001$) between the potential larval growth rate and larval survival on the different *Nothofagus* species (Figure 2.2). It was impossible to attribute larval mortality to an inherent host quality or to some exacerbation of leaf character by the mechanics of the assay process. To provide an alternative measure of host quality, growth rate was adjusted for larval mortality.

$$\text{Host quality} = \frac{\text{female larval growth rate } \mathbf{X} \text{ the number of surviving larvae}}{\text{50 (the initial number of larvae)}}$$

There was a significant difference in the adjusted female larval growth rate between species (ANOVA, F 11,19 = 19.11, $p<0.0001$) and a step-wise Least Significant Difference test showed the significant differences between the growth rates of larvae on different host species (Table 2.8). There was little difference in the ranking of species quality by either potential larval growth rate or survival adjusted larval growth rate.

Larval growth rates varied within and among sub-genera and landmass origins (Table 2.8). S. American species tended to support higher larval growth rates, but host quality could vary considerably within subgenera and landmass. There was no significant difference between the two varieties of *N. solandri* so they are treated as one taxon in further discussions.

The strong positive correlation ($P < 0.01$) between pupal weight and potential fecundity can be extrapolated to estimate a threshold pupal weight of about 175mg was required for a female to replicate herself (Figure 2.3).

There was approximately a 2% loss in pupal weight during pupation, with the loss highest at the beginning and the end of the pupal period. A plateau of weight loss occurred from about day three to day eight (Figure 2.4). The mean female pupal period was 11 days and there was no significant correlation ($P > 0.1$) between pupal weight and the rate of pupal development for the small sample of pupae for which this was recorded.

TABLE 2.5

Feeding scores, after 16 days, of 'Polish' gypsy moth on New Zealand indigenous plants compared to oak

Plant species	**Feeding score (0 to +++) site1 / site2**	**Highest instar development**	**% mortality**
Pseudopanax laetus	0	1	100
P. arboreus	+	1	100
Pittosporum eugenoides	+ / 0	1	100
P. eugenoides 'varigatum'	+	1	100
P. revolutum	+	1	100
P.tenuifolium	0 / +	1	100
P.tenuifolium ssp. colensoi	0 / 0	1	100
P.tenuifolium 'Garnettii'	0	1	100
P. bicolor	0	1	100
P. ralphii	0	1	100
Olearia cheesemanii	0	1	100
O. lineata	0	1	100
O. paniculata	+	1	100
Fuchsia exortica	+	1	100
Pseudowintera colorata	0	1	100
Grisilinia littoralis	+ / +	1	100
Sophora tetraptera	++	2	100
Metrosideros umbellata	+	1	100
M. robusta	+	1	100
Myoporum laetum	++	2	100
Hebe venustala	+	1	100
Hoheria sexstylosa	+	1	100
Dacrydium cupressinum	+	1	100
Dacrycarpus dacrydioides	+	1	100
Agathis australis	+	1	100
Quercus patraea	+++	3	8

TABLE 2.6

Feeding scores, after 20 days, of ‘New Jersey’ gypsy moth on New Zealand indigenous plants compared to oak

(0 to +++ represents a relative feeding score; 0 = no feeding)

Plant species	**Feeding score (0 to +++)**	**Highest instar development**	**% mortality**
Metrosideros robusta	0	1	100
Myoporum laetum	0	1	100
Pseudowintera colorata	0	1	100
Hoheria sexstylosa	+	1	100
Olearia. paniculata	0	1	100
Grisilinia littoralis	0	1	100
Hebe venustala	0	1	100
Pseudopanax laetus	+	1	100
Pittosporum eugenoides	+	1	100
Agathis australis	0	1	100
Dacrydium cupressinum	+	1	100
Quercus patraea	+++	3	0

TABLE 2.7

A summary of the growth rate results for gypsy moth fed different species of Nothofagus
*(0 indicates no survival on this species; *mis-identified as nitida by the arboretum directly above, ALF & MU; ** extrapolations from ♂= 0.54♀ + 0.07)*

Nothofagus species

	pumilio		***antarctica***		***betuloides***		***obliqua***		***solandri***		***solcliff***		***fusca***		***glauca***		***alpina***		***cunninghammii***		***menziesii***		***dombeyi***		**OAK**	
site	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**
AIF			10.75	20.35	9.25	16.16	13.76	26.26	8.47	15.11			4.77	8.42	7.7	11.14	9.17	16.45	5.89	12.92	0	0	9.21	19.23		
ANB			8.43	15.73			9.29	19.56									7.35	16.14					10.29	20.04*		
CW													5.50	10.04**												
llc			9.53	18.40	6.82	13.12							0	0			6.2	11.41	8.69	22.47	0	0	7.71	15.66		
DBG			7.98	17.71	7.48	12.72	11.13	20.23											7.06	9.64			6.99	16.10		
HA			9.72	16.91	6.07	10.78	11.74	24.09			5.64	10.59	5.99	12.91	8.3	10.06	15.28**	28.17	8.86	14.22			7.12	15.75		
F							10.80	21.46	6.06	13.97									6.22	11.71	0	0	6.70	13.75		
JFK			9.07	15.92	8.11	15.04	12.99	20.18					0	0			7.37	13.85		11.64	5.74	14.66	8.71	17.60		
MC	10.66	14.16					12.51	20.43			6.04	11.11	0	0					5.43	11.19	0	0	7.78	11.95		
MS			12.47	19.32	11.39	17.70	12.95	26.91						14.06			6.92	14.71	5.57	13.06			7.23	17.73		
MU	10.68	12.61	8.47	16.51	11.04	13.62	9.84	24.52	7.20	12.89			4.86	11.75			8.22	14.45	0	0	0	0	8.49	20.74		
RBGE	6.86	12.20	14.17	21.09	10.47	14.65	11.80	25.92	5.79	12.38			4.02	9.49			9.39	18.72			0	0	9.18	19.13*		
Ecl			17.98	27.36																						
RW			7.75	13.22			9.31	18.23	8.13	16.02	6.49	13.61	4.14	7.83			6.44	13.74	0	0			9.39	23.64		
WK	11.29	17.92	6.61	15.85	7.68	16.02	5.71	18.02	6.30	9.99	5.56	9.71	0	0	6.1	11.17	8.36	15.99	5.33	9.76	0	0	6.30	14.47		
Mean	**9.87**	**14.22**	**10.24**	**18.20**	**8.70**	**14.42**	**10.98**	**22.15**	**6.99**	**13.39**	**5.72**	**11.25**	**3.25**	**6.77**	**7.37**	**10.79**	**6.83**	**16.39**	**5.30**	**10.60**	**0.72**	**1.83**	**8.08**	**17.34**	**8.91**	**16.05**
SE	1.013	1.30	0.93	1.05	0.64	0.70	0.64	0.93	0.44	0.61	0.48	0.84	0.82	1.85	0.66	0.54	0.83	1.63	0.97	1.89	0.72	1.83	0.34	0.90	0.38	0.64

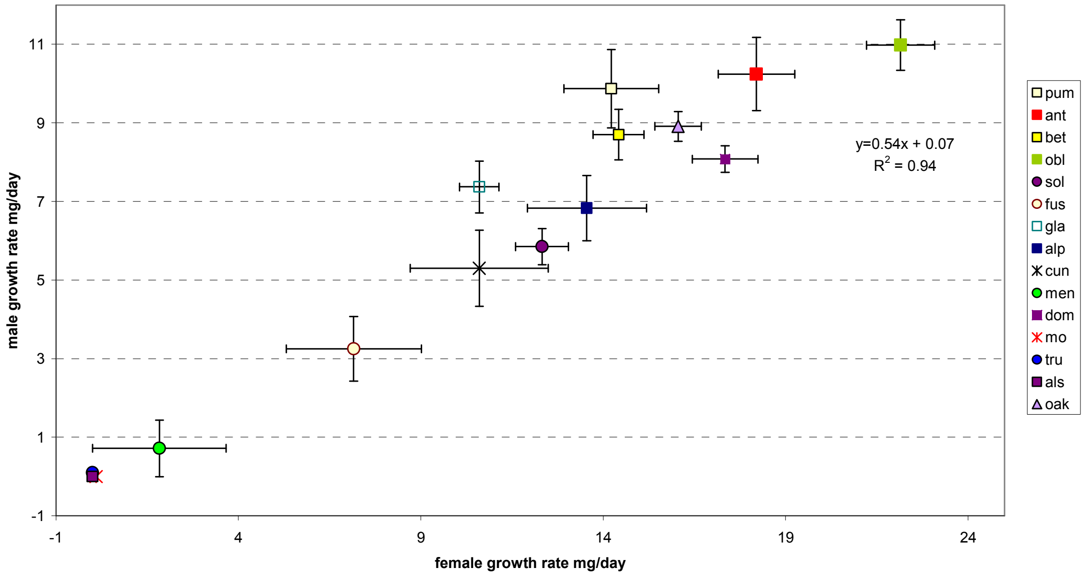

Figure 2.1. The larval growth rates of male and female gypsy moth on Nothofagus species and oak (P<0.001)

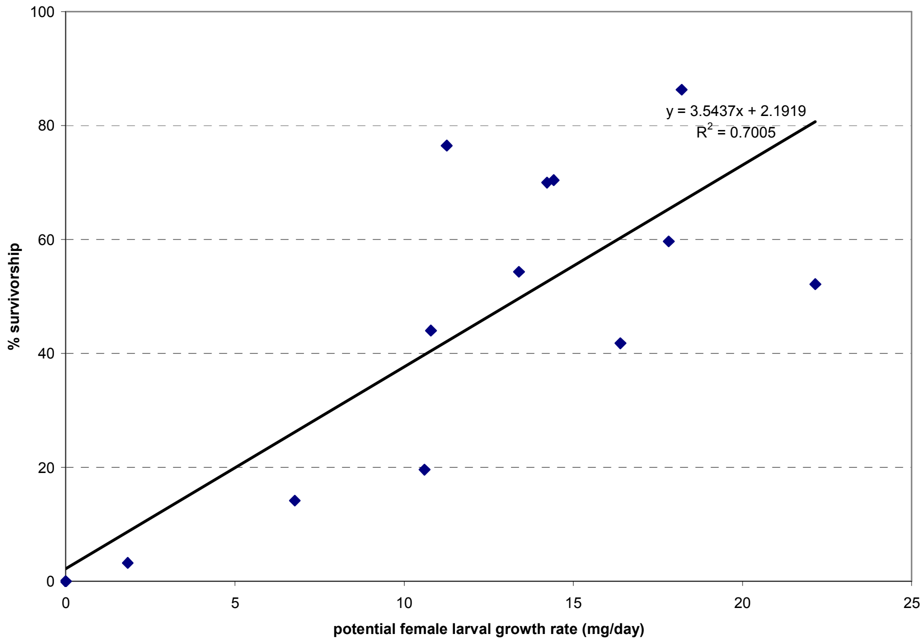

Figure 2.2. The correlation of survivorship with female gypsy moth larval growth rate when fed different species of Nothofagus (P< 0.001).

TABLE 2.8

Host plant phylogeny and origin, and mean gypsy moth female larval growth rates of surviving larvae (potential), and adjusted for mortality

– the adjusted values followed by the same letter are not significantly different (p = 0.05)

***Nothofagus* species**	**Sub-genus**	**origin**	**♀ larval growth rate (mg/day)**	
			potential	**adjusted**
N. antarctica	*Nothofagus*	S. America	18.20	15.6 a
N. obliqua	*Lophozonia*	S. America	22.15	12.6 b
N. dombeyi	*Nothofagus*	S. America	17.34	11.4 bc
N. pumilio	*Nothofagus*	S. America	14.22	10.2 bcd
N. betuloides	*Nothofagus*	S. America	14.42	9.9 bcd
N. solandri var *c.*	*Fuscospora*	New Zealand	11.25	8.6 cde
N. solandri var *s.*	*Fuscospora*	New Zealand	13.39	7.2 de
N. alpina	*Lophozonia*	S. America	13.55	6.0 e
N. glauca	*Lophozonia*	S. America	10.60	4.7 ef
N. cunninghamii	*Lophozonia*	Australia	10.60	2.3 f
N. fusca	*Fuscospora*	New Zealand	7.16	1.9 f
N. menziesii	*Lophozonia*	New Zealand	1.83	0.5 f
N. truncata	*Fuscospora*	New Zealand	0	0
N. alessandri	*Fuscospora*	S. America	0	0
N. moorei	*Lophozonia*	Australia	0	0

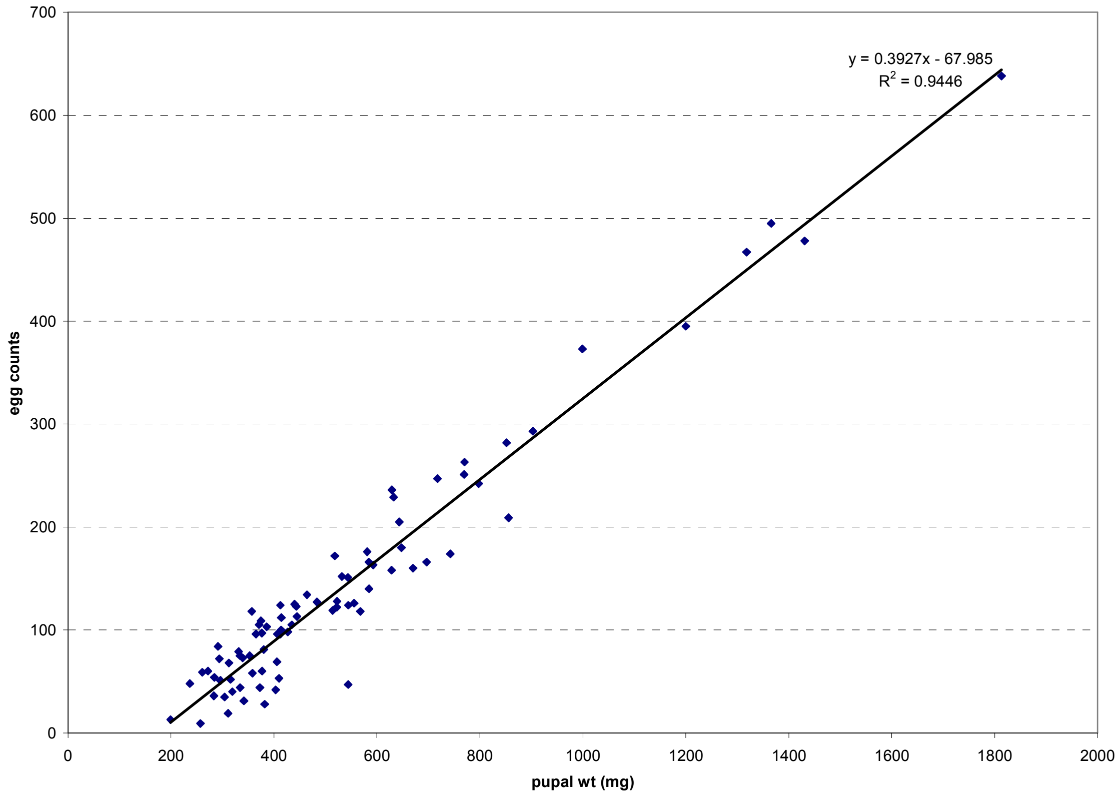

Figure 2.3. The correlation of gypsy moth pupal weight with potential fecundity (P<0.001).

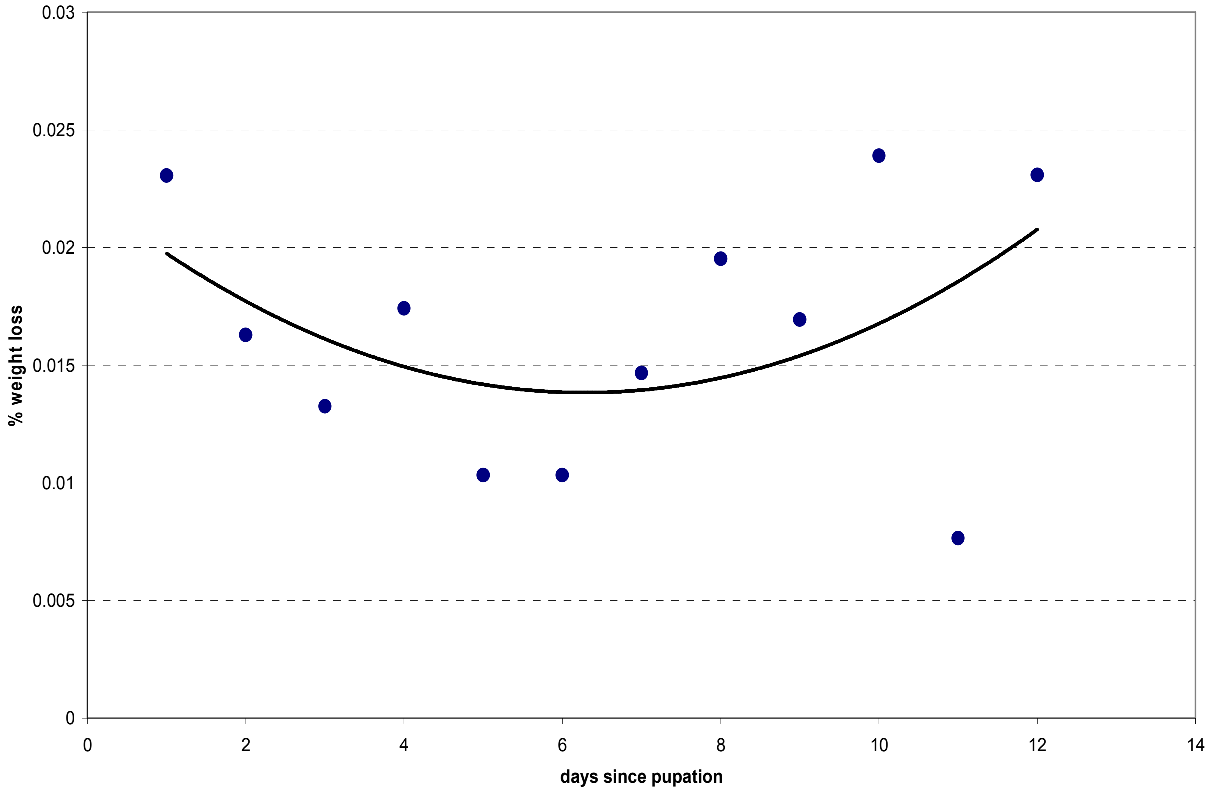

Figure 2.4. Gypsy moth pupal weight loss over time.

Fall web-worm

There was greater larval survival of fall web worm on New Zealand indigenous plant species than found for gypsy moth in 2002. However, many larvae failed to complete development, or had growth rates considerably lower than larvae feeding on the control plant *Morus*.

The unreplicated, neonate, Hungarian F1, no-choice feeding trials ran for only four days and the results are shown in Table 2.9. First instar fall web-worm larvae are extremely small and those larvae which showed no feeding appeared to be dead.

The survival and development of second instar larvae of the US provenance, transferred from *Prunus serotina* to the trial host plant in groups of approximately 20 larvae, is shown in Table 2.10. This was an unreplicated trial and the 20 larvae/treatment were not split into smaller groups as they developed. After 30 days larvae on *Morus* started to pupate. Those on *Nothofagus obliqua* were only a day or two behind. Larvae that survived on New Zealand indigenous plants were considerably slower in development (Plate 2.1).

A summary of the results of all the later-instar replicated feeding trials is produced in Table 11. However, they are best shown in Figure 5 as a plot of female against male larval growth rate.

For those host plants which produced pupae of only one gender that result was extrapolated for the other sex from a curve produced by first plotting only those host plants which produced pupae of both sexes. Only *Nothofagus obliqua* came close to achieving the results obtained from the natural host *Morus.* Frass production from the trials of third/forth instar larvae are plotted in Figure 6. The data are not adjusted for larval survival. Larvae on many New Zealand indigenous hosts produced negligible frass, but the amount of frass produced by larvae feeding on *Nothofagus menziesii* JFK was extraordinary. Both *Metrosideros kermadecensis* and *Leptospermum scoparium* supported some fall web-worm larval development to pupation and larvae on *O. macrodonta* would also have pupated in the curtailed US trial (Image 2.1).

TABLE 2.9

Fall web-worm neonate first instar larvae, feeding and survival on potential host plant species in no-choice trials

No feeding	**Feeding but no survival**	**Feeding and survival**
Nothofagus menziesii *WK*	Hoheria sexstylosa	Fuchsia exorticata
N. menziesii *JFK*	Metrosideros kermadecensis	Leptospermum scoparium
N. solandri var. *solandri* WK	Sophora microphylla	Hebe traversii
N. solandri var. *cliffortioides* WK		Nothofagus fusca *WK*
Griselinia littoralis JFK		N. obliqua *WK*
Coprosma rhamnoides		*Morus sp.*
Olearia macrodonta		
Pittosporum ralphii		

TABLE 2.10

*Survival and development, after 30 days, of fall web-worm second instar larvae, pre-fed black cherry, in a no-choice host trial. * see Image 11*

Host plant species	**% survivorship**	**Development stage achieved***
Hebe traversii	0	
Metrosideros kermadecensis	0	
Brachyglottis greyii	0	
Olearia macrodonta	95	5-6
Podocarpus totara	0	
Dacrycarpus dacrydium	0	
Dodonea vicosa	0	
Griselinia littoralis	0	
Nothofagus fusca JFK	10	
N. fusca ROW	25	3-4
N. fusca WK	80	3-5
N. menziesii WK	0	
N. menziesii JFK	100	5-6
N. solandri var. solandri WK	0	
N. solandri var. cliffortioides WK	0	
N. obliqua WK	65	Pre-pupae
Morus sp	85	pupation

TABLE 2.11

Growth and mortality statistics for Fall web-worm 3^{rd} /4^{th} larvae in no-choice feeding trials

		US 1/7				Serb 9/7				serb 17.7				US from1st.instar 1/7	
sp/site	**GR M**	**Gr F**	**% mort**		**GR M**	**Gr F**	**% mort**		**GR M**	**Gr F**	**% mort**		**GR M**	**Gr F**	**% mort**
Morus	8.38	12.4	60		7.31	8.65	52		8.33	11.14	28		3.34	5.57	15*
Obliq WK	6.58	8.64	40		4.35	5.61	36		6.72		76		2.84	2.17	35*
obliq RBGE									5.61	5.89	20				
sol RBGE					1.03	2.88	80								
sol WK	3.78	3.98	40			2.46	80								100
fusca WK	3.51	2.73	0		2.63	2.27	76								20*
fusca MTS					2.78	2.27	60		2.14	2.32	84				
fusca CW					2.44	2.5	72								
fusca RBGE									4.43	4.37	64				
fusca JFK					2.37	2.62	88								90*
fusca ROW															75*
GRIS LIT JFK	3.88	4.57	20		3.55	3.77	64								
GRIS LIT MST					3.6	2.95	92								100
GRIS LIT ROB					2.06	2.91	92								
MET ker		4.64	60		0	0	100								100
LEP. SCOP	3.65		60		3.15	2.98	48								
COP. RHA	2.74	2.69	40												
SOL CLIFF WK	2.84	3.36	60		2.09		96								100
MENZ WK															100
MENZ RBGE					2.55	2.42	92			2.27	96				
MENZ JFK					4.21	4.65	0								0*
HEBE SAL	0	0	100		5.71	5.13	72								100
ALP RBGE									4.1	4.78	32				
BET RBGE									5.22	3.5	76				
ANT RBGE									2.38	2.78	28				
DOM RBGE									3.02	3.17	48				
PUM RBGE									2.65	2.62	80				
COR BUD ROB					2.06		96								
DOD VIS	0	0	100		0	0	100								100
MET ROB					0	0	100								
OLE ALB	0	0	100		0	0	100								
OLE MAC	0	0	100		0	0	100								5*
OLE PAN	0	0	100		0	0	100								
PIT TEN CW	0	0	100		0	0	100								
PIT TEN ROB					0	0	100								
PIT RAL					0	0	100								
PSEU ARB	0	0	100		0	0	100								
PSEU COL	0	0	100		0	0	100								
Brach grey	0	0	100												100
DAC DAC	0	0	100		0	0	100								100
POD TOT	0	0	100		0	0	100								100
POD TOT HALL					0	0	100								

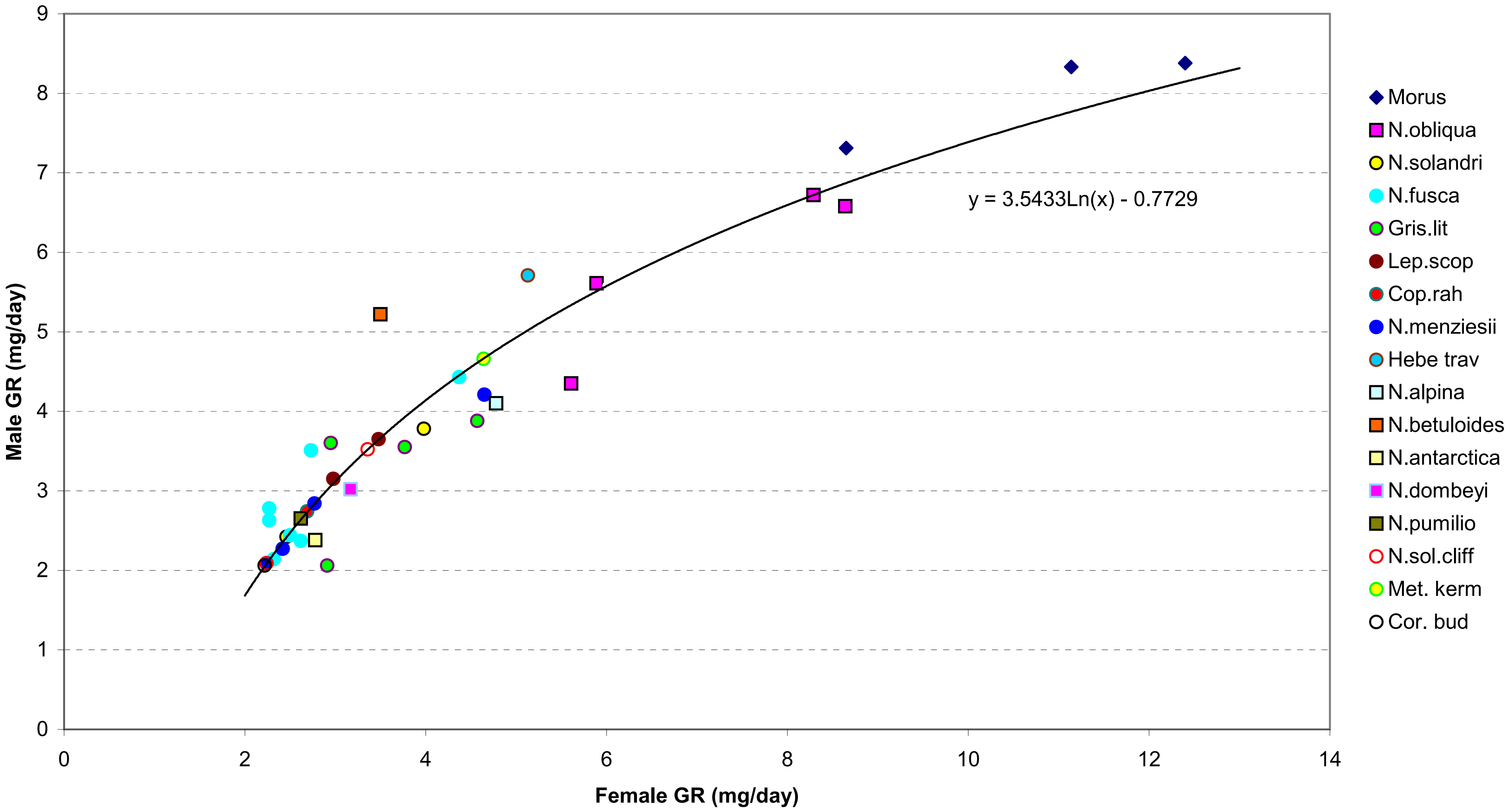

Figure 2.5. Fall web-worm larval growth rates on a range of plant hosts in no-choice trials.

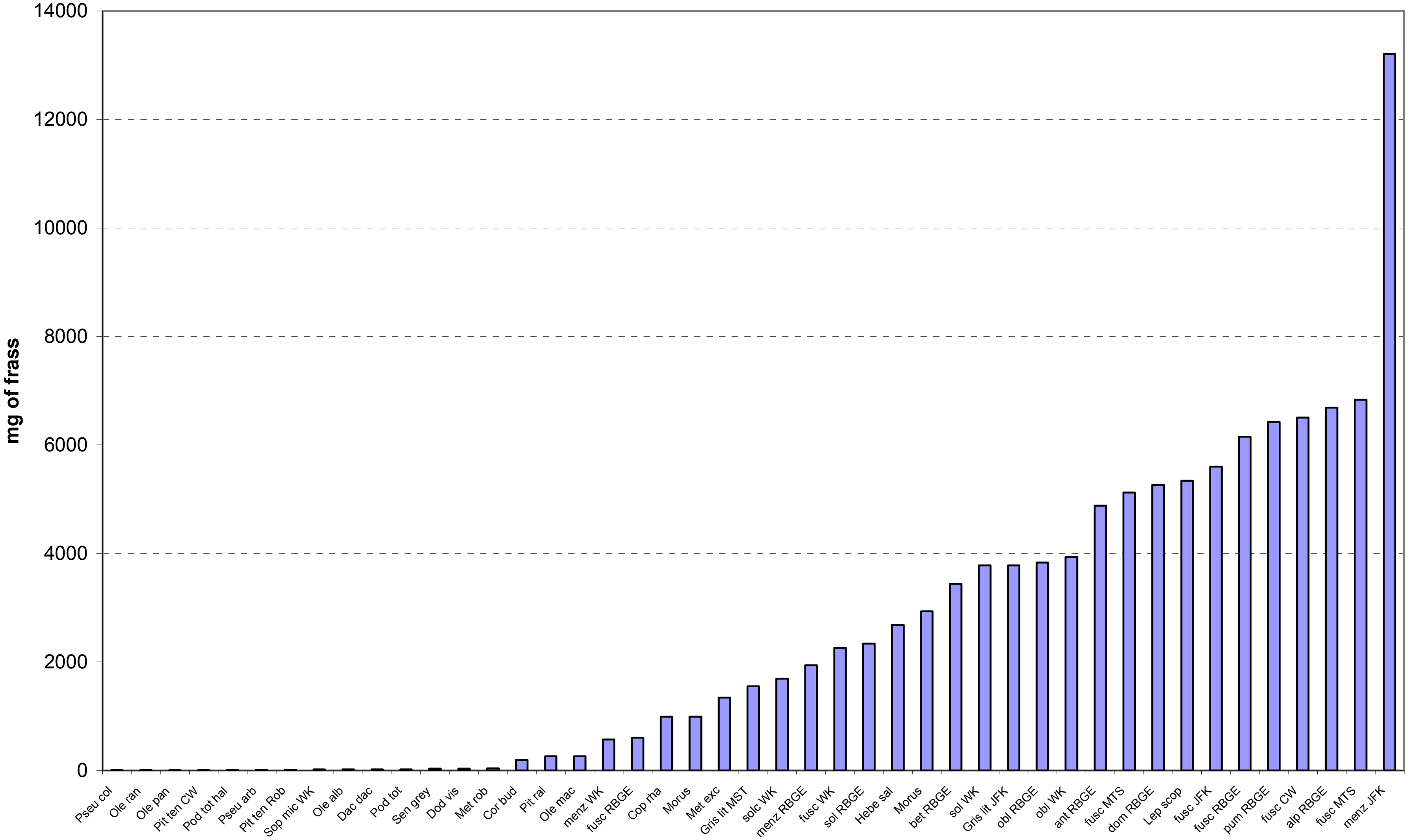

Figure 2.6. Frass production by FWW larvae on host species.

Plate 2.1 Development from second instar of fall web-worm larvae after 30 days on their respective host plants (clockwise from top left; *Morus, N. obliqua, Olearia*, *N. menziesii* JFK*, N. fusca* WK, *N. fusca* ROW).

Painted apple moth

As with gypsy moth and fall web worm the majority of New Zealand indigenous plants tested were not suitable hosts for *T. anartoides* (Table 2.12).Those from the Papilloniaceae were predictably more acceptable (Tables 2.13 & 2.14) but the few other species that did support larval development were not as good as the insect's natural host (Table 2.15).

The growth rates of both female and male insects were strongly correlated for the various hosts tested (Fig.2.7). Female growth rate was three to four times that of male larvae. However, the high mortality on less suitable hosts coupled with the shorter developmental time for male larvae, often resulted in only male pupae being produced. The parameters of host quality are therefore recorded in terms of male growth rate.

The potential fecundity, determined by dissection of weighed females, was strongly correlated to pupal weight (Figure 2.8). As host quality diminished so too did potential fecundity, survivorship and sex ratio (Figs 2.9 & 2.10).

Larval growth rates on *Nothofagus* species showed a similar pattern to those of gypsy moth and fall web worm. Larval development was remarkably good on *N. antarctica* (Table 2.16), and larvae failed to develop on *N.menziesii, N. truncata, N. moorei* and *N. alessandri*.

TABLE 2.12

Indigenous plant species unsuitable as hosts of painted apple moth

No feeding	**Feeding but no molting**	**Molting but no pupation**
Nothofagus menziesii	Pittosporum tenuifolium	Brachyglottis repanda
Geniostoma rupestre	Olearia furfuraua	Agathis australis
Pittosporum crassifolium	O. rani	Myoporum laetum
Melicytis ramiflorus	*Kunzea ericoides*	Planchonella novo-zealandia
Knightia excelsa	Leptospermum scoparium	
Hoheria populnea	Coprosma robusta	
Vitex lucens	C. lucida	
Fucshia exortica	Pseudopanax arboreum	
Weinmannia racemosa	Dysoxylem spectabile	
Charmichaelia muritai *C. crassicaule*	Dacrycarpus dacrydoides	
Beilschmedia tawa	Dacrydium cupressinum	
Metrosideros excelsa	Phyllocladus trachomanoides	
	Podocarpus totara	
	Prumnopitys ferruginea	
	Nothofagus fusca x solandri	
	N. truncata	
	Hebe stricta	

TABLE 2.13

Early larval development of painted apple moth larvae on indigenous Carmichaelia species

Host species	**Larval weight at 13 days (mg)**
Sophora tetraptera	162.90
Carmichaelia ramosa	164.49
C. carmicaeliae	160.06
C. astonii	124.55
C. williamsonii	117.13
C. kirkii	60.61
C. hollowayii	24.94
C. curta	19.56
C. stevensonii	13.65
C. apressa	10.89
C. arenaria	3.64
C. muritai	0
C. crassicaule	0

TABLE 2.14

Larval growth rates and mortality of painted apple moth on indigenous

Sophora species

Species	%mortality	♂ growth rate (mg/day)	n	♀ growth rate (mg/day)	n
Sophora cathamii	100				
S. prostrata	92	1.79	4		
S.longicarinata	100				
S.godleyi	98	1.51	1		
S.microphylla	100				
S.tetraptera	88	2.1	6		
S.fulvida	100				
S.molloyi	96	1.79	2		
Acacia mearnsii	20	4.42	24	11.92	16

TABLE 2.15

A summary of performance of painted apple moth on indigenous host plants

Species	Male GR (mg/day)	Female GR	Sex ratio	Surv. SHP%
Acacia mearnsii	5.12	17.25	0.65	76
Sophora tetraptera	3.66	13.95	0.35	84
Avicennia resinifera	3.18	10.92		46
Corynocarpus laevigatus	2.64			6
Sophora microphylla	1.48			10

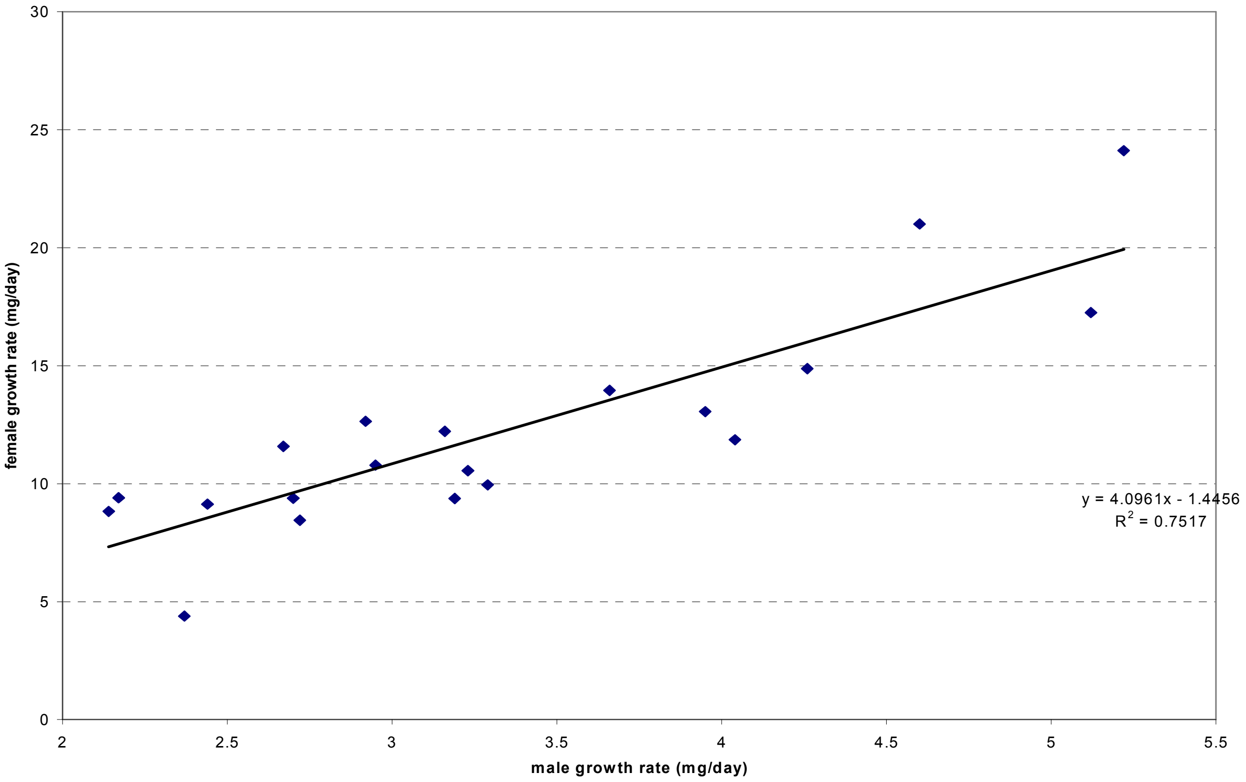

Figure 2.7. The correlation of male and female growth rates on a number of different host plants ($P<0.001$).

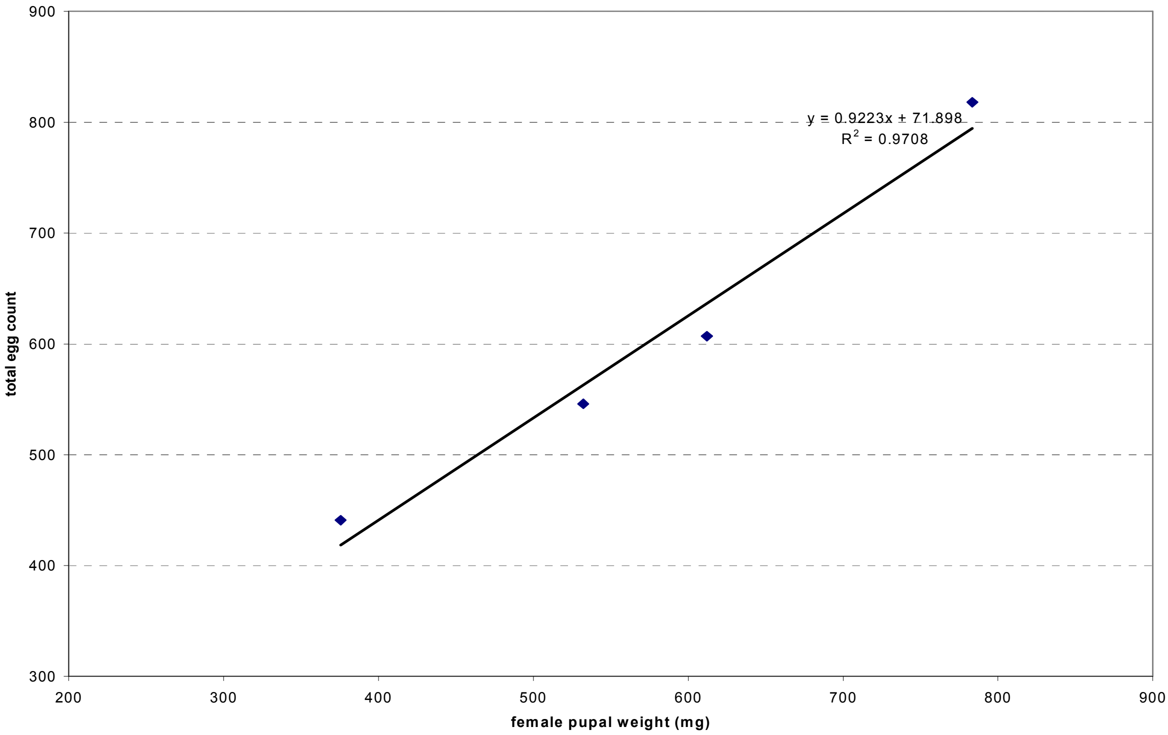

Figure 2.8. Potential fecundity (measured as female pupal egg complement) correlated with pupal mass.

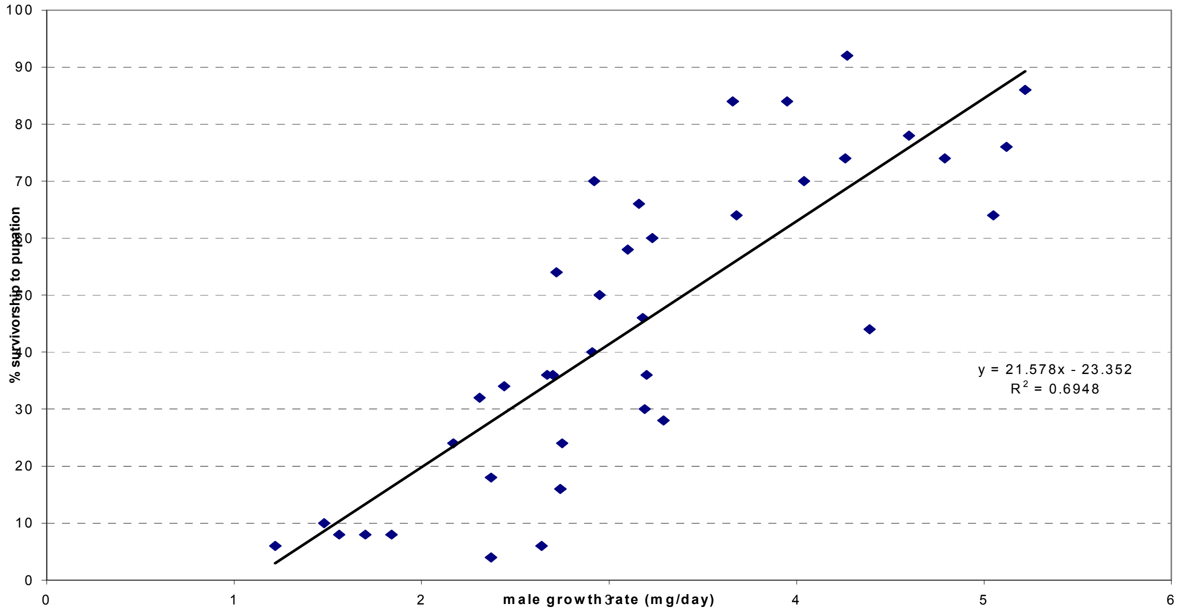

Figure 2.9. Percentage larval survivorship correlated with host suitability - measured as male growth rate (P< 0.001).

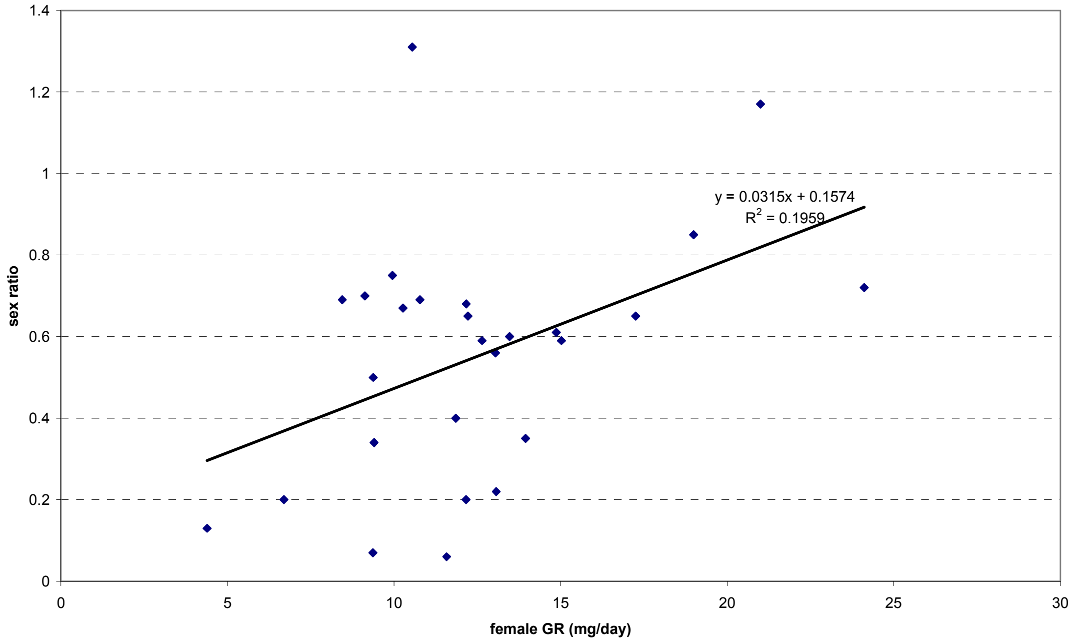

Figure 2.10. Correlation of host suitability – measured as painted apple moth female larval growth rate – with sex ratio (P<0.05).

TABLE 2.16

Parameters of growth, development and survivorship of painted apple moth on Nothofagus host species. (extrapolations of male growth rate data)*

Host species	**Female pupal weight mg**	**Growth rate (mg/day)**	**% survivorship**
N. antarctica S.Am.	650.04 ± 17.86	24.11 ± 0.43	46
N. obliqua S.Am.	490.83 ± 42.44	15.97 ± 1.69	60
N. alpina S.Am.	474.33 ± 23.60	12.78 ± 0.59	44.5
N. betuloides S.Am.	428.99 ± 30.00	14.87 ± 0.57	68
N. nitida S.Am.	469.50 ± 26.52	15.02 ± 1.21	84
N. dombeyi S.Am.	417.38 ± 40.29	12.83 ± 0.86	43
N. glauca S.Am.	-	2.35*	4
N. alessandri S.Am.	-	-	0
N. solandri cliff. N.Z.		6.89*	17
N. solandri sol. N.Z.	327.25 ± 63.83	6.31 ± 1.92	23
N. fusca N.Z.		2.19*	5
N. truncata N.Z.	-	-	0
N. menziesii N.Z.	-	-	0
N. moorei Aust.	-	-	0

Discussion

The pattern of host rejection and slow larval growth on a broad range of host plants was similar for all three polyphagous insects and is consistent with previous assessments with the Asian strain of gypsy moth (Matsuki et al. 2001) and the white spotted tussock moth, *Orgyia thyellina*, (Hosking et al. 2003). The broader effects of a slow larval growth rate will be covered in the next chapter, but the observed pattern of host quality suggests that a broad-spectrum defence is employed by the New Zealand forest flora. The pattern of host acceptance was one where continental host plants were generally more acceptable than insular plants. The odd exception, such as the acceptance of the insular *Metrosideros kermacadensis* as a satisfactory host for fall web worm, could be explained as a commercial aberration. This particular plant and *Leptospermum* were commercial ornamental plants which had undoubtedly undergone anthropogenic selection for floral display, probably at the expense of the plant's defence. *Sophora tetraptera* may also have fallen into this category; it has been a common ornamental species even in pre-European settlement (www.aoteamoana.co.nz.). Ornamental plants have often been selected for ease of production and/or floral display – the need for defence against invertebrate pests is supplanted by the use of insecticides.

That a number of host species and even individual plants were of similar palatability across two Lepidopteran families suggests that the defence has a similar physiological basis for polyphagous defoliators and that is not related to plant phylogeny. The painted apple moth, which could have been expected to have some evolutionary experience with the flora of the Southern Hemisphere, followed the same trend as the Northern Hemisphere defoliators.

The unexpected resistance to alien invertebrate defoliators may be a reflection of the high endemism of New Zealand's flora. However, the bioassays of *Nothofagus* puts the New Zealand flora into an ecological context that largely excludes the influence of phylogeny. Floristic novelty did not constrain larval growth rates from a number of S. American *Nothofagus*, and acceptance of other Southern Hemisphere genera such as *Eucalyptus* and *Corymbia* has been recorded (Matsuki et al. 2001). Humphries et al. (1986) concluded that phylogeny was not related to the host selection of beech specific moths. They found that the *Nothofagus* phylogenetic cladogram bore no correspondence with that of the Heterobathmid moths. A differential acceptance of host plant species within *Nothofagus* indicates that a differential selection pressure has been applied by invertebrate defoliators across the genus.

The resistance in the New Zealand flora to the three invasive, polyphagous, continental defoliators does not fit well with the perceived notion that islands should be vulnerable to continental species because of the availability of empty niches and/or the evolution-in-isolation of insular biotas (Whittaker 1998, Primack 2002). The biotic resistance hypothesis also argues that diverse ecosystems are highly competitive and resist invasion. However, accurate predictions for the invasibility of communities are tenuous (Kennedy et al. 2002) and both gypsy moth and the fall web worm have a proven ability to invade and naturalise in complex ecosystems.

Darwinian logic would predict that if the New Zealand flora has been continually exposed to unregulated invertebrate herbivores immigrating into enemy-free space there would be a strong selection for resistance to novel invertebrate defoliators. The resistance to invertebrates contrasts markedly with the susceptibility of the flora to alien vertebrate browsers (Craig et al. 2000). The vulnerability of New Zealand's indigenous flora to browsing ungulates and marsupials is understandable given that it has never been exposed to these organisms over an evolutionary time scale.

The need for New Zealand indigenous plants to invest in a strong defence against invertebrate herbivores may be reflected by other floristic traits that have previously been unrecognised as a reaction to invertebrate herbivory. Dioecy, hybridism, the evergreen habit, and the presence of domatia are comparatively common in the New Zealand flora (Primack and Lloyd 1980, Bawa 1982) and are traits that have or could be implicated in the resistance to invertebrate defoliators (Coley 1988, Jing and Coley 1990, O'Dowd and Pemberton 1998, Orians 2000). The significance of evolution in the low level of defoliation by forest insects in natural ecosystems is often overlooked.

An assumption of most plant defence theories is that herbivore resistance is metabolically costly and involves trade-offs with growth and/or reproduction (Rhoades 1979, Coley et al 1985 Herms and Mattson 1992, Koricheva 2002). It is possible that a significant allocation of resources to defence, or the evolution of a stoichiometric ecology to counter defoliators, explains the slow growth of New Zealand's endemic tree species when compared to sympatric exotic counter-parts. The mean annual increment for beech forest in New Zealand ranges from 4.6 –10 m^3/ha/ann. (Ogden et al. 1996) whereas for the exotic *Pinus radiata* plantations 25 m^3/ha/ann is the New Zealand norm (Beekhuis 1966). The fact that exotic forest species grow faster in New Zealand than in their homeland suggests that the growth of the New Zealand indigenous flora is not constrained by the abiotic environment.

Many simple ecosystems, such as bogs and oceanic islands, exist and remain stable if undisturbed by man. The high rate of endemism in New Zealand's flora (Allan 1982) and the host-specificity of its invertebrate herbivores (Dugdale 1975) suggest a long period of community stability and co-evolution. The robust defence within the New Zealand flora against invertebrate defoliators that are proven continental invaders, suggests that the functioning of insular forest ecosystems may be profoundly different to that of continental systems. This is not to say that the net outcome of community function will be any different for insular and continental ecosystems; just that it may be achieved by different process.

Chapter 3

The relevance of growth rate: the paradox revisited.

‘*So much of life is neither one thing nor the other... it's both things at the same time.*’
David Hyde Pierce

Abstract

The ecological relevance of larval growth rate was investigated here using the data from the larval feeding trials of two Lymantriids, the gypsy moth, *L. dispar* and the painted apple moth, *Teia anartoides* (Lepidoptera: Lymantriidae). The influence of larval growth rate on life-table parameters that could affect the population dynamics of the defoliators was identified. In addition, a potential synergy between slow larval growth rate and the virulence of a pathogen was investigated by evaluating the efficacy of a commercial pathogen-based insecticide Foray 48B – a formulation of *Bacillus thuringiensis* used to eradicate Lymantriid incursions in New Zealand and N. America – applied to a selection of host plants of the painted apple moth.

Introduction

Larval growth rate was used throughout this thesis as a measure of host plant quality. The larval stage of development is considered to be the most vulnerable period in an insect’s life and the population dynamics of most insects is determined in the larval stage. This is particularly true for exophytic defoliators whose exposed larvae must overcome a number of biotic and abiotic ‘hurdles’ during development (Southwood 1973, Janzen 1988). There may be some advantage in a slow larval growth rate for endophytic insects such as gall formers (Clancy and Price 1987), but for exophytic feeders, a rapid larval growth rate should assist in the avoidance of inclement weather and natural enemies (Southwood 1973, Price et al. 1980, Leather 1985, Isenhour et al. 1989, Stamp 1990, Montllor and Bernays 1993).

Slow larval growth may result from both genetic and environmental factors, but all else being equal, diet is the major determinant of larval growth rate (Scriber and Slansky 1981). Sub-lethal plant defences can inhibit, or reduce, the feeding of potential defoliators. Tree leaves are particularly poor fare for larval growth, although larvae may have some ability to compensate for the low 'apparent digestibility' (*sensu* Waldbauer 1968) of leaves. When larval growth rates and pupal weights are compromised by poor hosts, compensatory feeding by larvae and/or the employment of super-numerary instars, may assist the achievement of body mass norms. Typically this compensatory strategy results in greater leaf consumption (Slansky and Feeny 1977). Paradoxically then, plants that provide a poor diet as a defence against herbivores, have the potential to lose more foliage biomass than less defended plants (Moran & Hamilton 1980, Clancy and Price 1987, but see Wise et al. 2006). This apparent paradox may be resolved if slower larval growth results in higher larval mortality through stochastic abiotic trauma and/or an increased exposure to natural enemies (Williams 1999). The slow-growth-high-mortality hypothesis (SGHM) was formalised by Clancy and Price (1987). Specifically it proposes that sub-optimal host plants are defended by prolonging larval development and increasing the exposure of phytophages to natural enemies (Benrey and Denno 1997).

It has been shown that host plants can influence the vulnerability of a phytophage to its natural enemies (Hawkins and Lawton 1987, Bernays and Graham 1988, Holt and Lawton 1994, Lill et al. 2002). However, evidence for the assumed synergy between low larval growth rates and increased mortality from natural enemies is ambivalent (Benrey and Denno 1997, Williams 1999). Synergies have been demonstrated in laboratory studies (Price et al. 1980), but have been found wanting in field studies (Leather and Walsh 1993, Medina et al. 2005, Cornelissen and Stiling 2006, Wise et al. 2006). Indeed, the concept of enemy-free-space provided by novel, less salubrious hosts, may in fact increase the chance of survival for those insects, such as gypsy moth that are capable of host switching (Rossiter 1987). The inconclusive evidence of a synergy between host quality and the regulation of herbivores by natural enemies suggests that plants may benefit from slowing larval growth in some less obvious manner.

The vast majority of insect herbivores are specialist feeders (Bernays 1988). However, the polyphagous strategy offers access to a greater pool of resources and often allows defoliators to inhabit broader geographic ranges. However polyphagy requires a greater investment in reproduction and the maintenance of a suite of mechanisms to combat not only the defences of a range of host plants, but also the competitive, or predatory behaviour of a range of antagonists associated with those plants (Ahmad and Forgash 1978, Lindroth and Hemming 1990, Appel and Maines 1995). Generalist Lepidoptera tend to be larger than specialists; possibly to compensate for the unpredictability of their habitat (Loder et al. 1998), but this and other broad-spectrum defence/survival mechanisms of polyphagous insects are assumed to come at some metabolic cost (McPeek 1996). However, polyphagous insects do not perform equally well on all hosts and the allocation of resources within polyphagous insects is likely to be strongly influenced by the quality of its host plants.

The polyphagous gypsy moth is a renowned forest defoliator whose population dynamics are driven fundamentally by the availability of suitable host plants (Wallner and Walter 1979, Sharov et al. 1999). Although it is capable of development on a wide range of hosts, significant outbreaks of gypsy moth are usually confined to forests dominated by its primary hosts, oak or larch. Growth rates are slower on many of its secondary hosts (Liebhold et al. 1995) and a lack of outbreaks on them could be construed as support for the belief that natural enemies are more effective on these ‘secondary’ hosts. However, if natural enemies are limited (as in the case of gypsy moth in N. America) the quality, or ecological concordance provided by secondary hosts, must be less than that provided by the primary host plants.

A dilemma for ecologists and biosecurity policy makers is distinguishing between primary and secondary hosts. The relevance of ‘recorded hosts’ – published records of host plants from which an insect has been taken in the field; ‘physiological hosts’ – hosts supporting larval development as recorded by laboratory feeding trials; and ‘ecological hosts’ – host plants that sustain natural populations; are not necessarily closely aligned. The outcomes of new associations between organisms can be extremely variable and strongly influenced by their environment (Hokkanen and Pimental 1989). This uncertainty is captured in Williamson’s (1999) statement ‘predicting the ecological behaviour of a species in a new environment may be effectively impossible’, which highlights the frustration in assessing the risk of alien defoliators entering a novel habitats.

The ecological relevance of host quality was investigated here as a possible predictive measure of the ability of plants to sustain defoliator populations. Significant differences in the growth rates of gypsy moth, fall web worm, and painted apple moth were recorded across a variety of host plants (Chpt. 2). The potential for larval growth rate to influence life-table parameters that could affect the population dynamics of defoliators was investigated. In addition, a potential synergy between a slow larval growth rate and the virulence of a pathogen was investigated to help resolve the dilemma of host- or process-based larval mortality observed in the laboratory trials.

Methods

1. Analysis of the bioassay data from Chapter 2

- The bioassay data from the Lymantriid trials offered the most complete data sets. They were deemed free of potential maternal effects which may have influenced the F1 generation (Hunter 2002), because larvae of both gypsy moth and painted apple moth were derived from females from closed colonies that had been reared on standardised diets for many generations. Host related bioassay data were used to assess the influence of larval growth rate on mortality, fecundity and population sex ratio.

2. The synchrony of adult emergence

- The potential for host quality to disrupt adult emergence synchrony was investigated by comparing the difference in gender pupation times on different hosts.
- To determine the gender emergence synchrony of a natural population, pupae of gypsy moth were collected from an outbreak population in a scrubland of Quercus ilex at St Gely, France, in 2004. Pupae were placed on dampened sand within perforated containers and held at a constant 22ºC until emergence.

3. The larval growth rate of painted apple moth and the efficacy of a pathogen

Trials with the painted apple moth assessed the potential of host quality to influence the susceptibility of a defoliator to pathogens. A commercial pathogen-based insecticide Foray 48B – a formulation of *Bacillus thuringiensis* var. *kurstaki* (Btk) commonly used to eradicate Lymantriid incursions in New Zealand – was applied to a selection of host plants supporting differing larval growth rates and then fed to larvae of the painted apple moth. Test plants included three trees each of *Acacia mearnsii, A. dealbatum, A.*

decurrens, Paraserianthes lophanta, Sophora microphylla, Corynocarpus laevigatus, Nothofagus solandri and *Pseudotsuga menziesii.* Host plants were sourced from within an hour's drive of the quarantine facility. The *Acacia* species, *P. menziesii N. solandri* and *S. microphylla* were growing within the FRI campus. Foliage of *P. lophanta* was collected from Pyes Pa, Tauranga and that of *C. laevigatus* from a stand at Mt Maunganui.

The Btk was sourced from stocks used for the painted apple moth eradication programme. The Btk was applied to terminal shoots on a moving belt 'track sprayer' that passed under a stationary applicator. Belt speed and both Btk dilution and pump delivery rate was regulated to deliver doses by way of a controlled droplet applicator (ULVA 8, Micron sprayer) delivering droplets of 120µm volume mean diameter. This equipment mimics the conditions used in operational spray programmes and dose rates quoted here are given as litre/hectare equivalents. The recommended application rate is 5L/ha. The delivered dose was measured by the colorimetric analysis of the Btk deposition on mylar sheets that were run consecutively between the plant samples. For trials assessing the efficacy of Btk applied to artificial diet, the wheat-germ based diet was spread as a 1mm film on mylar sheets with thin layer chromatography apparatus. Btk was applied to the diet sheets on the track sprayer in the same manner as the foliage samples.

Larvae for the bioassays were provided from the painted apple moth colony maintained on artificial diet within the FRI quarantine facility. Trials were run at 22º±1C and 14 hour photoperiod within the same facility. Five replicates were run of each host plant in bioassays which utilised either 10 first instar larvae or 5 third instar larvae. Ten replicates were run for fifth instar larvae, with one larva per replicate. Each trial was run with an equal number of unsprayed larval controls. Control and treated plant samples were secured individually, each in a two-pot system as for the original bioassays. For each bioassay the control and sprayed replicates were arranged as five or ten randomised blocks within the quarantine facility.

Larvae were placed within the test arenas and mortality and/or development was recorded at one to three day intervals. Larvae from the control replicates were used to determine larval growth rates. At the end of trials larvae were killed in alcohol, then air-dried and weighed when they had reached a stable weight. Pupal fresh weights were used to determine the growth rate of fifth instar larvae.

- In an investigation of potential host effect on the efficacy of Btk, trials of first, third and fifth instar larvae on four different host plants were subject to a range of Btk dose rates.

- In a comparison between the effect of Btk on a natural host plant and artificial diet fifth instar larvae of painted apple moth were exposed to Btk applied at nominal dose rates of 2, 4 and 6 L/ha to samples of foliage of one tree of A. mearnsii and prepared sheets of artificial diet. The development time and weight of surviving larvae was recorded at pupation.

- The elimination of potential plant architecture effect on the efficacy of Btk was investigated by applying a sub-lethal dose 0.1 L/ha of Btk to foliage samples of 11 provenances of Douglas fir, Pseudotsuga menziesii that were then fed to third instar larvae. The mortality of those larvae was correlated with the growth rates of larvae on unsprayed samples of the same provenances.

Statistical Analysis

Simple linear or polynomial regression analyses were used to identify correlations between sex ratio and female growth rates, pupal mass and larval growth rate, potential fecundity and female pupal mass, larval survivorship and larval growth rate and larval mortality and Btk dose rates.

Results

The positive linear relationship between pupal weight and potential fecundity was described in Chapter 2. However, the relationship between larval growth rate and potential fecundity was curvilinear (Fig 3.1) partly because the relationship between larval growth rate and pupal mass is also curvilinear (Figure 3.2). Larvae on good quality hosts reach their pupal mass relatively faster than those on poor quality hosts.

There was a significant positive relation between larval growth rate and survival for both gypsy moth and painted apple moth larvae (Figs 2.3 & 2.8). For the gypsy moth survival was not gender specific and there was no significant relationship between larval growth rate and the ensuing adult sex ratio. However, the painted apple moth has a greater disparity in the duration of development of male and female larvae and there was a significant female skew in mortality and the resulting sex ratio of adults (Fig 3.3).

The emergence of adults from the natural St Gely population was protandrous. However, male emergence was protracted so that the peaks of male and female emergence were reasonably synchronous (Fig 3.4). The bulk of the emergence of females collected from the field population began four days after male emergence commenced and lasted eight days, while males were emerging for approximately 20 days. The adult emergence from pupae produced during the bioassays was not recorded. However the normal disparity of four days, in the onset of pupation between male and female laboratory reared gypsy moth, increased to seven days for larvae exhibiting the slowest growth rates (Figure 3.5). The trend was significant ($P < 0.02$) if the result for *N. fusca*, which had few surviving larvae, is ignored.

Larval mortality on poorer hosts was mirrored by the efficacy of Btk. Larvae on host plants that provided the highest larval growth rates had the best survivorship and required greater doses of Btk to effect mortality (Tables 3.1 & 3.2, Figure 3.6). Mortality was dose-dependent, with the larger later instars requiring a greater dose of Btk to effect mortality (Figure 3.7). The dose rates to effect mortality on poor hosts were at times a fiftieth the recommended dose rate and within the provenances of Douglas fir a dose rate of 0.1L/ha produced a significant negative correlation of mortality with larval growth rate (Figure 3.8). However, when Btk was applied to artificial diet, mortality was higher and faster for late instar larvae on the diet than larvae on the primary host *A. mearnsii*. (Figure 3.9), even though artificial diet supports larval growth rates equivalent to those of the primary host.

Significant dose-dependent, sub-lethal effects of lowered pupal mass and increased development time were found for late instar larvae (Figure 3.10).

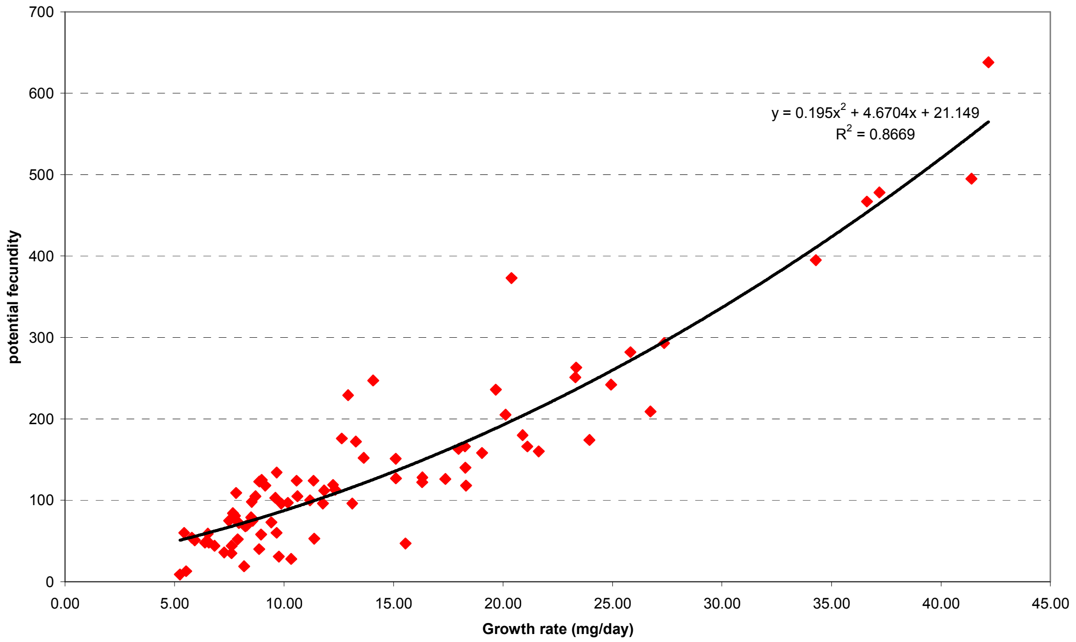

Figure 3.1. The relationship between female larval growth rate and the potential fecundity of gypsy moth.

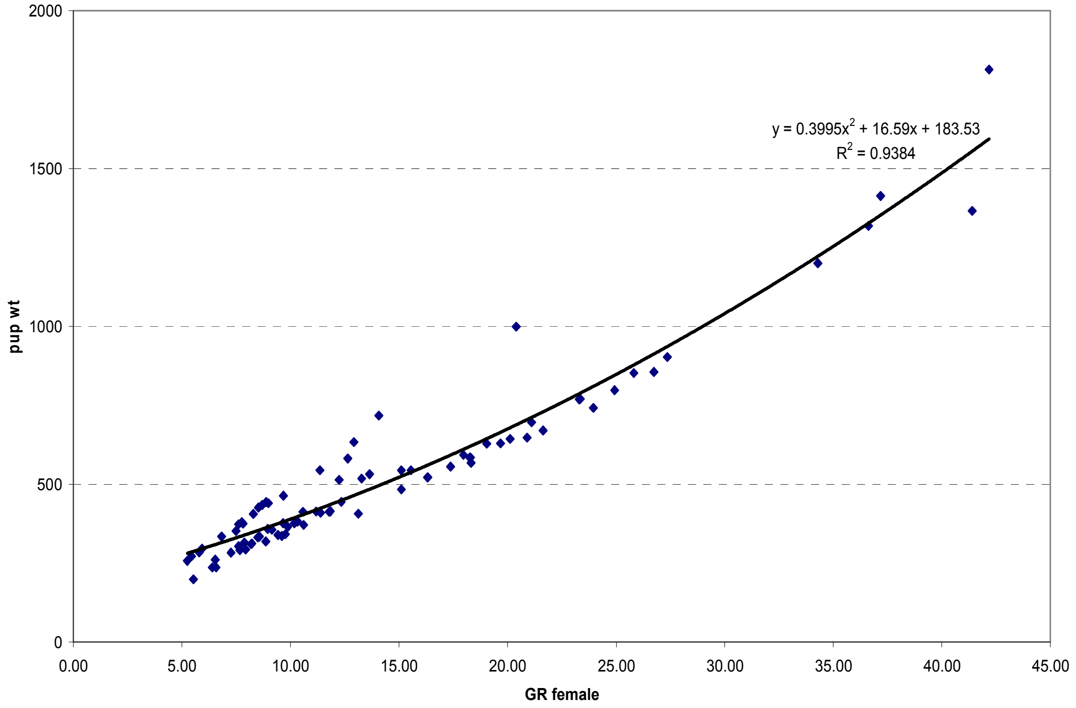

Figure 3.2. The relationship between female pupal weight and female larval growth rate of gypsy moth.

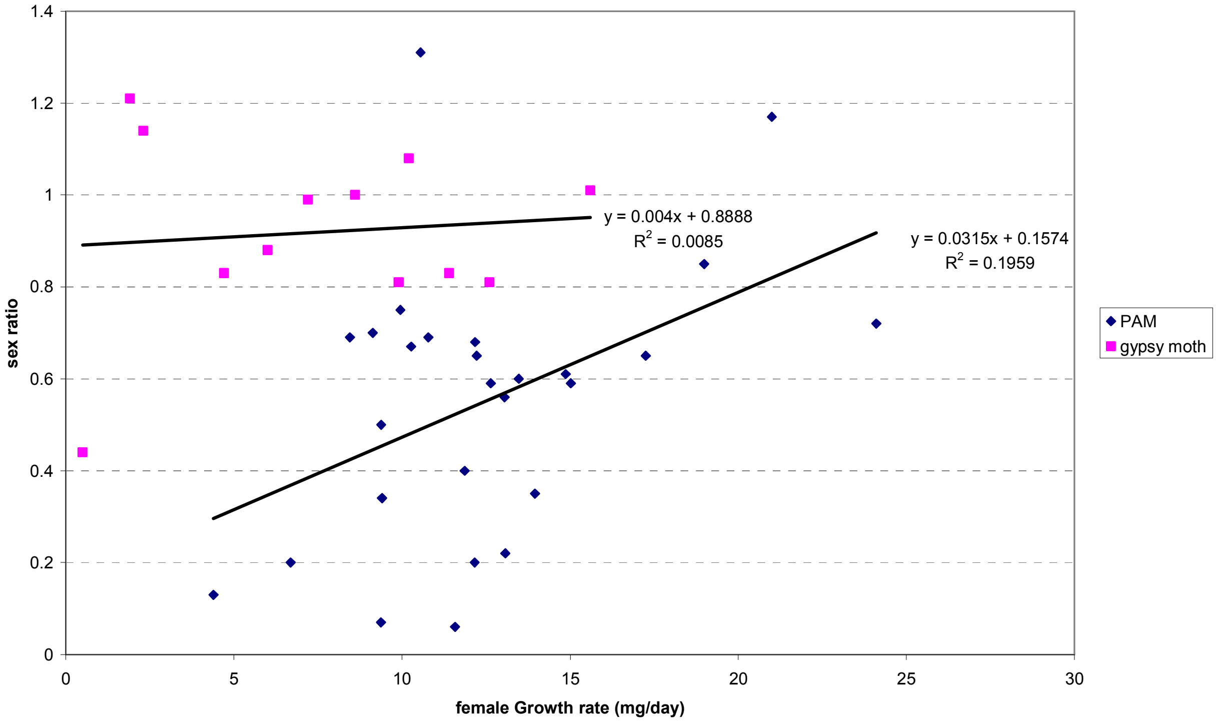

Figure 3.3. The relationship between female larval growth rate and the sex ratio of resulting adults ($P < .05$ for painted apple moth).

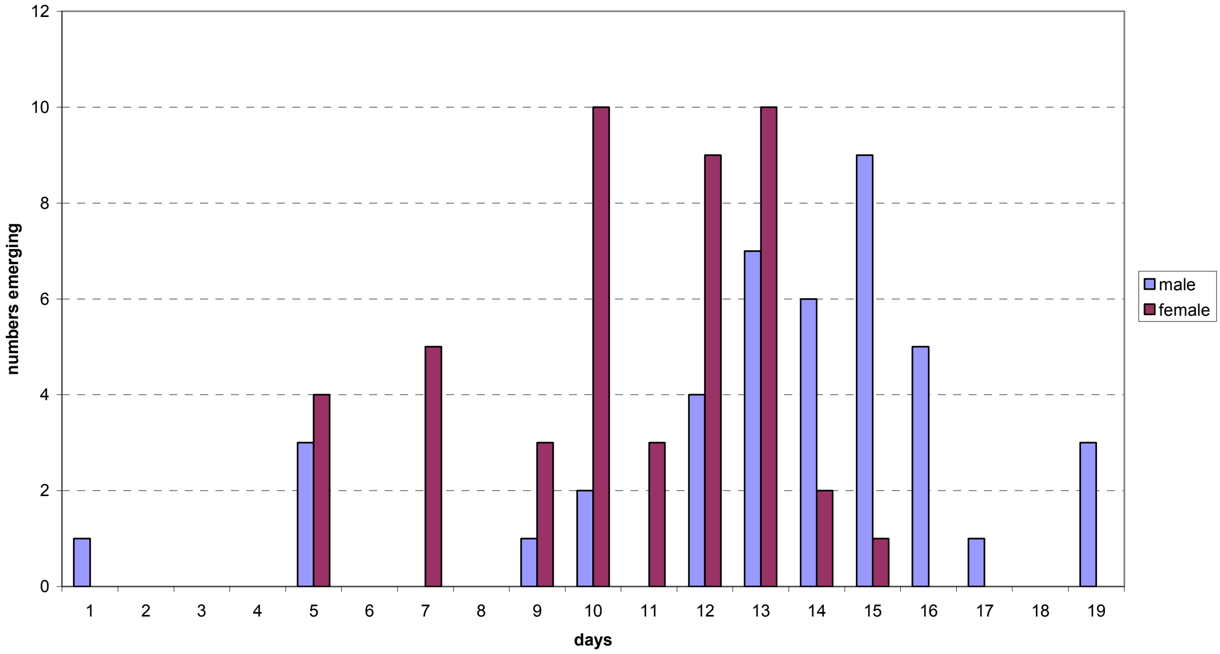

Figure 3.4. Moth emergence from pupae collected from a natural population at St Gely, France, 2004.

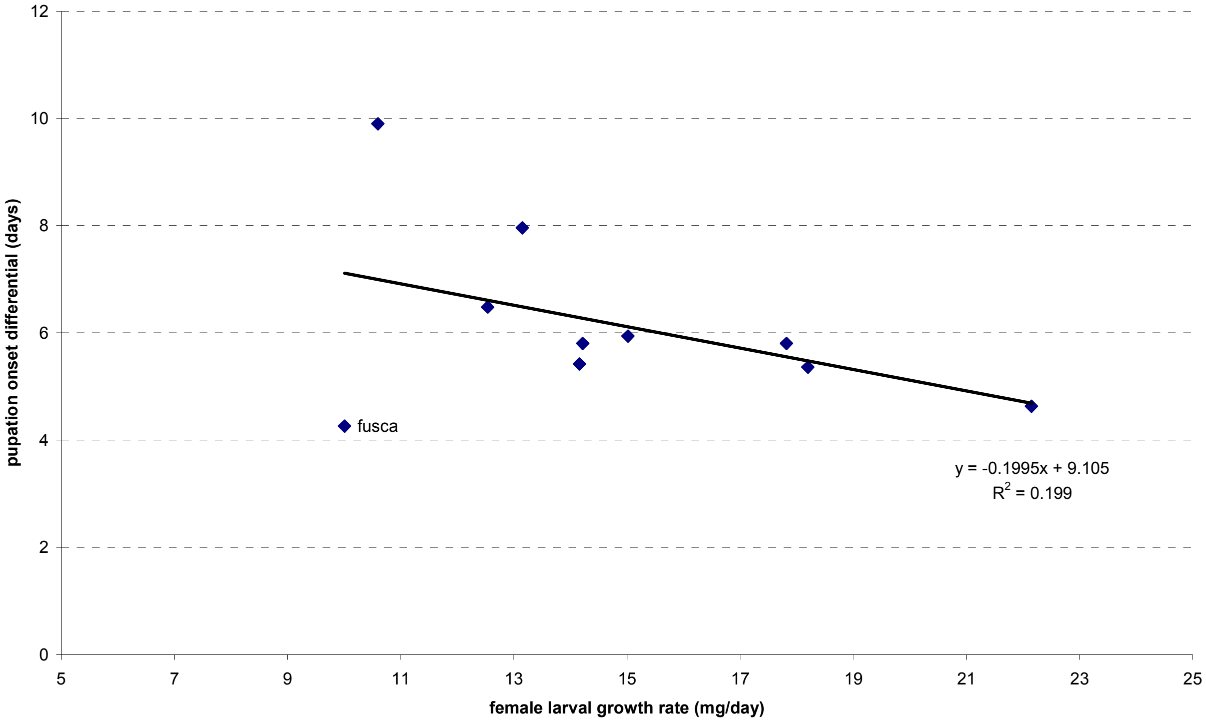

Figure 3.5. The correlation of gypsy moth female larval growth rate with the temporal difference between genders for the onset of pupation (without *N. fusca*, which had few surviving larvae, P <0.02)

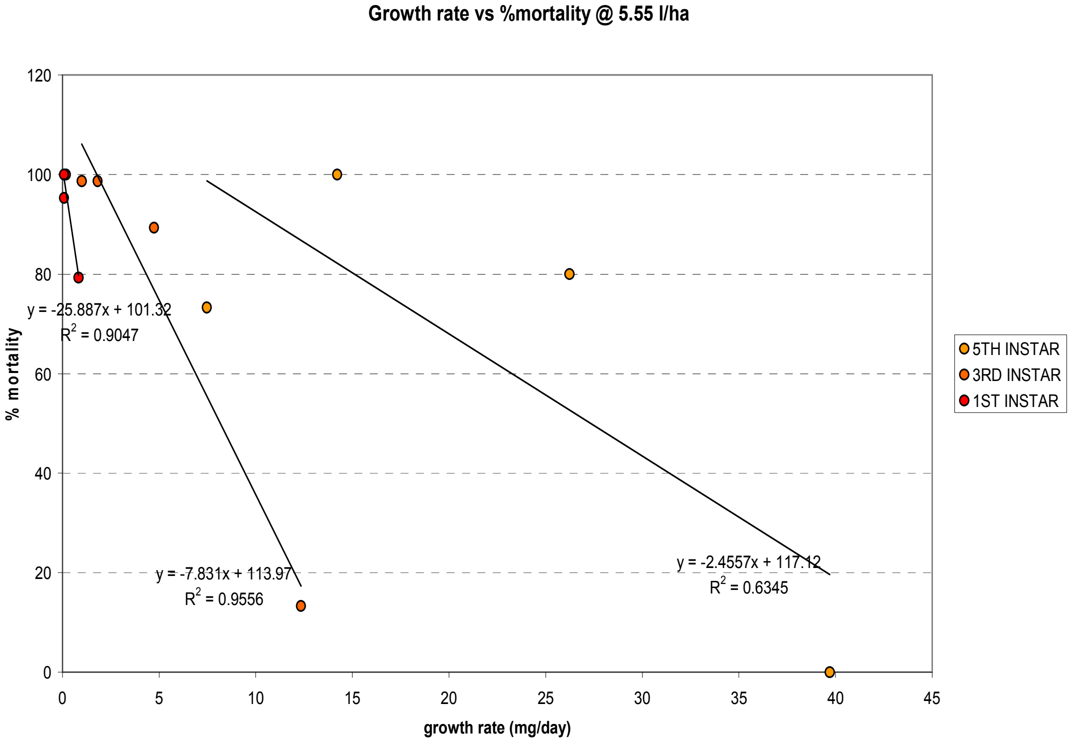

Figure 3.6. Correlations of mortality at a dose rate of 5.55L/ha Btk and the growth rate of larvae on four different host plant species across three instars of painted apple moth.

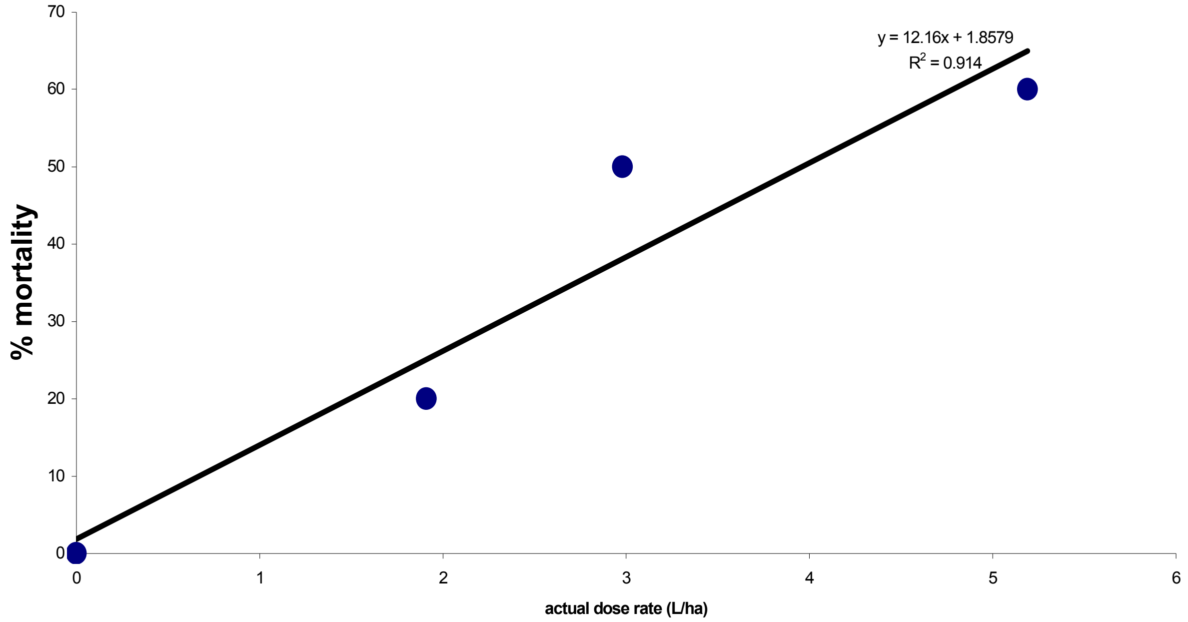

Figure 3.7. The relationship between Btk dose and the mortality of fifth instar (recorded at pupation) for painted apple moth larvae feeding on treated *A. mearnsii.*

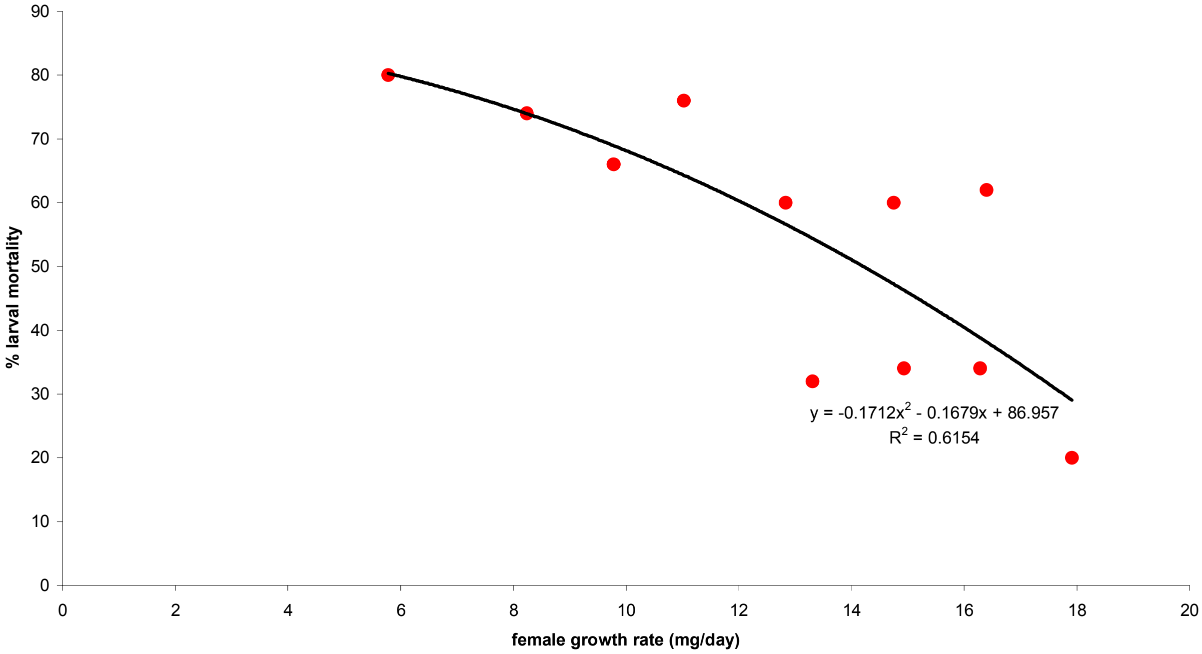

Figure 3.8. The relationship between the growth rate of painted apple moth larvae feeding on 11 provenances of Douglas fir and the mortality of larvae feeding on the same provenances treated with 0.1 L/ha Btk.

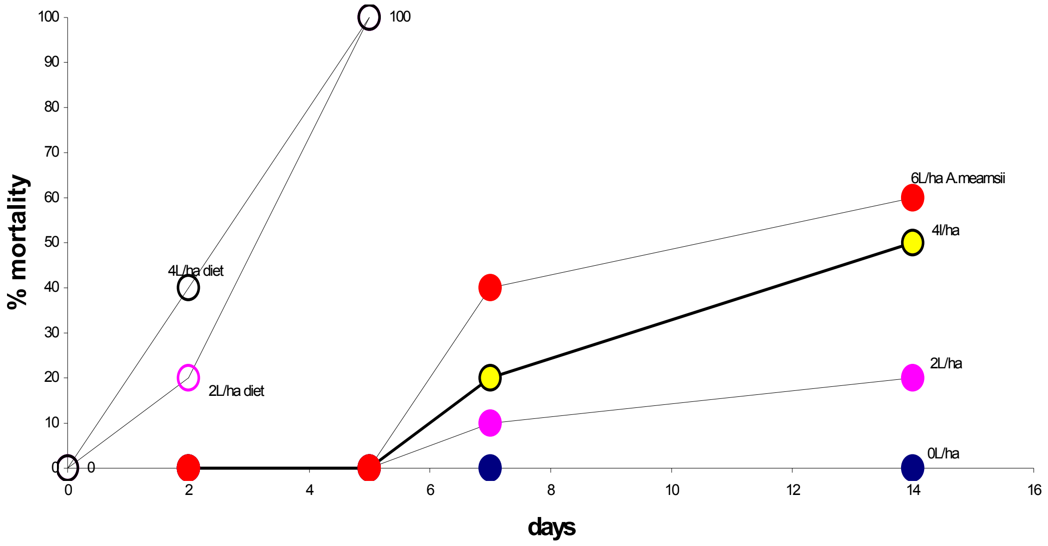

Figure 3.9. The mortality over time of fifth instar painted apple moth larvae feeding on artificial diet or *A. mearnsii* sprayed with Btk at various nominal rates

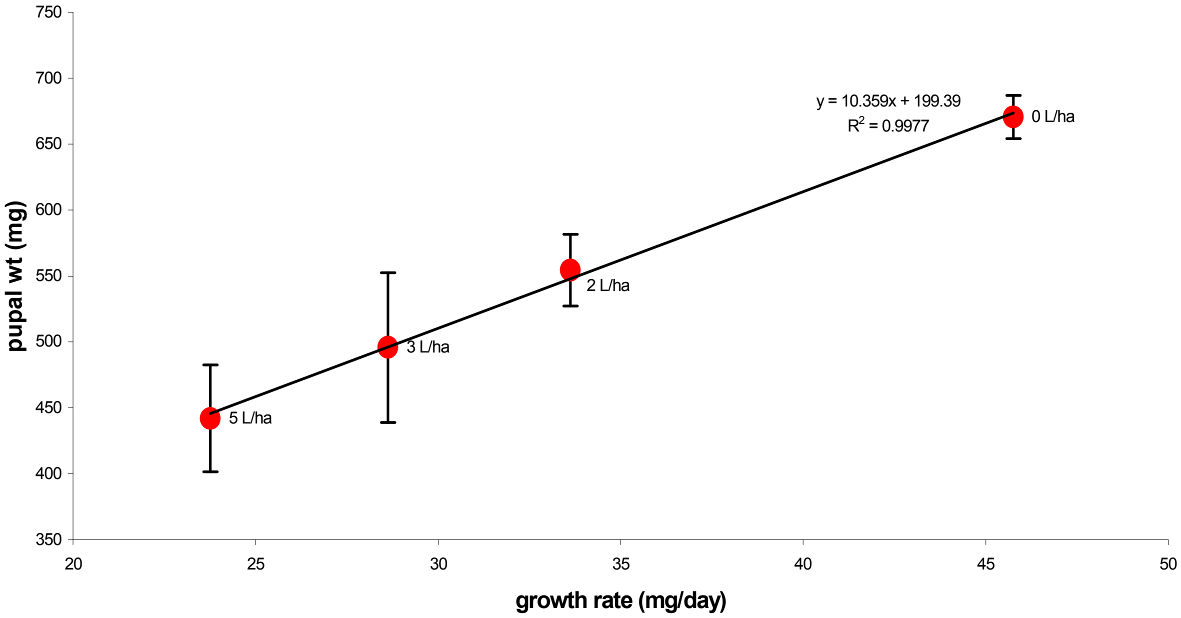

Figure 3.10. The effect of dose rate on the pupal weight and growth rate of fifth instar painted apple moth larvae feeding on treated *A. mearnsii*.

TABLE 3.1

Mortality of different larval instars on different host plants at different Btk application rates

Rate **Bt l/ha**	**%mortality 1st instar**			
	A. mearnsii	***C. laevigatus***	***P. lophanta***	***N. solandri***
0.165	12.7	98.7	52.7	72.7
2.57	37.3	100	100	100
2.59	50.7	100	100	100
5.55	79.3	100	100	95.3

Rate **Bt l/ha**	**%mortality 3rd instar**			
	A. mearnsii	***C. laevigatus***	***P. lophanta***	***N. solandri***
0.165	0	61.3	4	14.7
2.57	12	100	72	97.3
2.59	16	98.7	70.7	96
5.55	13.3	98.7	89.3	98.7

Rate **Bt l/ha**	**%mortality 5th instar**			
	A. mearnsii	***C. laevigatus***	***P. lophanta***	***N. solandri***
0.165	0	66.7	0	6.7
2.57	0	100	20	66.7
2.59	13.3	100	13.3	33.3
5.55	0	100	80	73.3

TABLE 3.2

The growth rate of control larvae on different host plants across all rate series trials

Series	Growth rate 1st instar			
	A. mearnsii	***C. laevigatus***	***P. lophanta***	***N. solandri***
0.165	0.36	0.09	0.047	0.055
2.57	1.61	0.6	0.12	0.16
2.59	0.98	0.047	0.092	0.078
5.55	0.38	0.005	0.067	0.047
Mean	**0.83**	**0.19**	**0.08**	**0.09**
SE	**0.30**	**0.14**	**0.016**	**0.026**

Series	Growth rate 3rd instar			
	A. mearnsii	***C. laevigatus***	***P. lophanta***	***N. solandri***
0.165	8.96	1.03	4.28	2.11
2.57	14.92	0.93	6.39	1.34
2.59	11.32	0.89	3.78	1.88
5.55	14.16	1.16	4.52	1.96
Mean	**12.34**	**1.00**	**4.74**	**1.82**
SE	**1.37**	**0.06**	**0.57**	**0.17**

Series	Growth rate 5th instar			
	A. mearnsii	***C. laevigatus***	***P. lophanta***	***N. solandri***
0.165	35.85	15.85	31.97	8.17
2.57	45.4	15	23.44	5.85
2.59	39.64	10.02	23.45	8.69
5.55	37.94	15.98	26.09	7.18
Mean	**39.71**	**14.21**	**26.24**	**7.47**
SE	**2.05**	**1.41**	**2.01**	**0.62**

Discussion

There is a good deal of theoretical and empirical support for the influence of host quality on the population dynamics of herbivores (White 1984, Hunter and Price 1992, Morris and Doyer 1997, Underwood and Rausher 2000). Host quality can be defined as the survival rate of larvae multiplied by their expected fertility (West and Cunningham 2002). Survivorship and reproductive capacity (*r*) are probably the most important parameters for the maintenance of any population. As long as *r* exceeds mortality a population has a chance of survival. The results show that larval growth rate is not only a good predictor of survivorship and *r*, but also indicative of mating success and potential inter-generational, maternal effects.

Plant defences that slow larval growth are usually referred to as sub-lethal defences. In this study slow larval growth rate on poor hosts often appeared lethal, but this may not have been intrinsically related to the quality of the host plant. The increased mortality at low larval growth rates may have been due to an increased susceptibility of larvae to pathogens and/or stress within the caged environs of the bioassays.

Price et al. (1980) suggested that there may be synergies between slowed larval growth rate and the susceptibility of larvae to pathogens and Anderson and May (1980) contend that pathogens, rather than invertebrate parasitoids, are major regulators of forest Lepidoptera. Many pathogens are characterised by achieving high host death rates by maintaining a high persistence in the benign, moist, shaded environment, typical of forests. In addition they are typically multi-generational within the generation time of their host. The behaviour of infected larvae also often facilitates pathogen dispersal, and pathogen infection rates tend to build throughout their host larval period – an effect compounded by slow larval growth (Campbell 1981).

The influence of within species host quality on the efficacy of *B. thuringiensis* has been recorded for gypsy moth (Hwang et al. 1995). A similar effect was recorded here for painted apple moth both within and among host plant species. It is possible that the apparent virulence of pathogens may be influenced by leaf characteristics, or plant architecture, which may affect the persistence and accumulation of pathogens on leaves. However, the within species result recorded here and by Hwang et al. (1995), should eliminate any plant architectural effect. The correlation of larval growth rate with apparent pathogen virulence suggests that some synergy exists between host plant quality and pathogen virulence and that larval growth rates adjusted for survivorship (as in Table 2.8) may be a legitimate measure of host quality. Even sub-lethal doses of pathogen appeared to be able to prolong larval development and reduce potential fecundity. If pathogen virulence is dose and body-mass dependent, as shown by the results of the Btk trials, hosts that provide the greatest larval growth rates offer the greatest benefit for population growth through both increased larval survival and greatest potential fecundity. For host plants an increased susceptibility of larvae to pathogens on secondary hosts would help maintain the resistance of those plants and essentially limit the resources available for the population growth of polyphagous insects.

Gender dimorphism and female aptery indicate a need to both conserve host resources and maximise *r* in gypsy moth and painted apple moth . Generally organisms need to maximise their fecundity just to overcome natural stochastic trauma. For the majority of Lepidoptera *r* is proportional to female pupal weight (Awmack and Leather 2002). A linear function exists between female pupal mass and potential fecundity in gypsy moth (Sharov and Colbert 1996) and was demonstrated in this study for both gypsy moth and painted apple moth. However, the correlation of potential fecundity with growth rate was found to be curvilinear, as body mass was achieved faster on higher quality hosts. However, potential fecundity does not necessarily equate to actual fecundity, or first instar survival (Leather 1998). Although the observed linear function between pupal mass and egg number suggests that eggs are of uniform mass, a number of studies have shown that individual egg dimensions may vary within an oviposition sequence (Rossiter 1991). Often, for species that oviposit *en masse*, the first laid eggs are larger. These are at the centre of the egg mass and are essentially protected by an outer layer of sacrificial smaller eggs. Therefore, the larger egg masses laid by females reared on better quality hosts should not only hold more eggs, but they are also likely to produce more viable offspring. In addition, Rossiter (1991) found that gypsy moth larvae from larger eggs had faster growth rates, higher fecundity and better resistance to Bt.

Diss et al. (1996) showed that although egg weight can vary for gypsy moth, it was the levels of two egg yolk proteins that influenced first instar survival and dispersal. This suggests that the best quality host plants provide the best conversion efficiencies that not only maximise the speed of development and fecundity, but also have beneficial intergenerational effects. Plant quality is a probably a key determinant of fecundity. Less salubrious hosts may have nutritional deficiencies or may require greater metabolic conversion costs and resources, to catabolise host plant defences and/or to overcome any physical barriers to digestion.

Other life history traits may also be affected by dietary deficiencies or conversion costs and, for dimorphic species in particular, there may be gender differences in any physiological trade-offs. In most insects there is a recognised trade-off between *r* and dispersal (Zera and Denno 1997), as both processes require distinct physiologies. Dispersal requires specific flight fuels, such as triglycerides, which are costly to synthesise. The bioassays using

Lymantriids showed that both gender were equally affected by host quality so increased conversion costs imposed by poorer hosts could affect male dispersal. Similarly, sperm load, the ability to compete for mates and even the detection of mates, could be compromised in male moths reared from sub-optimal host plants.

There are probably a number of subtle ways plant quality can influence the population dynamics of insects within and between generations. For polyphagous species the synchrony of the insect's life cycle to the availability of its host plant may not be critical, although host leaf quality may deteriorate with time (Feeny 1970, Stockhoff 1993). However, synchrony with other members of the adult population is obviously beneficial for the perpetuity of any species (Cole 1954), especially for univoltine, sexually reproducing, dimorphic species such as gypsy moth.

Normally a temporal overlap of the sexes insures greater female mating success (Ranlin and Kokka 2002). Gypsy moth is described as protandrous because males mature and emerge earlier than females. Robinet et al. (2007) imply that the peak of male and female gypsy moth emergence is asynchronous and a potential for reduced mating success occurs in insects such as gypsy moth, where individuals are only reproductively active for a limited time. A realistic longevity for adult gypsy moth is three days (Robinet et al. 2007).

The duration of the female gypsy moth pupal period recorded in this study did not appear to be related to pupal mass. However, the disparity in the onset of pupation between males and female showed a trend to increase inversely with larval growth rate, so that poor host quality not only has the potential to reduce adult numbers, but also may have the potential to create asynchrony in the emergence of adults and so decrease mating success. Mate isolation in time is equivalent to an Allee effect based on spatial isolation (McCarthy 1997, Calabrese and Fagan 2004). An asynchronous adult emergence leads to a temporal isolation of the sexes that decreases the number of males a female may mate with; decreases the probability of successful mating of contemporal individuals by effectively decreasing the number of males; and denies mating to a number of females. Reduced mating efficiency at low population densities, regardless of the specific cause, leads to an Allee effect and potential population extinction (McCarthy 1997).

For some insects ovipositing females have the ability to match offspring gender to host quality (eg Craig et al. 1992). However, apterous females can offer only limited parental care. In this study larval survivorship decreased with decreasing growth rate. For gypsy moth there was no gender bias in mortality towards the longer feeding female larvae. However, for the more dimorphic painted apple moth there was a significant female bias in mortality so that the adult sex ratio decreased with growth rate. Mathematically, greatest population growth is produced by female biased populations (Vlad 1989). The skew in sex ratio observed for painted apple moth lessens the number of females produced per mother, which should decrease population persistence (Craig et al. 1992, Doebeli and Koella 1994).

Plant quality has been implicated in the population dynamics of a number of forest defoliators (Baltensweiler 1977, Haukioja et al. 1987, Myers 1998). This study supports the growing recognition that poor host quality in its own right may be a potent form of resistance and that the addition of natural enemies may not be necessary to capitalise on a slow-growth-high mortality strategy (Williams 1999, Wise et al. 2006). Even the apparent paradox of increased feeding damage caused by slow growing larvae has been disputed (Wise et al. 2006) and was not apparent in this study. Rather, on poorer hosts, larval survival was reduced, growth was slower and the resulting pupae were smaller dramatically affecting the reproductive capacity of gypsy moth and painted apple moth. Furthermore, the sub-lethal effects of poor host quality could be exacerbated by pathogens. The effects of slowed larval growth rates were cumulative and had the potential to drastically affect population growth and conveyed that host plant choice is extremely relevant to the persistence of defoliator populations. It was interesting to note that pathogen susceptibility of painted apple moth larvae was high on an artificial meridic diet that provided high larval growth rates. This suggests that favourable host plants may provide some protection against disease and this maybe a significant factor in the evolution of host specialisation in defoliators.

On poor hosts the consequences of increased larval mortality and reduced fecundity on population dynamics would depend on the disposition of the environment. However, in all but the most benign environment larval growth rate could be considered a relevant measure of plant quality and should be included in any interpretation of a host plant. In the context of defoliator evolution, reduced survival, fecundity and mating success on poor hosts should provide a strong incentive for the specialisation of phytophagous insects.

Chapter 4

Nitrogen parsimony as a defence against defoliators in *Nothofagus*?

'The evidence for the generality of a relative shortage of nitrogen in the food of herbivorous insects is everywhere apparent' (White 1993)

Abstract

Bioassays with invertebrate defoliators have shown that the palatability of individual species of temperate *Nothofagus* is positively correlated with their geographic range. A mechanism to explain the differential palatability was investigated by examining the leaf nitrogen content of *Nothofagus* species, including those trees used in the original bioassays. Foliage from trees in the *Nothofagus* collections of ten European arboreta was sampled and analysed. There was a significant positive correlation between palatability (measured as larval growth rate in the bioassays) and leaf nitrogen for trees growing in these common garden situations. The findings suggest that the less palatable *Nothofagus* species may limit their uptake of nitrogen to avoid herbivory and that the stoichiometric ecology of specific *Nothofagus* ecosystems may have evolved in response to invertebrate herbivory.

Introduction

Theories of the trophic regulation of herbivore population dynamics have been dominated by the contrasting ideas of top-down regulation of defoliators by natural enemies (Hairston et al. 1960) and the bottom-up limitation of the resources available to defoliators by plants (Andrewartha and Birch 1961, White 1978, Andersen et al. 2004). While the regulatory actions of natural enemies are obvious, the specificity of bottom-up processes is often more difficult to prove because they may be multifunctional and contribute to other physiological plant processes. However, the evidence that plants defend themselves against defoliators is unequivocal (Herms and Mattson 1992, Karban and Baldwin 1997, Stamp 2003) and plants may limit the resources available to herbivores chemically, mechanically, temporally, or in any combination of these and/or additional strategies that include other organisms (Price et al. 1980, Larsson 2002).

A number of potential defence mechanisms against defoliators are exhibited by individual *Nothofagus* species. However, the correlation of palatability with the geographic range of *Nothofagus* species suggests that some form of quantitative defence, rather than a species-specific qualitative mechanism, may be responsible. Quantitative, dose-dependent, defences are considered to provide a broad spectrum barrier to defoliators and often take the form of mechanical structures that deter feeding, or digestion-inhibiting compounds.

Relative increases in leaf toughness or trichome density may provide mechanical barriers to larval feeding and digestion (Kanno 1996, Gutschick 1999) and some *Nothofagus* species exhibit dense trichomes (eg *N. glauca*) and tough coriaceous leaves are typical of some of the non-deciduous species (eg *N. menziesii* and *N. cunninghammii*). Leaf toughness increases with leaf age, however, the majority of the temperate *Nothofagus* species are deciduous and significant differences have been found in the palatability to polyphagous Lepidopteran defoliators within both evergreen and deciduous species (Matsuki et al. 2001, Kay 2003).

The growth and development of gypsy moth is affected by defensive plant compounds (Bowers and Puttick 1988, Berenbaum 1998). However, the Fagales, as a whole, has little in the way of unique chemistry (Bate-Smith 1962) that could categorically be defined as defensive, although *Nothofagus* species may possess ‘quantitative’ digestion-inhibiting, multifunctional, tannins, tri-terpenes, etc., typical of many ‘apparent’ (*sensu* Feeny 1976) tree species. However, the support for Feeny’s Apparency hypothesis is ambivalent (Forkner et al. 2004) as insects vary in their response to polyphenolics (Barbenhenn et al. 2003). Gypsy moth is reported to have a high mid-gut pH and surfactants that limit the ability of phenolics to block protein catabolism (de Veau and Schultz 1992). Some ‘qualitative’ chemical compounds with biological activity, have been extracted from the leaves of some *Nothofagus* species (Russell et al. 2000, Thoison et al 2004). However, it is always difficult to assign specific end uses for unique compounds extracted from leaves with unnatural solvents and it has been found that different insects may respond contrarily to different compounds within the same plant (Hare & Futuyma 1978, Sims & Rausher 1989, Marquis 1990, Maddox & Root 1990). A search for specific anti-feedant compounds to explain the differential palatability of *Nothofagus* species to polyphagous defoliators could prove to be an infinite and indefinite task.

One aspect of quantitative plant chemistry that is difficult for insects to counter, is the nutritional value of tree leaves. Gypsy moth growth and development is affected by diets low in vitamins and minerals (Lindroth et al 1991) and it is generally conceded that the growth rate of many defoliators is limited by nutrient deficiencies rather than the energy content of their diet (Sterner and Esler 2002). Plants are often nutritionally sub-optimal for insects (Gordon 1961, Schoonhoven 1969, Schoonhoven et al. 1998, Sterner and Esler 2002). The negative effects of nutritionally-imbalanced diets on insect development have been reviewed for a number of insects and nutrients (Dadd 1973), but the dominant role of leaf nitrogen in folivore diets has often been demonstrated (McNeill and Southwood 1978, Mattson 1980, Fagan et al. 2002, White 2005). The low nitrogen content of tree leaves is considered a particularly significant 'hurdle' for folivorous insects (Southwood 1973, White 1993) and Scriber and Slansky (1981) showed that larval growth rates of a range of insect species across a number of different forest trees and shrubs, were positively correlated with leaf nitrogen levels.

The potential role of nutrient imbalance as a plant defence against herbivory has been suggested (Moran and Hamilton 1980, Neuvonen and Haukioja 1984). Byrant et al. (1983) formalised the Carbon/Nutrient Balance hypothesis (CNB) that proposed that the relative availability of carbon (via photosynthesis) and nutrients to plants would determine the use of those elements in defensive compounds. However the failure of the CNB to account for many exceptions (Herms and Mattson 1992, Koricheva et al. 1998) has lead to suggestions that the domination of the CNB has forestalled the search for alternative hypotheses for the role nutrients in plant defence (Hamilton et al. 2001, Niato et al. 2002).

There is limited information about the leaf nitrogen content of *Nothofagus*. Foliar nitrogen analysis of New Zealand species suggests that nitrogen content proceeds as *fusca<menziesii<truncata<solandri-cliffortioides* (Adams 1976). Of the S. American species, *N. betuloides* has been recorded as having less leaf nitrogen than *N. pumilio* (Armesto et al. 1992). This study investigates to what extent leaf nitrogen equates with the differences in larval growth rates recorded for gypsy moth feeding on temperate *Nothofagus* species.

Methods

In June 2006 leaf samples were taken from the *Nothofagus* specimens in ten arboreta of UK and Ireland (Table 4.1) from which foliage had been obtained for the gypsy moth bioassays of 2002. Leaf nitrogen values can vary temporally and spatially (within the canopy and within landscapes), so every effort made to standardise sampling method and complete the bulk of the sampling within 14 days.

Where possible the foliage samples were collected from the same trees as those that were used in the 2002 bioassays. A number of arboreta had multiple specimens of *Nothofagus* species and foliage was taken from as many specimens of each species as was practicable. Over 75 trees were sampled. All arboretum curators believed that no fertiliser had been applied to the specimens, but all arboreta were probably subject to some degree of atmospheric nitrogen pollution.

Samples consisted of five terminal branchlets holding fully expanded new foliage. They were removed from the southern aspect of the canopy of each tree at about 2m above ground level. The shoots were placed in Ziplok™ plastic bags and kept on ice until the leaves were removed and combined (within 24 hrs) for oven drying to a constant weight at 50º. The dried leaves were transported to New Zealand where they were ground before nitrogen analysis was undertaken at the Veritec lab. Rotorua, using a Leco CNS-2000 analyser that utilises a modified Dumas method for nitrogen determination.

Larval growth rate data was taken from the extensive gypsy moth bioassays of 2002 (Chp. 2).

Statistical Analysis

Simple linear regression analyses were used to identify correlations between female larval growth rates and percentage leaf nitrogen. ANOVA and Least Significant Difference test were performed using SAS Version 3.2.2 software to identify species differences in percent leaf nitrogen.

Results

The ANOVA of results of the leaf analyses showed that there were significant differences between species (F = 8.09, p<.0001) in leaf nitrogen content. The differences tended to be species specific with the highest leaf nitrogen levels found in the South American species, while the lowest were predominantly from New Zealand species (Table 4.2).

For the trees that could be identified as having supplied foliage for the 2002 bioassays, there was a significant positive correlation (*P* < .01) of leaf nitrogen content with the recorded growth rate of female gypsy moth larvae (Figure 4.1). This was replicated (*P* < .01) in the correlation (Fig 4.2) of the mean species' values of leaf nitrogen from all trees of *Nothofagus* analysed (Table 4.2) with the mean growth rate of all female gypsy moth larvae reared on those species in 2002 (Table 2.2).

TABLE 4.1
The arboreta from which Nothofagus samples were taken for % leaf nitrogen analysis.

Arboretum	**Location**	**Number *Nothofagus* species sampled**	**Date of sampling**
Wakehurst Place	England	12	31.5.06
Rowallane	Nth Ireland	8	7.6.06
Mount Stewart	Nth Ireland	8	8.6.06
Earlscliffe	Ireland	1	9.6.06
Mount Usher	Ireland	9	10.6.06
Mount Congreve	Ireland	9	11.6.06
JF Kennedy	Ireland	8	12.6.06
Fota	Ireland	5	13.6.06
Hilliers	England	9	17.6.06
RBG Scotland	Scotland	9	19.6.06

TABLE 4.2

Percentage leaf nitrogen for species of Nothofagus from arboreta in UK 2006. (species followed by the same letter do not differ significantly, p= 0.05)

Nothofagus species	**Number of trees sampled**	**Mean % leaf nitrogen**	**LSD**
antarctica	9	2.79	a
obliqua	9	2.63	ab
pumilio	4	2.48	abc
alpina	9	2.30	bcd
fusca	8	2.09	cde
glauca	3	1.99	cdef
betuloides	8	1.90	def
dombeyi	8	1.95	ef
moorei	2	1.94	cdef
menziesii	7	1.76	ef
truncata	1	1.74	def
cunninghamii	8	1.73	f
solandri	9	1.71	f
alessandri	1	1.63	def

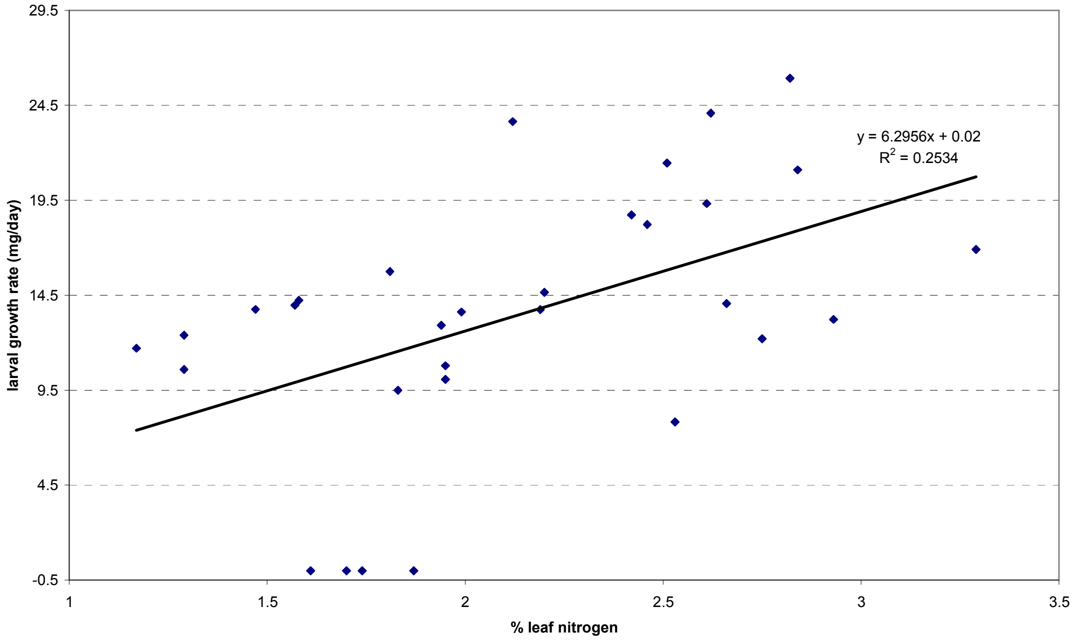

Figure 4 1. The correlation of the % leaf nitrogen in 2006 of individual *Nothofagus* trees of various species, with the larval growth rates of female gypsy moth reared from those trees in the bioassays of 2002 (P< 0.01).

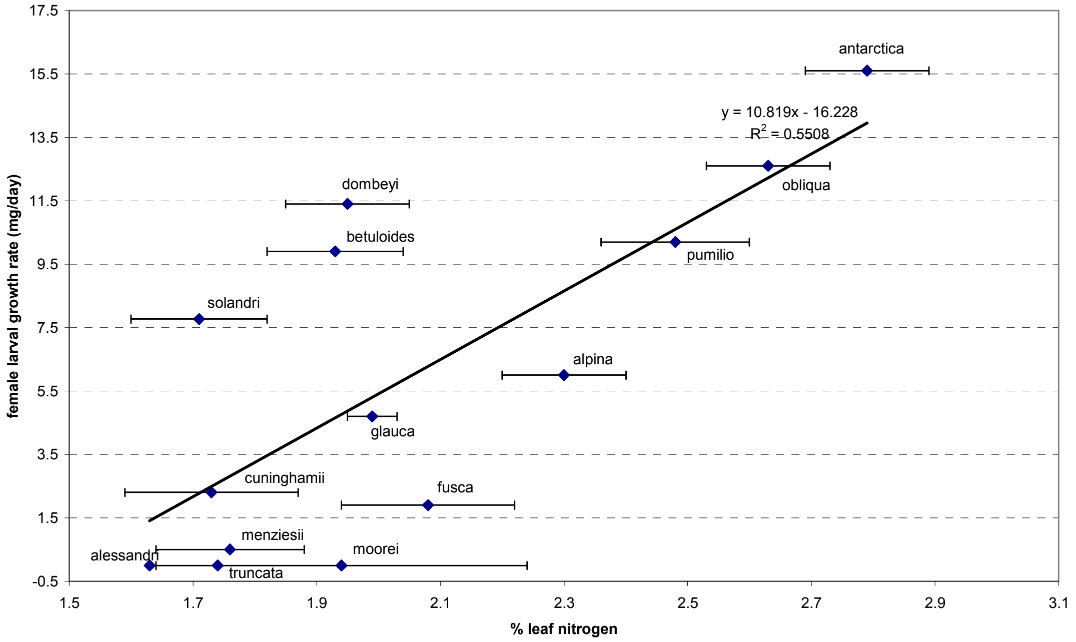

Figure 4 2. Correlation of the mean % leaf nitrogen of all trees sampled in 2006, with the mean larval growth rate of female gypsy moth recorded from those species in 2002 (P< 0.01).

Discussion

The leaf nitrogen analysis reported here took place four years after the larval gypsy moth bioassays. The leaf nitrogen status of individual trees may have changed over that time. However, the foliage sampled for this study came from trees in 'common garden' situations. As such, each species presumably had the same opportunity to acquire nitrogen, yet leaf nitrogen was relatively species-specific and apparently independent of available nitrogen. The results of the leaf analyses also concur with the limited published data for *Nothofagus* (Adams 1976, Armesto et al 1992), as well as the results from ten *Nothofagus* species in a Tasmanian arboretum (Kay and Smith 2005).

For plants, low leaf nitrogen could be an evolutionary adaptation to nutrient poor soils, but given the advantages to growth and reproduction that would result from increased nitrogen uptake, it is difficult to explain why 'low nitrogen' plants would not have a facultative response to increased nitrogen availability. That they don't, suggests that some plants benefit from a parsimonious nitrogen strategy.

Mooney and Gulmon (1979) suggested that the metabolic costs of unrestricted absorption of nitrogen may not necessarily be beneficial to plants, as it could lead to increased herbivory. Increased dietary nitrogen promotes insect larval growth and hence the population growth of insects (Scriber and Slansky 1981, Neuvonen and Haukioja 1984, Andersen et al. 2004, White 2005). Although the role of nutrient imbalance in plant defence has yet to be resolved (Niato et al 2002, Craine et al. 2003) the potential influence of stoichiometry on insect population dynamics has recently been more widely advocated (Esler et al. 2000, Fagan et al. 2002, Andersen et al. 2004, Moe et al. 2005).

Stoichiometric ecology – the balance of chemical elements in biological interactions (Sterner and Esler 2002) – highlights the tradeoffs between resource acquisition (usually in terms of carbon, nitrogen and phosphorous) and the functional consequences of organisms' biochemical composition (Kay et al. 2005). It provides a framework for linking variations in life strategies – particularly of plants – to food web dynamics and hence to the functioning of ecosystems (Sterner and Esler 2002).

Plants are pivotal to the development of terrestrial ecosystems. They are autotrophic, harnessing the sun's energy in a form that can be passed among heterotrophs. Plants also sequester the nitrogen essential for the proteins of the heterotrophic community. Nitrogen is the key element limiting primary production in most ecosystems (Vitousek and Howarth 1991). However, the nitrogen content of plants is far more variable, and a magnitude less concentrated, than that of their consumers (Esler et al. 2000, Sterner and Esler 2002).

The differences in nitrogen accumulation by plants have been recognised for some time (Knops et al 2002), with some plants appearing almost redundant to the ecosystem nitrogen cycle (Reich et al. 1997). The uptake and assimilation of nitrogen regulates plant carbon metabolism and photosynthesis and it is under strict genetic control (Scheible et al. 1997, Oliveira & Coruzzi 1999). The bulk of leaf nitrogen comprises the enzymes responsible for photosynthesis and there is a robust positive relationship between leaf nitrogen and photosynthetic capacity (Hollinger 1996, Glass 2003). It follows that the productivity of plant based ecosystems is not only nitrogen limited, but it is also sensitive their species' composition (Vitousek et al 1987, Wedin & Tilman 1990). However, the dynamics of the nutrient exchange between plants and their consumers within an ecosystem can be complex.

Differences in nitrogen accumulation by plants may be magnified by internal feedbacks (de Mazancourt et al. 1998), which may provide a stoichiometric mechanism by which plants can influence herbivory (Cebrian and Lartigue 2004). On the other hand, herbivores can influence the nutrient cycling and productivity of ecosystems (Pitelka 1964, Chew 1974, Mattson and Addy 1975). Even at endemic population levels, the activity of defoliators has been shown to affect the mobilisation of carbon and nitrogen between above and below ground systems (Bardgett and Wardle 2003, Frost & Hunter 2004). Herbivores are also capable of determining the plant species composition of ecosystems by selectively feeding on palatable plants (Louda et al. 1990, Schowalter 2000, Hunter 2001).

Presumably the species-specific variation in plant nitrogen accumulation is a reflection of the evolution of different plant life strategies, which in turn, influence the input of nitrogen to other trophic levels within an ecosystem (Gutschick 1999). The evolution of a stable ecosystem should therefore depend on the life strategies of the plant and consumer species within that community (Futuyma and Mitter 1997, Lerdau and Gershenzon 1997, Cornelissen et al. 1999, Agrawal 2004).

The leaf analysis of *Nothofagus*, when coupled with the larval growth data from the 2002 bioassays, reiterates the fact that host plants with low leaf nitrogen bestow low larval growth rates upon their defoliators (Slansky and Feeny 1977, Slansky 1978, Scriber and Slansky 1981). However, limited leaf nitrogen content could potentially be countered by herbivores through compensatory feeding and extended development (Slansky and Feeny 1977, Mattson 1980, Feeny 1991, Woodward et al. 1991). To advance plant fitness, any increase in leaf consumption by defoliators would have to be off-set by an increase in consumer mortality – the slow-growth-high-mortality hypothesis advocated by Clancy and Price (1987). Although compensatory feeding was not examined here, Chapter 3 showed significantly increased larval mortality and other effects detrimental to population growth, occurred when larvae fed on host plants that slowed larval development.

A defence based on nitrogen parsimony (NPD) would act as a broad spectrum defence that would be difficult for defoliators to circumvent – although there is some evidence for the influence of stoichiometry on the evolutionary diversification of insects (Fagan et al. 2002). Although NPD would constrain plant growth it should reduce the need for any additional metabolically-costly defences. It should also have synergies with an evergreen habit, as leaf nitrogen is negatively correlated with leaf longevity (Williams et al. 1989, Reich et al. 1997, Wright et al. 2004), as well as having a benign influence on defoliator natural enemies that may be vulnerable to secondary plant compounds (Barbour et al. 1993, Dyer 1995).

A defence based on a nitrogen parsimony that slows the larval growth of folivores would be in apparent agreement with resource availability hypothesis (RAH) (Coley et al. 1985) and the apparently universal trade-off between plant growth and defence (Fine et al. 2006). The RAH argues for the necessity of a defence for plants whose growth is constrained by the availability of nutrients. The RAH implies that slow-growing trees have limited ability to compensate for tissue loss and would benefit from a greater investment in defence (de Jung 1995), but this could represent a considerable metabolic drain to a 'slow growth' physiology and could necessitate continuous co-evolutionary adaptations (Erlich & Raven 1964, Farrell et al 2001). The NPD, although not excluding the possibility of other defence mechanisms, would argue that nitrogen is uptake is minimised to escape herbivory and that slow plant growth is a consequence of such minimalism.

Plant defence against herbivory is rarely the result of a single plant trait (Matsuki and MacLean 1994, Kause et al. 1999). Leaf toughness is often an impediment to first instar larvae (Lucas et al. 2000), but this was probably not an issue here as larvae were fed new season's foliage and slow larval growth occurred through all instars. Gypsy moth is a very large caterpillar and physically capable of coping with a wide variety of leaf types (Liebhold et al. 1995). However, constitutive or induced chemical defences may also play a role in the resistance of some unpalatable *Nothofagus* species.

Some plant defence compounds, such as phenolics, are carbon, rather than nitrogen-based, and the CNB (Bryant et al. 1983) would predict a preponderance of these compounds where nitrogen is a limiting resource. A number of the least palatable *Nothofagus* species arguably possessed sufficient leaf nitrogen to allow some larval growth or survival. Many defoliators live at the limits of their energy and nitrogen budgets (Mattson 1980, White 2005), but there must be a limit to which leaf nitrogen can be abated yet still allows a plant to maintain a competitive edge. There are undoubtedly some insects that will adapt to low extremes (eg Fox and Macauley 1977). Species such as *N. menziesii* and *N. truncata* appear to have sufficient leaf nitrogen to support some larval growth, yet they were consistently resistant to defoliators. This suggests that these species may utilise other defence strategies to bolster the NPD. *N. alessandri* had low leaf nitrogen but it has also been identified as being particularly well defended against herbivory – possibly by carbon based flavanoids and stilbenes (Russell et al. 2000).

Low leaf nitrogen was typically found in *Nothofagus* species from geographically constrained habitats and NPD may be a first line of defence for plants in island ecosystems. The unique island character of the New Zealand flora has been construed as a response to isolation in a habitat with a benign climate and a moderate to low soil fertility (McGlone et al. 2004). However, many of its floristic features could equally be explained as a response to invertebrate defoliation. Although leaf life strategies are undoubtedly the result of multifunctional synergies, the prevalence of the evergreen habitat in the New Zealand flora is consistent with invertebrate herbivore selection pressure, and the flora is renowned for its lack of response to fertilisers (Lee and Fenner 1989, Davis et al. 2004). It may also be significant that the New Zealand *Nothofagus* forests do not contain associate nitrogen-fixing species (Wardle 1984), whereas those of South America do (Veblen et al. 1996); and the introduction to Hawaii of a nitrogen-fixing tree dramatically changed the ecosystems where no native nitrogen-fixers had been present (Vitousek et al. 1987).

The understanding of the relationship between the response of plants to environmental factors and traits that determine effects of plants on ecosystem function is rudimentary, but Lavorel and Garnier (2002) predict it will most likely to be biogeochemical. Foliar defences against invertebrate herbivory undoubtedly affect litter fall decomposition and nutrient cycling (Wardle et al. 1998, Cornelissen et al. 2004). If nitrogen parsimony is a common defence against herbivory, it would be further evidence that invertebrates can influence plant productivity and ecosystem processes (Mulder et al. 1999). The idea that ecosystem dynamics is influenced by defoliators is not new (Chew 1974, Schowalter et al. 1991, Hunter 2001), but an NPD would highlight the role of stoichiometry in ecosystem function.

Chapter 5

A resource allocation hypothesis to explain the resistance of New Zealand flora to invasive defoliators.

"*the time is ripe for the synthesis of a novel paradigm of spatial ecology with the classical paradigms of top-down and bottom-up studies*." Gripenberg & Roslin 2007

Abstract

The demonstrable resistance of the New Zealand flora to 'sophisticated' continental defoliators does not concur with entrenched ideas of the inherent invasibility of islands. An hypothesis was developed to account for the resistance of New Zealand plants to invasive invertebrates. It argues that the low species: area ratio, typical of islands, results in simple food webs that limit the top-down regulation of herbivores by their natural enemies. Using *Nothofagus*, the dominant Southern Hemisphere forest genus, analysis shows that the geographic range of a plant species and/or the proportionate diversity of its associated invertebrates, are significant predictors of plant resistance to defoliators. The hypothesis contends that the resistance of plant species to invertebrate herbivores should be inversely proportional to their geographic range. Plants that are restricted to small isolated habitats such as oceanic islands, or form spatially restricted habitats in their own right, do not support complex food webs and must limit defoliator populations through bottom-up processes to maintain a 'green world' stability. Conversely, plants with large geographic ranges will have comparatively poor self-defence, because they support a greater trophic complexity that provides a top-down regulation of defoliators.

Introduction

The Southern beeches (*Nothofagus*) were long considered the only representatives of the Fagaceae in the Southern Hemisphere. Now they are more often placed in their own family, Nothofagaceae, but none the less are most closely related to the Fagaceae of the Northern Hemisphere. *Nothofagus* was a significant component of the Gondwanan continent in the late

Cretaceous and paleopollen data indicate that the three extant temperate subgenera were widespread prior to the tectonic fragmentation of the continent (Dettman et al 1990, Hill 1992, McGlone et al. 1996). Thirty-five species are currently recognised and about half of these, classified into three subgenera, are restricted to the temperate forest of New Zealand, Australia and South America. The subgenus *Nothofagus* is now restricted to S. America, but the subgenera *Lophozonia* and *Fuscospora* are present in S. America, Australia and New Zealand. A fourth subgenus, *Brassospora* is restricted to the montane regions of Papua New Guinea and New Caledonia (Linder and Crisp 1995). All of the *Brassospora* are evergreen, but deciduous species occur within the other three subgenera.

New Zealand has been geographically isolated from continental landmasses for about 65Myr. Although New Zealand has variously been described as a small continent or a large island (Daugherty et al. 1993), its isolation, coupled with periods of marine transgression and glaciation that at times may have restricted any surviving endemics to tenuous refugia (Fleming 1978, Stevens 1980, Trewick et al. 2007), has limited the existing endemic biota to a state considered depauperate even by island standards (eg bracken insects, Rosenzweig 1995, and ants Rosenzweig *pers. comm.*).

Insular biotas are typically described as relictual, depauperate and disharmonic (Paulay 1994). They hold significantly fewer species than equivalent mainland habitats (Rosenzweig 1995, Whittaker 1998), but are characterised by high levels of endemicity. New Zealand has a high level of endemicity (Allan 1982, Dugdale 1975, Patrick 1994), but a noticeable lack of vertebrates and significant gaps in the invertebrate fauna. Prominent Lepidopteran taxa are absent, despite the presence of potential hosts (Dugdale 1988). The renowned forest defoliators, Lymantriidae, are absent and higher taxa of the Hymenoptera that include many predators and parasitoids of other invertebrates, are also missing or under-represented (Valentine and Walker 1983).

It has been argued that ecosystems with little biodiversity lack a ‘biotic resistance’ to invasive species (Elton 1958, Carlquist 1965). The entrenched equilibrium theory of island biogeography (ETIB) contends that the simple island biotas are the result of a dynamic equilibrium between the continuous immigration and extinction on islands (MacArthur and Wilson 1967). There are abundant examples of species invasion and extinction in insular ecosystems colonised by man, so it is not surprising that the vulnerability of island ecosystems has become ingrained in mainstream ecology.

Island biogeography theory has also had a strong influence on the description and assessment of insect-plant interactions. Southwood's (1961) seminal study of the trees of Britain showed that the diversity of phytophagous insects associated with a tree species increased with the geographic range of that tree. Janzen (1968) proposed that the theoretical framework of the ETIB could be applied to insect-plant relationships by considering individual plants or species as ecological islands for their associate invertebrates. Strong et al. (1984) also suggested that plant patches could be considered as islands surrounded by other vegetation, and it is recognised that plant size or architecture can be equated to the habitat size and the diversity of associated invertebrates (Strong 1979, Southwood 1978, Denno and Roderick 1991). The species/host area concept was reaffirmed by Kelly and Southwood (1999) and Brändle and Brandl (2001) for the tree genera of Germany. It was refined with the inclusion of a function for host biomass within the British Rosaceae (Leather 1986), but interestingly, given the conservative host range of most phytophagous insects, host plant phylogeny was inconsequential and made no significant statistical improvement to the model (Kelly and Southwood 1999, Brändle and Brandl 2001).

Feeny's (1976) Apparency hypothesis related plant defences to their associated invertebrate load by suggesting that the potential for insect-plant interaction was determined by the numbers of phytophagous insects associated with the plant. He contended that plants with greater defoliator diversity would be more heavily defended *i.e.* plant species with greater geographic ranges would be at risk from more insects and therefore more heavily defended and less able to be 'invaded' by novel defoliators. However, the Apparency theory and other attempts to relate community structure to the evolution and deployment of plant defences have had little predictive success (Berenbaum 1999, Stamp 2003, Forkner et al. 2004).

The biogeographical concept of species/host area allowed Strong et al. (1984) to draw inferences of the ecological processes of insect-plant interaction, but little advancement appears to have been made since (Lill et al. 2002, Lewinsohn et al. 2005). The appealing logic of the ETIB has also failed to flourish as it is not well supported empirically (Whittaker 1998, 2000, Brown and Lomolino 2000, Anderson and Wait 2001, Davis et al. 2001, Hubbell 2001, Wilson 2001, Walter 2004). However, recently the benefits of biogeographical ecology have been advocated as providing a mechanism to understand multiple species interactions (Naeem and Wright 2003).

Large-scale biogeographic patterns are determined by species-level interactions. However, the extrapolation of paired species interactions, typical of insect-plant studies, often yield results contrary to those observed in natural communities (Sih et al 1985, Wootton 2002). Unfortunately the enormous resources required for multi-species experiments make detailed community research prohibitive, so the effect of multiple species interactions on the selection of plant traits, such as resistance to defoliators, remains difficult to elucidate.

The species composition of a community has a role in the evolution of plant defences (Hunter and Price 1992). Obviously the potential for species interactions within a community is determined by the biodiversity of that community. Biodiversity is a function of space (Rosenzweig 1995), so that space (habitat area, or the inter-connectedness of similar habitats) has a major influence on species interactions. It is becoming increasingly recognised that habitat area is important in regulating the dynamic behaviour of ecosystems (Levin 1992, Hanski 1998, Maurer 1999, Chase and Leibold 2002, Leibold et al. 2004, Roslin and Kotze 2005, Gripenberg and Roslin 2007). Rosenzweig (1995) makes a strong case for habitat area as the sole determinant of biodiversity, but there may be some amelioration of the influence of habitat area by habitat productivity, in terms of temperature, insolation and precipitation – the metabolic theory of ecology (MTE) (Allen et al. 2002, Brown et al. 2004).

The results of the bioassays described in Chapter 2 showed that plants in spatially constrained habitats were resistant to invertebrate defoliators. The results are contrary to both the normal expectations from the ETIB, invasion ecology and conventional plant defence theories. Here the differences in leaf defence of *Nothofagus* species with different geographic ranges, different leaf longevities, different habitat productivities and different invertebrate biodiversities, is explored to provide a plausible explanation for the bioassay results.

Methods

The bioassays of *Nothofagus* species with the gypsy moth in 2002 represent the most extensive data set and they were used in the formulation of the hypothesis. The measure of plant resistance to the gypsy moth was taken as the survival adjusted measurement of female larval growth rate recorded in Table 2.8.

The area (km^2) occupied by individual *Nothofagus* species was taken from a conversion of the latitudinal and longitudinal limits of their recorded geographic range (Table 5.1). The geographic and altitudinal limits of the New Zealand species were taken from Wardle (1984); for the Australian species from Read and Brown (1996); and for the S. American species from Donoso (1996) and Veblen et al. (1996). For some species, particularly those that have suffered from forest clearance, the extant range is considerably smaller than the recorded range limits.

The invertebrates known to be associated with *Nothofagus* species have been recorded by McQuillan (1993). He focussed on insects directly interacting as consumers of *Nothofagus* species. However, as he states, the sampling effort in investigating those invertebrates was very uneven between provenances. Recorded diversity is proportional to sampling effort (Rosenzweig 1995). The disparity of McQuillan's data set was overcome by using the invertebrate data of Russell et al (2000), who took standardised beat samples from New Zealand and S. American *Nothofagus* species during the 1995-6 summer. They recorded the total number of recognisable taxonomic units (RTUs) jarred from five trees of each species. Here the two taxa of *N. solandri* were considered as one species (as for Chpt 2) and the higher RTU value of *N. solandri* var. *solandri* was used in the analysis. The RTUs captured included all guilds from consumers, predators to 'tourists' and numbers were higher than those recorded by McQuillan (1993). The Russell et al. (2000) data set was supplemented by identical beats from the Tasmanian species, *N. gunnii* and *N. cunninghamii* in the summer of 2005-6 (Kay and Smith 2006 unpubl. report). Beat samples of *Nothofagus* were also undertaken at Wakehurst Place in June 2006. Defoliators were recorded from five separate beat samples about the lower canopy of each tree using a standard $1m^2$ beating tray. The caterpillars collected were identified by Nick Fielding, Alice Holt, UK Forestry Commission.

Habitat productivity of each *Nothofagus* species was taken as the mean annual temperature, as determined from the Hopkins bioclimatic rules (MacArthur 1972) for the mid-latitudinal, mid-altitudinal position of each species (Table 5.1).

Statistical Analysis

Simple linear or polynomial regression analyses were used to identify correlations between host species' geographic range and female larval growth rate, for both deciduous and evergreen host species, species geographic range and the number of species associated invertebrates and a log transformation of the same; the product of species geographic range and climatic modifier and the number of species associated invertebrates; product of species geographic range and climatic modifier and female larval growth rate, as well as the number of species associated invertebrates and female larval growth rate. An analysis of covariance was done to determine if there was any real difference between the regressions of deciduous and evergreen species. The growth rate of female gypsy moth larvae on 15 species of *Nothofagus* in relation to host species geographic range, a climatic modifier (MTE), species leaf longevity, species specific leaf nitrogen, the number of host species associated invertebrates, landmass origin of host species and their respective subgenus. An ANOVA, was followed by step-wise regression, and a Bayesian analysis considering all possible models.

Results

There was a significant positive linear correlation ($P < 0.001$) between species' geographic ranges and the survival adjusted growth rate of female gypsy moth larvae that fed upon them. The statistical significance was improved with as a curvilinear relationship (Figure 5.1), but a slightly less significant correlation was seen when the 'potential larval growth rate' (*sensu* Chpt 2) was used as a correlate ($R^2 = 0.61$). The correlation was seen for each sub-genus, with *N. obliqua* the most prominent outlier.

The relationship held regardless of leaf longevity. No significant difference was found in an analysis of covariance comparing the linear regression of larval growth rate for either deciduous or evergreen species (Fig 5.2)

A similar relationship was seen for the number of invertebrates associated with individual *Nothofagus* species (Fig 5.2). The statistical significance ($P < 0.05$) was improved ($P < 0.01$) with the inclusion of the Tasmanian species data. As with the correlation of geographic range with larval growth rate (Figure 5.1) *N. obliqua* was the most prominent outlier. This was remedied somewhat, and the relationship improved, with a log transformation (Fig 5.4) or by including a function for habitat productivity (Figure 5.5). However, this was not the case when the habitat productivity function was included for the larval growth rate correlation (Figure 5.6). *N. obliqua* showed better conformation, but the high altitude, high latitude *N. antarctica* became an outlier.

The correlation of either 'potential' or adjusted larval growth rate with the number of invertebrates associated with individual *Nothofagus* species was positive and statistically significant (Figure 5.7; $P < 0.01$). The significance was improved slightly with the inclusion of the data for Tasmanian species *N. cunninghamii*. (*N. gunnii* was not available for the original bioassays, and no beat sampling was done for the Queensland species *N. moorei*.).

The caterpillars collected beaten from foliage at Wakehurst Place were common polyphagous species (Table 5.2) and included the ubiquitous Lymantriid *Orgyia antiqua*. The catch reflected the palatability of the tree species and defoliators were only recorded from the South American beech species. No defoliators were recorded from the New Zealand beech species.

TABLE 5.1

*Geographic and climatic parameters of Nothofagus species (D= deciduous, E = evergreen) and the diversity of their associate invertebrates – from Russell et al. (2000) and * Tasmanian beat samples.*

Nothofagus sp.	Area $10^3 km^2$	Mid-latitude	Mid-altitude m asl	Latitude mean ºC	MTE range correction	Invertebrate diversity
betuloides E	104	48.33	600	5.7	250.7	53
dombeyi E	112	41.33	1250	10.8	438.0	48
nitida E	83	43.83	500	9.0	516.5	36
alpina D	39	38.25	500	13.0	400.5	56
obliqua D	70	37.25	900	13.7	615.6	103
pumilio D	150	45.13	1000	8.0	379.6	51
antarctica D	162	46	1000	7.4	307.8	64
glauca D	16	35.25	600	15.2	190.3	22
alessandri D	0.1	35.5	600	15.0	1.2	31
menziesii E	38	42	700	10.3	245.1	38
fusca E	37	41.75	500	10.5	286.1	34
truncata E	17	39.5	300	12.1	177.9	28
solandri E	62	41	700	11.0	444.9	64
gunnii D	2	42	900	10.3	10.7	10*
cunninghamii D	15	39.5	750	12.1	119.8	30*

TABLE 5.2

The catch from five beat samples of Nothofagus species at Wakehurst 28th June 2006. (n) = number of trees sampled.

Nothofagus *species* (n)	No. of oliators	Defoliator identity
obliqua (3) S.Am	4	2 late instar Noctuidae (*Orthosia cerasi*?) 2 late instar Lymantriidae (*Orgyia antiqua*?)
antarctica (3) S.Am	3	1 late instar Geometridae (*Biston betularia*?) 1 late instar Tortricidae (*Ditula angustiorana*??) 1 late instar sawfly (*Arge ustulata*??)
pumilio (2) S.Am	1	1 mid instar Geometridae (*Biston betularia*?)
betuloides (3) S.Am	0	
dombeyi (3) S.Am	0	
glauca (3) S.Am	0	
alpina (3) S.Am	0	
fusca (3) NZ	0	
solandri (3) NZ	0	
menziesii (1) NZ	0	

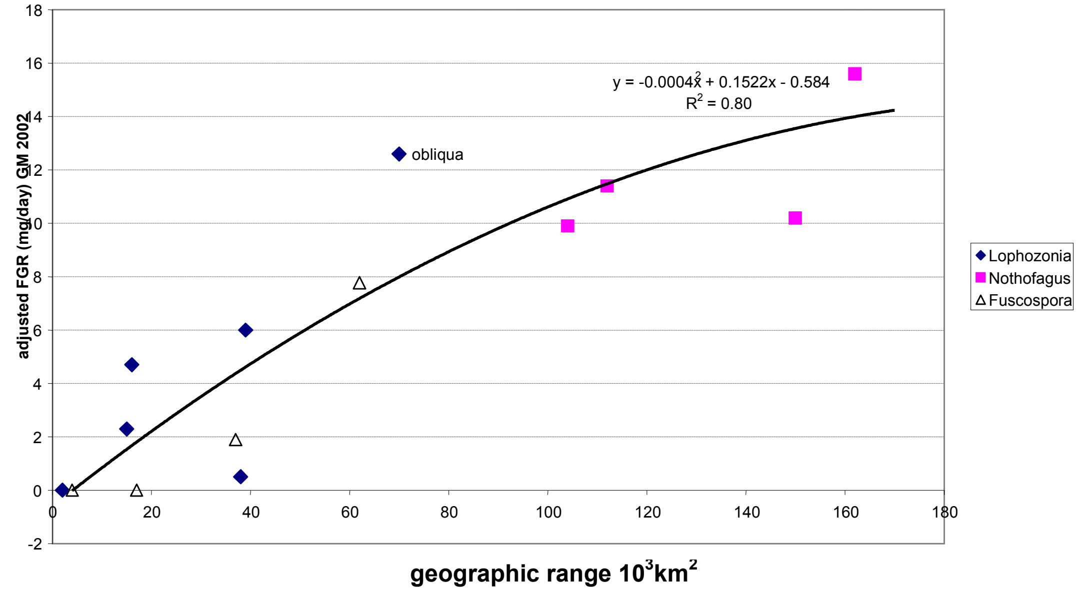

Figure 5. 1. The relationship between the geographic range of *Nothofagus* species from three subgenera, and the growth rate of female gypsy moth larvae adjusted for survivorship ($P < 0.001$). The S. American *N. obliqua* supports an unusually high larval growth rate for its geographic range.

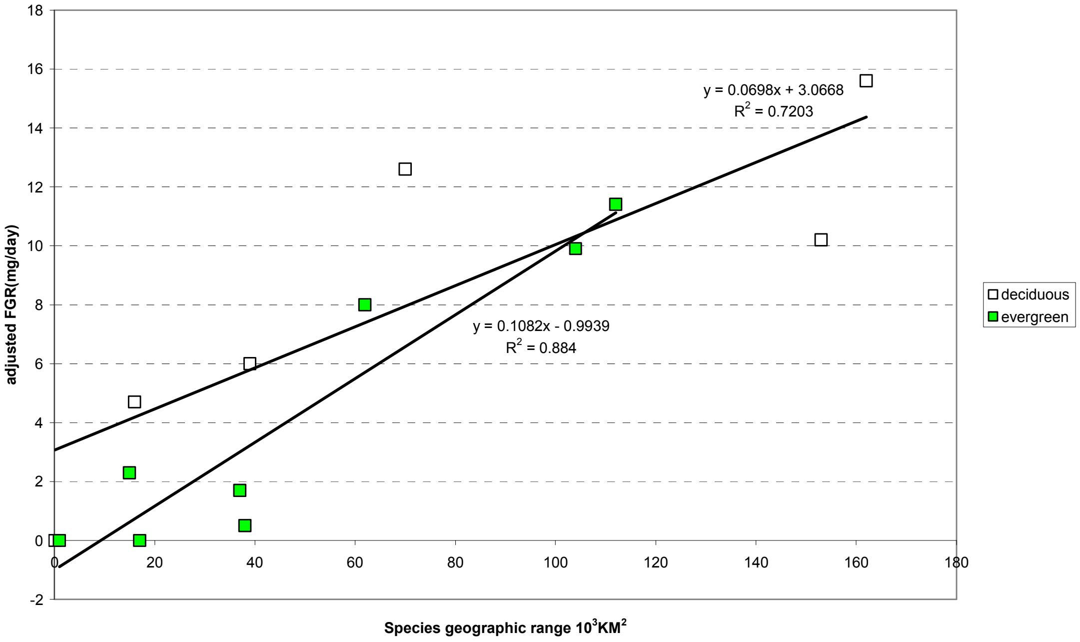

Figure 5. 2. Correlations for host species range and larval growth rate for deciduous and evergreen *Nothofagus* species. Analysis of covariance shows no significant difference between slopes or intercepts.

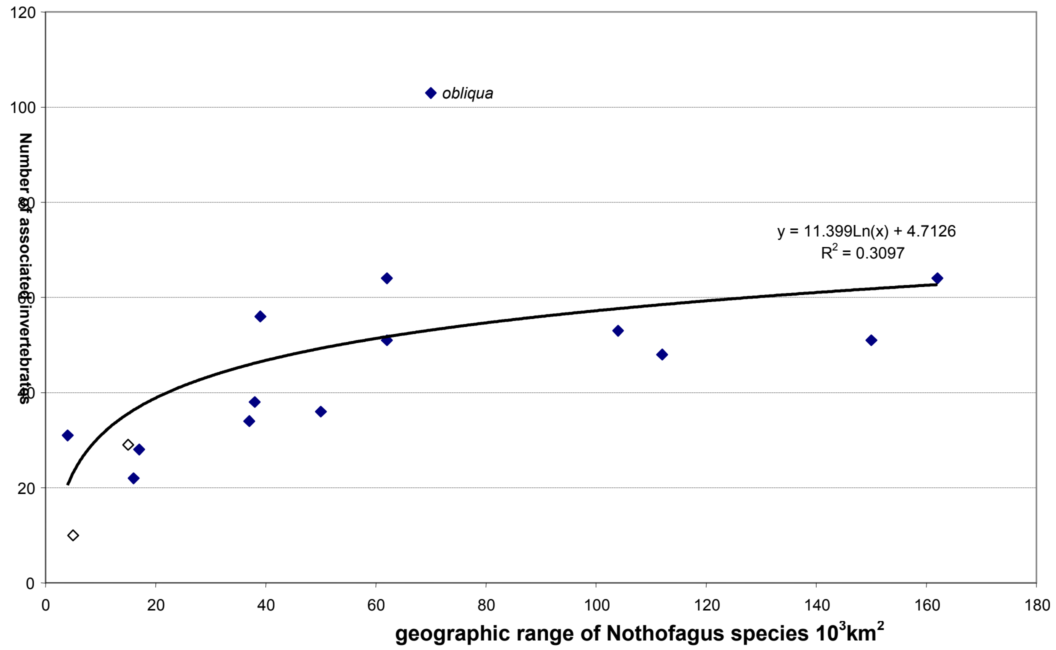

Figure 5. 3. The relationship between the geographic range of *Nothofagus* species and the diversity of their associate invertebrate community ($P < .05$). With the inclusion of the Tasmania species (◊) $P < 0.01$. *N. obliqua* supports an unusually high invertebrate diversity.

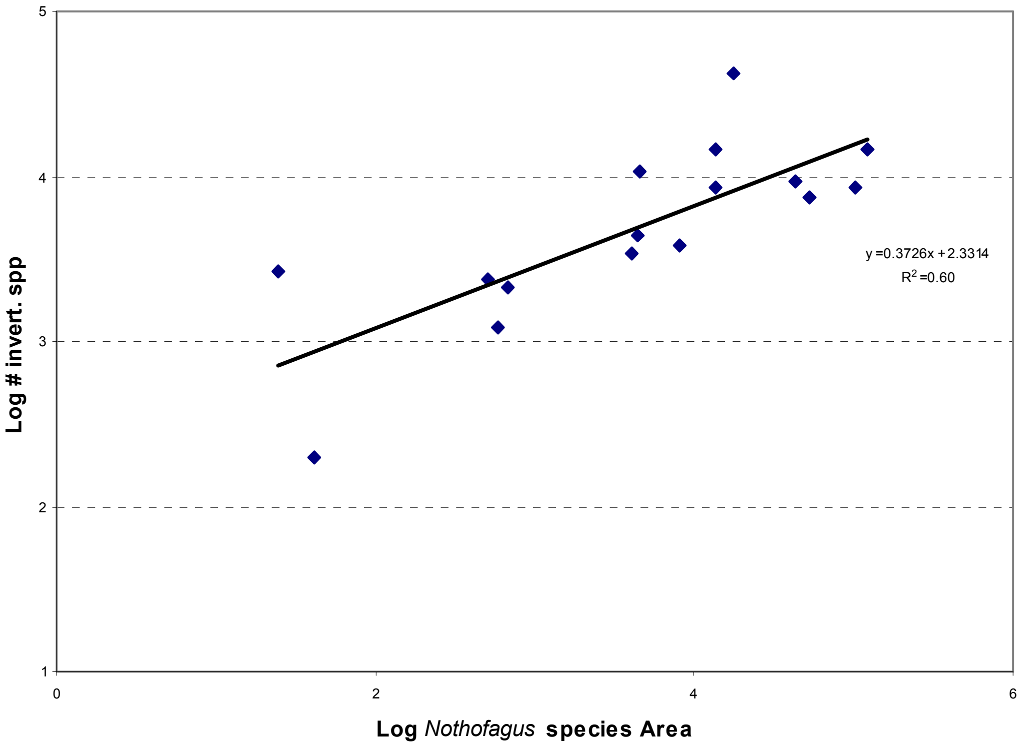

Figure 5. 4. The relationship between the geographic range of *Nothofagus* species and the diversity of their associate invertebrate community

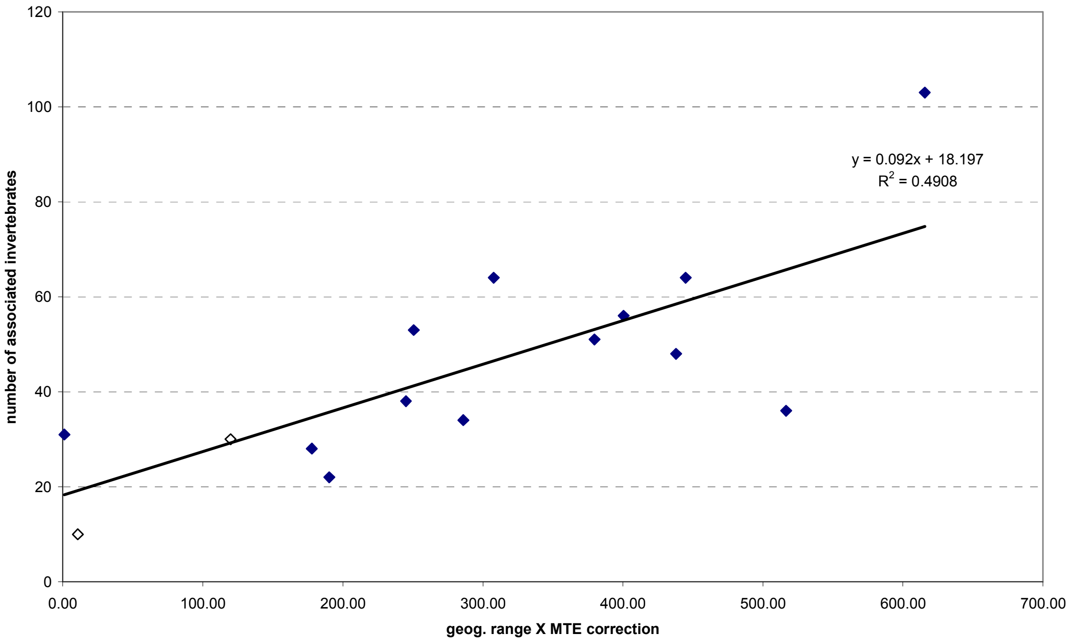

Figure 5. 5. The relationship between the geographic range of *Nothofagus* species adjusted with a mid-range function for habitat productivity, and the diversity of their associate invertebrate community ($P < 0.01$). With the inclusion of the Tasmania species (◊) $P < 0.001$.

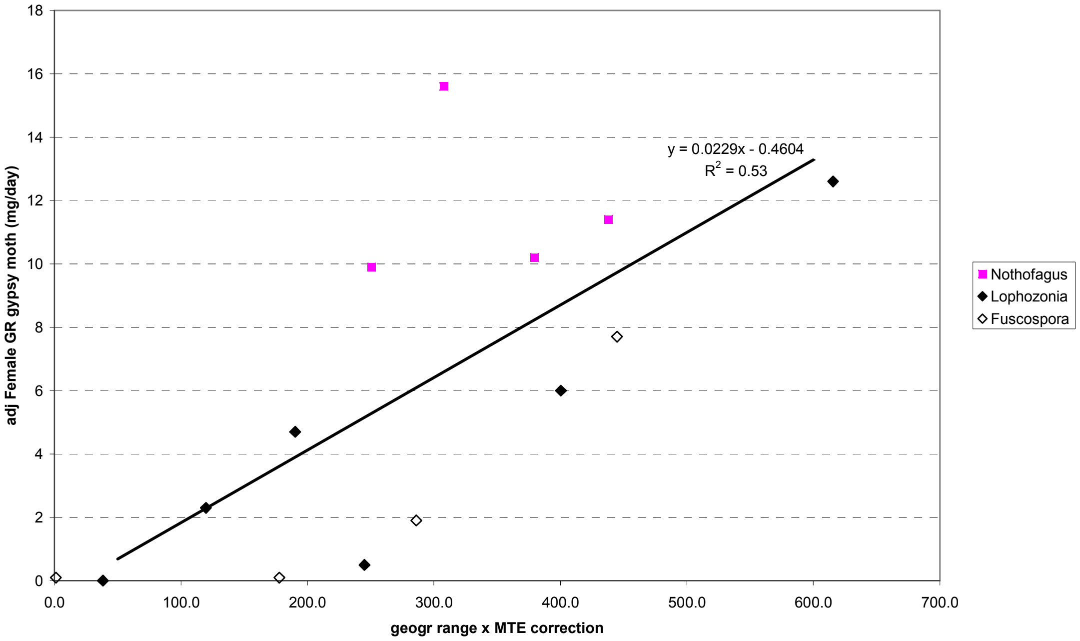

Figure 5. 6. The relationship between the geographic range of *Nothofagus* species adjusted with a mid-range function for habitat productivity, and the adjusted growth rate of female larval gypsy moth ($P < 0.01$). The outlier is the high altitude *N. antarctica*.

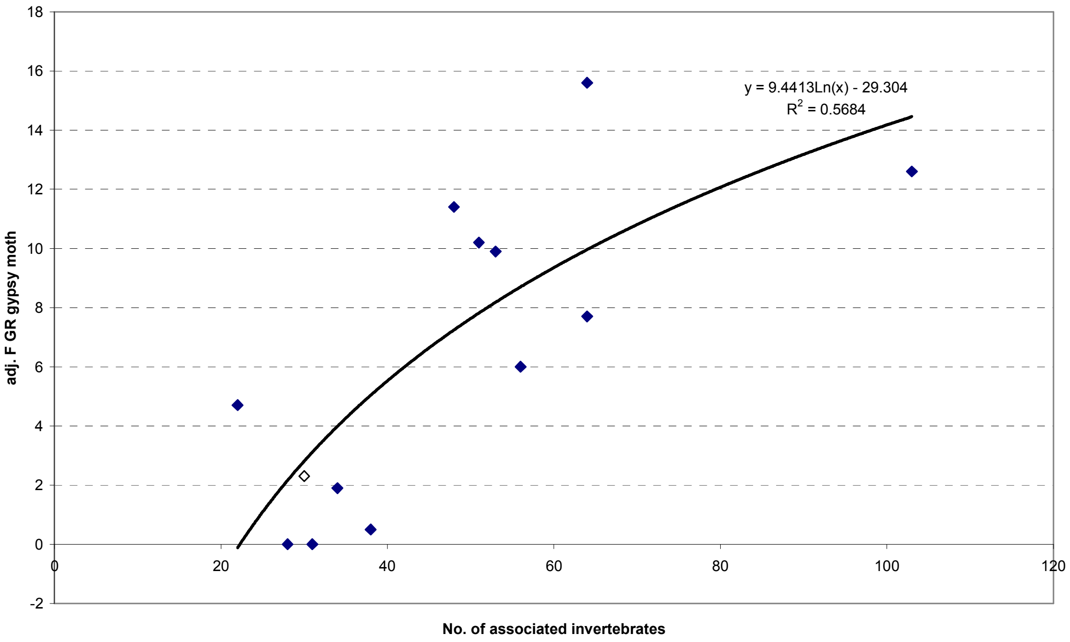

Figure 5. 7. The relationship between the diversity of invertebrates associated with *Nothofagus* species and the adjusted growth rate of female gypsy moth larvae feeding on those species ($P < 0.02$). With the inclusion of *N. cunninghamii* (◊) $P < 0.01$.

The analysis of all variables with larval growth rate shown in Appendix 1. All methods were consistent with a positive effect of host species geographic range or the number of invertebrates associated with the host species. The species area relationship posits that these two variables are correlated, but area was present in the most probable model from the step-wise regression or the Bayesian analysis. The Bayesian analysis quantified this most effectively, showing that there was good evidence (99.7% probability) of an increase in larval growth rate with the host species geographic range or the number of invertebrates associated with the host species.

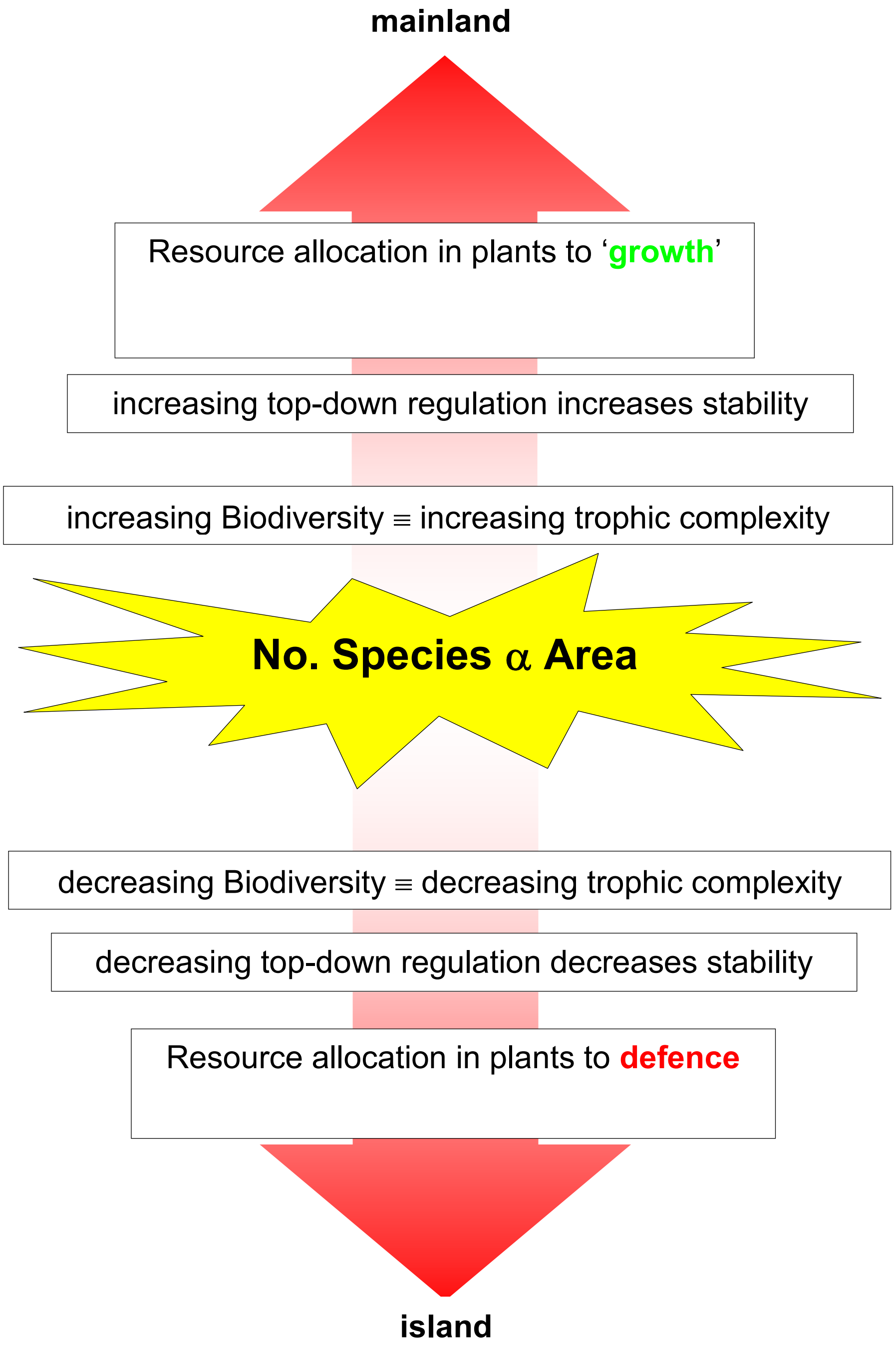

Figure 5. 8. A schematic of the Island Resource Allocation hypothesis. As habitat area decreases the allocation to plant defence increases and *vice versa*.

Discussion

That larger habitats hold greater species richness was confirmed by the positive correlation of the geographic range of *Nothofagus* species with the diversity of their associated invertebrates. This correlation is similar to that demonstrated for the New Zealand and S. American *Nothofagus* species (Dugdale 1975, Welsh 1988) and for Northern Hemisphere plant-phytophage associations (Southwood 1961, Kennedy and Southwood 1984, Leather 1986, Brändle and Brandl 2001). However, for this study all guilds of arthropods were included as the tree species was considered the foundation for a whole community.

Interestingly there was no distinction between deciduous or evergreen hosts. The inference drawn is that once leaves are produced they are available to defoliators and each *Nothofagus* species has a set of invertebrates associated with those leaves (Russell et al. 2000). This fauna will presumably only be present when leaves are available. So regardless of their longevity, leaves will be susceptible to attack and when the leaves are shed it is unlikely that the associate fauna will remain and will itself be adapted to a leafless over-wintering habit. Deciduousness could provide a degree of defence against generalist defoliators that may be active in winter, but equally there are defensive synergies between 'evergreen' habit and defoliator defence in the toughness of leaves which would deter late season defoliators. The beat sampling from Wakehurst (Table 5.2) and Welsh 1981 and Welsh and Greatorex-Davies (1993) show that the palatable *Nothofagus* species attract defoliators.

Host plants can be viewed as habitats for other species (Janzen 1968, 1973, Opler 1974, Strong 1979, Southwood 1978, Kuris et al. 1980, Denno and Roderick 1991 Frenzel & Brandl 2001) and their recruitment of herbivores, from a regional pool of species, is determined by the plant's spatial and temporal predictability (Straw and Ludlow 1994, Kelly and Southwood 1999, Brändle and Brandl 2001, Lewinsohn et al. 2005). The *Nothofagus* invertebrate sampling of Russell et al. (2000) did not distinguish between herbivore, 'tourist' or predatory guilds, but the assumption is made here that the same biogeographic recruitment principle applies to all guilds associated with a host. The inclusion of all guilds in the analyses was deliberate, as it is becoming recognised that species in all guilds, acting directly or indirectly, affect trait expression in plants (Werner and Peacor 2003, Ohgushi 2005) and are important in the functioning of ecosystems (eg, Menge 1995, Jordano et al. 2003, Ohgushi 2005).

The finding that S. American *N. obliqua* supports a high invertebrate diversity on only a modest geographic range appeared to be an anomaly. However, *N. obliqua* is the lowest latitude, lowest altitude, beech species in S. America. This should increase the productive potential and biodiversity of that habitat. The high diversity of arthropods associated with *N. obliqua* offers some support for the 'metabolic theory of ecology' (MTE) which was developed as an explanation of the higher biodiversity encountered at lower latitudes, and predicts that habitat temperature and precipitation (as a predictors of productivity) control species diversity (Allen et al 2003, Brown et al. 2004). The use of a mid-range temperature as a function of productivity in this study was relatively crude. A more sophisticated bioclimatic model including precipitation and insolation may have reduced the variance, especially for the correlation of larval growth rate with the climatically adjusted geographic range.

Possibly the greater apparent anomaly was that *N. obliqua* was one of the most palatable *Nothofagus* species trialled and that palatability of all species was positively correlated to geographic range. The result is supported by Russell et al.'s (2000) observation that *N. obliqua* and *N. antarctica* suffered the most defoliator damage while *N. truncata* and *N. alessandri* suffered the least.

That plants from islands or small geographic areas were found to be comparatively resistant to continental invertebrate herbivores appears to be counter-intuitive because it is contrary to the Apparency theory (Feeny 1975, 1976) and the long-held view that islands are inherently invasible. These paradigms assume that the low diversity of phytophage species in a simple community negates a requirement for metabolically-costly plant defences. This assumption was implicit in the work of Levin (1975) in which he suggested that higher levels of plant defence could be expected at the centre of a plant's geographic range. He argued that this would approximate the evolutionary centre of the plant and its co-evolved phytophage load, and, as Feeny (1975, 1976) also suggested, that the exposure to a larger array of herbivores would result in a greater suite of plant defences. Both authors, and most plant defence theory, neglect the role of tri-trophic interactions, yet the abundance and distribution of 'predatory' guilds are governed by the same spatial rules as those for herbivores.

An explanation for the comparative resistance of Nothofagus species – the IRA hypothesis

The break-up of the Gondwana continent represents a fragmentation of the *Nothofagus*-based forest ecosystem on a macroecological scale over evolutionary time. The remnants of that temperate ecosystem exist in Australia, New Zealand and South America. The size, isolation and inundative history of the New Zealand landmass has created a *Nothofagus* forest ecosystem typical of oceanic islands. On the continents of Australia and S. America the *Nothofagus* forest ecosystems may be more expansive, but stochastic events have marginalised some species so that as habitats, they too resemble mainland islands (Donoso 1996). The resistance of these 'insular' species, in comparison to their congenerics with greater geographic ranges, is a hitherto unrecognised pattern of plant defence.

The ecography of plant defence has not been well addressed. Bohm's (1998) limited review of insular secondary plant chemistry shows that island plant chemical profiles are somewhat ambivalent. They may be similar, simpler or enriched, when compared to the profiles of equivalent continental species. Carlquist (1974) described the Hawaiian islands as being exceptionally poor in poisonous plants and suggested that a relaxation of vertebrate herbivore pressure on islands led to the loss of defensive chemicals in island flora. The loss of cyanogenesis in the Galapagos Island plants has also been interpreted in terms of reduced herbivore pressure (Adersen et al. 1988) and a general loss of defences against vertebrate herbivores in insular plants is reported by Bowen & van Vuren (1997). So how do we explain 'insular plant resistance' to invertebrates?

It is generally accepted that in response to herbivore selection pressure, plants have evolved a multitude of physical, chemical, phenological and mutualistic strategies to provide a bottom-up limitation of the plant biomass available to consumers (White 1978, Edwards and Wratten 1980, Denno et al. 2003). These strategies may be complemented, or overshadowed, by the actions of natural enemies, which can effect a top-down regulation of herbivores (Hairston et al. 1960). The two processes are not mutually exclusive and a regulatory plurality is considered to exist in most ecosystems (Hunter and Price 1992, Denno et al. 2003), but it is empirically difficult to demonstrate the relative roles of each (Walker and Jones 2001, Gripenberg and Roslin 2007). However, it would appear logical that if insect herbivory does influence plant fitness, then, when a robust top-down regulation of defoliator populations by natural enemies is ineffective, or absent over evolutionary time, plants that cannot escape herbivory in space or time, should be selected to allocate resources to a ‘bottom-up’ defence.

Predators and parasitoids are the dominant biotic cause of mortality for exophytic insects (Cornell and Hawkins 1994), but the effectiveness of these natural enemies in regulating herbivores may be limited both temporally and spatially. Temporally, the plant has primacy in the food chain. It must establish first in any habitat and, excluding detritivores, the herbivores must be the second level to establish in order to support the advent of the third trophic level, comprising the herbivores’ natural enemies.

Arthropods are the most vagile of heterotrophic macro-organisms (Diamond 1974). For most ecosystems there is a continual rain of aerially borne adult insects (Johnson 1967). Phytophagous species probably arrive without their associated natural enemies, or have founding populations too small to accommodate the establishment of their associated natural enemies. There will be periods during the establishment and persistence of any community, where, in the temporal absence of predators and parasitoids, the bi-trophic interaction between the plant and its herbivores prevails (eg Schoener 1989, Schoener et al. 2005).

The spatial limitation of the natural enemies of herbivores is prescribed by the species: area relationship. Increasing habitat area not only increases species richness, but also trophic complexity. However, species richness is inversely related to trophic level (Schoenly et al 1991). Species in higher trophic levels are usually less diverse and less abundant, than organisms in lower trophic levels (Duffy 2002, Petchey et al. 2004, Vinebrooke et al. 2003). As the chance of extinction is proportional to population size (McKinney 1997, Purvis et al. 200, Jones et al. 2003) the natural enemies of prey are more prone to extinction than their prey (Stireman et al. 2005). Natural enemies may persist regionally by dispersal between small habitats that may not be large enough to provide sustainable predator-prey interactions. However, the isolation of small habitats beyond the dispersal capabilities of natural enemies will reduce any ‘rescue effect’ for their populations and will promote their extinction within those habitats (Holt 1984, Hanski 1998). The bias in extinction to the top trophic level is one of the clearest patterns of extinction and typically occurs on islands and perturbed or fragmented ecosystems (Whittaker 1998, Holt et al. 1999, Didham et al. 1998, Schoener et al. 2001).

The paucity or extinction of species in the higher trophic levels should have profound effects for food webs. Population demographics within communities have been demonstrated to be sensitive to the species composition of those communities (Losey and Denno 1999, Schoener et al 2005). The removal of functional groups – such as predators – can create dramatic regime shifts in ecosystems (Folke et al 2004). Although the effect of predator/parasitoid extinctions may be difficult to predict (Schoener et al 2003, Srivastava & Vellend 2005, Snyder and Evans 2006) the species interactions within small or isolated habitats, which are more likely to lose higher trophic levels, should be skewed towards plant-herbivore interactions.

Terrestrial food webs tend to be complex, with many interconnections within and between trophic levels. Species may interact directly through competition and predation, however, there is a growing recognition of the indirect effects of species interactions (Wootton 2002, Strauss and Irwin 2004). Low interaction strengths between many species characterise more diverse communities and tend to stabilise food webs (Jansen & Kokkoris 2003). Conversely, decreasing species diversity tends to increase the mean interaction strength between species and may promote instability (McCann 2000, Ives and Cardinale 2004). The interaction between predators and prey is always strong, but it is likely to be stronger, and therefore less stable, in small habitats. This should result in greater, or more frequent, population oscillations of herbivores (and natural enemies), which should evoke a stronger selection pressure for self-defence in plants providing, or inhabiting, small habitats. These 'insular' plants should differ fundamentally from 'mainland' plants in the strength and stability of their species interactions with herbivores and the consequent evolution of those interactions. Conversely, an increase in habitat area not only increases trophic complexity, and the potential predator synergies (Losey and Denno 1990) that promote the emergence of a top-down regulation of herbivores, but it is also likely to increase the stability of that regulation through processes such as facultative omnivory by predators (Reeve 1990, Worm and Duffy 2003). If the resulting top-down regulation is stable, then plants in large habitats can afford to relinquish what may be metabolically costly self-defence.

The Island Resource Allocation (IRA) hypothesis (Kay and Wratten 2006) was developed as an explanation of the resistance of insular plants to mainland defoliators and is schematically described in Figure 5.8. It contends that plants in small habitats, which lack the trophic complexity necessary to provide a stable top-down regulation of herbivores, must defend themselves. This defence will require the specific allocation of resources to a defensive strategy that will provide a broad spectrum of protection against folivores capable of long-distance dispersal. The IRA hypothesis offers the thesis that for plant species that cannot escape herbivory by dispersal, precocious seeding etc, **the inherent resistance of a plant species to invertebrate herbivores is inversely proportional to its geographic range.** Plants with expansive geographic ranges will be inherently less resistant to phytophagous insects than equivalent plants with lesser ranges.

The IRA hypothesis is a redefinition of the species: area relationship –possibly the strongest empirical generalisation in community ecology (May 1975, Rosenzweig 1995, Holt et al. 1999). Species diversity increases with area, but the relationship is more pronounced at higher trophic levels (Holt 1996). Habitat fragmentation studies (Schoener 1989, Kreuss and Tscharntke 1994, Lawton 2000, Komonen et al. 2000) and trophic level patterns in spatially discrete ecosystems (Schoenly et al. 1991, Holt 1996) show that the trophic components of invertebrate communities do not change uniformly with area. Rather, during habitat fragmentation, the higher trophic levels are lost prematurely or disproportionately, or cannot be maintained in small habitats. In redefining the species: area concept the *IRA* hypothesis contends that islands, or similarly geographically constrained ecosystems, inherently support lower biodiversity, have fewer trophic levels, and consequently have a lesser top-down regulation of herbivores by natural enemies. The hypothesis posits that if plant fitness is influenced by herbivores, then, when top-down regulation of herbivores is weak because of a lack of trophic complexity, plants that cannot escape in space or time will be selected to allocate resources to bottom-up defences. The correlation of host geographic range with larval growth rate, supports the contention that a high associate invertebrate load provides a stable top-down regulation of herbivores and allows the plant to relax its defences.

The IRA hypothesis relies on habitat area as a predictor of habitat diversity. Area is a strong determinant of biodiversity, but it may be improved with the addition of a function for habitat productivity (Whittaker et al. 2003). When the geographic ranges of *Nothofagus* were adjusted with a mid range temperature function to account for habitat productivity, *N. obliqua* conformed to the correlation of plant host range with the diversity of associate invertebrates and larval growth rate.

Nothofagus species with expansive geographic ranges had the least defence against defoliators, but had the greatest diversity of associate arthropods. Palatable plants do accumulate pests – le raison d'etre the pesticide industry. The Wakehurst beat samples (Chpt 4.) demonstrated that. It could be argued that the least resistant trees had the most invertebrates because they were so palatable, rather than that their geographic range was so great. However, this would mean the very significant correlation of palatability with host range was serendipitous and/or that invertebrate herbivores have no effect on plant fitness.

There is a common misconception that insects do not kill trees (eg Ohgushi 2005). This is possibly due to the 4-18% consumption commonly recorded within terrestrial ecosystems (Polis 1999). However, these systems have evolved to that status. Anyone who has witnessed forest caterpillar outbreaks resulting from novel associations, or the loss of natural enemies, can attest to the fact the insects indeed kill trees (Campbell 1979, Kay 1983, Terborgh et al. 2001). Lawton (2000) unwittingly demonstrated the potential for unregulated defoliators to kill plants when he moved bracken plants from their natural habitat to the university car park. Isolated from their natural enemies, bracken insects rapidly devoured his experiment. Isolated plants need time to evolve. Palatable plants must be well protected from defoliators by an associate third trophic level to negate the need of an investment in defence, although a complete lack of defence in plants might be evolutionarily inexpedient.

The New Zealand flora appears to be an extreme example of the IRA hypothesis. Resistance to 'sophisticated' continental defoliators was remarkably consistent across all plant families tested and New Zealand *Nothofagus* species tended to be more resistant than predictions from their geographic range. This is possibly a result of the extreme isolation and/or the unresolved, but certainly cataclysmic, extent of marine transgression on the spatial and temporal habitability of the New Zealand landmass (Trewick et al. 2004).

The IRA hypothesis contends that ecosystem processes on oceanic islands would be heavily biased towards insect-herbivore interactions. Immigrants would be predominantly *r*-selected super tramps (Diamond 1974) whose populations are capable of rapid expansion. Their arrival in enemy-free-space would not only promote their population growth, but also their host range expansion (Lomolino 1984, Schroener and Spiller 1987, Kay 2001). The 'predator' populations on oceanic islands are small and less populous than those on continents (Preston 1962). The extinction of organisms in the higher trophic levels would be common and any rescue effect would diminish with isolation, leaving the plants of oceanic islands at the mercy of generalist herbivores capable of long distance dispersal (Brown 1971).

The knowledge of the New Zealand invertebrate predator/parasitoid fauna is limited. There is a recognised paucity in the diversity of New Zealand Hymenoptera (Valentine & Walker 1991). For example, Mills (1992) found that Holarctic Tortricids typically support nine parasitoids, with a recorded minimum of four. New Zealand species on the other hand, typically support less than two, with a recorded maximum of four (Valentine & Walker 1991) – one of which, *Aphanistes kayi*, is more likely to be a parasitoid of geometrids (unpubl. data). There are also biogeographical examples of the absence of parasitoids from the New Zealand portion of the Southern Hemisphere *Nothofagus* invertebrate community, (Schlinger 1974). There are concomitant gaps in the defoliator fauna (Dugdale 1988), but defoliation is caused by defoliator abundance rather than diversity, and the lack of interspecific interaction among herbivores may even exacerbate defoliation (Damman 1989, Denno et al. 1995). Self-defence for the New Zealand flora would seem appropriate in the absence of significant invertebrate diversity in either herbivore or predator guilds.

There is an unreserved acceptance of the effect of predator release on New Zealand's avifauna and the effect of these large ground dwelling birds on the character of the shrub flora (McGlone 1988). The same principle applies to invertebrates. Moa did not climb trees. Our forest tree species are poorly defended against a hydrophobic maladroit browsing marsupial, but exceptionally well defended against defoliating insects.

Chapter 6

Marginal populations and plant defence in *Nothofagus truncata*: a test of the IRA hypothesis

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‘*geographic variation in food web dynamics could have interesting and important consequences for both ecological and evolutionary processes.*’ (Endler 1992)

Abstract

The Island Resource Allocation (IRA) hypothesis predicts that tree species in geographically small, isolated, habitats will allocate more resources to defence against consumers than those in larger, more trophically complex habitats. The hypothesis should also hold for the meta populations of a species and was tested here using bioassays of an Australian polyphagous defoliator, the painted apple moth (PAM), Teia anartoides (Lepidoptera: Lymantriidae) with disparate populations of hard beech, Nothofagus truncata (Fagales: Nothofagaceae). PAM larvae that were fed foliage of trees from the small isolated populations of hard beech at Haast and Omahuta exhibited higher mortality and slower growth rates than larvae fed foliage of trees from the larger contiguous hard beech populations of the central North Island or the Nelson districts. This pattern of plant defence is consistent with the IRA hypothesis, but contrary to plant defence hypotheses of ‘apparency’ and latitude.

Introduction

The central populations of species usually hold the greatest abundance of individuals and the most genetic diversity – the ‘abundant centre’ concept (Andrewartha and Birch 1954, Rapoport 1982, Sagarin & Gaines 2006). Consequently central populations are considered more resilient to environmental perturbation when compared with populations at the margin of a species’ range (Carson 1975). Marginal populations (*sensu* Stern and Roache 1974) typically become smaller and more isolated as they approach the ecological limits of the species (Thomas and Kunin 1999). It is intuitively obvious that these populations are most at risk of extinction, which is probably why they have often been deliberately ignored in conventional ecological studies. However, largely in response to the accelerating loss of biodiversity, there is a growing interest in range dynamics and the resilience of marginal populations (Brown and Lomolino 1998, Sala et al. 2000, Holt 2003).

A species' geographic range and genetic integrity is generally held to be a function of dispersal (Gaston 2003, Saether and Engen 2003, Böhning-Gaese et al. 2006). Marginal populations of mobile species can rely on the 'rescue effect' of immigration to maintain gene flow to isolated habitats (Hanski 1999). Mobile species therefore tend to exhibit fewer adaptations to local environments than do sessile species (Case and Taper 2000). Immigration is largely irrelevant to the marginal populations of sessile organisms (Guo et al. 2005) and a number of studies suggest that isolated populations of sessile species often perform poorly under the species' environmental norms, but are relatively better adapted to the unfavourable conditions encountered at their range margins. This is not surprising given the unique selection pressures and restricted gene flow at species' margins. As Antonovics and Levin (1980) pointed out, the entire geographic range of a species is not a seamless evolutionary unit and the average trait values for a species fail to capture the spatial dynamics of the ecology and evolution of species.

Typically, limited dispersal will increase genetic variation among sub-populations, but decrease variation within patches. Plants in particular, tend to rely on local seed production for the maintenance of local populations (Harper 1977), and even though a genetic rescue effect may be available in the form of pollen, genetic homology and asymmetrical gene flow have been shown to be more common at plant species' borders (Hoffmann and Blows 1994, Garcia-Ramos and Kirkpatick 1997). The resulting unique genetic structure of small marginal plant populations may lead to extinction (Newman and Pilson 1997), but may be equally relevant to speciation events (Brussard 1984, Rosenzweig 1987) and to community dynamics (Endler 1992).

The effects of space on the complexity of community dynamics is one of the main obstacles to the extrapolation of ecological parameters from one population to another. The inter-specific interactions of a species can be expected to differ between its central and marginal populations. The trophic structure of the respective communities may also be strongly influenced by spatial factors such as local habitat area and their connectedness to other similar communities (Holt 2002). Communities and their trophic structure become simpler as habitat area decreases (Schoenly and Cohen 1991, Rosenzweig 1995) and as some species are lost and new species encountered, inter-specific interactions will change and evolve to reach new equilibria (Grant & Antonovics 1978, Cornell & Lawton 1992, Endler 1992). In spatially isolated habitats, selection should favour different plant phenotypes to cope with these differences in species interactions.

Traditionally, competition has been the most reported interactive parameter in plant population studies, while the role of herbivory in climax plant population dynamics has often been discounted. However, herbivory has been found to be at least as influential as competition (Harper 1969, Huntly 1991, Hulme 1996) and plants may allocate considerable resources to defence against herbivores in what may escalate into an intense co-evolutionary contest (Mauricio 1998, Tiffin & Rausher 1999, Rausher 2006). The focus of plant defence theory has concentrated on these bi-trophic interactions (Bernays and Graham 1988, Janzen 1988, Stamp 2003) but current hypotheses remain unable to predict outcomes for the role of plant defence in complex inter-specific interactions (Berenbaum 1995, Stamp 2003).

Somewhat contentiously, complex heterotrophic communities have been considered self-regulating through the hierarchical top-down control exerted by natural enemies on herbivores, which limits the selection for plant defences against herbivory (Hairston et al. 1961). However, alternative community-based strategies proposed by Feeny (1976) and Levin (1976) stress bottom-up processes of plant defences in limiting herbivory, and argue that exposure to a variety of defoliators is correlated with the evolution of nutritional, physical and chemical plant defences. More recent community hypotheses invoke latitudinal gradients in plant defences, which suggest that both increased productivity and biodiversity allow, and demand, more potent plant defences at lower latitudes (Coley & Barone 1996, Dyer & Coley 2002).

The debate over the role of top-down and bottom-up forces in the regulation of herbivorous insects has at times been highly polarized (Murdoch 1966, Lawton and McNeill 1979), but most ecologists now accept that both processes, and even lateral, intra-guild, interactions (Lill et al. 2002), contribute to community stability (Chase 2000, Hunter 2001, Denno et al. 2005). However, there remains a lack of consensus and a dearth of empirical analyses of the relative strengths of top-down and bottom-up forces in terrestrial ecosystems (Walker and Jones 2001).

The Island Resource Allocation (IRA) hypothesis of insect-plant interaction (Kay & Wratten 2006) provides a resolution of the relative strengths of top-down and bottom-up processes and allows testable predictions of how the selection for defence against herbivory might vary with habitat area and/or community biodiversity. The IRA hypothesis posits that persistent plant species with limited geographic ranges will be at greater risk from herbivory than species with larger ranges, because spatially limited habitats constrain food web complexity, which limits the top-down regulation of herbivores by natural enemies. The same thesis should apply to populations within a species' range if the populations are sufficiently isolated to prevent the inter-population sharing of natural enemies. The IRA hypothesis predicts that small, marginal, plant populations within a species' meta-population should be better defended against herbivores than are their larger central populations *i.e.* a direct contradiction of Feeny's (1976) Apparency hypothesis.

Nothofagus truncata is the least common New Zealand beech species (Wardle 1984) and has the most discontinuous geographic range, with marginal populations at its extreme northern and southern limits. As such, it appears to be a good example of the 'abundant centre' distribution (Figure 1). The outlying populations, inexplicably at Haast (42º S) (June 1977, Mark and Lee 1985) and Northland (32º S) (Sexton 1941), are small and isolated from the large central population in the NW of the South Island (38º S). Plant species, such as *N. truncata*, which have limited dispersal abilities (Preest 1963), are most likely to respond, both genetically and morphologically, to the environmental nuances encountered in marginal habitats (Endler 1992).

As a test of the IRA hypothesis, the palatability of trees from marginal and central populations of *N. truncata* were compared in bioassays using PAM. Lymantriids are recognise forest defoliators, but are unrepresented in the New Zealand invertebrate fauna. PAM is endemic to Australia where it is primarily recorded from *Acacia*. However, it is considered polyphagous as it has been recorded from a number of host species unrelated to the Papilionaceae, but it has not been recorded from *Nothofagus*.

Methods

Larvae used as bioassays were taken from the PAM colony maintained for over 25 generations on artificial diet within the NZFRI quarantine facility. The trials utilized foliage from five to ten trees of each of the four *N. truncata* populations assayed. Five insect replicates were run of each tree, with each foliage sample and its control, receiving larvae from one of five different PAM egg batches. Bioassays utilized 10 newly eclosed, unfed first instar painted apple moth larvae per replicate. The larvae were caged with foliage in a two-chambered system, where the cut stem of the plant specimen was in a lower (595 ml) water-filled container and isolated from the foliage in the enclosed, upper (395 ml) arena. Insects were introduced to the foliage in the dry upper chamber. Foliage was renewed as required from pre-cut material held at 4ºC. The mortality and/or development of larvae were recorded. The time and the weight of surviving larvae at pupation were recorded to provide a growth rate.

The trials were maintained at 22°C ±1 and 70% ±10 RH; 16-h photoperiod. Replicates of each bioassay were arranged as five randomised blocks, with each block representing the progeny of one PAM female on subject and control trees.

Logistics and constraints of space within the quarantine facility prevented all trials running concurrently. The three separate trials were run over the 2004 and 2005 seasons. The control for each trial was foliage of *N. truncata* collected from trees in the Kaimai-Mamaku Forest (Mangorewa Gorge). Foliage from the same 'control' trees was used in each trial. Foliage from Northland (Omahuta Forest, February 2005), Nelson (Big Bush, April 2004) and Haast (MacFarlande Mound, February 2004) was couriered to Ensis from collectors in those areas.

The geographic size of each *N. truncata* population was taken from Wardle's (1984) Fig1.11, which was derived from the New Zealand Forest Service botanical survey. Dots in this figure represent the presence of the species in 100 000yard^2 grids (approx. 8ha) on New Zealand Map Series. The 'size' of each population was taken somewhat arbitrarily as the number of dots within a 5mm radius (equivalent to approximately 140 000ha) on Wardle's Fig 1.11., centred on the foliage collection point The measure was a combination of local population area and its isolation from adjacent populations.

Statistical Analysis

Simple linear regression analyses were used to identify correlations between female larval growth rates and percentage leaf nitrogen. Because the data set was so small due to excessive larval mortality Bayesian inference analysis was used to find the best fit explanation for larval growth rate with respect to tree population size and population latitude.

Results

Table 1 shows the mortality, growth rate and sex ratio of larvae reared on the foliage from the different populations of *N. truncata.* As expected from previous assays of this species (Kay 2003), larval mortality in all bioassays was high. However, it was highest on the foliage of trees from the marginal populations of *N. truncata*.

There was no significant difference in the larval growth rates on the Mangorewa Gorge control foliage between trials undertaken in February of 2004 and 2005. However, there was only one survivor from the control foliage for the Nelson trial undertaken in April 2004 and its growth rate was below the mean of the controls of the other two trials. Despite this, trees from Nelson, the central population of *N. truncata,* provided the highest percentage of acceptable host trees, the best larval survivorship and growth rate, and were the only trees which produced female pupae. (The painted apple moth is dimorphic with females three to five times the mass of males. Consequently female larvae have greater development times, pupal weights, growth rates and mortality. Only male data were included in the growth rate comparison). No larvae completed development on trees from the small, highest latitude, Haast population. Larvae on this foliage died within 12 days (Fig 2).

There was no relationship between larval mortality and the latitude of the host population, but even without adjusting for the discrepancy in the April trial control larvae, there was a significant positive correlation between larval growth rate and the geographic size of the host population (Fig 3).

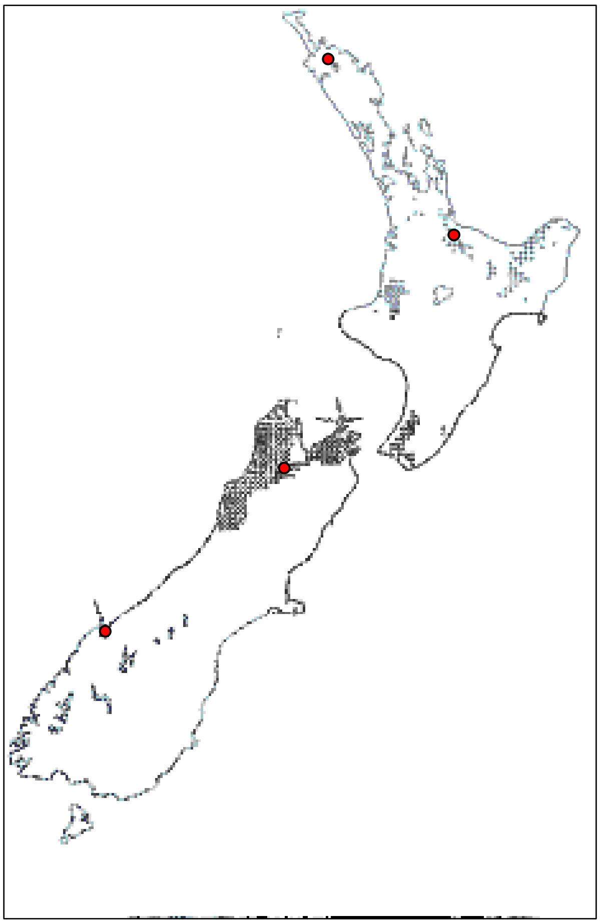


Figure 6. 1. The foliage collection sites marked on Wardle's (1984) Figure 1.11 of the distribution of *N. truncata*.

TABLE 6.1

Larval mortality and development on foliage of N. truncata from populations of different size and latitude

Population Location	Latitude S (± 5')	population size	No. Trees assayed	♂ larval growth rate (mg/day)	% trees supporting larval growth	Sex ratio ♂:♀	% larval mortality
Omahuta Forest	35° 15'	2	8	1.02 ±0.01	12.5	1: 0	99.3
Mangorewa Gorge	38°	12	6	1.28 ±0.18	22	1: 0	98.8
Big Bush Forest	41° 30'	28	10	1.87 ±0.06	70	4: 1	91.2
MacFarlane Mound	44°	1	5	0	0	0	100

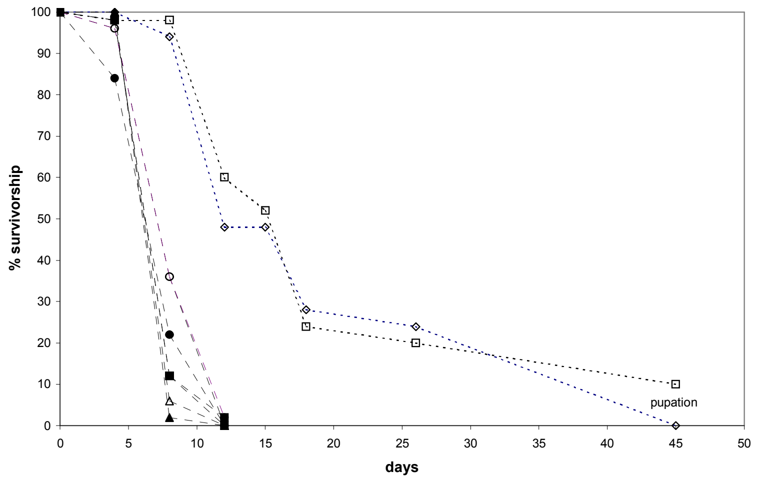


Figure 6. 2. The survivorship of painted apple moth larvae fed on Haast (solid) and Mangorewa (hollow) provenances of *Nothofagus truncata*.

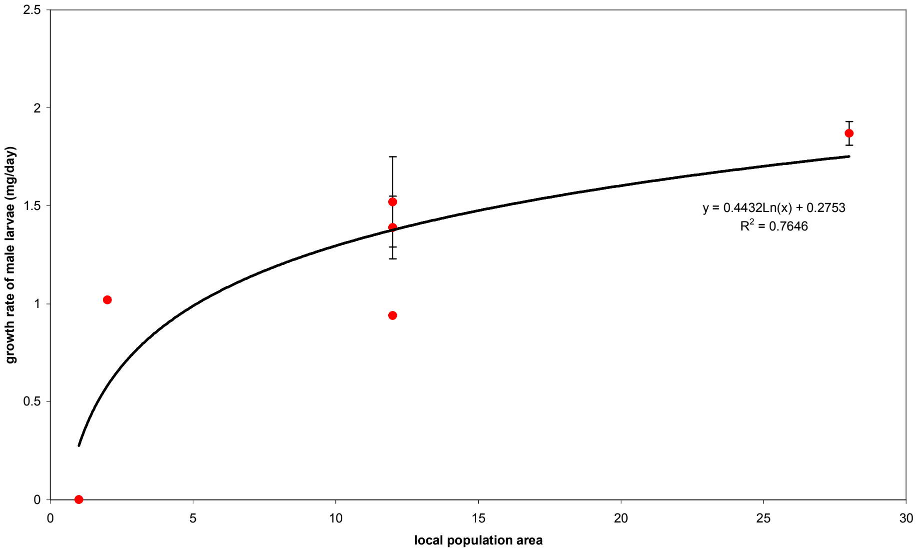
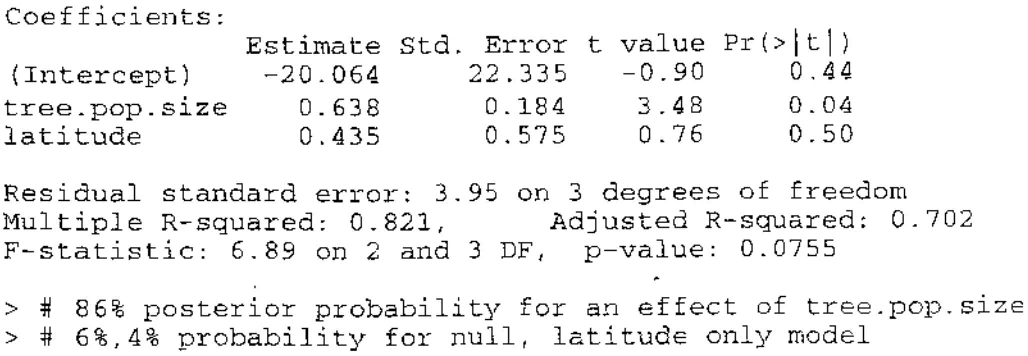


Figure 6. 3. The correlation of painted apple moth larval growth rate with the 'size' of the host plant population.

The Bayesian analysis treated the non-surviving larvae as having zero growth rate (Table 6.2). Of the two variables that may influence larval growth rate there was an 86% posterior probability for an effect of tree population size and only 4% for latitude – the null hypothesis was 6%. The odds are about 5 to 1 for a positive correlation of tree population size and larval growth rate. When only individual variables of latitude of population size were considered the probability of an effect of area increased to 89%

TABLE 6.2

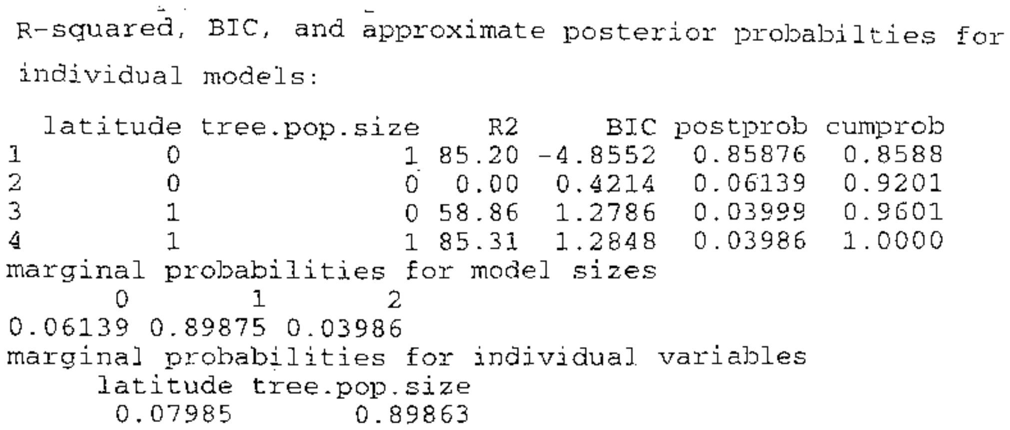
Bayesian analysis of the effect of foliage of N. truncata from populations of different size and latitude, on the growth rate of male painted apple moth larvae.



```
Coefficients:
                Estimate Std. Error t value Pr(>|t|)
(Intercept)     -20.064     22.335   -0.90     0.44
tree.pop.size     0.638      0.184    3.48     0.04
latitude          0.435      0.575    0.76     0.50

Residual standard error: 3.95 on 3 degrees of freedom
Multiple R-squared: 0.821,      Adjusted R-squared: 0.702
F-statistic: 6.89 on 2 and 3 DF,  p-value: 0.0755

> # 86% posterior probability for an effect of tree.pop.size
> # 6%,4% probability for null, latitude only model
```



```
R-squared, BIC, and approximate posterior probabilties for
individual models:

  latitude tree.pop.size    R2      BIC postprob cumprob
1        0             1 85.20 -4.8552  0.85876  0.8588
2        0             0  0.00  0.4214  0.06139  0.9201
3        1             0 58.86  1.2786  0.03999  0.9601
4        1             1 85.31  1.2848  0.03986  1.0000
marginal probabilities for model sizes
      0       1       2
0.06139 0.89875 0.03986
marginal probabilities for individual variables
     latitude tree.pop.size
      0.07985       0.89863
```

Discussion

Nothofagus truncata is the most resistant of the New Zealand fusca-type beech species to alien polyphagous invertebrate herbivores (Matsuki et al. 2001, Kay 2003). It also has the least diverse associate invertebrate fauna of the New Zealand indigenous *Nothofagus* (Russell et al. 2000). This study indeed showed that trees of *N. truncata* are quite resistant to painted apple defoliation but the data suggest that trees from small isolated populations are better defended against an alien invertebrate herbivore than are their counterparts from a large central population. The growth rate of larvae on the trees of the large central Nelson population could potentially be even higher than that recorded from the April trial. Leaves typically become less palatable with age and this may explain the poor result from the April control larvae compared with those of the February trials.

The results are consistent with the IRA hypothesis, but contrary to Feeny's (1976) Apparency Hypothesis and Levin's 'resistant central population' hypothesis. The results are also contrary to the inverse latitudinal distribution of plant defence promoted by Dyer & Coley (2002). For *N. truncata* the greatest resistance to the defoliator was found in the highest latitude population, at Haast. The lesser resistance of the only slightly larger Omahuta population may be due to chance –as the sample size was greater, or, in keeping with the IRA hypothesis, to a reflection of a greater biodiversity that could be expected at the lower latitudes (Allen et al 2002).

The IRA hypothesis is the only plant defence hypothesis which quantifiably includes a measure of community biodiversity. Biodiversity (here taken as the number of species) is proportional to habitat area (Rosenzweig 1995) and trophic complexity increases with biodiversity (Schoenley et al. 1991). The IRA hypothesis holds that the allocation to defence in plants is greatest in spatially constrained habitats because the lesser diversity of natural enemies within these small habitats limits the regulation of herbivore populations, thus increasing the selection for plant self-defence.

Much of the Earth's biodiversity is believed to be the result of co-evolution between plants and their natural enemies (Erlich & Raven 1971, Janzen 1980, Berenbaum & Zangerl 1988, Thompson 2005). There is considerable evidence to show that the co-evolution of species' interactions is geographically variable (Gomulkiewictz et al 2000, Thompson and Cunningham 2002). This variability has been conceptualised as a geographic mosaic of co-evolutionary 'hot spots' and 'cold spots'. Hot spots are said to occur where close reciprocal evolution takes place between two species, whereas cold spots reflect areas of neutral or ambivalent co-evolution. Thompson (1994, 1997, 2005) argues that the dynamics of species interactions are driven by selection mosaics. However, although complex patterns of phenotypic selection among habitats have been recorded, he acknowledges that predictions of the distribution of co-evolutionary selection are unknown.

Co-evolutionary 'hot' and 'cold' spots are consistent with, and can be predicted by the IRA hypothesis. Co-evolutionary cold spots should occur where the host plant population is large. In these large habitats the herbivores will be prey to a trophically more complex community and selection pressure on plants for a defence against herbivory will be low. Hot spots would be expected in small habitats, such as islands and isolated populations, where plants are forced to directly confront their herbivores without the benefit of the herbivores' own regulatory natural enemies. The interaction may be intense and it is possible that the limits of a species' range are characterised by extinction as a result of unbridled co-evolutionary interaction, especially if there is a trade-off between herbivore resistance and competitive ability.

The probability of extinction is a function of range size (McKinney 1997, Purvis et al. 2000, Jones et al. 2003). Demographic stochasticity may cause extinction even in favourable environments, but it is well known that species loss will occur more rapidly if numbers are low (Allee 1938, Shaffer 1981, Renshaw 1991, Lande 1998, Maurer and Taper 2002). For marginal populations, the metabolic cost of resistance to one or multiple environmental stresses may hasten extinction (Parsons 1990). Defences against natural enemies are assumed to carry a metabolic cost and the allocation of the host plant's resources to defence should diminish its allocation of resources to other life traits, such as growth and reproduction. As a population shrinks the IRA hypothesis predicts the necessity for an ever greater allocation to defence, at least until the host population is too small to support the consumer population. Such a commitment to defence may be a route to extinction. Alternatively, such a strong selection pressure, coupled with the genetic isolation from the parent population, may well drive speciation in marginal populations (Endler 1992, Holt 1996). *N. truncata* is the least abundant and the least palatable of the New Zealand beech species to exotic defoliators. The commitment of *N. truncata* to defence may compromise its competitive edge and may explain the species' restriction to the harsher of sites inhabited by the genus in New Zealand.

The IRA hypothesis and the results presented here also suggest an alternative direction for the 'community genetics' articulated by Antonovics (1992) and Wimp et al. (2005). Studies within host plant hybridisation zones have shown a correlation between plant genotype and the attendant phytophage community (Boecklen and Spellenberg 1990, Floate and Whitham 1995, Dungey et al. 2000). This atypical situation has been extrapolated to an expectation that insect community diversity will be driven by the genetic diversity of the host plant population (Wimp et al. 2005). However interaction between species is a two-way process and the study reported here suggests that invertebrate communities can shape the genetics of the host plant and supports the contention of Antonovics and Levin (1980) that both ecological and genetic factors are necessary to effectively describe a population *i.e.* a host plant is not just a Latin binomial, its provenance can influence its acceptance by invertebrate herbivores.

Chapter 7

Conclusions

'one of the major problems with ecology today is the existence of too much data and not enough theory, too many hypotheses and not enough testing, too many models and not enough verification' Price 2003 p3

Insect–plant interactions have dominated ecological research for decades (Moore 1995) and the evolution of such interactions is considered to be responsible for the high degree of biodiversity within the biosphere (Thompson 2001?). Despite the history and ubiquity of such interactions, which suggests they play a basic role in ecosystem function, research has focussed on the one-on-one co-evolution of insect herbivory and countervailing plant defences. This has resulted in a plethora of plant defence hypotheses (Stamp 2003), but no over-arching predictive theory (Berenbaum 1998) that would aid our understanding of ecosystem function.

The present study began as an investigation of the apparent anomaly of the resistance of New Zealand endemic plants to novel invasive continental defoliators (Matsuki et al. 2001, Hosking et al. 2002). Plant defence is usually considered to be proportional to herbivore pressure, where the measure of herbivore pressure is usually considered as the diversity of herbivores associated with a particular host plant (Feeny 1976). The species area relationship dictates that plants with geographically constrained ranges have fewer associated herbivores than plants with larger ranges (Southwood 1961, Brändle and Brandl 2001) and should therefore possess less potent defences.

The work presented in this thesis assessed the larval growth rate on three proven continental invasive Lepidoptera when fed elements of New Zealand indigenous flora.
However, there was a particular focus on the comparative defence of continental and insular species of *Nothofagus* using gypsy moth, *L. dispar*, as a bioassay.

Nothofagus is an iconic Southern Hemisphere temperate forest genus. It was long considered the only representative of the Fagaceae in the Southern Hemisphere and many specimens were collected and are present in the arboreta of the Northern Hemisphere. A great deal is known of its ecology, distribution and associated fauna (Veblen et al. 1996, Russell et al. 2000).

The gypsy moth is also thoroughly researched. It is a polyphagous defoliator of temperate forest tree species of the Northern Hemisphere. It has a broad host range with an ability to adapt to novel hosts, although it prospers ON host plants within the Fagaceae, possibly because this plant taxon tends to rely on quantitative leaf defences such as tannins (Feeny 1976) rather than qualitative defences such as alkaloids (Barbosa and Krischik 1987). On its accidental introduction to North America gypsy moth profoundly altered the species composition and growth of the indigenous oak forests of the Northeast (Kegg 1971, Campbell 1979, Davidson et al. 1999). This introduction is thought to have originated from a restricted Western Europe source and its host range is not considered as broad as that of the Eurasian gypsy moth populations (Rossiter 1987).

A number of studies have attempted to delineate the use of forest tree species as hosts for gypsy moth. However, in reviewing gypsy moth feeding trials Montgomery (1991) pointed out the difficulty in comparing analyses between the different studies because no two appeared to use the same methodology. Liebhold et al. (1995), in a comparison of seven gypsy moth laboratory feeding trials, came to the same conclusion and could only justify ranking host species use into the broad categories of ‘susceptible’, ‘resistant’ and ‘immune’. The strength of this *Nothofagus* study is the use of an iconic host genus, grown as mature specimens in the ‘common garden’ of the arboreta of Europe, and the use of a novel defoliator in no-choice bioassays. The gypsy moth, used as a bioassay originated from a laboratory colony perpetuated from the genetically restricted North American introduction and as such represents a very homogenous organism.

No-choice trials are the proven standard used by weed biocontrol practitioners for the evaluation of host acceptance by lepidopterous larvae (Sheppard 1999); although it is generally conceded that it defines a physiological, rather than an ecological host (Cullen 1990). Phylogenetic host assessments, where related plant taxa are exposed to larvae, as in this study of *Nothofagus*, usually as novel interactions, appears to be exclusively the domain of weed biocontrol practitioners, where it is used to evaluate host specificity of potential biological control agents (Wapshere 1974, 1989). There appears to be no application of this method to polyphagous insects – this guild of insects would automatically be excluded from weed biocontrol programmes.

Despite the strength of the experimental design for this study the research had a number of limitations associated with assessing novel interactions between insects and plants; not the least of which were the logistics involved in obtaining a ready supply of foliage from a common garden situation to assay in the quarantine conditions required for bioassays using proven invasive species. Common garden collections of subject plants are not that common and may contain collections with limited within species diversity. The provenance of most *Nothofagus* specimens within the European collections was unknown.and the assumption was made that the specimen trees used in these trials were chosen at random by the early plant collectors. The within species variation encountered during the trials would suggest that specimens were indeed taken from a number of populations.

In accepting the constraints, the explanation for the results is contrary to accepted hypotheses of plant defence and the ecology of invasive species. However, the hypothesis is eminently testable directly, and indirectly *via* the number of effects such interactions would produce in ecosystem processes. It offers a methodology to overcome the constraints imposed by ecosystem complexity by substituting habitat space for biodiversity.

Direct tests of consequences of the effect of space on plant defence

'The general failure of any single all-encompassing theory [of plant defence] *to gain acceptance to date may indicate that such a theory might not be a biologically realistic expectation.'* (Berenbaum 1995).

The IRA hypothesis was developed as an explanation of plant defence in spatially constrained habitats. However, the spatial explanation offers a dimension rarely included in autoecological investigations. In ecology space is synonymous with complexity. The complexity of inter-specific interactions increases exponentially with space and this has forced experimental ecology into a trade-off between manageable simplicity and realism. Dealing with space has become the realm of modellers using assumptions largely based on reductionist autoecological studies. Such pragmatism, apart from being dangerously circuitous, may be responsible for the lack of ability to extrapolate an ecological premise from one population to another, let alone to other species, communities, ecosystems or biomes.

Many natural populations exhibit geographic clines in traits from morphology to phenology. The evolutionary forces that shaped these clines have been the focus of many autecological studies (Nuismer et al. 2000). The multi-species diffuse evolution at a community level must also have the potential to present similar clines across landscapes and landmasses. Duffy et al. (2007) suggest that 'using biogeographic comparisons that detail the natural ecological associations between species diversity and productivity of large-scale whole ecosystems' may be one way to identify such patterns. This study focussed on that macroecological method to investigate of insect-plant interactions within fragments of a common ecosystem that had been geographically and/or ecologically, separated over evolutionary time.

The IRA hypothesis is a biogeographical explanation of the diffuse evolution of ecosystems that have been prescribed by space. There are many biogeographical processes which would allow the hypothesis to be tested directly. For example the adaptive radiation of colonising species offers the opportunity to test the hypothesis using endemic plants and defoliators without recourse to quarantined novel interactions. In New Zealand the defence within such genera as *Hebe* (Scrophulariaceae) and *Coprosma* (Rubiaceae) could be assessed with a polyphagous indigenous defoliator such as *Pseudocoremia suavis* (Lepidoptera: Geometridae). That the hypothesis appears applicable at the species level provides another opportunity for even less complicated corroborative research, by assessing marginal host populations with endemic defoliators. Chapter six indicates that host plants are not necessarily well represented by a Latin binomial and that the defence of marginal populations of plant species may differ significantly from their larger central populations. In hindsight, the comparison of central and marginal populations of such an unpalatable species as *N. truncata* was less than convincing, but any number of plants with large disparity in the distribution of its populations could be tested if the bioassay is neutral. The origins for this study came from an observation that mainland, but not island, populations of *Pinus radiata* were palatable to *P. suavis*. A re-investigation of this and similar novel interactions would be useful.

The IRA hypothesis is not restricted to an explanation of insular plant resistance. Plant defences should predominate wherever low biodiversity reduces the top-down regulation of herbivores *i.e.* islands, high altitude sites, 'unstable sites' lacking spatial or temporal predictability and sites of extreme abiotic conditions; or, habitats of limited biomass – when considering plants as habitats for other species. For example marginal tree populations, pioneer species and juvenile trees should be better defended than larger individuals or populations of the same or similar species. These suppositions could readily be tested.

Understandably plant defence research has had a strong phytocentric focus, but despite the plethora of hypotheses an over-arching theory remains elusive (Berenbaum 1995, Stamp 2003). The IRA hypothesis is phytocentric, but it is inclusive of community biodiversity and offers a general theory of insect: plant interaction and contends that if tritrophic interactions are included, a single all-encompassing theory of plant defence is possible.

Testable indirect consequences of the effect of space on plant defence

1. Biodiversity/productivity – Macro to Micro.

'integration of biodiversity-ecosystem functioning with food-web research poses an exciting challenge for ecology' (Worm & Duffy 2003)

There is an historical belief that biodiversity is a consequence rather than a cause of ecosystem productivity (Worm & Duffy 2003). This study offers the contrary view that biodiversity promotes ecosystem productivity. The idea that herbivores can regulate primary production of ecosystems is not new. Many studies have implicated herbivory in the cycling of nutrients (Chew 1974, Mattson and Addy 1975, Kitchell et al. 1979, Schowalter and Crossley 1983). Nitrogen is the main nutrient limiting ecosystem productivity. The IRA hypothesis contends that biodiversity may regulate community stoichiometry by imposing a parsimonious nitrogen economy on plants when trophic complexity is low, and allowing an unfettered nitrogen economy when trophic complexity is high. This is in apparent agreement with the Fretwell-Oksanen hypothesis that contends that longer food chains are supported by more productive habitats. Fretwell's model was designed for vertebrate grazers and invertebrates are not thought to comply with the hypothesis (Schädler et al. 2003). However this study suggests that it is the longer invertebrate food chains that are facilitating the greater habitat productivity of S. American *Nothofagus* forests. Leaf analysis of similarly distributed plants would reveal whether this was a common trait.

Differences in plant nitrogen use efficiency (NUE = biomass produced/ unit N uptake) may arise from allocation strategies such as tissue longevity and structure. Plants with greater leaf longevity tend to exhibit decreases in potential growth rate, leaf nitrogen, specific leaf area (leaf area/mass) and photosynthetic rates (Reich et al. 1992, Wright et al. 2004). However this study showed that differences in leaf nitrogen were correlated to trophic biodiversity rather than leaf longevity. The inference taken was that regardless of a leaf's longevity it is exposed to an associate herbivore guild which in turn is exposed to regulatory trophic guilds, and the plant must adapt accordingly, regardless of the longevity of its leaves.

These inter-specific differences should be important in structuring the ecosystem nitrogen cycle and can result in positive or negative feedback for nitrogen availability and productivity (Vitousek 1982, Wedin & Tilman 1990). Plant ecologists view a slow growth rate and efficient cycling of nitrogen as adaptations to plants on nutrient poor sites (Vitousek 1982). This study views them as a defensive adaptation and concurs with Mooney and Gulmon's (1979) suggestion that the metabolic costs associated with the absorption of more nitrogen may not be beneficial to plants, as it could lead to increased herbivory. This study would contend that this is particularly true for insular plants, although the adoption of a defence based on a parsimonious nitrogen economy may well have synergies with life strategies of plants on poor sites. For example, water stress negatively affects nitrogen uptake and the adaptation to low nitrogen and droughty sites and a number of leaf traits (leaf longevity, leaf toughness, low leaf nitrogen and water content) that deter defoliation, are common, and maybe complementary, in plants on less fertile sites. Many of these plants show no response to nitrogen fertilisation (Mattson 1980). If plant defence has a strong stoichiometric component then it must affect community nutrient cycling. For example, soil humus is the largest nitrogen pool in the ecosystem. If nitrogen parsimony is an element in the defence of *Nothofagus*, the depth and flow of nitrogen within the forest soil humus will depend on the biodiversity of invertebrates in the forest. With respect to the controversy of the slow-growth-high-defence hypothesis (Stamp 2003) – if stoichiometry is a basic mode of plant defence, then the slow-growth of plants it is not a cause for defence, but a result of defence and should be detectable as a spatial influence in ecosystem function. It should be detectable as a moderated flux of such processes as rates of decomposition of plant material, resorption of nitrogen from senescing leaves etc. Island floras are already noted for their inextricable paucity of nitrogen-fixing plants (Vitousek et al.1987) and the presence of qualitative nitrogen based defences, such as alkaloids, in insular nitrogen-fixing shrubs should be expected.

The potential role of nitrogen parsimony in plant defence, suggests a huge threat from anthropogenic nitrogen pollution for the earth's remaining large temperate forests. Humans have effectively doubled the natural rate of nitrogen fixation (Vitousek et al 1996). The anthropogenic fragmentation of forests not only results in the differential loss of upper trophic levels, but it is also coincident with this nitrogen pollution. Palatable forest tree species, which appear capable of utilising available nitrogen, may become more palatable (Throop and Lerdau 2004) and promote herbivore population growth while concurrently losing a degree of top-down protection as the natural enemies of the herbivores are lost.

2. *Diffuse evolution versus co-evolution*

'multispecies interactions significantly alter both the ecological and evolutionary outcomes of interactions in ways that could not be predicted from an understanding of pair wise interactions alone' (Strauss & Irwin 2004)

Although there has been a trend over the last decade to integrate evolutionary and community ecology, few attempts have been made to rationalise evolution, inter-specific interactions and space. Trophic interactions are probably the most important feedback phenomenon in ecosystems and co-evolutionary interactions between consumers and prey are probably the most intense. Many ecologists believe that much of the Earth's biodiversity has been generated by co-evolution (Thompson 2005).

The spatial influence on species interaction should not be confined to plants and their defoliators. The influence of habitat area, as a surrogate for biodiversity, should be identifiable in species interactions through all available trophic levels. Plant defence mechanisms will flow both up and down a community's trophic structure and herbivores and their predators and parasitoids are also bound by selection in the allocation of their resources.

Thompson (2005) recognised that the strength of co-evolutionary forces was geographically variable, but acknowledged a lack of prediction for this. The IRA hypothesis not only predicts a horizontal 'geographical mosaic of co-evolution', but may also reveal a vertical pattern of co-evolution. It posits that habitat space can account for the horizontal co-evolutionary mosaic. In spatially constrained habitats biodiversity and trophic complexity is low. Low biodiversity increases the strength of species interaction leading to greater co-evolution –

Thompson's 'co-evolutionary hotspots'. In large habitats with greater biodiversity there are more, but weaker, species interactions, resulting in less intense co-evolution –*i.e.* areas of cool or neutral co-evolution at the plant/herbivore level, but more intense interaction at higher trophic levels where there are fewer species.

In intense insect-plant interactions plant defences can be expected to be tracked by herbivore co-evolutionary counter-measures (Rosenthal and Janzen 1979, Bell and Cardé 1984, Edwards et al. 1991, Cornell and Hawkins 2003), which may in turn affect higher trophic levels (Awmack & Leather 2002). However, Janzen (1980) introduced the idea of diffuse evolution in recognition that communities may exert selective pressures that differ from the sum of pair-wise co-evolutionary interaction. If multi-species interactions mediate ecosystem function, they must have evolutionary consequences (Strauss & Irwin 2004). A corollary to the IRA hypothesis is that herbivores of 'resistant' island plants will be selected to allocate their own resources to catabolise the defences of their hosts. This co-evolutionary arms war is thought to drive host-specificity (Erhlich and Raven 1964) and may be responsible for the unusually high degree of host-specificity of New Zealand defoliators (Dugdale 1975). An allocation of resources for the catabolism of plant defences by herbivores may also be manifest as a decrease in fecundity, or, more likely on islands with fewer natural enemies, a decrease in defence against natural enemies. This may be demonstrated by comparing the New Zealand and Australian conspecific *Nyctemera* (Lepidoptera: Arctiidae).

The Australian *N. amica* is blown across the Tasman and readily hybridises with the New Zealand *N. annulata*. These two 'taxa' are a single species which has evolved in complex and simple ecosystems respectively. They both feed on *Senecio* and related plants and sequester the alkaloids from their hosts as a defence against natural enemies. The complex Australian community inhabited by *N. amica* includes several magnitudes more parasitoids and insectivorous species than that inhabited by the New Zealand *N. annulata*. Not surprisingly the warning colouration of *N. amica* is intense (Fig 7.1) and the larvae are protected with pro-thoracic urticating hairs, while *N. annulata* is dull with no urticating hairs (Kay 1980). The dull colouration and the lack of venomous species amongst many New Zealand endemic invertebrates could be seen as a result of diffuse evolution. If the lack of defence in *N. annulata* is an indication of predator release, its prevalence in other defence traits of New Zealand endemic invertebrates could be expected, and leave them vulnerable to exotic predators and parasitoids. The social Hymenopterous predators such as *Vespula* species have established readily in New Zealand, as have exotic parasitoids both accidentally and deliberately introduced (Charles 1998). The vulnerability of the New Zealand endemic invertebrate fauna predicted by the IRA hypothesis could be investigated by evaluating their behavioural and physiological responses, such as egg encapsulation, to novel parasitoids. A vertical pattern in co-evolution strength- may exist as biodiversity decreases with increasing trophic levels. Lower diversity at higher trophic levels should increase interaction strength between predator and prey, unless omnivory also increases at higher trophic levels.

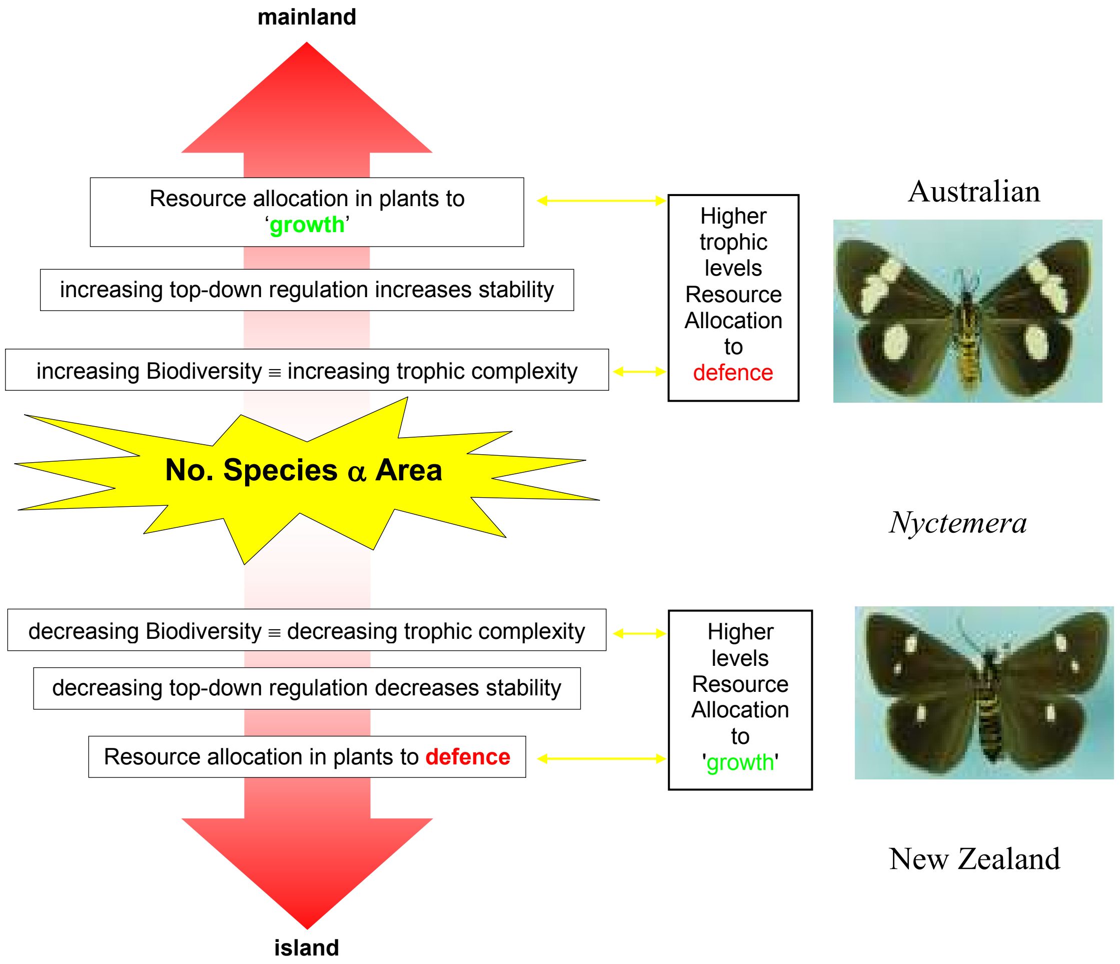


Figure 7. 1. A vertical shift in co-evolution as a result of increased community biodiversity. The Australian biotype of *Nyctemera* must allocate resources to its own defence in response to a greater array of predators. This regulatory top-down process allows its host plant to relax its defences.

3. Biodiversity and stability/invasibility

'The linkage between biodiversity and stability depends on the scale of inquiry' (Worm & Duffy 2003)

In light of increasing extinction rates (Lawton and May 1995) the role of biodiversity in ecosystem stability has become one of the most important questions in ecology (McCann 2000). Both habitat destruction and invasibility are the primary causes of the loss of ecosystem biodiversity. However, there are no general laws governing invasibility and the debate biodiversity/stability is ongoing. The ideas of 'complexity begets stability' and 'biotic resistance' (Elton 1958, Hutchinson 1959, Odum 1959) held sway to the 1970s, when it was challenged mathematically (May 1973, Pimm and Lawton 1978). Holling (1973) contended that different stability domains may exist or ecosystems may have multiple stable states (Holling 1996). Levin (1999) describes ecosystems as complex, but adaptive systems that are characterised by, among other things, 'historical dependency'. They may evolve or devolve to different stable states.

The conundrum for ecologists is that both simple and complex stable communities exist. Ecosystems can be easily perturbed, but there is only very weak equivocal evidence for any correlation between biodiversity and stability. The scarcity and contradictory results of experimental studies (Naeem et al. 1994, Fox and McGrady-Steed 2002) and the unpredictable effects of invasive species (Simberloff 1986, Snyder and Evans 2006) suggest that the issue is still far from resolution, but recent models suggest that the multitude of weak indirect interactions between species in highly diverse communities, promotes stability (McCann et al 1998, Jansen & Kokkoris 2003).

Both complex and simple ecosystems exist and may be functionally stable. It is invariably a dynamic stability and both systems can also lack resilience and be destabilised. That they do function with vastly different biodiversity suggests that stability for each may be reached by different processes. The IRA hypothesis allows predictions to be made about invasive abilities of species, the likely outcomes of alien species in novel habitats and the outcome of habitat fragmentation or reduction. Interestingly the loss or gain of top trophic level species appears to be the greatest perturbation to each system respectively.

The addition of predators (*eg* brown tree snake, predatory ants *etc*.) can be devastating for islands, whereas the loss of predators may be common and have little effect. Conversely the gain of predators may be of little consequence for complex systems but their loss can create cascades. However, as Cornell and Lawton (1992) suggested, a new order will establish among the remaining species. Stability is temporally relative, both systems need evolutionary time to adjust, but the time scales don't suit experimental observations.

The IRA hypothesis predicts that island invertebrates are defensively naïve and susceptible to 'sophisticated' parasitoids. The entry into New Zealand of these higher trophic levels, especially sophisticated invertebrate predators such as the social Hymenoptera, could well have more serious, albeit indirect, consequences for the indigenous flora. A scenario may already exist whereby the indigenous invertebrate defoliators, which provide a high protein diet for the fledglings of the forest's avian pollinators and seed dispersers, has been decimated by exotic natural enemies. We may not only lose our distinctive bird fauna, but in the long term elements of our unique forests as well.

On a more positive note, the biotas of islands are unlikely to be a serious invasive threat to continental ecosystems. Our slow growing plants are likely to be poor competitors for the continental flora, while our invertebrates are probably biologically naïve in terms of defence.

Confoundingly, the risk posed by alien invertebrates to New Zealand's indigenous forest may well come, not from continental herbivores, but from herbivores of insular, phylogenetically related communities. The IRA hypothesis predicts that the well defended New Zealand beech should not be at risk from insects associated with the beech species with large geographic ranges. However, specialist chrysomelids exist in the mainland island communities of the Australian beech *N. moorei* and *N. cunninghamii*. New Zealand lacks any significant arboreal chrysomelid fauna or their associate natural enemies. The introduction of such specialist defoliators may well result in the unregulated damage to the New Zealand beech forest by these insects that can cope with poor host quality. This could be readily tested by repeating the *Nothofagus* study, but utilising specialist insects from mainland islands as bioassays.

Interestingly the naturalised and endemic plants of New Zealand appear to be at opposite ends of the risk gradient for invasive invertebrate defoliators. The indigenous flora has allocated resources to defence, but the naturalised flora is largely continental and probably less inherently defended as it evolved with its herbivores regulated by suites of natural enemies. The introduction of an unregulated continental defoliator may pose a problem for naturalised plants, which may also be at risk from a number of indigenous polyphagous invertebrates that have adapted to the strong indigenous plant defences.

Habitat reduction or fragmentation should have little effect on simple ecosystems. The species interactions within these are already strong. If all herbivores were dispatched, plants would evolve without this selection pressure and re-allocate resources to growth and competitive ability, and become very similar to their continental congenerics. However, for complex communities, habitat reduction through fragmentation, perturbation or climate change, will have greatest impact on the least abundant upper trophic levels. The ensuing loss of herbivore regulation could result in the rapid loss of poorly defended plants that had evolved with the benefits of a strong top-down defence.

4. Top-down/bottom-up regulation of defoliators

" *the time is ripe for the synthesis of a novel paradigm of spatial ecology with the classical paradigms of top-down and bottom-up studies*." (Gripenberg & Roslin 2007)

The plurality of top-down/bottom-up (TDBU) regulation of phytophagous insects in ecosystems has largely been accepted (Price et al. 1980, Hunter and Price 1992, Forkner and Hunter 2000). However, the strength of both forces varies temporally and spatially. Experimental field studies providing empirical evidence of the relative strengths of each are rare and predictions for most systems are limited (Denno et al. 2003). Studies of TDBU on an evolutionary scale appear non-existent.

The current study reconciles TDBU in evolutionary time. When trophic complexity of a habitat is limited BU processes must prevail. With increasing trophic complexity, the regulation of consumers by predators, and the stability of that regulation will improve, and TD processes will pervade. The strength of TD regulation will increase with trophic complexity. This increase may be asymptotic, but, given the ever changing nature of Nature, it would be injudicious of plants to completely abandon BU abilities.

A majority of ecologists hold that top-down processes are more pervasive through food webs than bottom-up processes (Borer et al. 2006), but Denno et al. (2003) contend that bottom-up processes are more pervasive and dominate insect-plant interactions, due to small size, superior dispersal and higher rates of natural increase of many insect herbivores compared to their natural enemies. However, the difference in perspectives of TDBU processes may be observational. Trophic cascades resulting from the loss of predators may be more obvious than the subtleties of stoichiometric processes suggested as the major bottom-up process of the IRA hypothesis. Stoichiometry is more likely to be the basis of ecosystem function and Forkner and Hunter (2000) even suggest that upward cascades, due to improved nutrient availability, are possible.

5. Biodiversity and Ecosystem Function - the BEF debate

Ecosystem function (EF) research is primarily concerned with the fluxes of energy and matter within ecosystems. Inter-specific interactions are primarily responsible for these fluxes within and between ecosystems, but the pragmatism of ecological research has largely limited ecosystem function studies to synthetic autotrophic communities. Unfortunately there has been a preoccupation with the experimental manipulation of biodiversity to determine how ecosystems function. Such manipulation is not done in the context of the evolutionary stable re-arrangement of the interacting species (Cardinale et al. 2006). Macroecological studies attempt to avoid the constrictions of space and time by identifying patterns in ecological interactions and processes within and among ecosystems, as a means to understanding how the biosphere operates (Brown 1995).

There has been a trend to integrate evolutionary and community ecology over the last decade, but few attempts have been made to rationalise evolution, inter-specific interactions and space. A large number of ecosystem processes have been revealed and their application undoubtedly varies to meet different species assemblages. Multi-species interactions have evolutionary and demographic consequences (Strauss and Irwin 2004) and even simple genetic mechanisms can lead to major qualitative changes in the predictions of spatial and food web models (Lehman and Tilman 1997, Antonovics et al. 1998).

The IRA hypothesis offers an alternative way of looking at BEF. It provides an insight into how biodiversity affects the evolution of EF processes in common ecosystems. If, as the IRA hypothesis suggests, trophic diversity determines resource accumulation and allocation within plants, then biodiversity will have a profound affect on how ecosystems function. If the plant defences incur a metabolic cost, island plants may have a lower apparent productivity. There may also be a knock-on effect for all of the participants in the web. The ramifications of a stoichiometric defence in a foundation species such as *Nothofagus* should result in a diffuse evolution which differs with the biodiversity of the invertebrate community associated with each species. For spatially constrained habitats the resultant diffuse evolutionary outcome would appear to be slow plant growth supporting vulnerable herbivores.

Key trade-offs and feedbacks in ecology often involve strong stoichiometric mechanisms that affect the qualitative and quantitative nature of species interactions (Snyder and Evans 2006). An allocation of resources to stoichiometric or chemical defence systems in plants should have flow-on effects for all trophic levels including decomposers. For example secondary plant compounds affect litter decomposition rates (Findlay et al. 1996, Cornelissen et al. 1999) and Wardle et al. (1997) found that the accumulation of secondary compounds in the soil litter of islands increases inversely with island area.

In light of the anticipated sixth mass extinction the role of biodiversity in ecosystem function has become the great topical debate in ecology. Understanding the community- and ecosystem-level consequences of biodiversity is a prime objective of ecological research (Hooper et al 2005). The IRA hypothesis may be peculiar to forest species. Forests are, or were, the dominant global terrestrial ecosystems. Tree lineages typically experience low speciation and extinction (Petit and Hampe 2006) and insects are the dominant folivores. It is a green world, but the processes that keep it that colour appear to differ in space. Counter-intuitively it would appear the ecosystem function in small habitats may be quite resilient to perturbation, but possess a stoichiometric inertia that lowers apparent productivity.

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Appendix 1

Nothofagus growth rates, analysis for Nod Kay

Roderick D. Ball, Scion*

Nov 3, 2009

1 Nothofagus data

Data was given on growth rate of insect larvae on 15 Nothofagus species in relation to area, MTE, leaf longevity, leaf nitrogen,invertebrate diversity, landmass and sub-genus at the species level (Table 1.) The goal was to assess evidence for an increasing growth rate with increasing area of the host species location. Variables were mutually correlated, and it was recognised a priori that invertebrate diversity was almost a surrogate for area, since diversity increases with area. Methods used were analysis of variance, step-wise regression, and a Bayesian analysis considering all possible models.

Table 1. Species level data analysed.

```
> nothofagus.df
   Nothofagus     GR Area.103 MTE.adju Leaf.lon Leaf.nit Inverteb    landmass Sub.genu
1  betuloides    9.9    104.0     2.47        E     1.97       53        S.Am        N
2  dombeyi      11.4    112.0     3.91        E     1.95       48        S.Am        N
3  alpina        6.0     39.0    10.27        D     2.32       56        S.Am        L
4  obliqua      12.6     70.0     8.79        D     2.57      103        S.Am        L
5  pumilio      10.2    150.0     2.53        D     2.48       51        S.Am        N
6  antarctica   15.6    162.0     1.90        D     2.79       64        S.Am        N
7  glauca        4.7     16.0    11.89        D     1.98       22        S.Am        L
8  alessandri    0.0      0.1    12.00        D     1.63       31        S.Am        F
9  menziesii     0.5     38.0     6.45        E     1.79       38 New Zealand        L
10 fusca         1.9     37.0     7.73        E     2.09       34 New Zealand        F
11 truncata      0.0     17.0    10.46        E     1.74       28 New Zealand        F
12 solandri      7.9     62.0     7.18        E     1.63       64 New Zealand        F
13 gunnii         NA      2.0     5.35        D       NA       10        Aust        F
14 cunninghamii  2.3     15.0     7.99        D     1.73       30        Aust        L
15 moorei        0.0      2.0    29.57        E     1.94       NA        Aust        L
```

Note: this data was summarised from more detailed raw data.

---

*Scion is a trading name of the New Zealand Forest Research Institute Limited.

2 Analysis of variance

The first analysis was just to examine a simple analysis of variance with other possible covariates fitted before Area and Invertebrate diversity:

Table 2. Analysis of variance 1.

```
> # simple anova, with variables MTE.adjust, Invertebrate.diversity, Area last
> summary(aov(as.formula(paste("GR ~", paste(names(nothofagus.df)[c(5,6,8,9,4,7,3)],
+         collapse="+"))), data=nothofagus.df))
                       Df Sum Sq Mean Sq F value Pr(>F)
Leaf.longevity          1   13.9    13.9    4.17 0.1339
Leaf.nitrogen           1  176.5   176.5   52.79 0.0054
landmass                2   55.3    27.6    8.27 0.0602
Sub.genus               2    5.6     2.8    0.84 0.5117
MTE.adjust              1   17.0    17.0    5.08 0.1095
Invertebrate.diversity  1   34.2    34.2   10.22 0.0495
Area.103km2             1   21.3    21.3    6.37 0.0858
Residuals               3   10.0     3.3
2 observations deleted due to missingness
```

Note:

1. The '`Sum Sq`' column shows the sums of squares explained by fitting each variable after fitting previous terms in the table. From this we can see which variables are contributing to explaining the variance, e.g. `Leaf.nitrogen` has the largest sum of squares, (`Sum Sq=176.5`), followed by `landmass`, `MTE.adjust`,`Invertebrate.diversity`, and `Area` with sums of squares of 55.3, 34.2, 21.3.... respectively.
2. The sums of squares are sequential, meaning that the sums of squares for `Area` are conservative, and would increase if `Area` was fitted first.

Table 3. Analysis of variance 2 (analysis without invertebrate diversity).

```
> # analysis of variance without invertebrate diversity
> summary(aov(as.formula(paste("GR ~", paste(names(nothofagus.df)[c(5,6,8,9,3)],
+         collapse="+"))), data=nothofagus.df))
               Df Sum Sq Mean Sq F value  Pr(>F)
Leaf.longevity  1   28.0    28.0    6.96 0.03868
Leaf.nitrogen   1  167.7   167.7   41.66 0.00066
landmass        2   50.0    25.0    6.21 0.03454
Sub.genus       2   28.3    14.1    3.51 0.09780
Area.103km2     1   73.5    73.5   18.26 0.00525
Residuals       6   24.2     4.0
1 observation deleted due to missingness
```

Note: The sums of squares for `Area` has now increased to 73.5, now the second largest, and the p-value has decreased to 0.005.

Table 4. Analysis of variance 3 (analysis without Area).

```
> # analysis of variance without Area
> summary(aov(as.formula(paste("GR ~", paste(names(nothofagus.df)[c(5,6,8,9,7)],
+         collapse="+"))), data=nothofagus.df))
                       Df Sum Sq Mean Sq F value Pr(>F)
Leaf.longevity          1   13.9    13.9    2.14 0.2036
Leaf.nitrogen           1  176.5   176.5   27.09 0.0035
landmass                2   55.3    27.6    4.24 0.0837
Sub.genus               2    5.6     2.8    0.43 0.6705
Invertebrate.diversity  1   49.9    49.9    7.66 0.0395
Residuals               5   32.6     6.5
2 observations deleted due to missingness
```

Note: Now the sums of squares for `Invertebrate.diversity` has increased to 49.9, now the third largest, and the p-value has decreased to 0.0395.

3 Step-wise regression

The step-wise regression analysis searches for the model which best fits the data, according to the criterion. We have used the BIC criterion (selected by choosing $k = \log n$, where $n = 13$ is the sample size, (15 minus the number of missing values) in the options to the `stepAIC` R function (Venables and Ripley 2002). We have additionally considered only models which include `Leaf.longevity, Leaf.nitrogen, and landmass.` The method selects the model with the minimum value of the BIC criterion which is the most probable given the data, assuming all models are *a priori* equally likely.

Table 5. Step-wise regression analysis.

```
> fit1 <- lm(GR ~ Leaf.longevity+landmass+Sub.genus, data=nothofagus.df)
> sel <- with(nothofagus.df, !is.na(GR) & !is.na(Invertebrate.diversity))
> fit2 <- lm(as.formula(paste("GR ~", paste(names(nothofagus.df)[c(5,6,8,9,4,7,3)],
+            collapse="+"))), data=nothofagus.df[sel,])
>
> # best fitting model, BIC criterion (due to using k=log(n))
> # subject to ~Leaf.nitrogen + Leaf.longevity being in the model
> # GR ~ Leaf.longevity + landmass + Sub.genus + MTE.adjust + Area.103km2
> # NB: dropping Area, landmass or sub genus  would result in a large increase in AIC
> stepAIC(fit2,k=log(13),scope=list(
+         lower= ~Leaf.nitrogen + Leaf.longevity,
+         upper= ~Leaf.longevity+Leaf.nitrogen+landmass+Sub.genus+MTE.adjust+
+                 Invertebrate.diversity+Area.103km2))
Start:  AIC=22.28
GR ~ Leaf.longevity + Leaf.nitrogen + landmass + Sub.genus +
```

```
    MTE.adjust + Invertebrate.diversity + Area.103km2

                         Df Sum of Sq  RSS  BIC
- Invertebrate.diversity  1       0.2 10.2 19.9
<none>                                10.0 22.3
- MTE.adjust              1       3.3 13.3 23.4
- Sub.genus               2       6.5 16.5 23.6
- landmass                2      14.5 24.5 28.7
- Area.103km2             1      21.3 31.3 34.5

Step:  BIC=19.91
GR ~ Leaf.longevity + Leaf.nitrogen + landmass + Sub.genus +
    MTE.adjust + Area.103km2

                         Df Sum of Sq  RSS  BIC
<none>                                10.2 19.9
- MTE.adjust              1       4.0 14.2 21.7
+ Invertebrate.diversity  1       0.2 10.0 22.3
- Sub.genus               2      27.0 37.2 31.6
- landmass                2      37.9 48.1 35.0
- Area.103km2             1      55.3 65.5 41.5

Call:
lm(formula = GR ~ Leaf.longevity + Leaf.nitrogen + landmass + Sub.genus + MTE.adjust
    + Area.103km2, data = nothofagus.df[sel,     ])

Coefficients:
        (Intercept)     Leaf.longevityE       Leaf.nitrogen
            -7.4057              7.7287              0.0120
landmassNew Zealand        landmassS.Am          Sub.genusL
           -13.1110             -2.6264             -0.5284
         Sub.genusN          MTE.adjust         Area.103km2
           -14.1108              0.8557              0.2251
```

Note that the best fitted model (shown last) includes `Area`, but not `Invertebrate.diversity`, and the coefficient of `Area` is 0.2251, which is positive. In other words the most probable model posits an increaing growth rate with increasing area.

4 Bayesian analysis with posterior probabilities considering all possible alternative models

Assuming all variables were equally probable, a priori, posterior probabilities for all possible models were estimated by the BIC criterion. The analysis used the `bicreg.qtl` R function (Ball 2009), a modification of the `bicreg` R function (Raftery 1995; Raftery et al 1997, 2009). The `bicreg.qtl` function was modified for QTL mapping, but can be used more generally with the appropriate options.

Table 6. Bayesian analysis with posterior probabilities for alternative models.

```
> # Bayesian analysis with posterior probabilities for alternative possible models
> # prior 0.1 per variable, 36 models explain 99% of variation
> nothofagus.bic1p0.1 <- bicreg.qtl(X,y,prior=0.1,nvmax=9)
> summary(nothofagus.bic1p0.1, nbest=36)
R-squared, BIC, and approximate posterior probabilties for individual models:
   Leaf.longevityE Leaf.nitrogen landmassNew.Zealand landmassS.Am Sub.genusL
1                0             0                   0            0          0
2                0             0                   0            0          0
3                0             0                   1            0          0
4                0             0                   0            0          0
5                1             0                   1            0          0
6                0             0                   0            1          0
7                1             0                   0            0          0
8                0             0                   0            0          0
9                0             1                   0            0          0
10               0             0                   0            0          0
11               0             0                   1            0          0
12               1             0                   0            0          0
13               1             0                   1            0          0
14               0             0                   0            0          0
15               0             0                   0            1          0
16               0             0                   0            0          1
17               0             0                   1            0          0
18               0             0                   0            1          0
19               0             0                   0            0          1
20               0             1                   0            0          0
21               1             0                   1            0          1
22               1             0                   0            0          0
23               0             0                   1            0          0
24               1             0                   1            0          0
25               0             0                   0            0          0
26               0             0                   1            1          0
27               0             0                   1            0          0
28               0             1                   1            0          0
29               0             0                   1            0          1
30               0             0                   0            0          0
31               1             0                   1            1          0
32               1             1                   1            0          0
33               1             0                   1            0          0
34               0             0                   0            1          1
```

```
35               0             0                   0            0          0
36               0             0                   0            1          0
   Sub.genusN MTE.adjust Invertebrate.diversity Area.103km2    R2     BIC
1           1          0                      1           0 87.85 -11.587
2           0          0                      1           1 87.73 -11.456
3           0          0                      1           1 92.11 -10.241
4           0          0                      0           1 75.17  -9.257
5           1          0                      0           1 95.00  -9.205
6           0          0                      1           1 91.06  -8.613
7           1          0                      1           0 89.65  -6.715
8           0          1                      1           1 89.64  -6.702
9           1          0                      1           0 89.45  -6.462
10          0          1                      0           1 81.81  -6.341
11          1          0                      1           0 89.22  -6.180
12          0          0                      1           1 89.17  -6.125
13          1          1                      0           1 96.17  -5.723
14          1          0                      1           1 88.80  -5.687
15          1          0                      1           0 88.80  -5.681
16          1          0                      1           0 88.79  -5.678
17          0          0                      0           1 80.65  -5.535
18          0          0                      0           1 80.64  -5.530
19          0          0                      0           1 79.54  -4.814
20          0          0                      0           1 79.03  -4.489
21          1          0                      0           1 95.74  -4.324
22          0          0                      0           1 78.40  -4.108
23          0          1                      1           1 92.58  -4.084
24          0          0                      1           1 92.43  -3.822
25          1          0                      0           1 77.57  -3.618
26          0          0                      1           1 92.14  -3.328
27          1          0                      1           1 92.13  -3.320
28          0          0                      1           1 92.13  -3.318
29          0          0                      1           1 92.11  -3.287
30          0          1                      1           0 76.18  -2.833
31          1          0                      0           1 95.10  -2.508
32          1          0                      0           1 95.00  -2.251
33          1          0                      1           1 95.00  -2.248
34          0          0                      1           1 91.35  -2.089
35          1          1                      1           1 91.24  -1.915
36          0          1                      1           1 91.18  -1.827
   postprob cumprob
1  0.227311  0.2273
2  0.212905  0.4402
3  0.116014  0.5562
4  0.070925  0.6272
5  0.069104  0.6963
6  0.051384  0.7476
```

```
7  0.019900  0.7675
8  0.019763  0.7873
9  0.017528  0.8048
10 0.016499  0.8213
11 0.015227  0.8366
12 0.014811  0.8514
13 0.012117  0.8635
14 0.011898  0.8754
15 0.011864  0.8873
16 0.011843  0.8991
17 0.011028  0.9101
18 0.010999  0.9211
19 0.007692  0.9288
20 0.006536  0.9353
21 0.006020  0.9414
22 0.005404  0.9468
23 0.005339  0.9521
24 0.004683  0.9568
25 0.004229  0.9610
26 0.003659  0.9647
27 0.003644  0.9683
28 0.003641  0.9720
29 0.003584  0.9755
30 0.002856  0.9784
31 0.002428  0.9808
32 0.002135  0.9830
33 0.002132  0.9851
34 0.001969  0.9871
35 0.001805  0.9889
36 0.001728  0.9906
marginal probabilities for model sizes
        0         1         2         3         4         5         6         7
2.684e-04 7.510e-02 5.055e-01 2.902e-01 9.915e-02 2.602e-02 3.547e-03 2.125e-04
        8         9
5.628e-06 5.282e-08
marginal probabilities for individual variables
       Leaf.longevityE    landmassNew.Zealand           landmassS.Am
               0.13874                0.26075                0.08403
            Sub.genusN             MTE.adjust Invertebrate.diversity
               0.41919                0.06011                0.76549
           Area.103km2
               0.68407
attr,"prior")
[1] 0.1
attr,"intercept")
[1] TRUE
```

```
>
> w0.1 <- nothofagus.bic1p0.1$which
> w0.1[1:4,]
     Leaf.longevityE Leaf.nitrogen landmassNew.Zealand landmassS.Am Sub.genusL
[1,]           FALSE         FALSE               FALSE        FALSE      FALSE
[2,]           FALSE         FALSE               FALSE        FALSE      FALSE
[3,]           FALSE         FALSE                TRUE        FALSE      FALSE
[4,]           FALSE         FALSE               FALSE        FALSE      FALSE
     Sub.genusN MTE.adjust Invertebrate.diversity Area.103km2
[1,]       TRUE      FALSE                   TRUE       FALSE
[2,]      FALSE      FALSE                   TRUE        TRUE
[3,]      FALSE      FALSE                   TRUE        TRUE
[4,]      FALSE      FALSE                  FALSE        TRUE
>
> # models with invertebrate density or area
> AorID.models <- apply(w0.1[,8:9],1,sum) > 0
>
> # 99.7% probability either invertebrate density or area in the model
> sum(nothofagus.bic1p0.1$postprob[AorID.models])
[1] 0.997
>
```

Note:

1. A number of models are consistent with the data, as indicated by the `postprob` column, e.g. the 6 most probable models have probability greater than 5%. The 36 most probable models are shown and account for 99% of the total probability.

2. A variable is included in the model (corresponding to a numbered row in the table) if the entry is a 1.

3. The "`marginal posterior probabilites for individual variables`" summary is the total probability of all models containing that variable. The marginal posterior probabilities for `Area` and `Invertebrate.diversity` are 0.765, and 0.684, representing postive evidence for each of these variables since a prior probability of 0.1 was assumed.

4. The final calculation shows a probability of 99.7% that one or more of the variables `Area` and `Invertebrate.diversity` are in the true model.

5. The analysis was run with a prior probability of 0.1 per variable. This is appropriate if one is reasonably skeptical a priori about each variable. Other priors can be used including separately specified prior probabilities for each variable. The analysis was also run with prior probabilities of 0.5 and 0.3 (not shown). Naturally posterior

probabilities were higher with higher prior probabilities but qualitatively the conclusions were similar, i.e. there was good evidence for one or more of the variables `Area` and `Invertebrate.diversity` to be in the true model.

Table 7. Model averaged and conditional effects for variables in the Bayesian analysis with posterior probabilities for alternative models.

```
> effects <- with(nothofagus.bic1p0.1,
+      cbind(probne0,postmean=postmean[-1],
+            condpostmean=condpostmean[-1],condpostsd=condpostsd[-1]))
> effects
                     probne0(%) postmean condpostmean condpostsd

Leaf.longevityE           14.3  0.57630       4.0310    3.92647
Leaf.nitrogen              3.2  0.07863       2.4413    3.13901
landmassNew.Zealand       26.6 -1.45140      -5.4614    4.41485
landmassS.Am               8.6  0.16278       1.8880    1.64879
Sub.genusL                 3.3  0.02508       0.7705    1.93800
Sub.genusN                42.4  0.50841       1.1994    9.21562
MTE.adjust                 6.5  0.03359       0.5202    0.54352
Invertebrate.diversity    76.9  0.09072       0.1180    0.04050
Area.103km2               68.9  0.05926       0.0860    0.04619
```

Note:

1. This table shows the probability of selection `probne0` (interpreted as probability a variable is in the true model) and effects for individual variables. The `postmean` column shows model averaged effects, while the `condpostmean`, and `condpostsd` columns show effects conditional on selection and their posterior standard deviations.

2. The effects for `Area` of 0.059 (model averaged) or 0.0860 (conditional) are smaller than the coefficient of `Area` in the stepwise regression because `Area` and `Invertebrate.diversity` are competing to explain the variance here, while `Invertebrate.diversity` was not in the best fitting model selected by step-wise regression, so is not competing to explain the variance there. Nevertheless the effects of `Area` and `Invertebrate.diversity` are positive in both analyses.

5 Conclusions.

- All methods were consistent with an effect of area or invertebrate diversity. Area was included in the most probable model from stepwise regression or the Bayesian analysis.

- The Bayesian analysis quantified this most effectively, showing that there is good evidence (posterior probability 99.7%, assuming prior probability 10% per variable) for an increase in growth rate with increasing area or invertebrate diversity.

- The estimate effects of `Area` and `Invertebrate.diversity` are positive indicating an increase in growth rate with increasing area or invertebrate diversity.

References

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