The Use of Plant Functional Types as a Method of Determining Plant Biodiversity and Keystoneness on a Northern New Zealand Isocline.

A thesis presented in partial fulfilment of the requirements
for the degree of Master of Applied Science in Plant Science
at Massey University, New Zealand

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1999

Abstract

New Zealand vegetation, like the rest of the world, is undergoing increased perturbations due to global climate change. Whether anthropocentric in origin or part of a natural climatic cycle, increased CO_2, increased temperature plus changing regimes of precipitation have been recorded. Environmental change, especially at local levels, does affect community structure. New Zealand's ancient endemic trees and shrubs face the greatest threat of extinction, mainly due to habitat destruction by man for development and by introduced pests. The consequence could be that these trees and shrubs would not be able to migrate naturally in the time frame that climatic change will allow.

The use of Plant Functional Types in climate change research is extensive and these groupings are being used more frequently in the study of diversity response to environmental change.

The objectives of the Maunganui Bluff study were to develop a methodology to construct PFTs and to utilise these functional groupings in an analysis of the isocline. These analyses were; a diversity study based on richness and abundance, a site ordination and a group analysis. A total of forty-eight PFTs were constructed, then reduced to seventeen. The final seventeen functional groups were used in the following analyses.

1. *A diversity analysis*. While not appearing useful in comparing species evenness to PFT evenness over the isocline, the analysis did confirm that at that point in space and time when sampling was undertaken, PFTs did conform

to the assembly rule for groups. This rule states that there should be equal representation of functional groups at each site from the total available pool

2. *Ordination.* The second analysis was to determine the effect of the local environment on the spatial position of the PFTs on the isocline. Detrended Correlation Analysis (DCA), an ordination technique, was used to map the groups and the sites against environmental gradients. The results signified that a small number of groups were strongly influenced by potassium (K) but the majority of groups occupied specific sites, on an altitude – phosphorus and nitrogen gradient, due to competition for resources. This summation is supported by altitude being linked to precipitation and leaching, since most of the other environmental data, measured and analysed, were correlated to altitude.
3. *Group analysis using Indicator Species Analysis in the computer programme PCORD.* The statistical analysis highlighted three PFTs with high keystone rankings p*>.800), one of which was missed by a subjective analysis of the site map of PFTs distribution. When these three groups were deconstructed back to species, the membership of each group was only one species. Of these three species, only *Haloragis erecta* appeared to be out of place within the gradient. Four hundred metres in altitude is well beyond the plants recognised limit of approximately 120 metres. Since sea level to one hundred and fifty metres is the shrubland zone and site K is also, by species sampled, designated a shrubland, there is evidence that some environmental factor may be associated with these sites. Obviously, this cannot be tested, as there were no *Haloragis erecta* in the sampled sites from sea level to one hundred and fifty metres.

The analysis suffered from a lack of replication for the site under study, as well as comparative sites, to determine the validity of the methodologies. The results while encouraging only reflect a point in both space and time. The work would have needed a much larger range of environmental data, over a longer time frame to ensure that the results were not chance, and would be sustained under more detailed statistical rigor. Many of the premises that the work was based on are subjective.

However, despite the lack of statistical rigor, the study confirms the work being carried out using PFTs in other countries. New Zealand's endemic plants do have assembly rules and PFTs constructed with New Zealand natives are valid assemblages that can be used in statistical analysis, and may well turn out to be important in monitoring environmental change.

Certification

I, William Frederick Lee, certify that this thesis represents original work by me, except where acknowledged.

Acknowledgements

My sincere thanks are extended to my chief supervisor, Dr. Peter Kemp, for his valuable guidance and supervision throughout both this research and my postgraduate study. Thanks, also, go to Dr. Ian Valantine for his encouragement and suggestions for the ecological components of the thesis.

Special thanks are extended to my brother, A. J. Lee, for his guidance through the statistical analysis and to John Hastings for helping to interpret the data and outputs of the statistical analysis. To Janine McVeagh, for proof reading and help with grammatical structure. I would, also, acknowledge the contribution by Lisa Forester of the Department of Conservation for helping to identify the plant species sampled during the Maunganui Bluff survey.

To all my friends in Palmerston North, who supported me and discussed at length my work. Thanks for keeping me focused.

To my friends and colleagues at Northland Polytechnic, especially Alastair Wells for taking work pressures off me during final write up, thanks for the patience and encouragement. Special appreciation to Northland Polytechnic and the ASB grant committee for financial support throughout all my University studies.

Finally, very special thanks to my partner, Dot, for her encouragement and support. Without you, this work would not have been completed.

Structure of Thesis

This thesis is based on the premise that studying the effects of environmental change at the species level is too complex to be able to make predictions about changes to ecosystem structure and function both spatially and temporally. One methodology to reduce complexity is to group species into Plant Functional Types (PFTs).

The thesis is divided into two distinct sections. Chapter One (General Introduction) introduces the rationale behind using PFTs for biodiversity studies and identification of keystone species/groups with regard to monitoring environmental change. Chapters two to four (Literature Review) attempt to explain the major biotic and abiotic influences on, or as a consequence of, environmental change: CO_2, temperature, nutrient use efficiency, herbivory and fire. Chapter two deals specifically with the general theory of each of these abiotic influences in relationship to environmental change. Chapter three focuses on the effects of environmental change on the biota of New Zealand and looks at the effects of expected scenarios on the diversity of New Zealand's natural broadleaf – podocarp forests. Chapter four explores how functional groups evolved and examines the current theories regarding the use of functional groups to characterize changes in biodiversity and to identify keystone species or groups containing a keystone identity.

The second section discusses the application of the functional group theory to an altitudinal gradient analysis. Chapter five gives an overview of the survey site and details both history and biogeographical information. Chapter six is devoted to the methodology and analysis of the biotic and abiotic survey of the site. This includes the results of the construction of PFTs, the diversity analysis (Shannon H' and evenness), ordination (Regression and Detrended Correspondence Analysis (DECORANA)) and group analysis (Keystoneness) using the methodology of Dufrene & Legendre (1998). The results are discussed in chapter 6 and the major findings are summarised in Chapter seven (Conclusions).

The thesis is presented at three levels in relation to environmental change, species, PFTs and ecosystems. There is some repetition of environmental data, especially climate change, to set the scene for each of these chapters. This is done to remind the reader that environmental change has a differing effect on vegetation, depending on the hierarchial level the vegetation is studied at.

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Chapter 1 General Introduction

Vegetation all over the Earth is being subjected to massive disturbance in the form of wholesale exchanges of species between regions, introduction of alien predators and pathogens (Vitousek et al. 1997), over harvesting, habitat destruction, pollution, and in the future, climate change (Sutherst et al. 1996; Forseth 1997). Changes in land use in New Zealand over the past 100 years have created extensive areas of agricultural lands and early successional patches at the expense of late successional and climax communities (farm or scrub land instead of broadleaf – podocarp forest). Along with these changes are major reductions in population sizes and the extinction of species that depend upon the habitats which are being degraded or destroyed. The consequences of these changes to remaining remnants in New Zealand are not well known. Loss of species that may accompany forest destruction is irretrievable. Habitat loss can only be recovered over long periods of time.

Worldwide, ecologists have been concentrating on estimating the extent of species loss, identifying major causes of the losses, and developing ways to reduce the rate of species extinction. Conservation ecology in a myriad of forms has become a specialist branch of ecology. Habitat destruction has been highlighted as the most important cause of the estimated extinction of species since the advent of human change from hunter / gatherer to agriculturist. Less attention, however, has been paid to the consequences of the loss of species in terms of functional processes.

Research efforts are now being directed towards understanding species contributions to ecosystem functioning and to how the alteration of the species composition of ecosystems affects the maintenance of ecosystem processes (Woodward 1994). Specifically, how and to what degree do the key functional processes of ecosystems depend upon the richness of species in them, and how will these properties be changed by the losses of some of their component species (Berendse 1994; McNaughton 1994)?

The complex topic of the role of biological diversity in ecosystem functioning can be addressed in many ways and at population, community, and ecosystem levels. An important result of the past three decades of theoretical and empirical research into the causes of patterns in species richness is the demonstration that these patterns are the products of complex interacting forces that vary in relative importance in both time and space (Solbrig 1991). Similarly, the consequences of biodiversity for system-level processes are certain to be equally complex; their elucidation will require analysis of many factors operating at many spatial and temporal scales.

Lawton and Brown (1993) consider that *ecosystem processes*, *behaviour of ecological systems*, and *ecosystem functioning* are equivalent terms. Ecosystems process materials and energy. The productivity and stability of the process is likely to be influenced by biodiversity. *Biodiversity* means the number of species (species richness) and also the richness of the evolutionary lineage, the variety of functional groups of plants, and the variety of types of ecological communities. The number of species in ecological communities usually exceeds the number of major ecosystem processes. Since many species are involved in each process, groups of species that participate in a particular process are termed a *functional* *group* (Smith et al. 1993; Gitay & Noble 1997; Shugart 1997). A given species may participate in more than one ecosystem process and so be a member of more than one functional group.

When more than one species participates in a process there is *functional redundancy* (Walker 1997). This term does not imply that all species within a functional group can be substituted for one another with respect to maintaining that process. Because species differ in the quality and quantity of their contribution to a particular process, the loss of one species may not be compensated for by complementary performance of other species within the group (Orians 1997). However, if there is little change in the inputs or outputs of the process, then the functional system will be maintained within the ecosystem. Lawton and Brown (1996), while not disagreeing with the concept of redundancy and keystoneness, believe that in the plant kingdom the dominant species in a community is the usually the keystone species. Mooney (1997) lists only the dominant competitor as a keystone species among a list of animal keystone species. Lawton and Brown (1996) also note that it is still very unclear how keystone species may be identified a priori, as the dynamics of ecosystem functions change depending on community composition.

Functional redundancy makes sense only when referenced to some particular site and process. For example, because many plants on a site carry out photosynthesis using the same mechanism, there may be high functional redundancy in a community with respect to photosynthesis and primary production. However, these plants will produce highly distinctive litter (Hobbie 1992), and utilise nutrients from different parts of the soil profile. In regard to these processes, different species in the photosynthesis functional group may exert different influences on other ecosystem processes. Therefore, a species may be a *major actor* with respect to one process but a *minor actor* with respect to another. Walker (1995) refers to these interactions as *drivers* and *passengers*.

If the loss of a species results in a large effect on some functional property of an ecosystem, that species may be called a *keystone species* (Bond 1993). Keystone species are likely to be found in functional groups with few species or in functional groups having a species whose performance cannot be filled by other group members (i.e. no *passenger* species able to take over the role of system *driver*). Naeem et al. (1998) call this point the critical minimum species richness (CMSR). An example may be the role of nitrogen-fixing plants in plant communities. If nitrogen-fixing plants are removed, there may be some complementary redundancy by such plants as *Causarina spp*. However, quantity of nitrogen production will decline, thus influencing the dynamics of the system. Ecologists have looked for and identified keystone species by their effects on the species richness and composition of the community that they inhabit.

In regard to primary processes a keystone species may or may not significantly change the species composition of its community. Species within a functional group differ in the magnitude of their contributions, in terms of both their quantity and their quality. Species within a functional group may also differ in where they carry out these processes. For example, one organism might fix nitrogen on a branch high in the canopy of a forest, another in the soil. Where the fixation occurs, influences which other organisms have access to that nitrogen, and how the nitrogen moves through the ecosystem.

With respect to any particular process, the number of functional groups is termed the diversity (richness) of functional groups. The term diversity (richness) within functional groups refers to the number of taxa included in the group. Richness can therefore mean a simple listing of taxa, such as species or aggregates of them. Diversity is also applied to lists that are weighted by some meaningful ecological criteria such as plant morphology and physiology. In regard to processes this can be a functional group's response to external environmental factors that influence functional processes such as nutrient use efficiency, water use efficiency and productivity.

Analysing the functional significance of biodiversity is a difficult task because the richness of species in most communities is unknown and ecological roles of many described species are poorly understood. In addition, no accepted classifications of functional groups already exist, and no single classification can aggregate organisms appropriately for more than one major ecosystem process or for more than one instance in both a temporal and spatial sense. In other words, functional groups can only be constructed from available information for a set purpose. The groups formed, or the methodology (rules) of construction may not be applicable at any other location or point in time.

The Maunganui Bluff survey and analysis seeks to determine the value of PFTs constructed of non – numerical data in the form of traits, using a database and queries to construct the groupings, in a diversity study. Most studies, published in the Journals, use numeric data and construct the groups using Twinspan (Dufrene and Legendre 1997). These constructed groups were then used to test the rule concerning convergence of PFTs over a sampled altitudinal gradient, determination of the presence of groups in space and time in relation to the environmental data collected; altitude, light, soil temperature, soil nutrient levels and soil moisture. The same PFTs were analysed to determine group assemblages over all the sites and to place a value of the presence of any group occurrence at a site in relation to occurrences at all sites. The methodology used was devised by Dufrene and Legendre (1997) and available in the statistical package PCORD (McCune and Mefford 1997).

Chapter 2 Literature Review – Theory: environmental change

2.1 Introduction

There is consensus amongst the majority of scientists that CO_2 levels and global temperature will continue to rise. General circulation models (GCM) point to a doubling of today's CO_2 levels of 330 ppm to around 660 ppm by circa 2050 (Idso 1989; Morrison 1990; Bazzaz 1992; Jardine 1994). Pre - industrial atmospheric CO_2 has been estimated to have been 270 - 280 ppm, increasing to today's figure of 330 - 350 ppm. This represents a 21% increase in 170 years. The most rapid increase occurred from 1950 onwards (Mooney et al. 1991). The current rate of increase is about 4% per decade.

The major abiotic impact from this doubling of CO_2 will be a rise in global temperatures, though other factors will also affect this temperature increase. However, not all scientists are in agreement over the rate of increase or the ultimate level of the temperature rise (Idso 1989; Graham et al. 1990). The range predicted is 2°C to 4.5°C (IPCC 1990), with greater warming in the winter and warming increasing with latitude. Best guess of temperature circa 2050 is 2.5°C (Schneider 1993) to 4°C (Mullan 1988; Salinger & Hicks 1990; Salinger 1996). In Europe, a 3°C rise in temperature would equate to a 600km shift in latitude or 600m in altitude (de Groot et al. 1995). The present adiabatic lapse rate is 1°C per 100 metres altitudinal rise (Valantine 1999).

An increase in CO_2 will affect the growth and development of both individual plants as well as plant communities / ecosystems. At the plant level, there is much variation between species responses to enhanced CO_2. Often this variation can be attributed to the method of experimentation or to the influence of other factors such as temperature, nutrient availability or moisture levels. Most small-scale experiments take place under very controlled conditions and do not include interaction between plants (Carpenter 1996), which would occur if large scale natural communities were used. There is only a small body of knowledge that has been gained from large scale experiments such as Free Air CO_2 Exchange (FACE), forest gap dynamics and natural CO_2 sinks (Bazzaz 1990; Bazzaz 1996).

While many other environmental factors will affect plant growth and plant community dynamics, there is a distinct link between temperature, CO_2 and mineral nutrient use efficiency. This section of the literature review emphasises the interactions between CO_2, temperature and mineral nutrients by investigating the process of CO_2 fertilisation (the effect of rising CO_2 on the C_3 / C_4 pathways), allocation of photosynthates to biomass and to non structural carbohydrate storage, changing shoot : root ratios, the effect of increasing CO_2 concentrations on litter quality and litter decomposition rates, and mineral nutrient acquisition and use.

2.2 CO_2

The rate of photosynthesis in C_3 plants increases immediately following exposure to higher levels of CO_2. This response is often reduced with long term exposure to increased CO_2 (Korner 1993). Bazzaz and Fajer (1992) suggest that C_3 plants are more responsive than C_4 plants to rising levels of atmospheric CO_2.

Photosynthesis is enhanced by increased CO_2 but may decline over time. Other measured responses to enriched CO_2 include respiration rate changes, decreased transpiration rate (linked to stomatal opening), increased leaf area, increased shoot to root ratio, earlier flowering and increased fruit size.

At CO_2 levels of under 340 ppm, oxygen competes with carbon dioxide for the active RuBP carboxylase[1] site (photorespiration). If oxygen levels are high, then the plant loses energy because it fixes less CO_2. This wasted CO_2 is part and parcel of C_3 photosynthesis under ambient atmospheric levels of CO_2. As CO_2 increases, the likelihood of oxygen out - competing CO_2 for active RuBP[2] sites decreases, resulting in a loss of considerably less energy to photorespiration (Field et al. 1992). The outcome should be increased carbon gains that can be used for active sinks or increased non-structural carbohydrate storage.

Experimentation has shown that there is considerable variation between the responses of different species and variation even between plants of the same species (with all other conditions such as nutrient levels held equal). This may be due to the response of different plant parts, i.e. the size of the sink. An experiment on citrus trees subjected to 660 ppm CO_2 in an open topped chamber (OTC) for the past 7 years, with ample water and fertiliser, has shown that in the first few years experimental trees grew taller than the controls. However, seven years on the enhanced CO_2 trees and the controls are of equal height. Foliage density and yield is consistently twice that of the controls (Culotta 1995). Most plants grown in OTCs have a substantial biomass increase of fruit, shoots and roots. Biomass

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[1] Commonly termed RUBISCO, an enzyme that reacts with both CO_2 and O_2.

[2] Ribulose 1,5 – biphosphate, a five carbon sugar with two phosphate groups is the start and end compound in the Calvin cycle.

gain is very variable between species, but averages at 35% of dry weight (Hendry 1992). In the Idso (1989) citrus trial, total biomass of the CO_2 enriched trees, including above and below ground parts, has tripled compared to the control trees. These results would seem to indicate that with citrus apical dominance is of primary importance during initial growth, but is quickly replaced by a requirement to establish branching for increased fruit sinks. It would appear that usuage of extra carbon assimilation may be driven by sink size or potential sink size. The theory expounded by other authors (Pearcy et al. 1983; Bazzaz & Fajer 1992), is that meristems may be limited by the nutrient acquisition needed to keep pace with apical cell division and development. Consequently, after an initial burst of growth due to stored nutrients within the plant, growth slows as other limiting factors exert influence over metabolic processes. Available soil nutrients are translocated to the strongest sinks.

Numerous studies have been undertaken to study the effects of CO_2 enrichment on plants. The majority of these have used single species (monoculture) in glasshouses. These experiments have shown that C_3 plants respond to CO_2 enrichment by increasing P_n[3] along with an accompanying biomass increase over time. In C_3 plants carbon exchange increases by 30 - 40% and P_n by 50 - 100% (Hendry 1992). Temperature, moisture and mineral nutrients have been strictly controlled. Results from these types of experiments have a low probability of replication on plants within a diverse ecosystem, since plants grown under controlled conditions can be physiologically and morphologically different from plants grown in open fields.

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[3] Pn is the net products from the photosynthetic process before removing photosynthates for respiration, maintenance, reproduction and growth.

The first type of outdoor chamber was the Open Top Chamber (OTC), where experiments could be influenced by natural conditions. Unfortunately these were not totally successful as it was found that temperature inside the chamber was 2°C higher than ambient, light was attenuated by 10 - 15% (Hendry 1992) and wind speed was reduced with no gustiness, thus environmental stress was reduced. The main differences between free - air CO_2 exchange (FACE) and OTC are the difference in site size and the implications of less edge distortion. OTCs are typically < 3m and FACE = > 22m. Reducing edge distortion is of particular importance when studying CO_2 effects on perennials as the effects may be amplified over many years. Time is an important consideration of FACE experiments / trials. Because of the size of the experimental area, destructive harvesting for biomass analysis can occur without destroying the experiment's long term value. This has obvious advantages as ecosystem responses can lag behind individual plant responses.

Another large-scale experiment of note is the study of naturally elevated CO_2 springs. One such study has occured in a one ha bowl-shaped CO_2 spring near Sienna, Italy. Pure, naturally occuring CO_2 mixes with CO_2 in ambient air to increase average CO_2 levels ranging from 500 ppm to 1000 ppm at canopy level (Korner & Miglietta 1994). Immediately outside the spring area are similar plants in similar soils (and soil status) but with 335 ppm of CO_2.

This site has given Korner and Miglietta (1994) an opportunity to study the long term effects of CO_2 fertilisation on a natural ecosystem and make comparisons with a similar ambient CO_2 environment. The results are surprising but consistent with predictions, that plants in the experimental area did not grow faster or flower earlier than those in ambient CO_2. However, there was a large difference in total non - structural carbohydrates (TNC). Elevated CO_2 levels had no effect on sucrose levels; therefore the difference can be attributed to starch accumulation (Korner & Miglietta 1994). Also in line with current predictions, leaf nitrogen levels were lower under enhanced CO_2. This suggests that TNC accumulation and nitrogen depletion in leaves growing under enhanced CO_2 occur in ecosystems as well as in controlled short-term CO_2 enhancement experiments. The results also indicate that the effects do persist over a much longer period of time. There are two possible reasons for the TNC accumulation: (1) limited sink activity or (2) limited diffusion pathways between leaf chloroplasts and the phloem. Idso (1989) suggests that there will be a 33% increase in biomass in natural communities in line with the results of thousands of laboratory and field experiments. Korner and Miglietta's (1994) results suggest that there is still much uncertainty about whether plants in natural communities will accumulate more biomass. What the results do suggest is that leaf tissue composition will change, and that possibly other plant tissue will be altered.

The composition changes are as follows:

1. Plants will take up significantly more carbon than can be invested in structural biomass.
2. Downward adjustment of photosynthesis under high CO_2 is not complete.
3. Ruderals in high nutrient sites exhibit the same trend of TNC accumulation, which suggests that TNC accumulation does not just occur on nutrient-poor soils or in slow-growing stress tolerators.

The latter tends to be contrary to current thinking on the effects of CO_2 enhancement. The current thinking is that soil nutrient status will affect the response of CO_2 enrichment on plant biomass gains.

2.3 Temperature

Changes in atmospheric CO_2 will be accompanied by increased temperature and in some areas possible moisture deficits. C_4 plants perform well in warmer climates and are tolerant of high temperatures. Few C_4 plants perform well at low temperatures, and most suffer tissue membrane damage at around 10 °C - 12°C. Although there are exceptions, C_4 plants generally have higher optima than C_3 plants, and the difference is controlled by lower rates of photorespiration. Some C_3 plants such as bananas, cotton and sunflowers are tolerant of high temperatures in the range 30°C - 40°C (Loomis & Conner 1992). Most C_3 plants are able to handle temperatures down to 0°C without damage but some warm climate C_3's such as bananas are sensitive to chilling. The relationship between photosynthesis and temperature gives C_4 plants an advantage above 25°C, C_3 plants an advantage below this figure.

At low temperature, positive enhancement from CO_2 for C_3 plants occurs least. The enhancement increases continuously as temperature rises towards the optimum. The probable cause is the affinity of RuBP carboxylase for CO_2 that declines with increased temperature. Therefore, the temperature optimum for photosynthesis is generally higher at increased CO_2 levels (Pearcy and Bjorkman 1983).

2.3.1 Effects of enhanced CO_2 and temperature on plant processes.

Idso (1989) states that the positive effects of CO_2 atmospheric enrichment increase with rising temperature and that the optimum temperature for photosynthesis will increase in CO_2-enriched air. Temperature affects photosynthesis, respiration, growth, reproduction and water-use efficiency. Gifford (1992) singles out three important plant interactions in response to increasing temperature and CO_2. They are:

(1) The photosynthesis / photorespiration balance. Photosynthesis increases with temperature because plants are able to bind more CO_2 as enzyme activity increases with increasing temperature. In C_3 species, increasing temperature favours photorespiration and the Rubisco enzyme (Ribulose bisulphate carboxylase / oxygenase). With increasing CO_2 levels, oxygenation is inhibited. At high temperatures, diffusion of CO_2 and photorespiration become limiting factors and the positive effects of increasing temperature level off. At extremely high temperatures, the photosynthetic process breaks down and the rate decreases. The decline in whole-plant photosynthesis may continue to decrease (due to damaged plant tissue) even after temperature reduces to ambient. The decline in photosynthesis at high temperatures is probably due to stomatal conductance decreasing in response to increased CO_2. It would then be expected that as the stomatal opening decreases, conductance will also decrease. There should then be a direct proportional decrease in the transpiration rate. However, reduction in transpiration will lead to increased leaf temperature and increased water vapour pressure inside

the leaf (Pearcy and Bjorkman 1983). Therefore, the transpiration rate is not reduced in direct proportion to the reduction in stomatal conductance. Two experiments reiterate the above points. Under simulated field conditions, the increase in yield brought about by a doubling of CO_2 concentrations was found to be offset by a decrease caused by a temperature increase of 4°C above ambient. The effects of elevated CO_2 levels on plant growth can be reversed if temperature is altered, with differing effects between species. The results showed that the biomass of *Amaranthus retroflexus*, a C_4 annual, was increased by elevated CO_2 at 28°C but depressed at 38°C. For *Abutilon theophrasti*, a C_3 annual from the same site, elevated CO_2 had no significant effect on biomass at either temperature. There was an initial increase in relative growth rate (RGR) at 28°C (Atkinson 1992).

(2) The net photosynthetic / dark respiration balance. Maintenance respiration is highly temperature-sensitive. Growth respiration is not, being dependent on the chemical composition of new growth. Atmospheric CO_2 in the range of 300 - 1000 ppm decreases dark respiration, thus not increasing net primary production (Gifford 1992). Increased respiration due to higher temperatures will release more CO_2 to the atmosphere. This represents a positive feedback to both atmospheric CO_2 levels and increased greenhouse warming.

(3) The source sink balance. At high temperatures, it is expected that the demands of potential sink growth rates would not be met by a photosynthetic supply, so a huge potential for CO_2 stimulation should be available. At low temperatures, sink development rate is slow (Gifford 1992). Low temperatures, rather than photosynthate supply, restrict growth. When CO_2 is

enhanced at low temperatures, the expected potential accelerated growth does not occur. The photosynthetic rate seems to be inhibited by a metabolic feedback mechanism at low temperatures. A good example is an experiment carried out by Idso (1989), who measured the growth modification factor of carrots (*Daucus carota*) and radish (*Raphanus sativa*) at CO_2 levels of 640 ppm over a range of air temperatures. The expected growth response in carrots due to increased CO_2 did not occur until temperature reached 12°C. However radishes did show a photosynthetic response under 12°C. It appears that growth is suppressed in some species at low temperatures despite an increase in CO_2 (Idso 1989).

2.4 Nutrient Use Efficiency

The amount of carbon contained in ecosystems represents the difference between input (net primary production) and output (decomposition). Under conditions of increased CO_2 and temperature, the following responses have been indicated for leaf litter quality and decomposition.

Environmental change due to the Greenhouse effect will have an influence on soil organic matter, even if it is only to the extent of increased litter production. Sneider & Kay (1995) consider that under expected climate change scenarios, as more energy becomes available, the further a system will increase production to degrade the energy. Temperate and arctic plant communities should become more diverse and more productive. This increased productivity means that there will be more litter and consequently more humic material. The chemical constituents and the quality of these constituents of plant litter is an important determinant of the decomposition rate. Consequently, plant litter quality affects the rate at which mineral nutrients are recycled into plant available forms. Berendse and Elberse (1990) as well as Pastor and Naiman (1992) suggested that ecosystems dominated by different functional types should also differ in their rates and patterns of soil element cycling (cited in Shaver et al. 1997).

The effect of a northward or southward movement of vegetation will have an effect on the quality of these nutrient poor soils. As the humic content of these soils increases, so will the soils' nutrient status, mostly due to decreased nutrient leaching by waterlogging induced by a receding snow line (Couteaux et al. 1995). The expected productivity should manifest itself as larger leaf areas (as it should in tropical biomes, but to a lesser extent) and enhanced photosynthesis (temperature will be less of a limiting factor).

In natural ecosystems, there will still be limiting amounts of nitrogen, phosphorus and trace elements that will limit plant adaptation to increased CO_2 (Lamborg et al. 1983). Thus in nutrient poor soils, any substantial response to enhanced CO_2 would only occur long-term, if nutrient availability also increases (as per the arctic biome where decreased leaching will result in higher nutrient availability).

It is known that relative to other elements there will be increased carbon gains (due to increased carbon fertilisation). Thus the carbon: nutrient ratio in litter will increase. Leaf litter nitrogen concentrations should decrease as the concentration of atmospheric CO_2 rises, and since nitrogen is one of the factors (C : N ratios) controlling decomposition rate, a change in decomposition patterns is expected. Also, an increased rate of carbon mineralisation is expected in response to increasing temperatures (again it appears that the effects will be more noticeable in arctic or temperate biomes). In temperate regions, the season for decomposer lifecycles will increase thus augmenting nitrogen returns over a yearly period. In tropical regions, increased decomposition will probably be dependent on the canopy effect on soil surface temperatures. Much will depend on the plasticity of decomposer organisms to higher temperatures. Nitrogen mineralisation should increase in most biomes as a response to higher temperature, favouring plants with increased nitrogen availability.

The photosynthetic rate will increase with rising CO_2, in most circumstances. The debate, however, is whether plants will partition more photosynthates to roots for foraging and acquisition of nutrients (Pearcy & Bjorkman 1983). The probable result will be a balancing act. As the C : Nutrient ratio rises due to increased productivity, and as a consequence of decreased litter quality, a plant may have to allocate more photosynthates to root growth as opposed to stems and leaves to maintain the internal nutrient levels for increased photosynthetic rates. It is expected that plant community uptake for a nutrient is not just the physiological rate of uptake, but is also a result of the quantity of roots in the system (Jackson & Reynolds 1996). The other possibility is that plants in nutrient poor soils just may not show any long-term response. Some experiments show that after a period of very active increased growth, there is a falling-off in the photosynthetic rate due to decreased nutrients.

The other consequence of a climate change is a diverse pattern of precipitation. These changes will have an effect on litter quality and decomposition rates. As water availability changes - some areas will become wetter, others dryer. There will be an enhanced effect on litter quality. At low water levels there will be a further decrease in nitrogen availability with litter having an even more reduced quality (Hobbie 1992).

Experiments have shown that an increase in atmospheric CO_2 can enhance net primary production (NPP). In soils where inorganic nitrogen is limiting growth, a CO_2 increase can modify the nitrogen distribution within plants and lower nitrogen concentrations in plant litter. Other nutrients such as phosphorus, calcium and magnesium have shown no significant effects (Couteaux et al. 1995). Any change producing low quality litter may over time produce the following two conditions (taking the assumption that if nitrogen is available then plant productivity will rise):

1. Most factors will favour nitrogen fixation, since levels of atmospheric nitrogen (mostly unavailable to plants) will not change under climate change. Therefore, plants that have symbiotic relationships with nitrogen-fixing bacteria will take maximum advantage of increased CO_2. An increased % of these plants in a community will have a beneficial effect on all plants within the community, by producing high-quality litter, thus maximising their growth. Atmospheric carbon dioxide enrichment has been shown to directly stimulate the activity of nitrogen-fixing bacteria (Idso 1989; Sinclair 1992);

2. Plants with shorter life spans may be favoured over long-lived woody dicotyledons that store nutrients over a long time frame. Ecosystems may require faster turnover of litter - shorter plant life spans. The consequences may be larger leaf area, enhanced photosynthesis, shortened time spans from juvenility to maturity (increased precociousness).

Whatever the final scenario, unless nutrient levels increase at a proportional rate to carbon dioxide, then eventually enhanced growth will decline.

2.5 Herbivory

Herbivores are generally thought to enhance plant diversity via a number of mechanisms, but mostly through the direct consumption of competitively dominant plant species and the consequent indirect effects on plant inter and intra - specific competitions (McNaughton 1985; Crawley 1983; Crawley 1997). The effects of herbivores on plant species richness in a particular environment are a direct consequence of type and abundance. These effects can be either positive or negative. Natural populations of large grazing mammals are reported to increase plant diversity (Belsky 1992), which in managed situations can lead to a reduction in diversity. Insect herbivores often have weak or negative effects, although outbreaks of specialist herbivores on dominant plant species can increase plant diversity. Intermediate-sized, digging herbivores, such as rabbits *(Oryctolagus cuniculus)* create small areas of extreme soil disturbances that increase plant diversity (Olff & Ritchie 1998).

2.5.1 The positive or negative response to Herbivory

Variation in herbivore effects on plant diversity can arise from the spatial or temporal scales at which diversity is measured. Herbivores can influence species richness differently, at both the local scale and the regional scale. For example, possum browsing in a localised natural community would cause a loss of diversity initially. However, if the natural plant community were an isolated island in a much larger grassland system, then diversity would eventually increase as grass species migrated into the vacant niches. Local disturbances and selective grazing can enhance diversity at local scales, but strong selection for grazing tolerant plant species within the species pool might reduce diversity at larger scales.

Herbivore body-size also influences the rate of increase or decline of diversity. At the individual level a cow will consume much larger quantities of plant biomass than a possum or a green looper caterpillar. At the population level it is the extent of the sustainable source of food that determines both the level of continual herbivory and the length of time the population can be sustained. In the case of populations, an area may be able to sustain a cow or possum indefinitely through regrowth and migration but may not be able to recover from a continual infestation of insect pests. The temporal scale of herbivore effects is also important because short-term increases in plant diversity from herbivory can ultimately disappear owing to herbivory-induced succession to a few defended or tolerant plant species (Olff & Richie 1998).

2.5.2 Scales of plant species richness

The determinants of species richness in ecosystems are focused on the mechanisms that enhance resource partitioning and coexistence of plant species. These mechanisms include spatial variation in resource availability and limitation of plants by different resource. Other research stresses that colonization and regeneration (Berendse et al. 1992) determines local species richness. Both schools of thought are now being synthesised into the view that local species richness is maintained by a dynamic interaction between local colonization (via dispersal and establishment) from species pools at larger spatial scales and local extinction (e.g. because of competitive exclusion). This synthesis is inspired by island biogeography theory (McArther & Wilson 1967; cited in Wilson 1992). As a result, high plant diversity should occur when local extinction rates of species (relative to the number of species present) are lower than local colonization rates. The concepts of colonization and extinction as a result of resource competition are inclusive. Reduction of dominant competitors by herbivore grazing can enhance the persistence of plant species that colonize the disturbed areas generated by herbivores. Thus, the interaction of the two processes may further strengthen herbivore effects on diversity.

2.5.3 Herbivory across environmental gradients

Results of analysis of herbivore impacts indicate that herbivore effects vary predictably across environmental gradients (Gibson & Bosch 1996). The ratio of the supply of different plant resources determines productivity. For example in New Zealand's natural ecosystems, ungrazed, productive environments feature intense light competition from upper canopy trees and thus have greater potential for herbivores to increase local colonization rates of plant species. Due to the lower light levels, there is a more stable richness at ground level. If possum browsing increases light levels, there is a change in environmental conditions at ground level and potential sites become available to plants species previously excluded.

Olff & Ritchie (1998) have classified the effects of herbivory under the following four environmental gradients:

(1) **Low precipitation and infertile soils** result in low productivity and favour plants that compete well for both nutrients and water in the absence of

herbivores. Dominant species tend to be xerophytes and have water-retention mechanisms that operate through light reflection or transpiration reduction (via thorns, hairs, wax layers, woody structures and secondary chemicals). These mechanisms also tend to deter herbivory. Such plant communities may support a few small herbivores, and these herbivores are likely to select rare, palatable species. Herbivores will have little effect on plant competition and consequently will induce few plant coexistence mechanisms. Therefore, herbivory could increase extinction rates. Because of the low productivity and already extensive bare soil in these environments, herbivores would have little effect on colonization rates through opening of the plant canopy.

(2) **Low precipitation and fertile soils** favour competitively dominant plant species that tend to be palatable and will support high densities of many herbivore species. These conditions favour the major grasslands and savannahs. These plant species are likely to tolerate, rather than avoid herbivory, because of the good regrowth opportunities owing to the high nutrient availability in fertile soils. Exclusion of herbivores could have weak positive effects on diversity because only a few plants that are intolerant to grazing remain in the species pool to colonize ungrazed areas. Exclusion will favour migration of plants that have propagules that are carried long distances by wind.

(3) **Non - limiting precipitation on infertile soils** benefits dominant plants that are likely to have low tissue nutrient concentrations but are sufficiently productive to have a broad canopy that will induce light competition. These plants will probably only be used by grazers, which can tolerate low plant-tissue quality. Canopy grazing by possum might shift competition (locally) from light to soil nutrients, allowing more species to coexist. Such effects aid

smaller herbivores such as rabbits, which increase extinction rates of rarer nondominant species but balance this local extinction by enhancing the regeneration of these species through soil disturbance. Thus, herbivores can dramatically increase diversity in these environments.

(4) **Non - limiting precipitation on fertile soils** favours dominant plants that have high productivity. Light competition is important in the absence of grazing. Strong light competitors (woody trees) dominate these habitats in the absence of grazers, are likely to be unpalatable (because of the high stem: leaf ratios) to all but large herbivores when mature. Grazing by large herbivores opens the canopy so that a few grazing-tolerant plant species replace the tall species. This process is especially true of New Zealand circumstances. Possum browse the leaves from upper canopy trees, allowing encroachment from possum and stock tolerant/resistant species such as blackberry (natural defense) or grasses (monocot leaf : stem morphology ratios allow quick regrowth and minimal grazing damage). These tolerant species that are able to regrow quickly after being grazed, support high densities of grazers, imposing unacceptably high mortality rates on species that are less tolerant to grazing (broadleaf seedlings). Possum resistant trees such as Titoki (*Alectryon excelsus*) quickly become dominant within the plant community. Assistance by large herbivores may create opportunities for small, selective herbivores (e.g. insects and small mammals) that may further reduce plant diversity because they prefer rare, palatable species.

2.6 Fire

The scenarios predicted by Salinger & Hicks (1990) indicate that regionally the West Coast of New Zealand will become moister and the East Coast drier. On the East Coast the consequences to plant communities from increased fire outbreaks are:

- Much faster turn over in species assemblages.
- Communities that exist in fire hot-spots are never at equilibrium (Bond & Wilgen 1996).
- Changes in community structure from broadleaf podocarps to faster regenerating fire-tolerant or fire resistant species. As *Acacia spp.* and *Eucalyptus spp.* usually exist in these areas, these types of trees would form a local assemblage along with New Zealand scrubland plants such as *Kunzia ericoides* (Kanuka) and *Leptospermum scoparium* (Manuka).

On the West Coast, fire events may still occur but will affect succession and plant assemblages in a much different way. Precipitation will increase but will fall in much shorter time frames. There is a possibility that dry periods may be long enough to constitute a fire risk. Cyclonic events are predicted to increase (Salinger et al. 1996). The consequence will be increased debris within the West Coast forest systems that when dry will provide fuel for very intense fires. Fire frequency and degree are strongly influenced by the amount of available fuel and the weather. Fuel accumulation depends on productivity and the rate of decomposition; both are dependant on climate and in particular the seasonality of rainfall (Bond 1997).

Chapter 3 Literature Review – New Zealand Biota

3.1 Climate Change and the New Zealand Biota

Scenarios to date indicate that there will be an increase in global average surface temperatures of between 2°C and 4.5°C by the end of next century (IPCC 1990; see Chapter 2.1). For a working figure this author has chosen 4°C as a representative of worst case scenario over the next 100 years in accordance with Salinger and Hick's (1990) extreme prediction This would have profound effects on the distribution, structure, and functioning of terrestrial ecosystems (Mellilo et al. 1990).

In a previous study of southern hemisphere climate scenarios, Pittock and Salinger (1991), indicated that along with marked regional fluctuations in precipitation, general increases in temperature and evapotranspiration may occur, resulting in significant changes in soil moisture and runoff by as early as circa 2010. The identification of land systems (natural or agricultural) most susceptible to increased erosion, leading to loss in productivity, must be a priority for land-use planning (Blaschke et al. 1992).

The key feature of the major climate parameters (temperature, rainfall and solar radiation) is that the spatial patterns of change are not uniform. The major warming effect in New Zealand will be in the central North Island and in disparate regions of the South Island with some areas in the eastern North Island and south-eastern South Island showing minimal change. The model suggests a major increase in rainfall in the northern regions of the North Island and on the West Coast of the South Island, although little change is predicted elsewhere. In these models, minimum solar radiation is linked to rainfall and shows some of the same patterns. However, the overall effect is a decrease in rainfall, especially in the northern half of the North Island and much of the South Island. The overall effect is one of creating a potentially novel suite of climatic factors that bears little resemblance to recent patterns (Mitchell & Williams 1996). The effects of elevated $C0_2$ on the physiological responses of mature forests are likely to be small and more evident (Allen 1990) in eastern areas of New Zealand where more extreme soil water deficits are expected.

The effects of climate change on terrestrial biological processes are likely to be complex and influenced by interactions between the atmosphere, topography, land use, vegetation and soils at different scales. Environmental conditions are the basic controlling force on the functioning and distribution of most plant species (Woodward 1987). Climate, just one aspect of environmental change, shows wide spatial differences at both the global and regional scale. Relative to these scales of variation, most species show limited tolerance to a range of climatic factors, therefore climatic patterns can restrict species to particular regions. The long time-scales over which such climatic patterns have been established and their natural slow rate of change allow major speciation to occur (Jeffries 1997). It is quite clear from the Pleistocene pollen record that as climate changed into and out of glacial periods the species assemblage at any particular locality changed (McGlone et al. 1996). Thus climate provides the basic environmental boundaries within which species survive.

Variation in physical attributes may occur within environmental boundaries such as soil type, soil moisture, habitat quality, etc. The local environmental factors determine the specific assemblage of species (plant communities) at a site. Particular combination of species will be drawn from a pool of species that can survive within that climatic boundary. Specific and inter - specific relationships between the biotic components, for nutrients and light, may further refine the local subset of the available species pool for each site's plant community.

Plants, in their central role as autotrophs, provide energy to the rest of the ecosystem in response to the environmental boundaries. Plants are static, at least within the life span of individuals, and their ability to change in response to large perturbations in climatic conditions is limited. Normally, plants adapt to modified conditions through seed dispersal to more suitable areas; the original individuals dying as their tolerances are exceeded by the changing climate. Plants' ability to adapt to changed local climatic conditions is limited. Plant migration as a response to climate change can be seen over long time-scales in the Pleistocene pollen record (McGlone 1988). Plants will either migrate to more conducive sites or disappear totally from the biotic spectrum (Whitehead et al. 1992; Mitchell 1996). This response is not caused just by climatic conditions but may also be induced by site modifications by man.

3.1.1 Climate change and New Zealand's natural forests

New Zealand's land - use, from the arrival of Maori to the present time, has been dominated by deforestation, resulting in the destruction of about two thirds of the original forest over the past 1000 years. Grasslands are currently distributed over 10.6 million hectares, of which 6.5 million hectares are improved legume based pastures which contribute to about 50% of New Zealand's export income. About

5.1 million hectares of mainly disturbed indigenous forest remain, complemented by a rapidly expanding area in planted forest (1.3 million hectares). Scrub communities, including some grassland and forest on the poorer hill land, make up most of the remaining area (7.3 million hectares) of New Zealand (Tate et al. 1996).

The climate-model scenarios can only give indications about the future responses of New Zealand's forests to climate change. At present no real confidence can be ascribed to how natural systems will respond. Most of New Zealand's natural forests occur within an annual mean temperature of 10°C to 15°C and rainfall of 1250mm to 2250mm. With a temperature increase of 4°C by year 2070 (refer Chapter 2.1), more than 21% of forest will experience a mean annual temperature of 17°C. New Zealand's natural forest species have adapted to well-defined temperature regimes; so different responses to climate change by individual species and increased disturbance from introduced browsers will alter forest composition (Whitehead et al. 1992). Species migration will be restricted by the availability of sites. Possible results are increased dieback (already occurring in many areas due to possum damage), reduction in forest productivity and health, isolation of seed sources, and increased threat to survival of native bird and insect species (further detail in regards to the threat to biodiversity is given in Chapter 4.3).

Storage of carbon in soils generally increases from low to high latitudes, reflecting the slower decomposition rates in colder environments. Soil organic matter content is also influenced by factors such as plant community composition, land use, and the properties of soil. Small local variations can strongly influence the balance between production and decomposition, making larger-scale comparisons of carbon accumulation rates difficult to interpret (Tate 1992). In New Zealand, humus accumulation and intermittent water logging of soils appear to explain the wide variation in soil carbon turnover in some indigenous forests and grasslands (Tate et al. 1995). Global warming could threaten the future productivity of ecosystems through the loss of soil organic matter, with a resultant significant feedback of $C0_2$ to the atmosphere (Idso 1989).

In the case of endangered biota, the focus of research may need to be on a species by species basis. Species, however, do not truly function except within the communities and ecosystems. Because of changes in inter-specific interactions, competitors and predators may need to be controlled and invading weeds removed. On the other hand, if native species become locally extinct, or are lost because of physiological intolerance to climate change (Chapin III et al. 1993), then some invading species might need to be encouraged as ecological replacements for those that have disappeared. It is increasingly apparent that to understand the dynamics of terrestrial ecosystems, an understanding of the inter-relationship between species performance, physical factors, and the consumption and renewal of abiotic resources is required.

This raises the question as to whether it is feasible to fully analyse the requirements of a nation's biota, before the full effects of climate change occur. For example, it may not be feasible to identify the individual climatic requirements of the thousands of species in New Zealand. In this situation it might be more appropriate to study functional types rather than individual species. Studies might more appropriately address the question of functions and redundancy of species within ecosystems, rather than focus on single species.

Busby (1988) found that for New Zealand flora in his study, that much, if not all, their core range could become unsuitable (cited in Mitchell & Williams 1996). How species will survive or move naturally to new locations is unknown, especially if the climate of their habitat changes beyond the species tolerance e.g. alpine plants when climatic temperature increases by 4°C. The probable consequence is extinction.

In New Zealand, the wholesale destruction of continuous tracts of habitat has resulted in most species surviving in small fragments in an agricultural landscape. Climate change has brought into sharp focus the problems encountered by species moving around modern landscapes. Climate change, whether from anthropocentrically induced causes or as part of a natural climate cycle, adds to an already long list of threats to the future of biodiversity.

The large distances between fragments and the absence of habitat corridors mean that many species already have great difficulty moving around the landscape. There are no longer the continuous tracts of habitat that existed in pre-European times, through which species moved as the environment changed. In many cases, even the existing habitat fragments may not be enough to provide resistance against change at the patch level and species in these habitats are already under stress. If the climate changes at the rate suggested by the 4°C scenario, then species may not be able to move across landscapes fast enough to escape extinction. There is also the question of how far species may have to move. In the case of *Agathis australis*, climatically suitable habitat will be at least 150 km from the nearest extant population, which would require a rate of spread of roughly 2 km per annum between now and 2070 AD (Mitchell & Williams 1996). The only way in which this species may survive is by human intervention and relocation. Islands and mountain tops represent special cases of isolated habitat patches surrounded by unsuitable environments. Species that are restricted to such localities by a climatic restriction would face extinction, as there is simply nowhere for them to move to.

3.1.2 Climate change and soil organic matter – New Zealand ecosystems

There is a projected reduction in soil organic matter, which could be offset, at least partly, by increased plant residue inputs through three interrelated mechanisms:

1. As the annual productivity of ecosystems increases with temperature, so will the input of organic residues to soil.
2. Elevated CO_2 can stimulate plant growth (Idso 1989; Gifford 1992). The nth degree of this effect, however, may be considerably reduced by feedbacks from nutrient cycling (Woodward et al. 1998) and be much less pronounced for whole ecosystems than for individual plants. A particularly weak response to elevated $C0_2$ could be expected in humid, nutrient-limited ecosystems (Mooney et al. 1991); such as New Zealand's indigenous forests. Even in nutrient-rich ecosystems unlimited by water, $C0_2$-induced increases in net primary production may not necessarily be reflected in increased soil carbon storage (Newton et al. 1995).
3. The release of nutrients, including nitrogen, from the accelerated decomposition of organic matter is expected to increase plant production.

3.1.3 Consequences of climate change on New Zealand Plant Biota

New Zealand has geologically young landscapes and low biodiversity other than in the most Northern parts, which exhibit good zonation characteristic of soils that have escaped glaciation during the last glacial maximum. New Zealand is composed of two large and numerous small topographically varied oceanic islands, with climates which range from warm temperate (outer Northern Islands are considered to be subtropical) to high alpine. There are extensive ranges of hills and mountains, as well as areas of low relief. Climatically, much of the country is mesic: extremes of temperature rarely being experienced; rainfall is generally sufficient to abundant, with low inter-annual and inter-seasonal variability. Areas not within this paradigm tend to be spatially small or in Alpine regions. The main natural ecosystem of New Zealand was forest, except at the higher altitudes, where shrublands and tussock grasslands occur. Today, many consider 'natural' land to be modified agricultural ecosystems.

New Zealand has levels of endemism greater than 90% for many species (Statistics New Zealand 1993). Consequently, New Zealand has a global responsibility to maintain the biodiversity of our region. Throughout human occupation in New Zealand there has been a steady loss of biodiversity through direct extinctions (e.g. through hunting), as well as consequential extinction through loss of habitat. Habitat loss and habitat fragmentation continues today and is probably the greatest cause of extinctions in recent times. Climate change is yet another threat to natural ecosystems and to ecosystem biodiversity

3.1.4 Climatic effects - Temperature change

Climate change scenarios indicate that temperatures will rise; however this increase will not be spatially or seasonally uniform. Salinger et al. (1996) state that this may result in major changes to the thermal environment experienced by biota. It is also expected that there will be a greater impact on minimum temperatures than on maximum temperatures, in particular a proportionately lessened cooling at night, as compared to daytime temperatures (Tate et al. 1996). The overall effect will be a tendency towards a lower incidence of frosts and for more areas to experience heat stress. This can have a positive as well as a negative effect on plant distribution for individual species. Some areas of New Zealand may start to more regularly experience heat stress. The change in day/night balance may also affect plants. During the night, respiration would become more active and would need to be compensated for by additional daytime photosynthesis. The warmer conditions are also likely to increase the rate of soil processes (Tate et al. 1996).

3.1.5 Climatic effects - Solar Radiation change

It is unclear whether the levels of solar radiation reaching the planet surface will change. If it is assumed that levels arriving at the upper atmosphere remain at the present level, then any changes in atmospheric transparency will alter the quantity reaching the planet surface (Mitchell & Williams 1996). Solar radiation has been shown to have a strong relationship with the distribution of some plant species (Yee and Mitchell 1991; Leathwick and Mitchell 1992). Solar radiation also interacts with other environmental factors (one of the driving forces of transpiration). Therefore, any changes in solar radiation would result in changes in soil moisture (Garratt et al. 1996).

3.1.6 Climatic effects - Rainfall change

Rainfall is generally expected to show a general increase especially on the west coast of New Zealand (Salinger & Hicks 1990) and will potentially present biota with changed spatial and seasonal patterns. The general increase in rainfall will lower soil moisture deficits in many areas, but at the other extreme there may be an increase in waterlogged soils. Increased rainfall could result in any one of the following scenarios. If the increase in rainfall is met through:

(a) increased intensity of rain, but for the same duration, then the result will be an increase in variability of soil moisture. This will not affect solar radiation, but the net effect will be an increase in soil moisture levels;

(b) increased intensity but decreased duration, then soil moisture will become more variable, solar radiation will increase (increasing evapotranspiration), finally resulting in lowered soil moisture levels;

(c) an increase in duration of rainfall, then soil moisture variability will decrease, levels of soil moisture will increase and solar radiation will decrease.

Each possibility equates to different environmental consequences for plants. Overall, depending upon how climate changes, there could be a complex of new physical environments created, resulting in a quite unique and new spatial pattern. In an evolutionary context, the previous major climatic era was significantly cooler. This was recent enough in evolutionary terms that many of the current biota (especially very long-lived species such as trees) would show adaptations to cooler climates. The present rapid change is to a much warmer regime to which there may be little inherent adaptation (Tate et al. 1996).

Chapter 4 Literature Review – Functional Groups

4.1 Plant Functional Groups – an introduction

It is not feasible to develop models for every ecosystem nor to represent every species within the ecosystem (Steffen et al 1992). Plant Functional Types (PFTs) can be seen as groups of species that have certain functional attributes that are inherently common to each individual. These PFTs will respond as a single entity to environmental change (Skarpe 1996).

As the term *functional type*[4] indicates, physiological functions of organisms might provide a basis for classification. Even classifying into PFTs, especially when using physiological responses, may not show enough commonality to determine accurate responses in all situations. Even single entity PFTs have complex responses, since physiological processes are not independent but are interactive with other physical and chemical systems. An example being that the measure of photosynthate storage in plants may not be a good methodology (except in controlled experiments) for determining performance under enhanced CO_2, as sink strengths of individual plants will cause variation among a plant community. Varying sink strengths of species will affect the community dynamics especially in relation to resource acquisition and usage.

Any level of organisational elements that bear a certain set of common structural and/or process features may be treated as a functional group. At the species level this may include taxonomic groups as well. No distinction is required between

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[4] Functional types are the representation of the key attributes defining a functional grouping.

structures and processes in the sense that one is literally non-functional while the other is functional. Structures represent something that is static but can exert dynamic influences on functions which may be equal to, or have even greater significance than, certain processes. This equates to functional groups that can be formed at any level within the hierarchy and for any sort of function(s).

The ultimate goal for defining functional groups is to establish criteria for making some predictive assumptions about vegetation in relation to some biotic or abiotic event. In constructing PFTs, essential steps are:

(1) Selecting traits which are related to different plant functions then;

(2) Screening large numbers of plants in the community for these traits, since not all traits are immediately obvious (Grime et al. 1988, MacGillivray 1995). A trait matrix is then developed, from which a classification of PFTs for the plant community is defined. These classifications of PFTs are then used to build predictive models (Grime et al. 1997). These predictive models must be constructed with consistent, testable data. Unvalidated models will not retain credibility (Nemai & Running 1996).

The functional type concept has been implicit in literature for a long time (Knight & Loukes 1968), but has gained renewed interest because of the need to predict the response of plants to rapid and possibly substantial environmental change. The expectation is that PFTs will be based on a minimum set of functional attributes that are considered to be the most critical in reliably predicting the present day distribution of plants from climatic variables (Steffen et al. 1992), so the models developed can be used to predict the future distribution from changes in environmental data.

This chapter of the literature review sets out to consider the history and development of PFTs, the rationale involved with construction of PFTs, PFT use in comparative studies and the role of PFTs in determining key players and functions in ecosystem processes. The chapter follows the rationale and use of PFTs based on the model (Fig. 4.1) which shows the linkages between species and functional groups in studies of diversity and ecosystem functioning.

4.1.2 PFTs -History

Historically, the thread of thought that has led to the present definition of plant functional types can be traced back to Theophrastus, circa 300 BC. The modern part of this thread began with Root (1967), who defined the ecological concept of guilds. He iterated that guilds were *a group of species that exploit the same class of environmental resources in a similar way.*

Cummin (1974) developed the concept of functional grouping of organisms to highlight important ecological processes (cited in Noble & Gitay 1996). Botkin (1975) was the first to suggest that species could be aggregated into a smaller number of functional types and that these groupings would still *allow consideration of important population interactions* (cited in Gitay & Noble 1996).

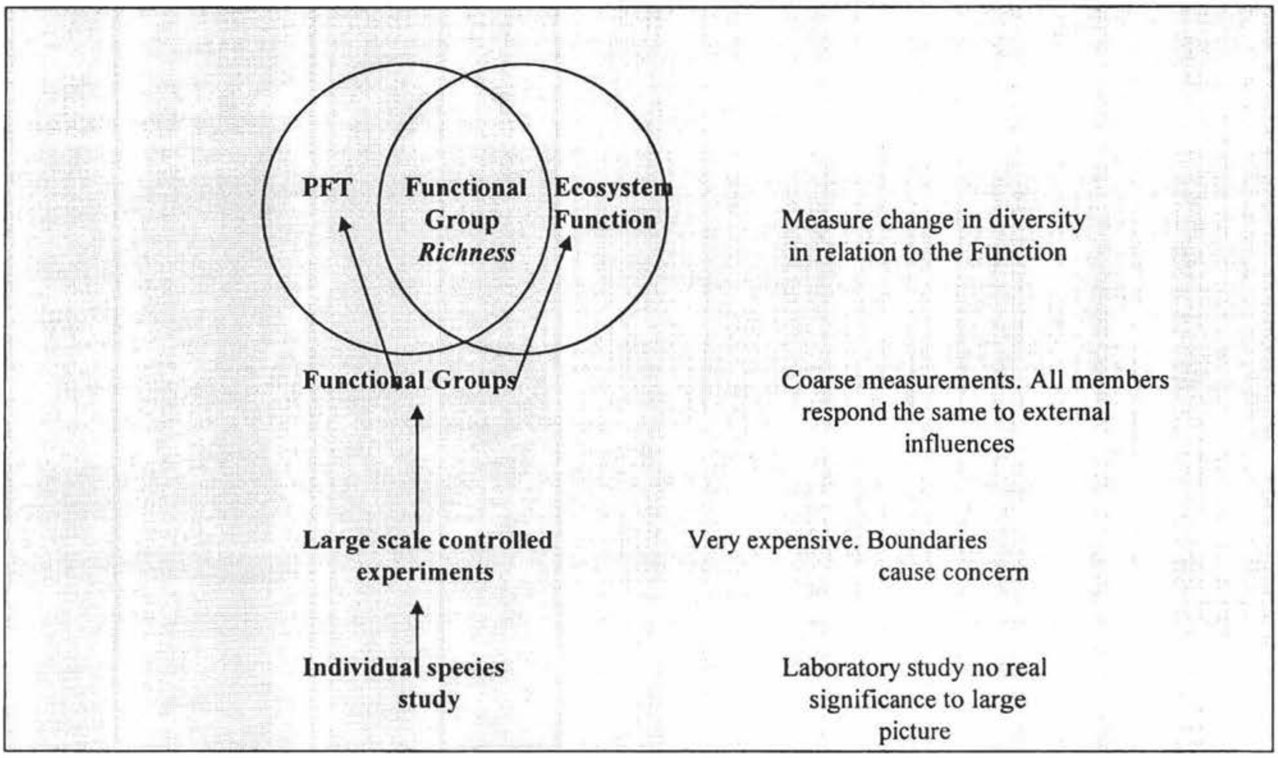

Fig 4.1. A hierarchical model of the linkages from the study of species to whole ecosystem studies using functional groups (Lee 1998).

Other terminologies associated with functional roles are character or adaptive (Gitay & Noble 1997) syndromes which are used to describe certain characteristics (traits; author's own interpretation) which cannot be discarded from inquiry because the characteristic contributes to a common functional role (Swain & Whitmore 1988; cited in Gitay & Noble 1997). Another is the 'vital attribute' proposed by Noble & Slatyer (1980) which was developed to predict the dynamics of plant communities after disturbance by fire (cited in Noble & Gitay 1996). Noble and Gitay (1996) use 'method of persistence', in response to disturbance, as a vital attribute to group plants into a functional classification.

Plant species can be classified not only according to their taxonomical relationship within genera or families, but also in relation to their types. This concept has been clear to botanists since the advent of botanical science (Du Rictz, 1931 cited in Boutin and Keddy 1993). They use the term *guild* to describe PFTs, since member species use the same class of resources. The term *guild* is used to describe groups of functionally similar species in a community (Root 1967; Pianka 1983; cited in Boutin and Keddy 1993). This leads them to point out the traits to be considered when relating plants to the role they play within a community. These three traits are remarkably similar to a redefinition of Grime's (1979) life form attributes. These are matched to the traits of Boutin and Keddy (1993) (Table 1).

4.1.3 PFTs - role in ecological studies

One of the most difficult problem areas of ecological study is where to focus experiments and to what level of integration (Fig 4.2). The fear of failure has meant that most experiments are fixed at low levels of complexity. Small-scale experiments can rarely be used to explain ecosystem functioning. Ecosystems are complex arrangements of biotic and abiotic components at a variety of spatial and temporal levels. A single-species study of nutrient uptake and utilisation should never be confused with or scaled up to ecosystem nutrient cycling, i.e. a model for a plant process should never be scaled up to represent an ecosystem process.

There was a need to find a linkage between species and ecosystems. From this need came PFTs, which were able to address issues at both levels of complexity. Certainly the literature shows that at the trait level, PFTs have fulfilled an important role, but the real value of PFTs will be their integration into ecosystem studies and to provide clearer views of the importance of complex associations to ecosystem functioning.

4.1.4 PFTs ' Role in Climate Change Studies - a brief introduction

In relation to global climate change, PFTs can be defined as follows:

1. the effects of plants on the environment
2. the function of plants in the ecosystem
3. the response by individual plants to environmental constraints
4. the response by plant populations to these constraints (Skarpe 1996)

PFTs constructed from 1 & 2 will determine the rate of ecological processes and the effects on the environment and ecosystem but will not indicate how the ecosystem will respond to environmental change. The opposite holds true for 3 & 4. Skarpe (1996) stresses that all factors (1 to 4) must be constructed into PFTs that will have relevance in determining the rates and effects of climate change.

The Global Change and Terrestrial Ecosystem (GCTE) group has made the study of PFTs a high priority task. GCTE have determined that their focus will be on changes in biological composition of species functional types and ecosystem structure at the patch scale.

Table 4.1 A comparison between Boutin and Keddy's (1993) guild traits and the Grime's (1979) life forms.

Boutin and Keddy 1993 guild traits	Grime 1979 Life forms
The ability to forage for essential elements in the absence of neighbours	Ruderals
Traits associated with interaction with other plants.	Competitors
Traits associated with the ability to withstand agents such as fire, flooding, grazing, etc.	Stress tolerators

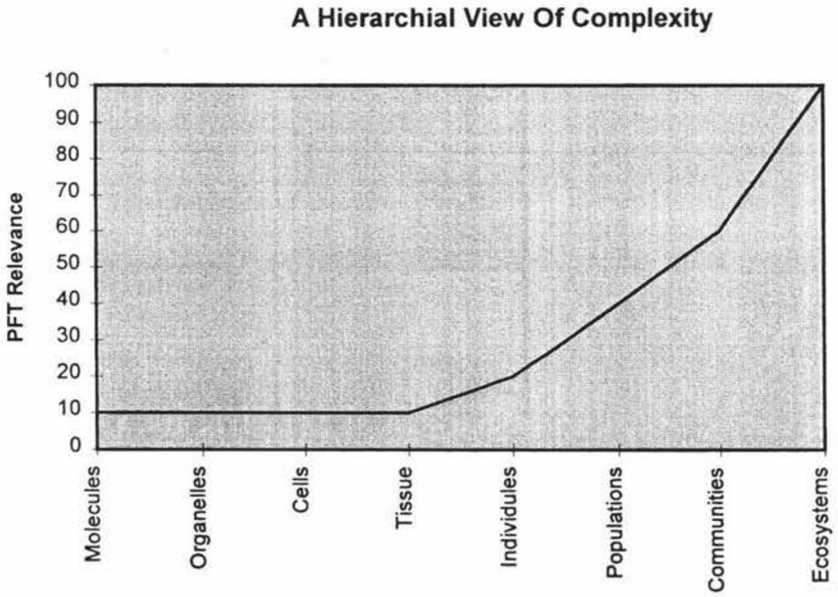

Fig. 4.2 A hierarchical view of complexity in plants and the level of integration for PFTs.

GCTE has prioritised its focus to the following tasks:

Task 1:	Classification of functional types.
Task 2:	Characterisation of functional type responses to key climatic variables and CO_2.
Task 3:	Linkage between community dynamics and ecosystem processes.
Task 4:	Climate-induced changes by fire and other disturbance regimes that affect community composition and ecosystem physiology.

Using the C_3 attribute PFT (Task 1) as an example to illustrate Task 2, elevated CO_2 increases the photosynthetic rate in C_3 plants when other resources are not limiting. This increase is tied to increases in water use efficiency (WUE) and nutrient use efficiency (NUE) - plants produce tissue with higher carbon/nutrient ratios (Bazzaz 1992).

Many plants acclimatise to increased CO_2 and growth rates fall off. However, this is not the case with all species. It would be advantageous to determine the functional attributes of NUE and WUE. Empirical measurements of soil and litter quality, precipitation, evapotranspiration rates etc., could be used to build a hierarchical signature for C_3 species that may maintain elevated growth rates indefinitely. This study could be accomplished under controlled conditions. Selected species from the trial would then be transfered to a large-scale controlled experiment to determine if the response was similar in plant communities (Condit 1997). If growth rates were not overly affected by community interactions, then selected representatives of the PFT could be monitored over the long term to determine if the carbon/nutrient ratios were increasing under increasing anthropocentric CO_2 levels.

The other effect may be a shift in boundaries between C_3 grasslands and C_4 dominated forests (Vitousek 1994), as per the North American work of Paruelo and Lauenroth (1997) cited later in the literature review.

4.1.5 PFTs' Role in Comparative Studies

A method for determining plant responses to environmental change may be to use PFTs constructed of a single strict attribute for global models or PFT vegetation maps. A better method may be to have PFTs with a sequence of attributes that can be compared at local, regional and across large geographical distances. By using statistical analysis and dendrological trees (for comparative purposes) on a global scale, comparisons may have more statistical reliability over a greater geographical range for inclusion in models. The functional sequence would become this group's signature. Advantages of this method are:

1. The group is more tightly defined.
2. Still relatively large - but smaller in comparison to individual species analysis.
3. Able to be more precisely compared to an exact same grouping for correlating environmental responses within a plant community.

This signature can be used to describe a PFT that may exist on Barrier Islands off Queensland, Australia and South Carolina in the U.S.A. A comparison can then be made between PFT responses in similar groups in both the Northern and Southern hemispheres. Even though species that make up the PFTs are likely to be different in Northern and Southern Hemisphere groups, there is now commonality based on functional traits and functional responses. The PFT can now be compared between sites.

The relationship between physiological systems and PFTs' responses to a changing environment is far more complex than a simple, deterministic predictive link between cause and effect (Steffan 1996). PFTs only have meaning in the context of the model in which they are used. The definition used by Steffan (1996) for PFTs is of a hypothetical biological entity characterised by two sets of properties:

(1) Properties of interest to users of the model's output;

(2) The environmental response function required to stimulate the dynamics of the system and used to describe the PFTs' response to the drivers of change (e.g. increased temperature, decreased moisture and enforced disturbance).

If rates of resource use are easily comparable, then broad functional groups can be established. Two such groups immediately become obvious; (1) C_3, C_4 and CAM utilisation of atmospheric CO_2 and (2) shade-tolerant and shade-intolerant groups employment of PAR. Species within each of the groups have a similar response to resource supply (Grime 1977; Tilman 1990). Since each group within the resource type has a different utilisation of the resource, these groupings allow for comparative studies with regards to fluctuations or large scale changes to the resource.

Steffan, 1996, considers that rather than classify species and their functions into PFTs, scientists should be refining the models used to determine environment change. In regard to the model, define the functional requirements of the PFT (if the model was to be used to determine the effects of rising temperature on coastal islands then the PFT in the example (Fig 4.3) may be the appropriate grouping). All other functional attributes that each species may have can be ignored. However, it must be reiterated that while this applies to the model in use, another set of functions may be more appropriate for a new model or for a further refined model.

While many classification systems have tried to specify functional groups as either morphological, physiological, taxonomic or life strategies, it would appear that combinations of these groups may well be the best way of describing any set of species with some common attribute. Hierarchical groups can represent functions at any level of complexity i.e. the more functions that are accumulated or grouped together the total number of species within each functional group would seem to decrease.

An example of this multiple attribute system is:

TYPE	**ATTRIBUTE SIGNATURE**
Coastal Salt Marsh Shrubs	Angiosperm - dicotyledon - C_4 - cold intolerant - moisture deficit tolerant - salt (Na) tolerant - high percentage of sclerenchyma tissue - evergreen - shrub.

Fig 4.3 Attribute signature of a coastal salt marsh shrub

An example of a physiological life strategy is C_4 plants, which account for approximately 18% of the total plant population and are determined to be a single attribute functional type. If we seek to remove complexity, this is an ideal starting point. 18% of all plant species have a functional response to CO_2 fertilisation that follow the same pathways. Researchers can therefore analyse plant responses to CO_2 fluctuations or changes in anthropocentric CO_2 on any species having a C_4 pathway and expect to have the same type of response.

In reality, this has not turned out to be true. Many other factors influence carbon fertilisation and thus the accumulation of photosynthates or any other carbon-based products within the plant. It is known that the age, the form, and the reproductive or the life stage of the plant at any particular time can influence partitioning of photosynthates within the plant. This may be in short-term usage such as cell division, cell elongation, or maybe in long-term storage (storage organs such as modified stems and roots). While variable strength sinks are available, then partitioning of carbon within the plant can differ from plant to plant even within the same species. It is necessary here to point out that the ameliorating effect of having a large number of species within a PFT may mean that overall there will be no change in output for a particular ecosystem process.

What are the repercussions? For any relevant use of C_4 as a PFT for measure of carbon fertilisation, the results of each replicate should be consistent. While physiologically the process is the same, there is variation between species and between individual plants of the same species. Replication would be difficult in a field situation. This would appear to be the main reason against the use of very broad single functions as a representation for a group. An exception would be forest distribution on a global scale using global information systems (GIS) data from which major tree types are easily identified.

There **should** be further distinctions - more factors should be involved. The addition of each additional trait should fine tune the PFT (Kemp 1997). The end result could be a PFT with only one or two species within it. This has significance when trying to determine which PFT construct displays keystoneness for an ecosystem function. This concept is discussed later in the thesis. While complexity is increased slightly, it is still well below that of individual species studies. The most convenient method of grouping species into functional types would incorporate both the species response to environmental change and the effect of species on ecosystem functioning (Chapin III et al. 1995). If there are different traits and/or ecosystem processes in response to each environmental factor, then there would be separate functional groups for each factor. In the long term, there may be as many functional groups as there are species. The defining and use of functional groups would lose all modelling and experimental value.

On a global scale, the use of a single-trait PFT such as C_3/C_4 (a complex plant physiological process) to determine shifting boundaries between grass and tree dominated landscapes may be appropriate depending on the scale of prediction required. Global PFT models by necessity need to be coarse. When using this attribute to define a PFT at local regional or even national levels, the boundaries tend to overlap or display patchiness that is difficult to map or model.

The use of PFTs, when associated with more environmental data, has turned up new and interesting reasons for vegetation dynamics. Time can now be spent collecting and grouping environmental data, since this data does not have to be used with every species for functional representation. In temperate grasslands and shrublands of North America, temperature has always been considered to be the main controlling factor determining the distribution of C_3 and C_4 species. Paruelo and Lauenroth (1997) have now determined that mean annual precipitation, mean annual temperature and the proportion of summer precipitation accounted for 66% of the variability of the PFT response. C_3 grass abundance decreased with a temperature decline but rose with the proportion of winter precipitation.

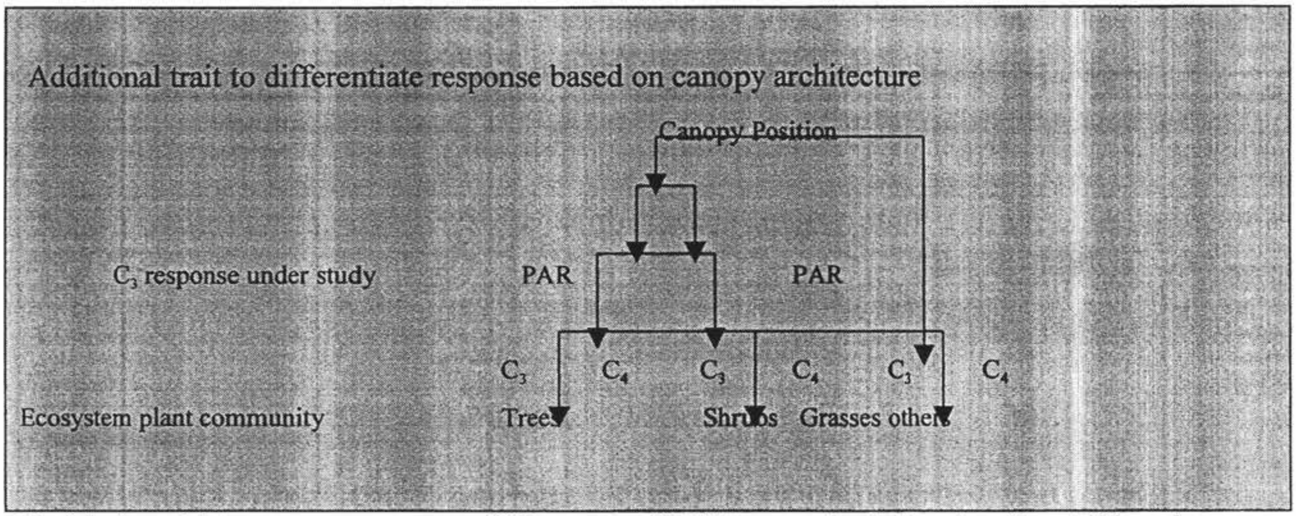

Fig 4.4 A model to compare responses of C3 grasses with C3 trees or shrubs based on the addition of canopy architecture.

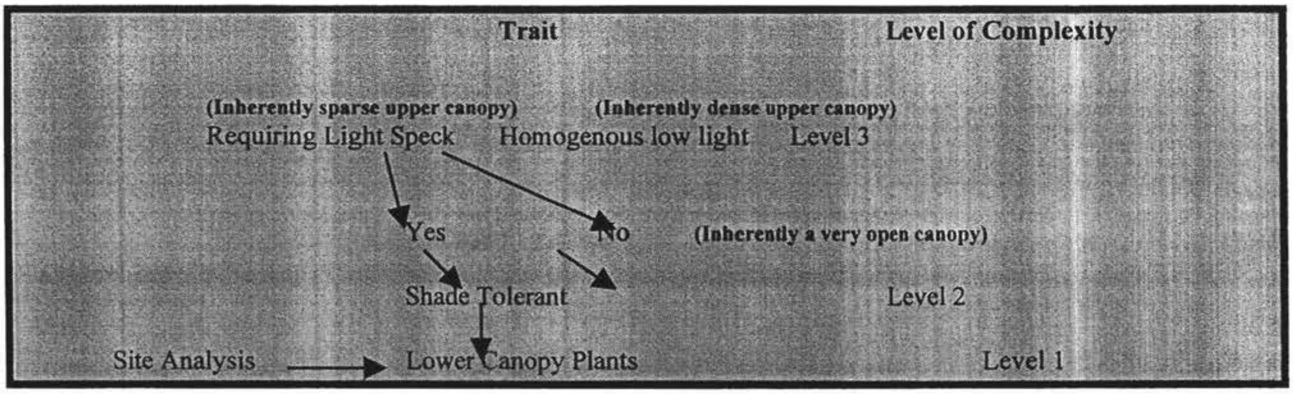

Fig 4.5. Hypothetical experiment of leaf litter quality - a comparative study between shade tolerant and shade intolerant groups. Will the inclusion of Level 3 complexity provide groups with distinctly different response to groups constructed at level 2 (Lee 1998)?

The interesting point made is, that as a result of studying a PFT rather than species, two other factors emerged that explained abundance and range over a large geographical area, even if only 66% of this variability was accounted for.

Is this enough? As a scientific query the answer has to be yes (in ecological terms 66% is a very high level of determination); however, if North American policy makers are planning for the future of their agricultural base, the answer may not be definite enough. The next step would be to continue to increase the complexity of the PFT, one attribute at a time, till the percentage of accounting for variability was closer to 100% (Fig 4.4).

The vertical position of plants within the canopy is another grouping to consider. Distinction can be made between the upper, middle and lower parts of the canopy in relation to both the diversity of the plants within the community in relation to differing environmental effects at each structural level. Open boreal type forests that are exposed to harsh winter conditions, but which allow a minimal amount of light in through the canopy during summer, would have a very low diversity at the lowest level of the canopy (the forest floor). A rain forest with several layers of canopy (typically evergreen) has a more stable environment in regards to temperature and light levels - light levels at the equator tend to be more uniform than those found in the other climatic regions of the earth.

Conversely, can / will the inclusion of one more trait (key plant attribute) distinguish a group of plants with distinctly different ecological responses? For example (Fig. 4.5), if a lower canopy PFT was constructed, the main attribute would be shade tolerance. Would a further distinction such as a lifestyle adaptation requiring sunspeck light as opposed to an even, low light make any difference in the assessment of litter quality? Complexity within the PFT definitely increases, but will the experimental results differ from the larger scale PFT at a lower hierarchical level? Will this group use and retain nutrients and contribute to ecosystem function in a distinctly different way?

Another functional group is the below ground spatial position of plants i.e. what position the root systems take up within the lower or upper strata of the soil. Also another attribute to consider when constructing this group is plant association with VAM fungi and VAM's ability to aid plants in competing intraspecifically and interspecifically with other plant species.

If VAM fungi turn out to be keystone species or an indicator of environmental stress, then plant species that have a specific VAM association similar to another plant could be placed within the same functional group. Bearing in mind that there are abundant numbers of VAM fungi; and one would have to do a detailed study to determine if the VAM and plant associations were similar. If the VAM fungi showed a faster response to environmental change (at either extreme in environmental conditions) and signalled this response by disappearing, then it might well be an indicator that some sort of change was taking place within the plant community. This would have an effect on the successional process and may well cause, in the long term, a change in species abundance / biodiversity within any particular plant community/ecosystem.

Competition for resources is also another area that may be used to contrast functional groups (Hooper 1998). A plant's ability to scramble or to make use of

VAM fungi to gain a competitive advantage over other plants could be because they have a greater resilience to change than do those plants without a similar VAM. VAM could also have some type of competitive root strategy to combat nutrient depletion within the soil strata. The presence of these types of attributes - resilience and resistance - can give some indication of where a successional process will head.

Progress in broad ranging comparative studies of PFTs will be enhanced by using the huge amount of data sets of functional attributes contained in existing literature. According to Duarte et al. (1995), most of the scaling functions that have been derived have been produced by compiling data scattered through the literature (as per the Maunganui Bluff analysis in Chapter 6).

For comparative PFTs to become recognised as legitimate tools for predictive analysis there is a need to develop a set of guidelines for methods, measuring techniques and analysis (MacGillivray & Grime 1995; Duarte et al. 1995). Data should be gathered in all categories that are accessible at the time of the analysis. Parsons (1976) and Grimes et al. (1988), have classified plants into ecological groups by assembling a data table of plant attributes without prejudging which attributes are the most important. Using statistical analysis, vital attributes were determined.

Another legitimate methodology is to make *a priori* judgements, then to construct and test a PFT against the environmental conditions e.g. hot and dry environmental conditions would lead to an *a priori* judgement that the majority of plants have C_4 or CAM metabolisms. From available data at these sites a methodology can be developed to test these predictions. Box (1981) developed such a model which has been under utilised (Westoby & Leishman 1997).

To recap on this topic of comparative studies and the construction of PFTs, the following areas are highlighted:

Plant functional types are functionally similar plant types. (Box 1996). On a global scale PFTs should cover the following criteria.

1. PFTs should represent the world's most important terrestrial plant types, in natural vegetation and ecosystem interactions.
2. Such plant types must be characterised by functional behaviour, not species responses.
3. The set of PFTs should as a whole provide complete geographically representative coverage of the main vegetation types of the world's land areas.

This author also suggests at the local level, PFTs should:

1. Have a response to a localised environmental condition e.g. plant groups that have a tolerance of moisture stress versus those that do not.
2. Be representative of the major variations in vegetation such as trees, shrubs and grasses. These can be then assessed as high canopy, mid canopy and understory.
3. If they are representatives of refugia, will show distinct migration patterns under environmental change e.g. contain a genus of a much larger family whose other representatives are found in tropical climates.

4. Have an attribute that is not limited by taxonomic constraints e.g. divarication which occurs across a range of genera.
5. Form mutualistic associations with soil biota that may be more sensitive than plants to environmental perturbations e.g. VAM fungi.

One way to determine multiple functions could be the use of dendrological trees with pathways on the tree representing a group of function; incorporating taxonomic, physiological and morphological responses. Another is to use comparative searches based on accumulated data held in a database (used by this author to construct PFTs from site data for the Maunganui Bluff plant survey). This approach would be especially effective at the local level, as in Grime et al. (1988) comparative study of common British species.

4.2 The ecosystem concept and biodiversity

The concept of ecosystems has gained greater recognition in literature since the 1950s. The concept is that a whole community of plants (and animals) plus the chemical and physical environment they inhabit is a dynamic system (Odum 1971). The ecosystem concept emphasises the interdependence and complex relationships between component parts. Not only do individual plants adapt to the geochemical environment, but, by concerted action (feedback), plant communities adapt this environment to their biological needs. Ecosystems are said to be *holoceonotic*[5] (Jeffries 1997). This interdependence and interaction by plant communities with their environment means that a response by one component to some form of change may be modified or enhanced by another within the system.

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[5] An all-encompassing term to describe complex linkages, flows and processes between component parts of an ecosystem

Changes in the limiting factors are reflected in the whole system, because even minor changes, e.g. invaders or small fluctuations in the climatic gradient, can have far reaching effects. The changes initiated by these effects are almost always irreversible (Lange et al. 1993).

The sum total of ecosystem services: gas and water purification and recycling, soil formation, nutrient recycling and storage, growth and development, is termed ecosystem function. Ecosystem function depends on the organisation of the system, the diversity of the taxonomic groups, the number of species and their distribution within the system. Some species play a keystone role in some ecosystems, e.g. nitrogen fixing (not an ingredient in New Zealand's natural systems with only the Kowhai having a true symbiotic relationship with *Rhizobia spp.*). Biota having similar roles with ecosystem function, including a similar use of resources, are called functional types and are considered to be the drivers of ecosystem processes.

One premise is that if researchers were able to determine the important driver functional groups and keystone species then we could both monitor (for functional change) and preserve (for functional integrity). The problem is that not enough is known about the complex relationships within ecosystems and that this approach may constitute 'too many eggs in one basket'. By concentrating only on key species and driver functional groups, researchers say that diversity in ecosystems will decrease (composition) though total numbers may not shift markedly if the key species is the largest member of the group. Evidence suggests (though this premise does not hold true in all circumstances), that with increasing diversity of species, stability and productivity increases (Tilman et al. 1996). Hooper and

Vitousek (1997) believe that the composition of functional groups may be more important to ecosystem process than functional group *richness*[6].

The term biodiversity was not at first associated with ecological sciences, but with politics and environmental technology (Ghilarov 1996). Scientists were obliged to incorporate the terminology to show the general public and policy makers (Bengtsson et al. 1997), the possible role of biodiversity as a requirement of ecosystem functioning. Biodiversity within the context of this essay is interpreted as *biological diversity* (Lamont 1995). Biodiversity comprises three components - composition, structure and functions (Noss 1990 cited in Lamont 1995). A comparison can be drawn between these characteristics and the characteristics of PFTs (Table 4.2).

For the purposes of this literature review, all currently accepted models of biodiversity relationships and dynamics are accepted. These include the species - time hypothesis, species - area relationship, species - energy hypothesis, stability - time hypothesis, redundancy hypothesis, species abundance patterns and the intermediate disturbance hypothesis. While no accepted hypothesis is singled out for a negative response, the redundancy hypothesis (Walker 1992) appears to this author to fit the linkages of keystoneness, driver functional types and ecosystem resilience in response to changing environmental factors.

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[6] Richness is an arbitrary term used to measure the total number of individuals that make up any group.

Table 4.2. **Relationship between biodiversity and PFT composition, structure and function (Lee 1998; after Noss1990).**

	BIODIVERSITY	PFTs
COMPOSITION	Abundance	Number of species exhibiting the same functions
STRUCTURE	Spatial and temporal make up of an ecosystem	Construction of the PFT - the number of functions selected
FUNCTION	Nutrient flows, productivity etc.	NUE, WUE, LAI, RGR etc.

4.3 Biodiversity, ecosystem processes and the redundancy hypothesis

The redundancy hypothesis advanced by Walker (1992) proposes that certain species have an ability to expand their jobs in ecosystems in order to compensate for neighbouring species that go extinct. His hypothesis was based on the work of Ehrlich and Ehrlich (1981; cited in Johnson et al. 1996). If a species within a functional group becomes extinct, then a species with the same functional attributes will replace it and will exhibit the same functions within the plant community/ecosystem. By definition then, PFTs with keystone species will show no redundancy because the keystone role cannot be replaced by another species. The overall effect on the ecosystem process will lead to instability and a successional change.

Biodiversity does not occur at random, but changes across environmental gradients. The most obvious gradient is the increase in biodiversity from high latitudes (the poles) to low latitudes (the tropics). Within this latitudinal gradient are changes in light, temperature, moisture and season, which facilitate change in diversity. The decrease in diversity over increasing altitude is a similar gradient. Both biodiversity and PFTs are affected by disturbance. Chapin III et al. (1996) states *a sustainable ecosystem is one that over the normal cycle of disturbance events, maintains its characteristic of major functional groups, productivity, and the rates of biogeochemical cycling.*

Because of anthropocentric changes in land use, natural ecosystems have become fragmented. This has imposed pressures on these systems that have decreased their resilience in response to climatic and other geochemical fluctuations. Species within the New Zealand Broadleaf – Podocarp forests may have difficulty in surviving the climatic changes due to projected increases in CO_2 levels and temperature over the next century (refer Chapter 3). Examples are: (1) *Akamia rosaefolia*, where a warming of $4^{O}C$ would render all current locations unsuitable with no other suitable locations apparent. *Akamia rosaefolia* would become extinct. (2) For *Vitex lucens* and *Agathis australis* under the same $4^{O}C$ rise, the number of climatic suitable locations would decrease. Because no migration corridors are available (except by human intervention) there is a probability that both species will become extinct (Mitchel & Williams 1996). It is important to identify functionally distinct groups from which *a priori* predictions can be made about extinctions within ecosystems (Johnson et al. 1996) or full ecosystem change due to the loss of keystone species that mediate ecosystem functions.

The above example is used to illustrate the distinction between species that are able to migrate (but cannot do so because of ecosystem fragmentation) and those that will have no suitable habitat independent of human intervention. Maintaining a diversity of functionally equivalent species within ecosystems enhances resilience – the capacity to recover from a disturbance that affects species' composition within ecosystems (Tilman & Downing 1994; Walker 1996).

While climate change scenarios indicate an overall trend of temperature increase, there is much variation at the regional scale (refer Chapter 3). New Zealand is small spatially and the ameliorating effect of being surrounded by sea may mean that New Zealand will have a reduced rise in temperature, meaning less pressure on species and ecosystem composition. However, degradation of ecosystems and a lowering of natural forest biodiversity through possum browsing may in fact make New Zealand ecosystems less stable and less resilient to change. This is especially true if some of the species browsed by possum turn out to be keystone species and members of plant functional groups that are intrinsically tied to important ecosystem processes.

The most important point to consider is that species that make up PFTs are not similar in all respects. In a relatively stable ecosystem, plants may respond differently along a climate continuum, but overlapping within the PFT is compensatory and the ecosystem process will continue in a relatively stable fashion till disturbance causes a shift to a new relatively stable point. Species may be very important players in one PFT but only play a minor role in other PFTs. Walker (1995), as well as mentioning driver (or keystone) species within PFTs, describes two other divisions:

(1) Passengers that contribute to ecosystem function and which may become redundant without affecting the overall ecosystem processes.

(2) The inert passengers who exert little influence but which under severe disturbance may take a driver's role.

4.4 Biodiversity – productivity and stability

Many studies have been done on the scale, pattern and architecture of ecosystems and how these effect biodiversity. In studying the effects of increased environmental disturbance to ecosystem diversity, the aim is to understand how these ecosystem attributes (pattern, scale and architecture) are changed. Will this change enhance or decrease biodiversity? The comparison of ecosystem functional properties, which are characterised by different levels of diversity, may not necessarily demonstrate the importance of diversity in ecosystem functioning. Attempts to carry out the work of determining the relationship between productivity and diversity have not yet clarified whether PFTs are useful measures or whether it is the productivity of individual species within the PFT that really contributes to the diversity – stability and productivity debate (Naeem et al. 1994; Tilman et al. 1996).

Walker (1995) believes that the experimental manipulation of structure by Naeem et al. (1994) was a good demonstration that biological diversity is a key determinant of ecosystem function. This is backed up by later experiments. A field experiment that compared plant species diversity to plant functional diversity in a controlled savanna – grassland environment showed that functional diversity had a greater impact on ecosystem processes (Tilman al. 1997).

Chapter 5 Maunganui Bluff – Vegetation and History

5.1 Introduction

Maunganui bluff (latitude 35° 46′, longitude 173° 33′) was chosen as the site for the gradient analysis because it is the highest promontory, within the Hokianga – Dargaville area, offering enough environmental perturbations to warrant testing the validity of PFTs in diversity/disturbance analysis.

The other rationale was that the Auckland Botanical Society had carried out a previous study, and an unpublished species richness list (provided by the Department of Conservation) was available for the entire bluff reserve to construct PFTs *a priori*. A vegetation history was also available (Esler & Dodbins 1977). The following sections (Chapter 5.2 to Chapter 5.4.3) were developed from Esler and Dodbins (1977) report and brought up to date (circa 1998) through personal observation by the author and Lisa Forester (DOC botanist). The author has found no other published vegetation lists or history of the Bluff. Consequently, while specific events are referenced, the majority of these sections are strongly influenced by Esler and Dodbins (1977) report.

This chapter is intended to build up a vegetation history of the bluff, highlighting events that have shaped the plant communities that exist today. Also, the chapter specifically states large-scale categories that the sampled communities are reflective of, e.g. vegetation classes, geographical, and geological influences.

5.2 The Bluff Reserve

Maunganui Bluff is a biological reserve of some significance. While it may not have any endemic plant species peculiar to it, the reserve is a haven for native flora while other native communities nearby are being eliminated or modified. The Bluff contains two plants with very restricted distribution: *Hebe speciosa*, a spectacular koromiko and *Cotula rotundata*, a little matted bachelor's button (Forester 1997).

Maunganui Bluff is a massive domed promontory with the seaward face eroded away. A depression separates it from the high country of the Tutamoe Range, but it is all part of the same series of basalt flows stretching half way across Northland. The seaward face is fairly steep, but the lee side falls away gently. Cliffs run nearly the full length of the reserve. The cliffs rise to a prominent, sharply indented rim reaching to 300 metres in most places. A depression in the rim near the centre point is the saddle at the head of the Waiotapu Stream. In the south the seaward face ascends from the cliff tops through an amphitheatre to a high ridge where the radar trig stands at 459 metres. This seaward face, from 50 metres above sea level to the radar trig (459 metres) was the study site for the gradient analysis.

The cliffs change in form along the 6 kilometres of coast. In the south the cliff is represented by a series of bluffs curving inland a short distance. They have talus[7] at the foot. Then for 3 kilometres the cliffs rise very steeply to the indented rim. On the seaward side of Waiotapu saddle the cliffs are almost vertical at the base then the slope ascends less steeply to the rim. This part, negotiable on foot with caution, is referred to as the coastal slope. In the higher, forested parts of the south slope, the talus slope is composed of large boulders. Below this, the terrain is quite irregular (apparently because of lumping); there is less rock and more soil with some sand blowing inland near the beach. The lowest slopes are very wet in winter.

The foreshore for most of its length is a narrow beach backed by an embankment a metre or so high, which is composed of soil studded with boulders and occasional tree stumps. Sand blows up off the beach and inland for a short distance

The views are panoramic (Appendix II, Photographs 5.1 to 5.4). To the south - east lie the Kai Iwi Lakes and the long straight coast running to the Kaipara Harbour mouth Photograph 5.1). To the north - west lie the heads of the Hokianga Harbour at the end of another long line of sandy coast (Photograph 5.2). Waipoua Kauri Forest is about 5 kilometres to the north and slightly inland.

The nature of the Maunganui Bluff is best appreciated from the rim above the cliffs, particularly between the Waiotapu saddle and the radar trig. From here there are distant scenes as well as views of the sea cliffs, which cannot be seen from the highest parts of the reserve. The reserve forms a strip about a kilometre wide with a finger pointing inland for 2 kilometres from the sea. The area is 495 ha.

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[7] **Talus slope:** An accumulation of fallen rock debris which has formed at the foot of a steeper declivity.

5.3 Historical Background

The land was reserved in 1911 under the Scenery Preservation Act 1908. The vegetation on the site tells something of its past. Prior to the Aranga area being converted to farm land, the original vegetation on more sheltered parts was similar in nature to that of Waipoua Forest. Kauri (dense in places and sparse at others) with podocarps and northern rata reached far above a canopy of tawa and taraire in areas where kauri numbers were low. All useable timber was removed, probably early this century (Esler & Dodbins 1977).

Since then there have been many fires. Cattle have grazed and browsed all the accessible parts for a long period of time since the land was reserved, probably continuously until recent times. The boundary of the reserve has now been well fenced and, unless gates are accidentally left open by hikers, there is no stock access. There was no evidence of recent stock access and understory plants were recovering.

A minimum amount of land was cleared in 1942 for the site of the RNZAF radar station. The earliest air photos show forest close to the buildings on all sides with trees between the buildings. A fire some time later is said to have destroyed some of the vegetation at the radar trig. The buildings were dismantled in 1957 (Esler and Dodbins 1977).

5.4 The Effect Of Environment

The effects of salt-laden winds are evident from the structure and composition of the vegetation. However, not all of the reserve is exposed. The lee slope is relatively sheltered and there are parts of the seaward face that are partially protected. The amphitheatre is screened in many parts because the wind ascending the cliffs sweeps over the top. Small ledges on very steep parts of the seaward face give similar protection where otherwise exposure may be expected to be greatest. The canopy of the vegetation on these ledges is deformed, but within the community the air is calm. The formation of a wind roof of this nature in exposed places enables many species to survive that do not have a high tolerance of wind-borne salt. If, through slips or the loss of tree species, the canopy becomes broken and the wind is not shed so effectively, plants that have become isolated will desiccate, eventually leading to necrosis.

Where previously there has been burning and browsing in these windswept places, grassland has developed. Grass species are slowly encroaching into bush margins, mainly due to human vectors, since the advent of the national walkway and the increased popularity of tramping in "wild" exposed spots with spectacular scenery.

Nearer the shore, and in places where a wind roof cannot form, the effect of the salt blast is to eliminate all but the hardiest species. In some places, hardy plants create enough shelter for more sensitive plants to succeed. All the broken topography of the reserve lies on the seaward face, meaning that, as well as exposure to wind, the plants have to endure thin soils with little reserve of moisture and an insecure root hold. Plants are of generally low stature. Many of them have strap-shaped leaves. Some plants thrive here because competition for meagre resources is minimal.

Where cattle and fire have worked together in the past, the forest has suffered severely. However, grazing has not been systematic enough to maintain grassland in all places, particularly where there is shelter from wind. The return to forest is indicated by the abundance of flax, bracken, manuka and other shrubs. Grazing did not always have an adverse effect. There appear to be some places where grazing and burning have created a habitat conducive to the growth of *Hebe speciosa.* The grassy strips along the cliff tops that cattle helped to maintain are an asset to the reserve because they improve access and views (Esler & Dodbins 1977).

Although possum numbers appear to be fairly high their effects are not clear. There are many dead northern rata trees and it is likely that possums are to blame. It is significant that there appears to be little damage to pohutukawa, a species high on the possums' preference list. The leeward side of the bluff, which has the most extensive forested areas because of the lesser effect from salt-laden air, is now extensively poisoned (for possum) from bait stations.

There are rats and mice in the reserve, but there is still uncertainty in regard to rat species or their impact. Certainly, evidence from Waipoua and Trounson Park, where there is extensive monitoring of rat and mice populations, indicates that bird species suffer from egg predation and that seed availability is lessened for birds and consequently for plant regeneration. The rats' habit of living in the crowns of nikau palms suggests that they are *Rattus rattus* (Esler & Dodbins 1977).

5.5 Vegetation - General

5.5.1 Forest

Forest covers most of the reserve. The coastal forest dominated by pohutukawa forms only a small part of the total. The rest, referred to here as sheltered forest, has a remarkable degree of uniformity, comprising the same set of species occurring in most places but differing from them in height due to age and exposure.

Over the top of regenerating forest, the relics of the old forest can be seen. Kauri occurs in only a few places. A few northern rata are still alive (most are dead or dying). There is good regeneration of northern rata in the sections that are poisoned for possum. Most of the other emergent trees are rimu, miro and kahikatea. In a few places, puriri are emerging above the main canopy. As is common for puriri, many have collapsed and sprouted again from the reclining limbs.

The main canopy is made up of two classes of trees - the transitory species, which are there because the canopy is low and the vegetation is young, and the permanent canopy species (Forester 1997). A typical short-term species is *Coprosma arborea*, which has low palatability. The principal permanent canopy species is taraire, which although not forming a continuous cover, is the predominant emergent species. Regeneration of taraire is high because of stock-proof fencing. Kohekohe and karaka are of lesser importance in the canopy. Rewarewa, in more sheltered places, is able to emerge above the cover (which varies from about 6 m above the ground to 15 m). At higher altitudes the shorter species such as cabbage tree are fewer, and nikau becomes an understory plant along with silver tree fern.

Epiphytes are fairly conspicuous on the larger trees, particularly the emergents, and on the fairly level branches of puriri and taraire. *Collospermum hastatum* is much more abundant than *Collospermum microspermum* and *Astelia solandri*. Kiekie and supplejack are fairly widespread climbers and the white climbing rata (*Metrosideros perforata*) is quite common.

In the shrub layer, *Coprosma areolata* deserves some mention. *Coprosma areolata* is particularly suited to northern coastal areas. The plant can form a small tree canopy in sheltered areas and a low shrubby canopy in very exposed sites. *Coprosma areolata* is a very common emergent on very steep exposed (seaward) sites. *Coprosma areolata* does not appear to be palatable to browsers, either cattle or more recently, possum. Most other Coprosma species (except for *C. rhamnoides* and *C. parviflora*) were too palatable to survive when cattle were present. Other Coprosma species are slowly infiltrating the majority of habitats available on the Bluff. *Coprosma lucida*, a species usually common in unbrowsed vegetation of this kind, is becoming increasingly more common, albeit in small numbers. Hangehange is well represented throughout all non-grassland sites, another good indicator that browsing by cattle is much reduced. A large number of hangehange plants have now grown above the browse level and appear to be seeding profusely (Esler & Dodbins 1977).

The coastal forest has a distinctive composition; pohutukawa stand alone where conditions are too harsh for other woody plants but in many places grow with some of the following: kohekohe, karaka, ngaio, rangiora, *Coprosma macrocarpa*, taupata, kawakawa, kowhai and *Astelia banksii*. Vegetation of this nature is a feature of forested areas near the shore. The effects of the coastal influence are probably greatest here, because wind funnels among the bluffs and carries with it a large amount of sea spray laden with salt from the waves dashing against the rocks below.

5.5.2 The coastal slope vegetation

Vegetation intermediate between coastal forest and cliff communities can be seen on the coastal slope at Waiotapu saddle. In some places the soil is eroded by wind; in others, gravity is pulling boulders downslope. It is not just instability that prevents forest from developing; wind is an important factor, as well as past fires.

The first impression is the grassy appearance of the slope; flax and toetoe are widespread. The main shrubs on the slope are rangiora, hangehange, *Hebe speciosa*, kawakawa, mingimingi, *Helichrysum glomeratum* and five finger with some *Rhabdothumus* where it can find enough shelter. Bracken is scattered throughout. Most of the dwarfed pohutukawa, karaka, kohekohe and mapou grow in depressions and on rocky outcrops.

The smaller grasses are mostly on minor ledges, on thin soil over rock and on unstable soil. There are some native grasses but not in any significant numbers.

Among the exotics: ratstail, cocksfoot, tall fescue, sweet vernal, wild oat, paspalum and shivery grass are present in large numbers.

5.5.3 Cliff vegetation

On the cliff rim there are plants from different communities, which are able to withstand the buffeting from the wind and the salt that it carries. It is usual to see pohutukawa, mapou, five finger, flax and many others clinging to a ledge on the seaward edge. If the ledge is wide enough a minor forest has developed in this relatively sheltered pocket. On the rim itself the most common plant is *Coprosma neglecta*, looking like *Muehlenbeckia* with its creeping intertwining stems (Esler & Dodbins 1977).

The cliffs are very steep, but rise in a series of steps presumably representing the 40 or so separate lava flows which formed the Bluff (Esler & Dodbins 1977). On larger ledges there are pohutukawa, kohekohe, *Olearia albida* and mapou present. Smaller ledges have *Astelia solandri,* flax, pohutukawa and kowhai. But in the more extreme habitats only the plants with strappy leaves survive.

5.5.4 Grasslands

Native plants have only a minor place in the grassland areas. There is a wide range of exotic species. Esler & Dodbin (1977), in relation to the grassland areas, have determined that the abundance of species at any site is more important than presence or absence of particular species. Esler & Dodbin (1977) believe that this is due to the plasticity of all the exotic species available from the total pool on the Bluff. The fairly sheltered grasslands on the lower part of the bluff favoured in the past by cattle have fairly fertile soil. This habitat has a predominance of clumped grasses - tall fescue, prairie grass, cocksfoot and perennial ryegrass - with some mat-like species such as Yorkshire fog and paspalum. The main legumes are white clover and Lotus spp.. Weedy species are relatively few because the grass here grows fairly rank.

A shift towards medium fertility on the cliff tops and behind the beach excludes none of the above, but swings the balance towards browntop and sweet vernal as well as some annual grasses such as shivery grass. Wild carrot grows in abundance and there are conspicuous amounts of weeds such as narrow-leaved plantain, slender winged thistle, Scotch thistle, fleabane, hawksbeard and hawksbit.

5.5.5 Site Description

As mentioned, the area of study was on the southern slope of the Maunganui Bluff Reserve (Fig 5.1). The eleven study quadrates were spaced at 50 metre altitudinal increments along the gradient. Distances between sites varied from several hundred metres on the steepest parts of the slope to a kilometre (approximate only, no instruments used for precise measurements) along ridges. The topography changed from talus slopes to thin soils over consolidated basalt lava. Vegetation classes were determined by environmental conditions such as wind, salt laden air, geophysical factors such as slope and soil depth and consequential nutrient status, aspect and a history of fire and grazing. The sites were on a basaltic outcropping that changed from solid bare rock through to varying degrees of soil development depending on topography and vegetation history.

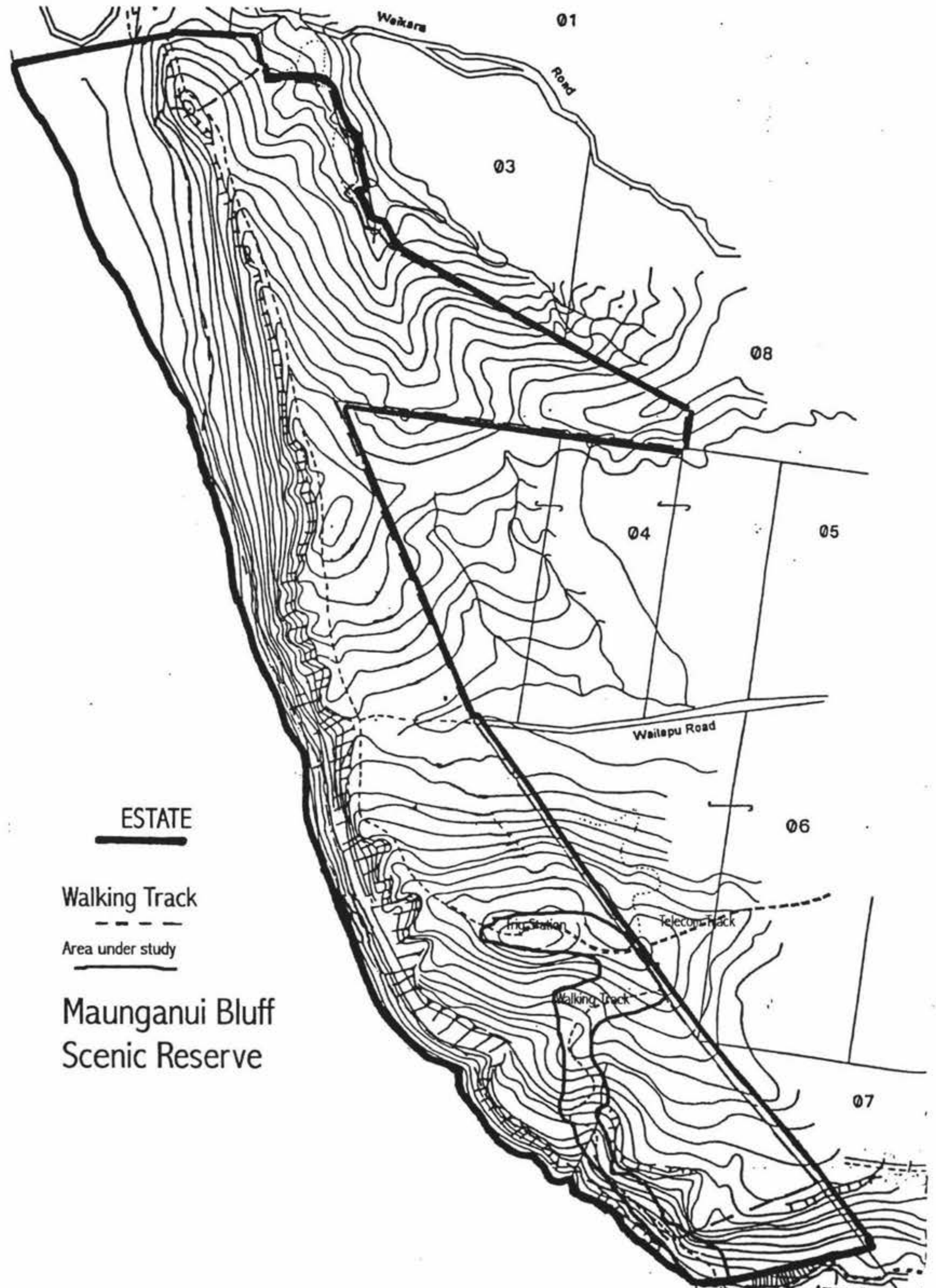

Fig 5.1 Map of the Maunganui Bluff Reserve. The boundary of the estate is marked in heavy lines. The area of study has been inserted by the author and is the thin freeform solid line stretching from Aranga Beach to the Trig station (Lee 1998).

These topographical features ranged from varying degrees of midslopes, interfluvials[8], a convex creep[9] slope and a toe[10] slope. The Lands and Survey vegetation classifications were taken from a Site of Significant Biological Interest (SSBI) survey carried out by the Department of Conservation (DOC 1995). The structural classes were checked with the national classifications (Landcare 1995); see Table 5.1. As part of this author's survey, these classifications were correlated with the dominant canopy species to see if the classes remained constant. The comparisons were strongly correlated as to composition (Table 5.2) both with the old survey and between the classes (Forester 1997); no attempt was made to determine if richness had changed as there were no comparable data.

5.5.6 Soil

The soil on the bluff is classified as Katui clay loam. While there are many site differences due to steep transportational slopes that preclude the buildup of more than a rudimentary "A" horizon, the soil type at each site has not been evaluated. The soil description is therefore based on Katui clay loam, which is formed from andesite and basaltic rock, mostly older than 50, 000 years.

These soils are popularly known as semi-volcanic soils, but are officially named brown granular clays. Granular soils are clayey soils in which kaolin-group minerals are dominant, and are usually associated with vermiculites. Granular Soils are mainly found in the area north of Dargaville and Whangarei; of which

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[8] **Interfluve**: An elevated surface bounded by a head slope or shoulder or upper slope or a gully or a stream. An interfluve area has slopes of less than 5° and is more than 20m wide and is more than 10 times long as it is wide.

[9] **Convex creep**: Shape of land is like the outside of a circle with slow, gradual, more or less continuous, non-reversible deformation sustained by soil and rock materials under gravitational stresses.

[10] **Toe**: The lowest part of a slope or cliff: the downslope end of an alluvial fan.

120,000 ha are mountainous and steep and an equal area is hilly, rolling or flat (Molloy 1993).

The profile morphology tends to be dominated by a moderately developed-to strongly developed-nutty structure throughout the "A" and "B" horizons. The small granules, prominent in the topsoil, are highly resistant to pressure while dry, but when wet are easily broken down by pugging, resulting in an unpleasantly sticky soil. The clayey subsoil is relatively structureless with the result that water percolates very slowly. Consistency is sticky and plastic. After heavy rain, a high perched water table may persist for considerable periods. In dry periods, vegetation growing on many of these soils suffers more severely from drought than on many of the freely draining soils. Clay contents are generally high (from 40 to 80%). Workability and trafficability of these soils are constrained by stickiness and plasticity after heavy rainfall. Reserves of phosphorus, potassium and magnesium tend to be low (McLaren & Cameron 1996).

Table 5.1 Geophysical and major (tree/shrub) vegetation overview of Maunganui Bluff's South slope

Site	Geophysical	Aspect	Altitude	Structural Class	Dominant Tree/Shrub Composition
A	*40° midslope. Basalt rock*	*westerly*	*50*	*Shrubland*	*Phormium tenax, Macropiper excelsum.*
B	*45° midslope. Loose basalt rock on surface*	*westerly*	*100*	*Treeland*	*Corynocarpus laevigatus, Macropiper excelsum, Brachyglottis repanda.*
C	*30° midslope. Soil over basalt*	*South westerly*	*150*	*Shrubland*	*Phormium tenex, Rhopalostylis sapida, Macropiper excelsum, Geniostoma rupestra.*
D	*45° midslope. Predominantly fragmented basalt rock, free draining*	*South easterly*	*200*	*Forest*	*Beilschemedia taraire, Geniostoma rupestra, Myrsine australis.*
E	*15° toe slope. 60% rock, 40% soil moderately drained*	*East*	*250*	*Forest, coastal broadleaf*	*Beilschemedia taraire, Geniostoma rupestra, Rhopalostylis sapida.*
F	*15° interfluvial. No surface rock, stable soil structure, moderately well drained*	*South east*	*300*	*Forest, coastal broadleaf*	*Beilschemedia taraire, Geniostoma rupestra, Rhopalostylis sapida*
G	*15° midslope. Occasional rock, soil stable with good structure, moderately well drained.*	*South west*	*350*	*Treeland*	*Rhopalostylis sapida, Hoheria populnea, Melicytus ramiflorus.*
H	*35° transportational midslope. Rock uncommon, deep litter layer.*	*North east*	*400*	*Forest*	*Rhopalostylis sapida, Melicytus ramiflorus, Geniostoma rupestra, Aristotelia serrata.*
I	*Convex creep slope. Very thin soil layer over fragmented rock.*	*Westerly*	*450*	*Shrubland*	*Coprosma parviflora, Phormium tenax, Myrsine australis.*
J	*5° interfluvial slope. Thin soil over fragmented rock, well drained.*	*South east*	*459*	*Grassland*	*Phormium tenax, Hoheria populnea, Carpodetus serratus.*
K	*15° midslope. Good soil structure with 30% rock, moderate to well drained.*	*North-westerly*	*450*	*Shrubland*	*Geniostoma rupestra, Hoheria populnea, Coprosma areolata,, Haloragis erecta.*

Table 5.2 **Diagnostic criteria for recognising vegetation structural classes (adapted from Landcare 1995).**

Structural Class	*Qualitative criteria for rapid recognition*	*Qualitative criteria for precise definition*
FOREST	*Woody vegetation dominated by trees, shrubs and treefems in which tree cover exceeds shrub cover and trees are of major importance in the canopy; e.g. pine forest.*	*Combined cover of trees, shrubs and treeferns in the canopy: > 80% tree cover:> shrub cover in canopy : > 20%. Trees are woody plants => 100 mm trunk diameter measured 1.4 m above ground.*
TREELAND	*Vegetation in which the canopy is formed by a discontinuous layer of trees that overtops a lower layer of predominantly non-woody vegetation or bare ground; e.g. mahoe/bracken treeland*	*Tree cover: 20-80 :> cover of any other growth form or of bare ground. Note: vegetation consisting of a discontinuous tree layer above a lower layer of shrubs or tree ferns is classified as forest, scrub or treefernland depending on the proportions of trees, shrubs and tree ferns in the canopy.*
SHRUBLAND	*Woody vegetation in which shrubs are the predominant growth form but which do not form a semi continuous canopy as in scrub; e.g. manuka shrubland*	*Shrub cover: 20-80 % : > cover of any other growth form or bare ground.*
GRASSLAND/ SEDGELAND/ RUSHLAND	*Vegetation in which grasses, sedges or rushes are the predominant growth form; e.g. paspalum grassland. Note: tussock grasses tussock sedges and tussock rushes are excluded from these structural classes*	*Grass/sedge/rush cover: 20-100%: > cover of any other growth form or of bare ground.*

Chapter 6 Maunganui Bluff Survey - Methods and Analysis

6.1 Introduction

Species whose presence or abundance reflects some aspect or measure of an ecosystem are called bioindicators. An ability to readily identify these indicators would lead to a reduced amount of site biotic analysis over time, especially in long-term experiments to determine the effect of environmental change. Dufrene and Legrandre (1997) suggest an approach to determining bioindicators that *derives indicators from any, a priori or a posteriori, hierarchical or non hierarchical site classification* (McGeoch & Chown 1998). The association between each species or site group is determined independently of the clustering method.

A plant survey was carried out, along a transect, at each 50 metre altitudinal rise. The transect[11] followed the access path from sea level to the highest point, the trig station. At each 50 metre point, plants were identified and counted from a 4 metre by 5 metre quadrat[12]. Any plant whose stem was inside or touched the quadrat perimeter was included in the sampling. Plant function groups were calculated from a dataset of all available species from the locality, based on *a priori* assumptions of plant attributes (taxonomic, physiological and life history) that would most likely determine plant distribution across the altitudinal isocline. For each of the functional groups, sampled species from each of the eleven sites were retained. All other species were removed from the functional group (these species may or may not be present in the locale, but were not sampled). A presence and

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[11] A transect is a line across a habitat and is most often used for assessing the distribution of species across an environmental gradient.

[12] A quadrat is a frame used to isolate an area so all organisms within the area can be counted.

absence table for each functional group across each of the eleven sites was compiled.

6.2 Site survey

6.2.1 Species survey

While abundance of species may be useful for constructing biodiversity indices, occurrence (presence/absence) data are important in most techniques used to statistically analyse datasets. Hayek and Buzas (1997) emphasis the value of a full dataset for the locality under survey; compiled by others, if possible. The availability of this dataset allows the use of small sampled sites and an assumption of normality. For the Maunganui Bluff site a previously compiled dataset of the vegetation present at the locality was available. The paper only-dataset (list) was compiled by the Auckland Botanical Society. The author with the aid of a Department of Conservation botanist, Lisa Forester, sampled the eleven sites.

6.2.2 Site selection and randomness

The term random does not describe the dataset; instead the term describes the method by which the dataset at each quadrat is obtained. Hayek and Buzas (1997) state that a random process should guarantee that each possible biotic sample has an equal chance of being selected – not, as often erroneously defined, as each individual in the population having an equal chance of being in the sample. This is evident from the criterion that the researcher must accept every individual in the sampled quadrat.

> *Only samples generated by a random process will have known patterns that can be used in statistical methods* (Hayek & Buzas 1997).

Randomness of the sample unit was derived at the Maunganui Bluff site by using an altimeter. A decision was undertaken to sample a 4 m×5 m quadrat (20 $m^{2)}$ on the right hand side of an existing walking track (provides the only **safe** access along the bluff) at a distance of 3 metres and 90° from the track. Two criteria contributed to ensuring randomness:

1. The author had no personal prior knowledge of the track (never walked the track prior to sampling) or of the spatial position of the vegetation; so no personal bias influenced the decision to sample on a 50 metre altitudinal rise.
2. The altimeter had a ± 10 percent error ensuring that the site being sampled could not be calculated and fixed on a topographical map in advance.

The 50 metre altitudinal rise between sites was determined as suitable to obtain distinctly different environmental data and different co-existence of species i.e. the effect of salt laden winds and the moisture content of the soil should change over a 50 metre rise (though distinct micro – climatic conditions may cause this to be indistinct in the data). There should also have been a distinct temperature gradient from sea level to 467 m that would be reflected in the 50 metre sampled sites.

Quadrats were structurally set up using a prepared length of twine with pegs at 4 metre, 9 metre and 13 metre. The total length to form the rectangular quadrat was 18 m. A plastic right-angled triangle was used to ensure a 90° angle from one peg to the next. All trees, small trees, shrubs and lianas were counted so long as the stems touched or were within the quadrat. Seedlings were counted but not utilised in the study due to uncertainty over the eventual number of newly germinated seedlings that would survive to contribute to community function. A decision was made to discount all seedlings that were less than 10% of the height of mature trees within the quadrat. The survey of species from the eleven sites was carried out over two days in spring 1997.

6.2.3 Environmental data

The criteria for collecting environmental data were influenced by the distance to the site (a two hour drive) and the difficulty of the terrain (4 – 5 hours climbing and sampling to cover the eleven sites). A decision was made to sample all but the soil cores seasonally over a one year period from Autumn 1997 to summer 1997/1998. The summer 97/98 sample was not taken due to the author having a broken collarbone. The climb up the bluff was considered to be too risky and may have resulted in more permanent damage. Only environmental data that could be easily obtained (no expensive specialist equipment or equipment too heavy to easily carry) set the rationale for the dataset to be collected. The factors used to determine the environmental data to be collected are based on the model (Fig. 6.1) proposed by Woodward and Kelly (1997). Temperature limits define plant survival boundaries. Temperature within these boundaries influences the resource capture of light capture by photosynthesis, uptake of water and nutrients and shade tolerance. Woodward and Diament (1991) advocate integration of functional types (groups) with these environmental filters. Essentially, at all sites, all functional groups present in the locale have an equal opportunity to occur. The filtering is carried out by environmental factors.

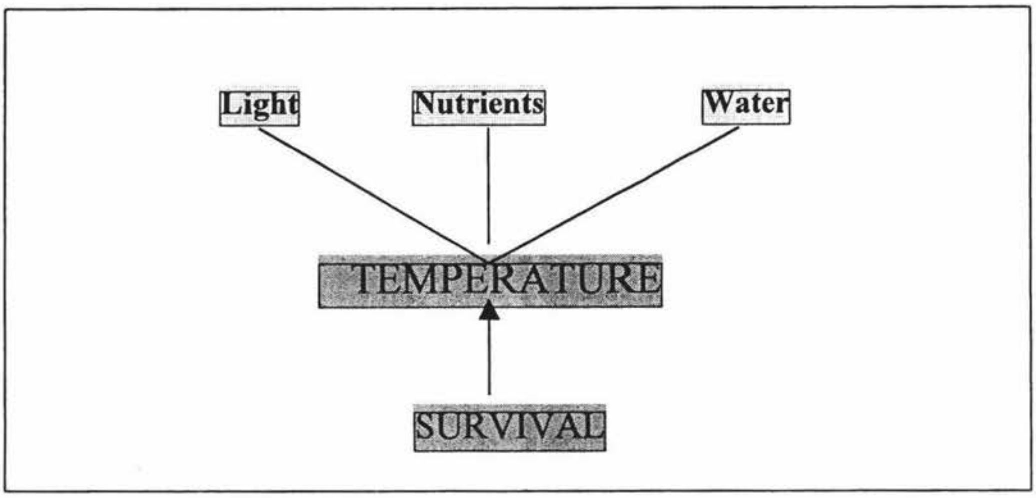


Fig 6.1 A general model for survival based on temperature which influences light, nutrient and water resource capture (Lee 1998; after Woodward & Kelly 1997).

The environmental factors sampled are as follows:

- Elevation – (see Chapter 6.2.2 for methodology). Elevation is an indirect measurement of precipitation (Velazquez 1994).
- Soil nutrient status - data was obtained by taking six core samples at random from a site and amalgamating the material. A proportion was then removed and sent to a soil-testing laboratory for analysis. This was repeated for the eleven sites (Table 6.1). The testing laboratory used Plant Root Simulator (PRS) technology to measure the ions of each nutrient available in the soil and is based on the exchange of ions between the soil and a synthetic resin. The technique is analogous to nutrient ion exchange between plant and soil (Saggar et al. 1990)
- Temperature – soil temperature reflects external air temperature without having to take into account the short-term fluctuations associated with air temperature data. Soil temperature is more consistent over time, lending itself to seasonal sampling (Table. 6.2). Six samples were taken at each site. The mean of these samples was the final result. The rate of change was calculated to determine if

there was a pattern of soil temperature change (Table 6.3). Even though the site temperatures changed seasonally, there was no real difference in the rate of change between autumn and winter. As there was no summer figure to compare spring to, autumn temperatures were accepted as representative of change between each site and were used in the ordination.

Table 6.1 **Soil analysis for all eleven Maunganui Bluff sampled sites.**

Site	pH	N	P	K	S	Ca	Mg	Na
A	6.30	3.80	3.70	5.70	8.00	50.00	45.40	288.00
B	7.30	3.00	5.90	4.70	4.00	72.00	33.10	241.00
C	6.50	3.80	1.00	5.70	2.80	62.00	44.10	221.00
D	6.50	1.70	1.30	3.60	7.00	64.00	37.70	209.00
E	6.50	1.50	0.40	4.60	4.00	52.00	38.70	201.00
F	6.50	1.60	1.40	4.70	13.00	46.00	39.60	226.00
G	6.00	1.60	0.40	9.10	2.80	49.00	30.30	82.00
H	6.00	1.30	0.40	5.30	6.00	56.00	27.50	98.00
I	5.80	0.90	0.40	8.20	5.00	34.00	23.80	59.00
J	5.80	2.50	0.40	5.80	2.80	59.00	26.20	48.00
K	5.40	0.90	0.70	6.00	9.00	46.00	33.80	182.00

Table 6.2 **Mean seasonal soil temperatures at each site**

Site	Autumn 97	Winter 97	Spring 97
A	15.68	14.42	18.88
B	15.5	14.83	18.13
C	14.65	14.10	18.2
D	14.84	13.94	16.22
E	14.8	14.21	15.3
F	14.63	13.98	15.1
G	12.45	11.24	16.26
H	10.45	10.10	15.7
I	8.41	7.62	20.9
J	6.55	6.1	18.8
K	7.65	6.4	18.15

Table 6.3 **Rates of change of temperature between sites over the seasons**

Site	Autumn 97	Winter 97	Spring 97
A - B	0.13	0.41	0.75
B - C	0.9	0.73	1.07
C - D	0.19	0.16	1.99
D - E	0.04	0.27	0.92
E - F	0.75	0.23	0.2
F - G	2.18	2.59	1.16
G - H	2.00	[illegible]	0.56
H - I	2.04	2.68	[illegible]
I - J	1.46	1.59	2.1
J - K	1.10	[illegible]	0.45

Table 6.4 **Percentage of total radiation (Watts m^{-2}) outside the canopy measured inside the canopy.**

Site	Autumn	Spring
A	7.73	0.75
B	10.48	1.13
C	87.1	1.5
D	7.14	1.38
E	30.41	0.5
F	45.71	0.88
G	47	1.63
H	35	5
I	24.62	27.5
J	20.51	5.25
K	14.17	32.5

- <u>Light levels</u> - The differential between the light levels outside and under the canopy was used to reflect the amount of leaf/stem area cover of the canopy. The technique lends itself to seasonal sampling since the differential is calculated at a point in time. The result should not be influenced by overhead conditions provided the inside and outside samples are taken at a close point in time. Measurements inside the canopy were taken as close as possible to the underside of the upper canopy (within the constraints of reach) and a second reading at ground level (Table 6.4). Six sets of readings were taken at each site and then meaned. The ratio of inside canopy light to outside canopy light became the data to be further analysed (Table 6.4). As the data indicates, the vagary of the cloud cover determines the amount of light entering the canopy at any point in time. The autumn 1997 measurements had the only consistent outside light levels. The other days spent data collecting at the bluff were plagued by winds and constantly changing light levels. Autumn light levels were chosen to represent the percentage light differential at each site for the statistical analysis.

- Soil Moisture – soil moisture reflects overall precipitation, modified by slope and soil type along with the organic matter content of soil. Taking soil moisture samples is suitable for seasonal collection of data to reflect seasonal variation in rainfall. Soil moisture was measured using a TDR. The TDR relies on measuring the current drop between two probes as current passes through the soil solution. Unfortunately, the majority of the sites are made up of unconsolidated basaltic rock with very shallow soils, which precluded the insertion of the probes to the required depth. Out of the eleven sites results from only three sites could be confidently used. Soil moisture sampling was therefore discarded from the survey.

6.3 Functional Groups

Fox and Brown (1993) introduced an assembly rule for functional groups of mammals that could also be used to predict pattern in any assemblage of plants (Weiher et al. 1998; Keddy 1992). The species pool for communities can be divided into a number of distinct functional groups. These functional groups will show an unusual tendency to be equally represented in any local assemblage (the probability is high that a species entering into the community is from a functional group not represented at the site but is represented in the locale). Functional groups do not reflect forbidden combinations of species, but only *favoured* or *unfavoured* states. These states equate to presence or absence tables when functional groups are constructed. Favored states have equal (or nearly equal) representation by each functional group and are predicted to occur more frequently than would be expected by chance. However, in regard to plant communities, Wilson and Roxburgh (1994) as well as Wilson and Whittaker (1995) have found little evidence to support this pattern.

Gotelli and Graves (1996) use the following example: if a species pool is composed of three functional groups, then a local three-species assemblage with all groups represented (1, 1, 1) would be a favoured state. A four-species assemblage with (2, 1, 1) would also represent a favoured state, because the mix of species is maximally even. In contrast, a three-species assemblage with a (0,1,2) mix would represent an unfavoured state, because there are no species from the first functional group but two species from the third group.

Competition for resources is thought to be responsible for the uniform frequencies of different functional groups (Wisheu & Keddy 1992). Different functional groups exploit resources in different ways that are presumed to promote coexistence. The availability of these resources is a function of the habitat (Cramer 1996). If resource limitation is severe, how can two or more species from the same functional group coexist? A superior competitor might be expected to exclude all other species within a functional group. However, competition for resources may not be the only determinant of local assemblages. Because many of the functional groups are composed of closely related species, historical processes such as allopathic speciation may also be responsible for the orderly composition of local assemblages; also, soil biota such as VAM fungi may influence the assemblage (Watkinson 1998). Whatever the role of interspecific interaction, phylogeny and history determine the mix of local species available for colonization (Cornell & Lawton 1992).

Functional groups by the nature of their assemblage (construction) may be more phylogenetically diverse and could include unrelated species that are united by common morphology and foraging strategy. Species in different functional groups may be aggregated by body size (e.g. tree, shrubs or grasses), which has been used as a convenient character to define functional groups (Fox & Kirkland 1992). Whatever criteria are used to define functional group membership, Fox and Brown (1993) consider that functional groups must be defined *a priori* and independently of the co-occurrence data.

6.3.1 PFT Construction

In reference to the theory in chapter 6.3, a decision was undertaken to construct Plant Functional Groups without *a priori* knowledge of the species sampled on the Maunganui Bluff sites. The full Maunganui Bluff species richness survey carried out by the Auckland Botanical Society was utilised to construct a computer database. The full dataset of 362 species (Common Name, Genus and Species was transcribed into Microsoft Access (1994), a relational database. Lifestyle attributes (preferred by this author over body size) and other traits were added to the form field for each species and the database was sorted into hierarchical order. Weiher et al. (1998) agree that while the PFT trait list chosen is not exhaustive and others would immediately suggest additions, they consider it important to look for pattern that can be immediately recognisable and easily obtained.

Due to the focused scope of the study, all non-native New Zealand species were excised from the database table. A further reduction left only woody angiosperms and gymnosperms (monocotyledons and dicotyledons) species still in the database. The final species count for constructing Plant Functional Groups was 108 (on attached cd-rom, Microsoft Access query – 'Trees and Shrubs'). From the literature (Brockie 1992; Dawson 1988; Dawson & Lucus 1996; Fisher et al. 1988; Metcalf 1987; Poole & Adams 1963; Salmon 1980; Smith-Dodsworth 1991; Webb et al. Undated) the following list of attributes was added (sample output, Table 6.5):

<u>Family</u>	to determine if specific families were over represented in the total species pool.
<u>Climate</u>	to trace the climatic origins of the family's gene pool.

Salt tolerance	tolerance or non-tolerance to salt spray would determine spatial positioning for species on the Bluff site.
Wind tolerance	wind tolerance would determine presence or absence at specific sites. May also point to co-existence with wind tolerant plants that will provide shelter.

Queries were then developed in Microsoft Access to construct the Functional Groups utilising the four climate zone attributes as the base line (Fig 6.2)

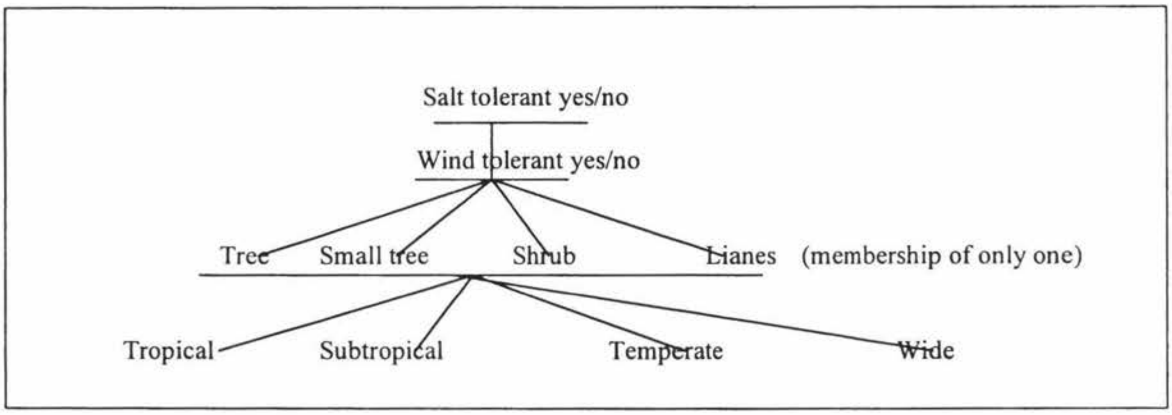


Fig 6.2. Hierarchical model showing the selection criteria for generating the 48 functional groups (Lee 1998).

The database generated 48 functional groupings, each of which contained some combination of taxonomic, lifestyle and physiological attributes. Within each functional group a presence and absence table was built from the species sampled at each site on the Bluff (Table 6.5). The 48 groups were generated again with a count of each species at each site within every functional group. All species that were not sampled at any of the sites (but were part of the original Bluff richness survey carried out by the Auckland Botanical Society) were removed from each functional group. Some functional groups had no sampled presence and were removed from the analysis.

The remaining groups were then compared for presence/absence at each site and were sorted into similar patterns (Table 6.6) to facilitate further reduction in the number of groups. Group keys for Table 6.6 are found in Table 6.7. These 'like' groups were then examined to determine if any one group accounted for all of the species present. If so, then these groups were amalgamated. After analysis of all functional groups at each site, the number of groups was reduced to 17. These 17 groups were then statistically analysed with the environmental data.

Table 6.5. **Sample of final table in Microsoft Access from which Functional Groups were generated (Lee 1998)**

GENUS	SPECIES	COMMON NAME	LIFESTYLE	TAXON - FAMILY	Na TOLERANT	WIND TOLERANT	GYMNO - ANGIOSPERM	CLIMATE ZONE
Ackama	rosifolia	makamaka	tree	Cunoniaceae	no	semi	dicot	sub
Agathis	australis	kauri	tree	Araucariaceae	no	yes	gymnosperm	trop
Alectryon	excelsus	titoki	small tree	Sapindaceae	no	semi	dicot	trop
Aristotelia	serrata	wineberry	small tree	Elaeocarpaceae	no	yes	dicot	trop
Beilschmiedia	tarairi	taraire	tree	Lauraceae	no	semi	dicot	trop
Beilschmiedia	tawa	tawa	tree	Lauraceae	no	semi	dicot	trop
Brachyglottis	repanda	rangiora	shrub	Asteraceae	yes	semi	dicot	wide
Carmichaelia	aligera	broom	small tree	Fabaceae	no	yes	dicot	wide
Carpodetus	serratus	putaputaweta	small tree	Escalloniaceae	no	semi	dicot	sub
Clematis	paniculata	clematis	liane	Ranunculaceae	no	no	dicot	temp
Clematis	cunninghamii	yellow clematis	liane	Ranunculaceae	no	no	dicot	temp
Coprosma	arborea	mamangi	small tree	Rubiaceae	no	yes	dicot	trop
Coprosma	areolata		shrub	Rubiaceae	no	yes	dicot	trop
Coprosma	crassifolia		shrub	Rubiaceae	yes	yes	dicot	trop
Coprosma	grandifolia	kanono	shrub	Rubiaceae	no	no	dicot	trop
Coprosma	lucida	karamu	shrub	Rubiaceae	yes	yes	dicot	trop

Table 6.6. Functional groups sorted by site and pattern into a reduced number of groups based on similarity of assemblage and presence of individual species (Lee 1998).

PFT Class	SITES PFT	E	A	D	C	F	I	B	J	G	K	H	COUNT	PFT GROUPS
tsm	2					P2	P2				P2	P2	4	16
tss	11		P11		P11		P11	P11		P11		P11	6	15
tsw	19		P19		P19		P19	P19	P19	P19	P19	P19	8	14
tsww	23		P23		P23	P23	P23	P23	P23	P23	P23	P23	9	13
wsm	6			P6	P6	P6	P6	P6	P6	P6	P6	P6	9	12
wt	5	P5			P5	P5			P5	P5	P5	P5	7	11
tlw	20			P20									1	9
tlww	24			P24									1	9
tsms	10											P10	2	6
tsmw	18											[illegible]	2	6
tsmww	22											[illegible]	2	6
tsmws	34											[illegible]	2	6
tsmwws	38											[illegible]	2	6
wsw	27										P27		1	17
wsws	43										P43		1	17
wsww	31			P31				P31			P31		3	5
ws	7			P7				P7			P7		3	5
wss	15			P15				P15			P15		3	5
wswws	47			P47				P47			P47		3	5
wsmwws	46											P46	4	8
wsms	14											P14	4	8
wsmws	42											P42	4	8
wts	13					P13			P13	P13	P13	P13	5	2
wtw	25					P25			P25	P25	P25	P25	5	2
wtww	29					P29			P29	P29	P29	P29	5	2
wtws	41					P41			P41	P41	P41	P41	5	2
wtwws	45					P45			P45	P45	P45	P45	5	2
tsws	35		P35		P35		[illegible]	P35	P35	[illegible]		P35	7	4
tswws	39		P39		P39		P39	P39	P39	P39		P39	7	4
wsmw	26			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	P26	P26	9	3
wsmww	30			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	P30	P30	P30	9	3
ttws	33	P33	P33	P33	P33		P33	P33	P33	P33	P33	P33	10	10
ttwws	37	P37	P37	P37	P37		P37	P37	P37	P37	P37	P37	10	10
tt	1	P1	P1	P1	P1	P1	P1	P1	P1	P1	P1	P1	11	1
tts	9	P9	P9	P9	P9	P9	P9	P9	P9	P9	P9	P9	11	1
ttw	17	P17	P17	P17	P17	P17	P17	P17	P17	P17	P17	P17	11	1
ttsww	21	P21	P21	P21	P21	P21	P21	P21	P21	P21	P21	P21	11	1
ts	3	P3	P3	P3	P3	P3	P3	P3	P3	P3	P3	P3	11	7
		8	12	16	16	16	21	22	23	24	25	30		

Table 6.7 **Definitions of keys for PFTs derived from Microsoft Access. The table was derived after the first sort – all groups having nil sampled members were excluded.**

KEY	DESCRIPTION
tsm	Tropical small tree
tss	Tropical shrub salt tolerant
tsw	Tropical shrub wind tolerant
tsww	Tropical shrub wind semi or fully wind tolerant
wsm	Wide small tree
wt	Wide tree
tlw	Tropical liana wind tolerant
tlww	Tropical liana semi or fully wind tolerant
tsms	Tropical small tree salt tolerant
tsmw	Tropical small tree wind tolerant
tsmww	Tropical small tree wind semi or fully tolerant
tsmws	Tropical small tree wind and salt tolerant
tsmwws	Tropical small tree wind semi or fully tolerant and salt tolerant
wsw	Wide shrub wind tolerant
wsws	Wide shrub wind and salt tolerant
wsww	Wide shrub wind semi or fully tolerant
ws	Wide shrub
wss	Wide shrub salt tolerant
wswws	Wide shrub wind semi or fully tolerant and salt tolerant
wsmwws	Wide small tree wind semi or fully tolerant and salt tolerant
wsms	Wide small tree salt tolerant
wsmws	Wide small tree wind and salt tolerant
wts	Wide tree salt tolerant
wtw	Wide tree wind tolerant
wtww	Wide tree wind semi or fully tolerant
wtws	Wide small tree wind and salt tolerant
wtwws	Wide tree wind semi or fully tolerant and salt tolerant
tsws	Tropical shrub wind and salt tolerant
tswws	Tropical shrub wind semi or fully tolerant
wsmw	Wide small tree wind tolerant
wsmww	Wide small tree wind semi or fully tolerant
ttws	Tropical tree wind and salt tolerant
ttwws	Tropical tree wind semi or fully tolerant and salt tolerant
tt	Tropical tree
tts	Tropical tree and salt tolerant
ttw	Tropical tree wind tolerant
ttsww	Tropical tree wind semi or fully tolerant and salt tolerant
ts	Tropical shrub

6.4 Statistical techniques

6.4.1 Introduction to the analysis

Three specific questions were statistically examined:

1. Would the derived functional groups show convergence over the bluff sites?

The richness and abundance of both species and PFTs at each site was transformed into a comparable index. The chosen index was the Evenness index derived from the Shannon Diversity index. The results were then graphed over the eleven sites. The evenness was used to determine if PFTs constructed from non numeric datasets would display adherence to the assembly rules (Chapter 6.3) over all the sites in the gradient analysis. Samuels and Drake (1997) suggest that functional group proportionality over a range of communities should converge.

2. Would the bluff gradient display broad vegetation scales usually associated with large gradients or would vegetation dynamics be determined by localised environmental conditions?

The hypothesis under test was that *PFT richness on the bluff gradient is determined by localised environmental gradients such as wind, salt saturation and nutrient deficiencies due to leaching,* as opposed to distinct vegetation changes associated with large altitudinal gradients. The literature suggests *that species richness decrease with altitude*, however, a 467m isocline next to an ameliorating body of water may not have enough climatic variation to exhibit a distinct vegetation trend. Detrended Correspondence Analysis (DCA) was used to determine the uncorrelated relationship between the environmental data and the functional groups. Microsoft Excel's correlation function was used to determine cross correlation of the environmental data. DCA was applied once again on the reduced dataset. The qualitative (Chapter 6.5.1) assessment of a traditional gradient was based on the Department of Lands and Surveys classifications (Table 5.1). The results of the DCA are in Chapter 6.5.4.

3. Can PFTs be used to discern potential keystoneness?

The presence of a functional group over all of the sampled sites would indicate that there is overlapping of that group through all realised niches. The isolation of a particular functional group at a site would indicate that there is no overlapping and may well indicate a functional group that is 'stuck' and may not be able to migrate. Either functional group would be a strong contender for further analysis to determine if some measurable attribute could be included in a long-term study to investigate environmental change. Both extremes could indicate a functional group that displays keystoneness. The former could indicate members that are important to a particular ecosystem function within all sites' communities. The latter may indicate a group whose members are 'stuck' in a marginal site and are unable to migrate. This aspect of general potential keystone groups was assessed using the site PFT map (Table 6.13) and the statistical methods of Dufrende and Legendre (1997).

6.4.2 Diversity indices

Diversity is more than just a count of the number of species present. Diversity incorporates richness, commonness and rarity. The term diversity is a simple measure of community characteristics that takes into account both abundance patterns and richness. A common methodology used is the Shannon Diversity index.

$$H' = -\sum_{i=1}^{S} p_i \ln(p_i)$$ where p_i is the proportion of the community that belongs to the i^{th} species

(Magurran 1988)

Shannon indices were generated for both species present and the functional groups present. The abundances for the functional groups were generated from the reduction of the original 48 groups to the final 17. For example, group 1 is made up of 4 subgroups, group 2 of 5 and group 17 of 10. Reducing both species and functional groups to Shannon indices allowed for a graphic display of diversity across the gradient and permitted comparison between the two methodologies. The technique was used to determine if *PFTs could be used to substitute for classic diversity analysis?*

An evenness graph was also constructed so that species and functional group evenness could be compared to see if the PFT methodology could be substituted for a similar species analysis. Evenness (E) is a measure of the equability or dominance at each site; whether species are more or less evenly represented. E is constrained between 0.0 and 1.0 where 1 represents a situation where all species are abundant (Magurran 1988). The index used is Pielou's (1969) ratio of the Shannon H' (observed diversity) to the maximum value of H' that could occur in a community.

6.4.3 Detrended Correspondence Analysis (DCA) – a multiple scaling technique

DCA is a multidimensional scaling technique. Multidimensional scaling is a general term for a set of multivariate techniques that allow relationships among a set of elements to be represented as inter-element distances in low dimension space (Manly 1994). The technique generates maps from a distance matrix that shows relationships between data. In the Maunganui Bluff analysis, a relationship between the functional group dataset and the environmental dataset was sought. The DCA statistic in the computer programme PC-ORD (McClune & Mefford 1997) produces tabulated data for three dimensions and can generate a graphical map in two dimensional space for any two combinations of the three dimensions (see Appendix I). The axis detrending of DCA yields a better scaling than other correspondence analyses (Hill & Gauch 1980; cited in Jobbagy et al. 1996). Others such as Oksanan (1988) say that that DCA removes meaningful data from the ordination plane and may decrease the stability of the solution (cited in Jobbagy 1996).

In consideration of the above, a decision was undertaken to check the relationships of the data in Microsoft Excel (1993) after the first analysis of the full dataset with PCORD (McClune & Mefford 1997) to determine if either meaningful data was removed during the DCA analysis or that uncorrelated data may be obscuring an important relationship. The ordination would be run again looking for significant variation in output.

6.4.5 Dufrene and Legendre indicator analysis

The methodology of Dufrene and Legendre (1997) allows for the calculation of indicator values using any hierarchical classification for any combination of sites.

$$\text{Bioindicator value} = \text{Specificity} \times \text{Fidelity}$$

$$\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100; \quad \textit{where}$$

Specificity is the uniqueness of species to the site group

$$A_{ij} = \text{Nindividuals}_{ij}/\text{Nindividuals}; \quad \textit{and}$$

Fidelity is the abundance and spread of species within the sites

$$B_{ij} = \text{Nsites}_{ij}/\text{Nsites}$$

(see appendix 1 for a full description from the statistical package PC-ORD)

A high indicator value indicates that the species is present only in that functional group and that group has low occurrence over the gradient. Just as important are species that occur more frequently in a particular group of sites than in any other site groups.

6.5 Results and Discussion

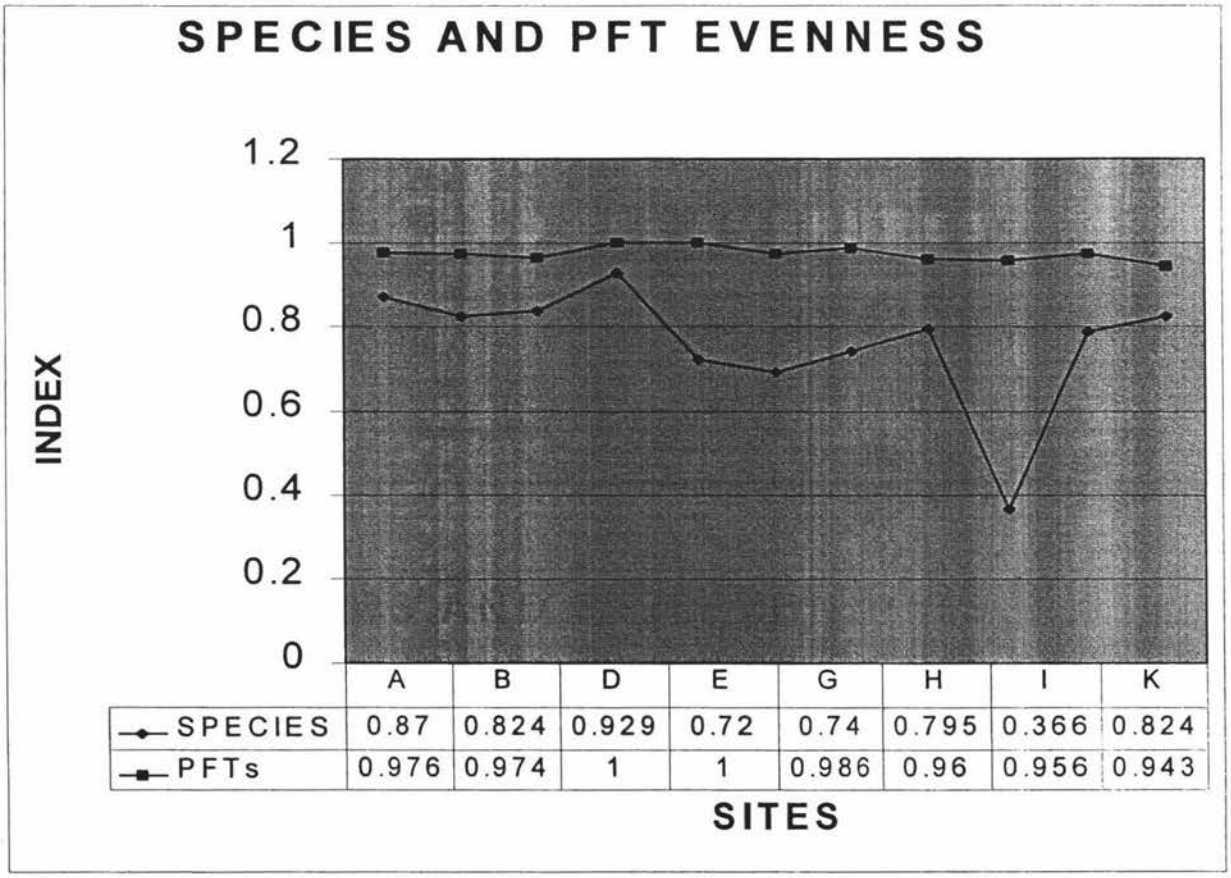
6.5.1 Diversity

The results (Table 6.8) indicate that there was a high percentage of similarity between the two assemblages (species > PFT). When graphed (Fig. 6.3), this similarity became discernable over all of the sites except for site I. This is an unexpected result. It was expected sites with abundance heavily related to low species richness would equate to low PFT richness. That is, there would be 1 or 2 PFTs with low abundance and 1 PFT with high abundance to give a similar index. However, this is not an anomaly. Given another set of circumstances, the reverse could be true. A site could contain only one species with very low abundance, but the functional groups richness and abundance could be high, as that particular species by default can be a member of more than one PFT at any point in space or time. This factor is a precept in the construction of PFTs. While PFT evenness may not be a substitute for species evenness, the methodology appears to be satisfactory for deriving PFT evenness and interpretation of the richness and abundance of PFTs at each site based on the total available pool of PFTs.

An approach that discerns regularities in community development focuses on pattern derived from coarse scale attributes of functional groups (Fox 1987; Wilson & Roxborough 1994; Wilson & Whittaker 1995; see Chapter 6.3). The non-numerical attributes used to construct the PFTs fit these criteria. Fox's (1997) assembly rule states that *community development proceeds while maintaining nearly equal representation of functional groups*. Though only a snapshot in time, the evenness graph (Fig 6.3) indicates nearly equal representation of functional groups at each site from the total available pool. These patterns apply generally and are not intended to be a substitute for a individual community analysis (Samuels & Drake 1997).

Table 6.8 **Evenness index for each site (species and PFT) based on Shannon H′.**

SITES	SPECIES	PFT
A	0.87	0.976
B	0.824	0.974
C	0.839	0.964
D	0.929	1
E	0.72	1
F	0.693	0.975
G	0.74	0.986
H	0.795	0.96
I	0.366	0.956
J	0.787	0.973
K	0.824	0.943



	A	B	D	E	G	H	I	K
SPECIES	0.87	0.824	0.929	0.72	0.74	0.795	0.366	0.824
PFTs	0.976	0.974	1	1	0.986	0.96	0.956	0.943

Fig 6.3. Graph of evenness indices (species vs. PFT) across the altitudinal gradient at each sampled site.

6.5.2 Vegetation dynamics

Observation - The distinct vegetation types found at each site (Table 5.1) can in part be described by knowledge of the locale rather than by statistical analysis. From sea level to 150m the track meanders with only a slight gradient increase over approximately a kilometre. The Treeland (refer Table 5.1) at site B (Photograph 5.6) is an anomaly in a vast expanse of grasses and shrubby Coprosma species. The presence of the Treeland class of plants is strongly associated with the presence of a large pohutukawa, which is providing localised protection from salt and wind, as well as decreased light levels for the broadleaf understory. In the overall biogeography of the isocline there is a distinct graduation from shrubland to forest marked by a transitionary belt that still includes shrubland species but has a wider diversity of species. This belt marks the appearance of nikau palms and cabbage trees (Photograph 5.7).

From 200 metres to 400 metres, there is a distinct forest belt before a return to grassland/shrubland (refer Table 5.1; Photograph 5.5 and 5.8). The ready access to the first 150m and the effects of man on these sites are possible causes for the vegetation type – certainly the predominance of grass species (non-endemic) can be attributed to burning and grazing as the Aranga area (Photograph5.4) was colonised. Newly introduced grass species were probably carried on to this area by trampers and tourists since the reserve was formed and fenced off to stock.

The 400 metre to 467 metre section of the isocline was burned and felled, post 1945. A fire destroyed the radar trig. Telecom in recent times has built a relay station on the site. The area has panoramic views in all directions and trampers/tourists move freely over the whole of the pinnacle, thus trampling any newly germinating seedlings of native plants. Telecom vehicles and workers have access to the site from a neighbouring farm (Photograph 5.4); obviously a certain amount of weed/grass seed is transported in this manner.

The distinct zonation does follow a classic gradient, often correlated to altitude. However, the altitude of the zone changes and in particular the change back to grassland/shrubland at the 400m mark indicates that the primary factors in the derivation of the present vegetation were fire, grazing and the influence of man. The question this poses is *how much influence do environmental effects such as wind, salt and nutrient status have in maintaining or altering these community assemblages?*

Ordination – In general, ordination is the ordering of objects along axes according to similarities. The major objective is to achieve an effective data reduction, expressing many-dimensional relationships in a smaller number of dimensions. This amounts to extracting the strongest correlation structure in the data (using correlation in the broad sense). The correlation structure is used to position objects in the ordination space, i.e. create a map. Objects close in the ordination space are generally more similar than objects distant in the ordination space (McCune &.Mefford 1997).

There was a concern that the environmental causes were not specific to the relationships. Altitude may well be accounting for everything else and the other environmental data was unfairly weighting the eigenvalues, so a true picture of the each axis was not being reflected. A decision was undertaken to carry out a correlation analysis (Microsoft Excel) on the environmental data to determine what categories of data could be excluded (results Table 6.9).

Correlation analysis measures the linear relationship between two datasets that are scaled to give a coefficient independent on the unit of measurement. The population correlation calculation returns the covariance of two data sets divided by the product of their standard deviations. The Correlation tool determines whether large values of one set are linearly associated with large values of the other (positive correlation), whether small values of one set are linearly associated with large values of the other (negative correlation), or whether values in both sets are unrelated linearly, correlation near zero (Microsoft 1993). The relationship was tested for significance using Pearsons' product moment correlation coefficient (PMCC). Using statistical tables for critical values of r^* for eleven sites, any value over 0.685 is significant at the .02 level. It can be seen that there is difficulty in separating out pH, nitrate, phosphorus, magnesium, sodium and temperature from altitude. All have a negative correlation with altitude, i.e. as altitude increases all these environmental factors decrease.

A correlation between causes and effects was also undertaken using Excel's correlation function (Microsoft 1993). Again $r^* > 0.685$ is significant at the 0.02 level, which indicates a direct relationship. Relationships clearly exist between temperature and PFT 7. Clearly, this relationship relates to coldness, as the relationship is negative. Also, PFT13 and PFT 14 have a relationship with potassium (K). The relationship is positive. PFT 12 has a relationship with sodium (Na).

The relationships in Excel (Microsoft 1993) are pair-wise and there is no taking into account where the environmental (causes) and PFT (effects) are mapped with regards to sites. In order to determine the relationship between the environmental data and the functional groups at each of the sites an analysis was undertaken using the DCA ordination function within the statistical package PCORD (McCune &.Mefford 1997). The results of this analysis are shown graphically in Fig 6.4.

Table 6.9 **Cross-correlation of environmental factors to determine where substitution is occuring and to determine which factors are significant. Key: Alt = Altitude, Temp = Temperature, L low = Lower canopy light levels, L up = Upper canopy light levels, Na = Sodium, Mg = Magnesium, Ca = Calcium, S = Sulpher, K = Potassium, N = Nitrogen, pH = concentration of Hydrogen ion.**

	Alt	**Temp**	**L low**	**L up**	**Na**	**Mg**	**Ca**	**S**	**K**	**P**	**N**	**pH**
pH	**-.8000**	**.8213**	-.4069	.0466	.6182	.4479	.6562	-.0723	-.5218	**.7178**	.5128	1.00
N	**-.7652**	.4962	-.4120	.2065	.5276	.5924	.5465	-.2558	-.2099	.5810	1.00	
P	**-.7328**	.5229	-.2872	-.3739	.6353	.3198	.5072	.0737	-.3197	1.00		
K	.4400	-.4338	.3004	.2325	-.6072	-.4709	-.5880	-.3433	1.00			
S	-.0007	.1395	-.2619	-.2221	.4247	.3181	-.3478	1.00				
Ca	-.5337	.3936	-.4487	-.0198	.3383	.2322	1.00					
Mg	**-.7827**	**.7762**	-.5999	.2260	**.8930**	1.00						
Na	**-.8466**	**.7941**	-.5497	-.0717	1.00							
L up	-.0043	.1552	-.3344	1.00								
L low	.5634	-.6386	1.00									
Temp	**-.8952**	1.00										
Alt	1.00											

Table 6.10 **Cross-correlation of Causes and Effects to determine major significance.**
Key: P = PFT = Plant Functional Type.

	pH	N	P	K	S	Ca	Mg	Na	Light Up	Light Low	Temp	Altitude
p1	-.2616	-.1956	-.0434	.4921	-.3511	.1280	-.5302	-.4938	-.0355	-.0539	-.3869	.3794
p2	-.5559	-.4280	-.4309	.2489	.2588	-.2236	-.4092	-.4831	.1008	-.0603	-.5472	**.6773**
p3	-.3098	-.1787	-.2956	.4542	-.3161	.0909	**-.6066**	**-.6912**	.1964	.0639	-.5319	.5432
p4	-.1095	.5582	.1077	.4538	-.5029	-.0321	-.1601	-.2750	.2011	.1871	-.2172	-.0705
p5	.2059	-.1137	.4288	-.3998	.1629	.4328	.0249	.3287	-.5267	-.1204	.0471	-.1610
p6	-.3258	-.4446	-.2953	.3045	-.0548	-.4093	-.6119	-.5427	-.0037	.3044	-.4153	.4623
p7	**-.6586**	-.0612	-.2720	.3486	-.0866	-.2053	-.4532	-.4881	.1167	.3145	**-.8265**	**.6078**
p8	.0600	.0340	.1439	.2284	-.4840	.4076	-.5846	-.4961	-.0584	-.0322	-.2663	.2135
p9	.1713	-.1108	-.0290	-.4481	.1187	.3294	.1450	.1630	-.3205	-.2365	.2472	-.1955
p10	-.4820	-.2750	-.5098	-.0442	.1041	-.0433	-.3358	-.4528	.2208	.0388	-.5619	**.6325**
p11	-.4945	-.2394	-.5127	-.0217	.1120	-.0701	-.2815	-.4239	.2265	.1116	-.5764	**.6338**
p12	-.3098	-.1787	-.2956	.4542	-.3161	.0909	-.6066	**-.6912**	.1964	.0639	-.5319	.5432
p13	-.3699	.2122	-.0746	**.7731**	-.2709	-.4411	-.3160	-.4315	.2474	.2917	-.4018	.2265
p14	-.3582	.1871	-.1818	**.7546**	-.3873	-.2460	-.3908	-.5470	.4603	.1832	-.4751	.3457
p15	-.1095	.5582	.1077	.4538	-.5029	-.0321	-.1601	-.2750	.2011	.1871	-.2172	-.0705
p16	-.4222	-.5855	-.3273	.0619	.4419	-.4207	-.4159	-.3191	.0280	.0234	-.4216	.5568
p17	-.5434	-.3607	-.1418	.0490	.3259	-.2428	-.0348	.0540	-.2219	.1180	-.4516	.3663

In Fig 6.4, axis 1 describes the greatest variation in the data, in this case 63 percent (Table 6.11). The second axis explains 32 percent of the variation percent (Table 6.11). Fig 6.4 is taken to be a three-dimensional map with only two dimensions showing (the eigenvalues of the first two account for approximately 95% of the variation). The third dimension explains the remaining 5% and is sufficiently small not to require further discussion (see Table 6.11). The first axis is almost exclusively associated with potassium abundance. The axis represents potassium levels from high to low and from Fig 6.4, it can be seen that site D has particularly low potassium levels. PFT 9 (strongly) and PFT 5 are associated with this low level of potassium. Very little else influences this grouping.

The second axis is a contrast between altitude and phosphorus and nitrogen level. PFT 17, PFT 16, PFT 10, PFT 11, PFT 2 and sites E, F, H and K contrast high altitude with low phosphorus and nitrogen. PFT 17 does have a moderate relationship with potassium. PFT 14, PFT 5, PFT 13, PFT 8, PFT 4, PFT15 and sites I, B and A contrast low altitude with high levels of phosphorus and nitrogen. PFT 6, PFT 7 and sites G, and C are of approximately equal low values of altitude and the contrasting nitrogen and phosphorus. Potassium (K) is a very strong regulator of where some functional groups are found on the bluff.

The results are consistent with expectation. The altitudinal gradient probably accounts for all the major environmental effects, sodium levels from salt-water spray, temperature changes as altitude increases, and the majority of nutrient changes between sites. Sodium is a matter of physical criteria, the strength of the winds and the exposure of the sites where measurement took place. The remaining factors that altitude accounts for can probably be attributed to changing precipitation and levels of leaching which have been shown to be strongly correlated to altitude (Velazquez 1994). At the Maunganui Bluff site, the analysis only highlights potassium (K) as a strong influence on some localised vegetation structure. The way to test whether PFT 9 is influenced by potassium is to set up a trial where potassium (K) levels are manipulated and all other environmental controls are constant, then assess productivity against that of a control group.

The gradient analysis supports the theory that altitude can account for the majority of influences in vegetation structure on an isocline. There is some local variation due to potassium (K) at the Bluff site, based on the analysis, other than potassium (K) there is no obvious factor for influencing vegetation structure. It must be assumed that since the altitude / potassium relationship is weak in most cases then the major determinant of community structure is by default, competition for limited resources. Resources may be limited in summer by lack of precipitation and during winter by the amount of leaching, probably influenced by the grade of the slopes, and where sites are positioned.

Table 6.11 **Eigenvalues of the three axes (No downweighting and no rescaling) in the relationship analysis (PCORD, DCA ordination).**

Axis	Eigenvalue
1	0.264205
2	0.131326
3	0.021823

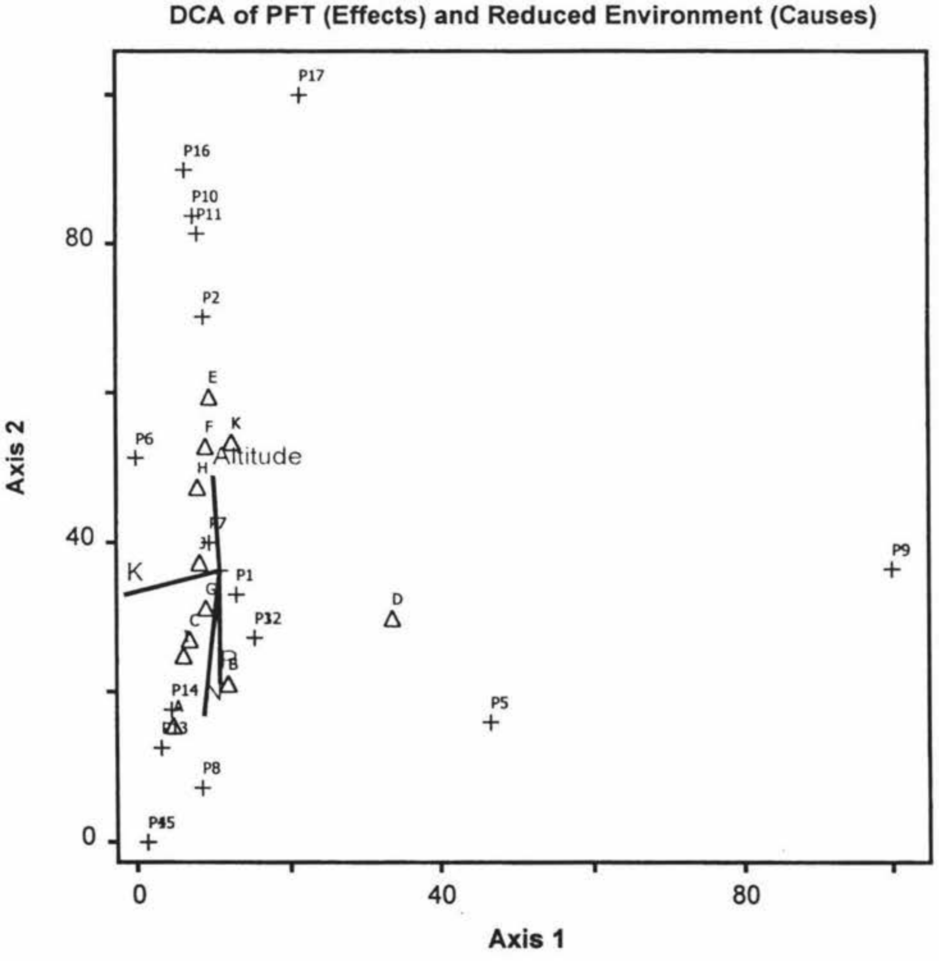


Fig 6.4 Detrended Component Analysis of the PFTs (Effects) and the site environment dataset (causes).

6.5.3 Group analysis – assemblage and keystoneness

The initial step in determining keystoneness was to perform a cluster analysis on the PFTs. The clustering was based on the site classes (Table 5.1) as these give a broad index of the vegetation type at each site. These classes were given a numeric ranking based only on the class. The purpose was to discern whether a statistical clustering of the PFTs fitted the Landcare vegetation classes. The rankings were:

1 Shrubland
2 Forest
3 Treeland
4 Grassland

The results (Fig 6.5) indicated that there was close matching to the clustering of the groups at each site to the site vegetation classes. The exception was site K (shrubland), which the clustering indicated, had more similarity in PFT makeup to Site J, the grasslands.

The methodology utilising vegetation classes as the hierarchical ranking system correlates well with the Landcare class assessment. The Landcare vegetation rankings were defined for the general localised area and may not reflect the randomly selected sampled sites. In order to utilise the ranking system for the Indicator Species Analysis, there was a need to change the ranking of only one site to match the sampled area. After deconstructing the PFTs present at this site to determine species present, Site J's ranking was changed to a Shrubland structural class.

```
                  Distance (Objective Function)
    2.500        26.011        49.523         73.034        96.545
    |-------+-------+-------+-------+-------+-------+-------+-------+
                Information remaining (%)
   100.000       75.000        50.000         25.000         .000
    |-------+-------+-------+-------+-------+-------+-------+-------+
A    ---|--------------|
C    |--|              |-------------------|
I    |                 |                   |
B    --------|---------|                   |------------------|
G    --------|                             |                  |
D   -|-------------------------------------|                  |
E   -|                                                        |
F    -----|-----|                                             |
H    -----|     |------------|                                |
K    -----------|            |--------------------------------|
J   -------------------------|
```

Fig 6.5 Cluster analysis of PFTs based on vegetation classes. Dendrogram produced with PCORD.

Dufrene and Legendre's (1997) methodology of selecting keystoneness was then undertaken using the ecology statistical package, PCORD (McCune and Mefford 1997; see Appendix I for details of the computer package). A subjective analysis was undertaken in the first instance (using Table 6.13 as a gradient map for PFT richness) to give a benchmark for comparison with the results of Dufrene and Legendre's (1997) methodology. The subjective analysis highlighted PFT 17, PFT 9, PFT 5 and PFT 6 as the most likely candidates to contain either a species that may be an indicator or a group of species that maybe 'stuck' in a site and unable to migrate because no other similar sites are available. The results of the Dufrene and Legendre's Keystone analysis (Table 6.12) fit well with this primary subjective appraisal. The variation at higher indicator levels is PFT 2, which did not appear to be significant in the primary subject appraisal.

While Dufrene and Legendre's original methodology was carried out using species, there does not appear to be any restriction to grouping prior to analysis. As stated earlier (Chapter 6.1), the value of the methodology is the ability to calculate values independent of other groups within the sites assemblage.

Table 6.12 Indicator values for PFTs (* proportion of randomized trials with indicator value equal to or exceeding the observed indicator value).

Column	Value (IV)	Mean	S.Dev	p *
P1	50.0	40.9	4.47	.034
P2	24.2	41	15.14	.832
P3	39.6	43.4	7.65	.730
P4	56.3	42.3	12.27	.163
P5	25.6	33.3	16.50	.712
P6	19.7	31.7	16.19	.833
P7	50	40.9	4.88	.025
P8	67.8	36.2	17.41	.093
P9	25.6	34.7	17.45	.721
P10	41.7	43.6	10.29	.572
P11	43.8	42.8	12.51	.457
P12	39.6	43.4	7.65	.730
P13	44.4	43.9	8.03	.521
P14	44.4	43.9	8.03	.521
P15	56.3	42.3	12.27	.163
P16	39.5	36.7	17.48	.307
P17	20.0	27.7	11.34	.999

The assembly rule concerning functional groups (Chapter 6.5.1) only takes into account heterogeneity of the total assemblage across all sites from the available functional group pool. This analysis provides an index based on the value of that functional group out of the pool of functional groups at each site, over all sites. The maximum indicator value not only identifies PFTs with the highest indicator values but also the level for which it is most representative (McGeoch & Chown

1998). The results (Table 6.12) of the analysis highlights the following PFTs, in descending order, as worthy of follow up investigation, PFT 17, PFT 6, PFT 2 and at the next level PFT 12, PFT 3 and PFT 5. When the first three PFTs ($p^* > .800$) were investigated at the species level, each of the PFTs was represented by only 1 species. A research-based study was carried out on the member from each group (the traits of the group are found in Table 6.13 and the key to these traits are in Table 6.7) to determine if any characteristics were appropriate for further study.

Haloragis erecta (shrubby haloragis), the sole representative for PFT 17 is a member of the family, Haloragaceae. This is an ancient family from the Cretaceous period (Dawson 1988). *Haloragis erecta* appears to be the only member still found in New Zealand, though the family is still well represented in Australia. *Haloragis erecta* is a herbaceous plant that is found on coastal sites, from sea level to approximately 120 metres (Watson and Dallwitz 1998), and tolerates wet conditions. There does appear to be a need for some recognition to be given to the altitude factor, as from this researchers experience there was not an indication of waterlogging at site K during any of the seasonal visits. The appearance of *Haloragis erecta* at this altitude may be associated with all high coastal sites in Northland. Without further study or a comparative site no hard evidence exist to categorically state that this plant is 'stuck' due to some very localised factor. Despite this, *Haloragis erecta* does appear to be a plant to carry out further studies on and may exhibit some keystoneness in relation to the edaphic factors at this site.

The other two functional groups were PFT 6 and PFT 2. Each contained a very common plant of lowland forests. PFT 6 has *Pseudopanax aboreus* and PFT 2, *Hoheria populnea*. These two plants, while common in lowland forests, are species that appear very early in the successional process. The presence of both species in the shrubland sites indicates that canopy development is taking place (Dawson 1988). This successional process is very common after fire, and the presence of *Pseudopanax aboreus* and *Hoheria populnea* indicate that a state change is in progress, from the scrubby primary shrub and tree vegetation (manuka and kanuka) after fire to the establishment of lowland forest. When these broad-leaved plants form a canopy the bracken, manuka and kanuka gradually die out as light levels fall. The podocarp conifers then establish (Dawson 1988).

Small newly establishing *Hoheria populnea* and *Pseudopanax aboreus* could be monitored to determine if the sites were progressing along a recognised successional pathway. While not exactly in the category of keystone species, they would certainly be suitable to determine the effects of expected storms. If the upper canopy of manuka / kanuka and the shelter from perching pohutukawas was damaged, then the progression to broadleaf podocarp forest would be inhibited.

Table 6.13 **Structural classes of each site based on Landcare's rankings and the general assessment by Forester (1997). The table is also a map of the positions of PFTs across all sites.**

Sites	E	A	D	C	F	I	B	J	G	K	H		
PFT Class	Forest	Shrubland	Forest	Shrubland	Forest	shrubland	Treeland	Grassland	Treeland	Shrubland	Forest	Richness	PFT
ttsww	P1	P1	P1	P1	P1	P1	P1	P1	P1	P1	P1	11	1
wtwws					P2			P2	P2	P2	P2	5	2
wsmww			P3	P3	P3	P3	P3	P3	P3	P3	P3	9	3
tswws		P4		P4		P4	P4	P4	P4	P4	P4	7	4
wsww			P5				P5			P5		3	5
tsmwws						P6					P6	2	6
ts	P7	P7	P7	P7	P7	P7	P7	P7	P7	P7	P7	11	7
wsmws							P8	P8	P8		P8	4	8
tlw		P9	P9				P9					3	9
ttwws	P10	P10	P10	P10	P10	P10	P10	P10	P10	P10	P10	10	10
wt	P11			P11	P11			P11	P11	P11	P11	7	11
wsm			P12	P12	P12	P12	P12	P12	P12	P12	P12	9	12
tsww		P13		P13	P13	P13	P13	P13	P13	P13	P13	9	13
tsw		P14		P14		P14	P14	P14	P14	P14	P14	8	14
tss		P15		P15		P15	P15		P15		P15	6	15
tsm					P16	P16				P16	P16	4	16
wsws										P17		1	17

Conclusions

While there are many inconsistencies arising from work carried out by scientists, there does appear to be a trend concerning plant responses towards climate change. This response will be an increased photosynthetic rate in C_3 plants due to the increased availability of CO_2 within the stomata - the constraint will be other limiting factors such as temperature, and nutrient availability. It can be concluded that if the increased photosynthetic rate response to CO_2 occurs, there will be an advantage for C_3 crops over C_4 weeds in areas where C_4 weeds have summer dominance over C_3 weeds. Consequently C_4 crops will be disadvantaged by increased growth of C_3 weeds. Some plants will utilise increased photosynthates for increased growth, though experimentation has shown that after an initial enhanced growth period, growth rates return to the level prior to the doubling of CO_2. However, there will be an average increase in biomass, attributed to partitioning of photosynthate to non-structural carbohydrates.

There are discrepancies between the results of small-scale experiments extrapolated to large natural communities and large-scale experiments, such as Free Air CO_2 Enhancement. These discrepancies can be attributed mostly to the difference in complexity between the different plant communities. Small-scale experiments are usually carried out in very controlled circumstances, so that results can be replicated. In natural communities, environmental and competitive fluctuations vary the amount of resources available to individual plants, thus varying the response of plants to both temperature and CO_2.

Availability of nitrogen appears to be the major limitation in most biomes for plant communities not maximising increased CO_2. Nutrient poor soils promote nutrient poor litter. This process of recycling between plant - soil - plant degrades, through each recycling as the C:N ratio increases. Nutrient rich soils - not those enhanced by fertiliser additions or those on newly formed soils - will also degrade over time, as the ratio of C:N increases. This will result in increased turnover rates, making nutrients available for successive generations and an increase in stress tolerator plants as nutrient supply becomes a limiting factor. Nitrogen fixing trees will have a competitive advantage by being able to maximise CO_2 fertilisation.

The main area of study for the future appears to be towards large-scale models and experiments that might indicate the extent that enhanced CO_2 and temperature will affect growth, development and cycling within natural plant communities. It may well be that there is no simple answer. Community and ecosystem interactions between biota and with environmental factors may be so complex that each system will show a varying response. Experimentation and modeling by scientists may only ever show trends. Complex systems may not have simple rules governing responses to CO_2, temperature and nutrient availability.

The implications of $C0_2$ enrichment on growth and yield of trees and shrubs within natural forests are still unclear. Laboratory studies on growth rates and yield of plants grown in elevated $C0_2$ environments have documented increased rates of photosynthesis, lowered plant water use requirements, increased carbon sequestration. Increased soil microbial activity results in higher rates of nitrogen fixation, thereby stimulating growth. However in a natural ecosystem, where animals graze on plants, disease organisms cause damage and tree death, and plants compete for available light, water and nutrients, there are serious doubts that production would actually increase. In addition, higher growth and yield could be offset by higher losses due to fire, insects and disease.

To date, little work has been done to test the effects of higher $C0_2$ concentrations on forests or other natural plant communities over extended time frames. Therefore the net effects of climate change on forest growth and yield are uncertain. When temperature and rainfall patterns change, the ranges of both animal and plant species change. As the Earth warms, species tend to shift their distributions toward higher latitudes and altitudes. For each 10°C of warming, tree ranges in the Northern Hemisphere have the potential to expand 100 kilometres northward while the southern boundaries retreat. There is ample evidence in the fossil record that plants have undergone significant range shifts in response to changing climates. Shifts in the ranges of tree species could be important for several reasons. First, there are indications that climate could change faster than some tree species can respond through migration. Second, new sites may not be edaphically suitable for the migration of species.

Shifts in the natural ranges of animals and plants will take place in response to the requirements of individual species and not necessarily the ecosystem as a whole. Therefore some realignment of species associations can be expected should the climate change. Species may shift altitudinally as well as latitudinally. If the climate warms as predicted, species will shift upwards. Generally a short increase in altitude corresponds to a major shift in latitude. Because mountain peaks are smaller than the bases, as species shift upward in response to warming, they typically occupy smaller areas, have smaller populations and may become more vulnerable to genetic and environmental pressures. This could affect the distribution and abundance of endemic species whose natural ranges are already confined to high elevations.

Increased climatic anomalies are predicted to occur as part of climate change. A higher incidence of droughts, storms, frosts or periods of excess rainfall will put additional stresses on trees and forests making them more susceptible to attack by pests and disease. Episodes of forest decline may also increase. These are the result of a complex interaction of forests with climate, site, pests and disease and, in many cases, human activities

As the structure, composition and biomass of forests respond to changing climate, so will the behaviour of fire. Some expected changes include increases in the frequency and severity of fires and a lengthening of fire seasons in areas which are already prone to fire events. Droughts can drastically change the fuel conditions and flammability of the vegetation. If precipitation decreases then drought episodes will increase causing forest vegetation to shed leaves progressively as stress increases. In addition, the moisture content of surface fuels is lowered; while fallen woody material and loosely packed leaf litter contributes to the build-up and spread of surface fires. One of the more uncertain effects of predicted climate change is the possibility of an increased frequency and intensity of tropical storms. This would increase the levels of combustible fuels. Additional fuel accumulation resulting from the direct effects of tropical storms would also increase the hazard of fire.

In general, plant ecologists believe that plant species with broad geographic ranges and many populations will be the most likely to survive climate change. Rare or geographically restricted species would be at greater risk of extinction. This is especially true of species restricted to high elevation zones, which would ultimately be unable to shift their ranges further upslope in response to a warmer climate. Other ecologists argue that the risk of extinction of plant species and resultant loss of biodiversity is minimal because plants possess genetic variation that allows them to adapt to changing environmental conditions. Genetic variation is a prerequisite for evolution and a powerful mechanism that allows both animals and plants to change and adapt.

An ecosystem becomes more simplistic due to habitat restructuring through human impact. There may be a loss in some functional properties. Evidence suggests that redundancy will occur and that processes will continue either through invasion of new species (niche filling) or by increased numbers of another member species with the same functional attributes. However, there is still no real hard and fast evidence to suggest that stability of ecosystems especially in regard to richness and abundance can be maintained under climate change or that new interactions at the species level will not interfere with ecosystem functioning. Analysis of a plant community is dependent on the number of factors measured, the spatial size of the community and the point in time that the measurements take place. In a given location, higher temperatures could result in more generations of insect pests per year, thus increasing their destructive potential. This is especially true for those insects that already have more than one generation a year.

There is a general trend among ecologist to accept that species richness of communities increases productivity and stability. This richness provides either resistance or resilience to change. However, species-rich communities may do better, not because of the number of species in itself, but merely because they contain representatives of a few key functional groups. Recent studies carried out by Tilman et al. (1997) and Naeem et al. (1998) have determined that community productivity and stability are enhanced with the addition of functional groups, not increased species numbers within functional groups. The assembly rule for functional groups tends to support their findings. Functional group richness in a local area, even with a disparity of niches, tends to converge. Sites with low species richness can have high functional group richness. On Maunganui Bluff, increased species numbers in any functional group may result in very little change to the way the group interfaces with ecosystem functions. The addition of a functional group that is not present can have a large effect on these ecosystem processes. A functional group containing a nitrogen fixing plant will affect overall productivity. Hooper and Vitousek (1997) confirm that the type of interaction with functional processes determines the importance of the group to the ecosystem. Hooper and Vitousek (1997) say that the type of group is more important than the number of groups. Within these groups, there are probably key species.

The number of plant functions to be incorporated into the PFT should be determined by the model, which represents the criteria under analysis. This may appear to be defeatist when considering that PFTs are supposed to reduce complexity by allowing a group response to replace responses at a species level. The purpose of comparative studies is to allow one or more species to be selected and monitored as (an) overall representative(s) of a large number of functional types. This one species then becomes the representative of the much larger group and the methodology fulfils the criteria of decreasing complexity at the species level. Whether a one attribute or multi-attribute PFT is constructed is only constrained or required depending on the model under study.

The research was carried out to determine the effectiveness of functional groups in diversity analysis and the identification of possible keystoneness. The scope of the study was not intended to investigate, to any depth, individual species to correlate the importance of the members of functional groups within communities. However, three species emerged as being potential keystone species. Each came from a one species group (this species by way of reduction of the original forty-eight groups to seventeen groups represented higher numbers of species), resulting from the keystone statistical analysis (group assemblage) of Dufrene and Legendre. Of these, *Haloragis erecta* appears to have the most potential to monitor the effects of environmental change, as spatially, it is well past its altitudinal limits. Both, *Pseudopanax aboreus* and *Hoheria populnea*, from the other two PFTs, appear to represent natural change in the successional process from shrubland to lowland forest.

While no absolute keystone species or groups have emerged from the analysis, the study has confirmed several natural ecosystem processes, without making ecological judgements *a priori,* based on species sampled. The technique, using trait-developed functional groups generated by computer, may tend to remove bias from any ecological analysis. Based on the data collected and the construction method for PFTs, the study has confirmed that at a point in space and time, functional groups are conducive to diversity analysis and possible identification of keystone groups or keystone species. One can argue the value of the group assemblage analyses, but the study has indicated that more detailed study be carried out using a larger number of replicates.

The Maunganui Bluff study, while appropriate in determining the validity of the assembly rule for functional groups, mapping functional groups on gradients to determine the environmental influences that place groups at any one site and determination of key species within key functional groups does have a major omission. This omission is that the study has not taken into account the influence of animal diversity. It is therefore unknown if animal diversity has a stronger effect on how well the ecosystem functions, than plant diversity does. Browsers (insect or mammal) have a profound effect on the plant species present in ecosystems.

Even if natural ecosystems could lose many of their species and still work reasonably well, this does not mean that ecologists should stand aside and watch species become extinct. Diversity has other benefits, including genetic resources for plant breeding and new therapeutic drugs. Researchers may not yet have the technology or skills to identify rare species that will in some way impact on ecosystems as environmental perturbations increase. While the redundancy theory is valid, sacrificing species not credited with importance to present day functions may threaten the survival of these ecosystems in the future. Despite all best efforts, change is inevitable and natural. Ecosystem processes will continue with new groupings of species, however, these ecosystems, may not be supportive of the species that we as humans place great value on. Some of today's minor species may be the perfect candidates to become tomorrow's dominants as climate changes and one ecosystem evolves into another. All we as researchers can do is to develop methodologies that will allow us to make informed decisions in appropriate time.

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Appendix 1 – Statistical Packages

The following methodologies from the statistical package PC-ORD (McCune & Mefford 1997) are edited notes from the *Help* files.

Dufrene and Legendre's Method – PC-ORD

A very common goal in community analysis is to detect and describe the value of different species for indicating environmental conditions. If environmental differences are conceptualized as groups of sample units, then Dufrene and Legendre's (1997) method of calculating species indicator values provides a simple, intuitive solution. The method combines information on the concentration of species abundance in a particular group and the faithfulness of occurrence of a species in a particular group. It produces indicator values for each species in each group. These are tested for statistical significance using a Monte Carlo technique.

Groups are commonly defined by categorical environmental variables, levels of disturbance, experimental treatments, presence/absence of a target species, or habitat types. Dufrene and Legendre (1997) also use this method to choose a stopping point in cluster analysis. If groups are too finely divided then indicator values will be low. On the other hand, if groups are too large, then the internal heterogeneity will reduce the indicator values. Dufrene and Legendre found that indicator values peak at some intermediate level of clustering, and that this peak will vary by species. Taken collectively, the method can be used to decide on an appropriate level of clustering for species data.

Detrended Correspondence Analysis (DCA, DECORANA)

Detrended correspondence analysis (DCA; Hill and Gauch 1980) is an eigenanalysis ordination technique based on reciprocal averaging (RA; Hill 1973). DCA is geared to ecological data sets and the terminology is based on samples and species. With other kinds of data, DCA may not be suitable, and for other types of data the terminology in the output must be translated to match the particular data set.

Like RA, DCA ordinates both species and samples simultaneously. The arch that is almost inevitable with more than one dimension in RA is squashed with DCA. This arch effect is squashed by dividing the first axis into segments, then setting the average score on the second axis within each segment to zero. Another fault of RA, the tendency to compress the axis ends relative to the middle, is also corrected with DCA. Axis compression is corrected by rescaling the axis to equalize as much as possible the within-sample variance of species scores along the sample ordination axis.

Also like its parent technique, DCA implicitly uses a chi-squared distance measure. Although DCA and CA do not require an explicit calculation of a matrix of chi-squared distances, it can be shown that RA is equivalent to an eigenanalysis of distances in a space defined by the chi-squared distance metric.

DCA has been quite popular in ecology. Recently its faults have been made more apparent. A lack of robustness has been found and there is erratic performance of DCA as compared to NMS using a wide variety of simulated data sets based on a range of assumptions about the underlying distributions of species along environmental gradients. This is attributed to poor performance to two factors, properties of the implicit dissimilarity measure, and the behavior of the detrending and rescaling processes.

DCA is performed with a modified version of DECORANA from the Cornell Ecology Program series (Hill 1979). Earlier versions of DECORANA were unstable because of lax criteria for stability and a bug in the rescaling algorithm (Oksanen and Minchin 1997). These problems have been corrected in PC-ORD. Oksanen and Minchin's "super strict" criteria of tolerance=0.0000001 and maximum number of iterations = 999 is now applied. The bug in the rescaling algorithm that is present in DECORANA beginning with the Cornell Ecology Program series and repeated by the versions in CANOCO and PC-ORD has been corrected in PC-ORD. This bug caused sensitivity of ordination results to sample order, mainly on the third axis and higher.

Cluster Analysis

Groups | Cluster Analysis

The purpose of cluster analysis is to define groups of items based on their similarities. Program CLUSTR performs eight variants on the general class of cluster analyses that are hierarchical, agglomerative, and polythetic. In this context, "hierarchical" means that large clusters are composed of smaller clusters. "Agglomerative" means that the analysis proceeds by joining clusters rather than by dividing clusters ("divisive" cluster analysis, e.g. TWINSPAN). "Polythetic" means that many attributes of the items are used to decide the optimum way to combine or divide clusters. See Sneath and Sokal (1973) for a comprehensive discussion of clustering methods; Gauch (1982) and Greig-Smith (1983) have good discussions of clustering for ecologists.

W. M. Post and J. D. Sheperd wrote the basic algorithm, which was then adapted for PC's by B. McCune.

APPENDIX II Photographs

Photograph 5.1 View of Aranga – Kauri Coast District (South) from the top of Maunganui Bluff (459 metres).

Photograph 5.2 View from Top of Bluff towards Waipoua Forest (North).

Photograph 5.3 Site A – 50 metre elevation, showing predominance of exotic grasses. The monocot flax is the dominant native species.

Photograph 5.4 Aranga and surrounding farmland from 350 metres

Photograph 5.5 Site J, the top of the Bluff (459 metres), beside the trig station.

Photograph 5.6 Site B, a small anomaly in a vast area of shrubland. A perching pohutukawa on the coastal slope was modifying light levels and was reducing the effect of salt-laden wind.

Photograph 5.7 Site C, the presence at the 150 metre mark of nikau palms and increased native shrubs signals the transition to forest.

Photograph 5.8 Site I, redesignated to shrubland from grassland due to the sampled site having a large population of shrubs and small trees.