Environmental and Management Factors as Determinants of Pasture Diversity and Production of North Island, New Zealand Hill Pasture Systems

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Phillipa Karen Nicholas

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ABSTRACT

Hill pasture systems are inherently variable due to both environmental (e.g. rainfall, temperature, altitude, slope, aspect and microtopography) and management (e.g. stock type, stocking rate, grazing behaviour and soil fertility) factors. Fertiliser application and grazing pressure are the two main tools used for hill pasture management, as hill pastures are non-arable and the success of oversowing into existing pastures has been limited. One aim of pasture management is to increase the percentage of desirable species (e.g. *L. perenne* and *T. repens*) by changing composition rather than the addition of new species. Pasture botanical composition affects production directly through the productive capabilities of species present, but it is hypothesised that the number of species present play a role in pasture productivity and stability of hill pasture systems.

A field survey and two glasshouse experiments were performed on hill pasture swards to identify the effects of imposed management and environmental factors on botanical composition. The relationship between species diversity and productivity was also investigated.

Ten field survey data sets were collected from two research farms. These data sets reflected different management history, climate, season and time (28 year time lapse). Information collected for each data set included botanical composition, Olsen P, hill slope, standing green biomass, and species growth rate over a one month period. The results of the survey indicated that the same species were present on all sites surveyed, but the abundance of those species changed. For example, *L. perenne*, *A. capillaris* and *T. repens* were most abundant on the high fertility sites, *A. capillaris* was the dominant species on the low fertility sites, flatweeds were more abundant on the dry sites, and *Muscii* spp. were more abundant in spring than summer. There was no direct relationship between species diversity and pasture production, but factors such as hill slope, fertility and season appeared to play a role in a more complex, undefined relationship between species diversity and productivity.

The first glasshouse experiment involved the application of two simulated management factors (i.e. defoliation height and treading) to hill pasture turves. The turves were removed from three hill country farmlets that had different management conditions imposed on them for 20 years. The abundance of *A. capillaris*, *L. perenne*, *A. odoratum*, *Poa* spp. and *T. repens* increased with the tall defoliation height, which was a positive effect, as was the increase in abundance of *T. repens* with treading. *L. perenne* and *H. lanatus* abundance decreased whilst treading was occurring, which was a negative effect.

The second glasshouse experiment involved the application of a simulated environmental factor (i.e. moisture deficit and excess moisture) and its interaction with a management factor (i.e. treading) on the same turves. The abundance of *H. lanatus*, *Poa* spp., *T. repens* and other legumes decreased under the moisture deficit treatment. *L. perenne* abundance was unaffected. The abundance *of C. cristatus*, *A. odoratum, F. rubra* and *L. perenne* decreased under the excess moisture treatment, all others increased. *T. repens* abundance was increased with a combination of treading and excess moisture.

Functional groups were developed as part of the objectives of this research programme, to simplify the system being studied. In response to the management and environmental factors applied to the turves, the functional groups were described as being increasers, decreasers or static. The results of the turves experiments were used to validate the definition of the functional groups. For example, the high fertility responsive grass functional group was more abundant on the high fertility turves and *L. perenne,* which is also responsive to high fertility conditions, was found to be in a functional group of its own because of its ability to recover from treading. *A. capillaris*, which like low fertility tolerant grasses was abundant on low fertility sites, was separated

into a group of its own because of its great abundance and dominance of the sward.

No definitive relationship between species diversity, production and stability of production was observed in the turves experiments. That *A. capillaris* was particularly dominant in all swards may have significantly influenced the relationship. As with the field survey, however, all species were observed on all turves, and just the abundance of those species changed.

The results of this experimental work showed that pasture composition can be altered to a more desirable (leafy green with legumes and adapted to the environment in which they are occurring) form with the use of management factors such as fertiliser application, defoliation height and treading. That composition was changed without a change in the number of species present, suggested that such composition changes are reversible. The work also highlighted the importance of an environmental factor, that cannot be controlled by land managers (i.e. soil moisture), and its interaction with management practices in maintaining a desirable and stable pasture composition.

“*Real generosity towards the future lies in giving all to the present.*”

Albert Camus (1913-60), French-Algerian philosopher, author.

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1. Introduction and Objectives

1.1 Introduction

With the enactment of the Resource Management Act in New Zealand, and the need for farmers to become more efficient to maintain economic viability, there has been an increasing interest in recent years in the concept of sustainable agriculture. This is an issue of particular importance to hill farmers in New Zealand, as the land resource being used is particularly susceptible to degradation, has limited agricultural use (pastures or trees) and markets and prices for products are cyclic.

The term sustainability has no fixed definition (Pretty, 1994), but it is widely accepted that sustainable land use has ecological, social and economic components. Blesing (1992) described sustainability as the capacity of a land use system to maintain net productivity of biomass over a time frame of decades or centuries. Schaller (1990) described a sustainable system as one that over the long term enhances environmental quality and the resource base on which agriculture depends, provides for basic food and fibre, is economically viable, and enhances the quality of life for farmers and society as a whole. Not only does this definition recognize the need to conserve the natural resource base, but to also improve it for future generations. It also emphasizes the importance of several components including productivity (plant and animal), ecological stability and economic viability (Michalk and Kemp, 1994). Ikerd (1990) stated that although ecologically sustainable management practices might conflict with short term economic sustainability, long term economic performance must be related to conservation of the resource base.

Resilience, resistance to damage through natural environmental cycles (e.g. drought), flexibility, robustness, stability, endurance and ability to cope with change are all useful concepts in understanding agricultural sustainability

(Blesing, 1992). In assessing whether a farming system, such as a North Island hill pasture system, is sustainable or not, a key issue is the rate of change for components, rather than the value for components at one point in time (Michalk and Kemp, 1994). This leads into the concept of stability, and in agricultural systems, particularly pastoral systems, the rate of change in soil, plant and animal parameters. Some parameters are more useful than others in indicating the sustainability of a system. Commonly used measures relate to animal performance (e.g. animal liveweight), but this was considered a poor measure (Michalk and Kemp, 1994) as animals can act as a buffer to soil and pasture changes through processes such as selective grazing. Pasture production may also be used as an indicator of stability, though this is inherently variable both within and between years. A more sensitive measure of change could be pasture composition and pasture demographics. The rate of change of pasture composition and the direction of change may be useful indicators of pasture stability, which would in turn affect whole system sustainability. Lambert *et al.* (1996) identified pasture botanical composition (particularly content of high fertility responsive grasses and weeds) as being a good indicator of North Island hill pastoral farming sustainability. There has not been a study, however, of the role of species diversity in pasture stability and production in the plant communities that support North Island New Zealand hill pastoral systems.

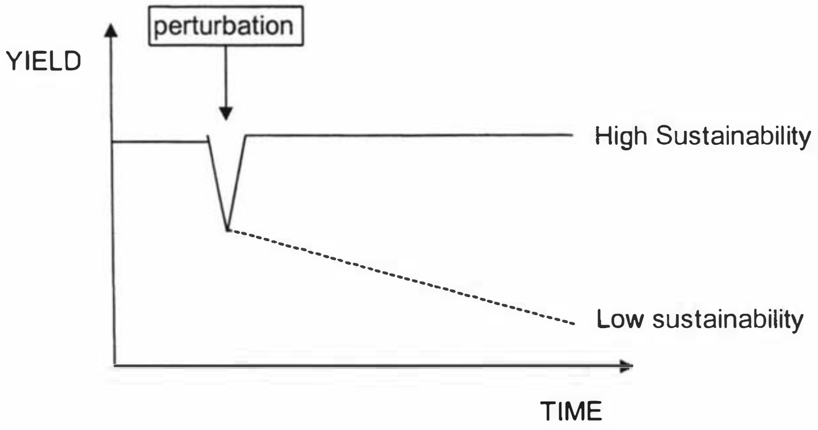
1.2 Objectives

Consequently, the objectives of this thesis were to:

- Survey the botanical composition of typical North Island hill pasture and identify how this composition changes under different environmental and management conditions in the field, so that optimal management practices can be implemented to achieve a desired pasture composition.
- Identify the relationship between pasture species diversity and productivity in a North Island, New Zealand hill pasture to identify if more diverse pastures are more productive.

- Identify functional groups in a North Island, New Zealand hill pasture as an aid to management by simplifying the hill pasture ecosystem.
- Under controlled glasshouse conditions identify the effects of imposed management conditions on the botanical composition and production of a North Island, New Zealand hill pasture so that improvements in pasture botanical composition (by increasing leafy green grass and legume content) can be achieved.
- Identify the effects of an environmental stress (i.e. moisture stress) and its interaction with a management stress (i.e. treading), on botanical composition and production of a North Island, New Zealand hill pasture so that undesirable changes in botanical composition (e.g. increased dead matter, flatweeds and other species content) can be avoided.

Figure 1.1 An illustration of a sustainable and unsustainable pasture system under the influence of a perturbation.



2. Review of hill pasture biodiversity

2.1 Hill country pastoral farming

In New Zealand hill pastures account for approximately 5 million hectares of the 14 million hectares in pasture (White, 1994). Hill pastures are those that were surface-sown on unploughable hill country that originally grew podocarp rainforest, fern or scrub, and occur mainly in the North Island of New Zealand (White, 1994). These pastures account for nearly one third of the export earnings derived from agriculture (agriculture comprises 60 - 70% of total export earnings), hence are an important resource for the New Zealand economy (Trustrum *et al.* 1983).

Most hill pastures were developed from native forest and scrub in the late 1800's (Levy, 1955). A technique of clear felling, burning and oversowing with introduced pasture species such as browntop (*Agrostis capillaris*), chewings fescue (*Festuca rubra*), danthonia (*Rytidosperma* spp.), crested dogstail (*Cynosurus cristatus*) and white clover (*Trifolium repens*) (Hilgendorf, 1936), was used to establish pastures, which were subsequently stocked with sheep and cattle. Often these pastures reverted back to native scrub and fern due to an incorrect mix of stock and stocking rates, which when implemented correctly would promote pasture growth over native scrub species (Levy, 1955). Up until the 1950's, hill pastoral farming was primarily concerned with maintaining these introduced pasture species at existing levels of fertility, which were often low (White, 1994). There were very few legumes in these pastures and improvement of soil fertility through nitrogen fixation was minimal.

Improvement of hill pastures occurred with the advent of aerial top dressing in the 1940's, when superphosphate and lime were commonly applied (White, 1994). The combination of superphosphate application and oversowing legume seed resulted in vastly improved pastures. The superphosphate fertilizer stimulated legume growth, which in turn fixed atmospheric nitrogen, which encouraged grass growth. This improvement of hill pastures meant a shift from low feed quality species like chewings fescue and danthonia, to more desirable species such as perennial ryegrass (*Lolium perenne*). Browntop continued to significantly contribute to pasture composition.

Prices paid for products (wool and sheep meat) produced on hill country farms, are often variable and cyclic. Though inputs for production (such as fertiliser) are relatively low compared to a dairy farm, for example, they are still vital for retaining a productive pasture and for preventing reversion to native scrub. The cost of these inputs remains the same regardless of the prices being paid for products and this may result in the economic viability of some hill farms being compromised.

Different aspects (e.g. pasture management) of hill pastoral farming need to be examined to improve their economic and ecological viability in the long term. The changes in the composition of pastures under different environmental and management conditions may result in improved pasture production. Also, the role that pasture species diversity plays in the long term production of pastures is unclear. Improvements in pasture quality and production may be achieved, at low cost through changes in management, by developing a more desirable pasture composition.

Hill pastures are extremely diverse, compared to other pastoral farming systems in New Zealand, both on a single farm or even a hill paddock scale (Chapman and Macfarlane, 1985; Scott *et al.* 1985). This diversity is caused by both environmental factors such as rainfall, temperature, soil moisture, altitude, slope, aspect and microtopography, and management factors such as stock type, stocking rate, grazing behaviour and soil fertility.

It is very difficult to maintain a homogenous pasture composition over an entire hill farm because of the factors described above. It could be achieved, but the inputs required to do so would be prohibitively expensive, and the costs associated with such an action would be unlikely to be offset by profitable increases in production. Pasture composition is dependent on the environmental and management conditions imposed on it. As land managers have no control over the environment, changes in management and controllable inputs are a useful way to alter pasture composition from one state to another. The direct costs of implementing a composition change and the long term costs of maintaining it, in terms of the inputs required, need to be considered to be sure that these costs are offset by increased production.

2.2 Botanical composition of hill pastures

The composition of hill land pastures is diverse compared to lowland pastoral systems in New Zealand (Matthew *et al*. 1988). Lambert *et al*. (1986a) identified approximately 20 species in a survey of a North Island, New Zealand hill pasture. Some species typical of these pastures were grasses such as *Lolium perenne*, *Agrostis capillaris*, *Anthoxanthum odoratum*, *Cynosurus cristatus*, *Holcus lanatus*, *Poa* spp., *Festuca rubra*, *Rytidosperma* spp., legumes such as *Trifolium repens*, *Trifolium dubium*, and *Lotus pedunculatus* and other species such as flatweeds (e.g. *Plantago lanceolata*, *Hypochaeris radicata* and *Leontodon taraxacoides*), *Centella uniflora*, *Nertera setulosa* and *Muscii* spp. (Lambert *et al*. 1986a). This diversity is brought about through both management of the pasture and the wide variety of environmental conditions present on most hill farms.

Management factors that affect species composition include stock type, grazing regime, defoliation intensity, stock treading intensity and pasture improvement techniques such as fertilization and oversowing. In a pasture composition survey of low fertility hill pasture in the North Island (Grant and Brock, 1974), topography was found to have the greatest influence on pasture composition. Topography had largely determined composition because of its influence on stock management, animal behavior and nutrient transfer. Composition differences caused by soil type were not great, except where they appeared to be related to soil moisture characteristics (Grant and Brock, 1974). In another hill pasture survey (Lambert *et al.* 1986a), fertiliser application, grazing regime (sheep or cattle, rotationally grazed or set stocked), slope and aspect were all identified as influencing pasture composition.

Pasture botanical composition itself can affect the pastoral agricultural system in many ways. It can directly influence farm production through feeding value of herbage, seasonality of herbage accumulation and rate of herbage accumulation (Lambert *et al.* 1986a). Some species, particularly legumes and grasses such as *L. perenne*, have a higher feeding value than other species such as *Rytidosperma* spp., *Muscii* spp. and flatweeds. The abundance of the more desirable species in the sward will significantly influence the feeding value of the pasture (Ulyatt, 1978). The seasonality of individual species will also affect production. *A. capillaris* is winter inactive, resulting in decreased growth in the winter months. The abundance of this species in the sward in winter will have a large influence on herbage production. Species composition needs to be balanced so that peaks of production of individual species are spread throughout the year, ensuring a more even feed supply. Herbage accumulation rate can be affected by pasture botanical composition in several ways. Some species such as *L. perenne* and other grass species have a faster growth rate than species such as *T. repens*. Therefore, the abundance of these types of species in the sward will determine total herbage accumulation rate. The susceptibility of some species to defoliation and treading damage, and the abundance of these species in the sward will affect herbage accumulation rate. The tolerance of species to environmental perturbations such as periods of water stress, and the ratio of tolerant to intolerant species in the sward (Kemp *et al.* 1997), will also affect herbage accumulation rate.

Pasture botanical composition has an influence on other non-production related factors in hill pastures. For example, the abundance of legumes in the sward will determine the amount of nitrogen fixation that occurs. Soil stability on hill sides may be affected by the ratio of deeper rooting plants (e.g. grasses) to shallower rooting ones (e.g. moss). A sward consisting of species that are more resistant to treading will be less likely to be an open sward which may be susceptible to soil loss through surface runoff, and weed invasion. There are other processes such as the relationship between pastures and soil fauna, that pasture botanical composition may have a role in, and that may be beneficial for hill pastures. There may be other relationships like this in which pasture botanical composition has a role, but this role is unknown. It is apparent however that all the functions of botanical composition are contributed by a diverse range of species. While the roles of some species are known, the roles of others (e.g. *C. uniflora* and *N. setulosa*) are unknown, but may be important for sustainable hill pasture production.

2.3 Biodiversity

The contribution of biodiversity to hill pasture farming systems is relatively unknown. Biodiversity can be defined at three levels, genetic diversity within individuals, species diversity and ecological or community diversity (West, 1993). West (1993) described biodiversity simply as the variety of life and its processes, including the variety of living organisms, the genetic differences among them, the communities, ecosystems and landscapes in which they occur, plus the interactions of these components. This study of hill pastures deals with diversity at the species level. This encompasses the number of species present and is influenced by resource availability and disturbance. Wayne and Bazzaz (1991) identified the problems associated with the unit of species as a measure of diversity, such as plant taxa being generally unreliable units for quantifying the ecological diversity perceived and utilized by most organisms in communities. Species diversity however is commonly used (Magurran, 1988).

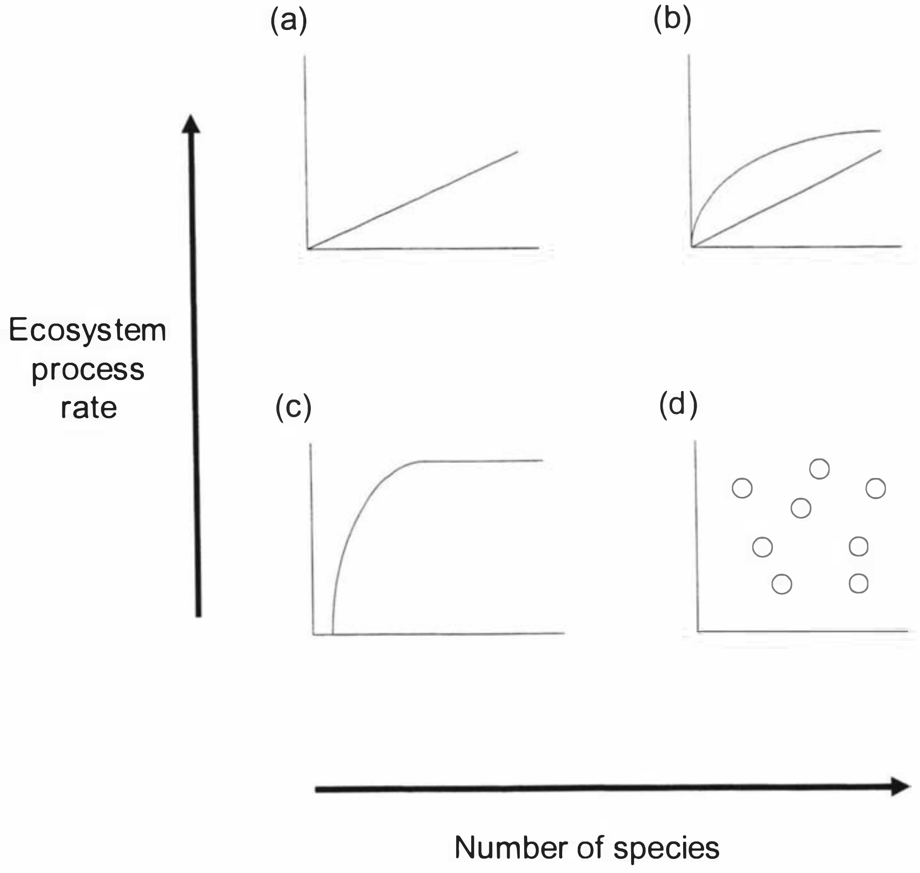
Biodiversity is regarded as being important in ecosystems for four main reasons (West, 1993). The first is morality, as many humans believe they have a moral obligation to preserve other species. The strength of this reason for preserving biodiversity depends on an individuals religious and philosophical orientation. The second reason is aesthetics. Humans derive pleasure from being able to observe a wide variety of natural organisms and ecosystems. The third reason is economic. Direct benefits of biodiversity include provision of a wide range of foods, medicinal products, fuels and building materials. There are many more species present in nature, besides those currently being used by humans, that may have potential use in the future. The fourth reason is the array of essential services provided by ecosystems such as nutrient cycling, gaseous exchange, decomposition and waste disposal. No single species carries out each of these services, and it is unknown exactly which combination of species results in the best provision of these services. Loss of diversity therefore may result in loss of some of these services.

2.4 Biodiversity, production and stability

There are four prevailing hypotheses regarding the relationship between biodiversity, production and stability in ecosystems (Johnson *et al.* 1996). These are the Diversity-Stability hypothesis (MacArthur, 1955), the Rivet Popper hypothesis (Ehrlich and Ehrlich, 1981), the Redundancy hypothesis (Walker, 1992) and the Idiosyncratic hypothesis (Lawton, 1994) (Figure 2.1). The Diversity-Stability hypothesis (MacArthur, 1955) defined stability as the temporal constancy of population numbers. In the other three hypotheses, stability is defined in terms of the ability of a community to resist change in its ability to maintain ecosystem function (resistance) and to recover to normal levels of function after disturbance (resilience) (Johnson *et al.* 1996). Pimm (1984) provides further definition of the term stability.

The Diversity-Stability hypothesis (MacArthur, 1955) postulated that increasing the number of trophically interacting species in an ecosystem should increase the collective ability of member populations to maintain their abundance after disturbance. The Rivet Popper hypothesis (Ehrlich and Ehrlich, 1981) suggested that ecosystem resistance can decline as species are deleted, even if the system's performance appears outwardly unaffected, resulting in sudden catastrophic collapse of the system. In this situation, resistance is described as the ability of the system to absorb changes in abundance of some species without drastically changing ecosystem performance, such as biomass production (MacGillivray and Grime, 1995). Ehrlich and Ehrlich (1981) likened ecosystems to aeroplanes. The removal of a dozen rivets (or species) from an aeroplane (ecosystem) may have no effect on the planes performance, but the plane is inherently weakened. The removal of a thirteenth rivet (or species) from a wing flap (or vital ecosystem process), may result in a collapse of the aeroplane (ecosystem). The Redundancy hypothesis (Walker, 1992) states that some species may be expendable from an ecosystem as long as an existing species can take the place of the extinct species in the community. The Idiosyncratic hypothesis (Lawton, 1994) states that there may be no pattern, or an indeterminate relationship between species diversity and ecosystem function.

Figure 2.1 Hypotheses for the functional role of species diversity in ecosystems, (a) Diversity-Stability hypothesis, (b) Rivet popper hypothesis, (c) Redundancy hypothesis and (d) Idiosyncratic hypothesis. Figure adapted from Johnson *et al.* (1996).



All four hypotheses are phylogenetically related. Walker (1992) used MacArthur's (1955) Diversity-Stability hypothesis in the development of the Redundancy hypothesis, Lawton used the Rivet, Redundancy and Idiosyncratic hypotheses together to address the rate of ecosystem processes (Johnson *et al.* 1996), and Tilman and Downing (1994) stated that the Redundancy hypothesis was an alternative to the Diversity-Stability hypothesis.

Many experiments have been carried out to investigate the relationship between biodiversity, production and stability (McNaughton, 1994; Naeem *et al.* 1994; Tilman and Downing, 1994; Vitousek and Hooper, 1994). Support for species diversity being essential for maintaining ecosystem function, has come from experiments in a controlled laboratory environment called the Ecotron (Kareiva, 1994; Naeem *et al.* 1994) and from plant community responses in field experiments conducted in both natural grasslands or simulated mixes of natural grasslands (McNaughton, 1977; Frank and McNaughton, 1991; McNaughton, 1994; Dodd *et al.* 1995; Silvertown *et al.* 1994; Tilman and Downing, 1994; Tilman, Wedin and Knops, 1996). A summary of the results of these experiments are presented (Table 2.1).

In Tilman's (Tilman and Downing, 1994) early experiment, biomass and species diversity were negatively associated, but in a later experiment (Tilman, Wedin and Knops, 1996), there was a positive association between biomass production and species diversity. Naeem *et al.* (1994) also identified a positive relationship between biomass production and species diversity. In experiments carried out by Dodd *et al.* (1995), McNaughton (1994) and Silvertown *et al.* (1994), there was a negative relationship between biomass production and species diversity. The relationship between diversity and stability also varied in the experiments mentioned, though more showed a positive relationship between diversity and stability.

Table 2.1 Summary of selected diversity/ecosystem function studies in grasslands. (+) indicates a positive relationship, (-) indicates a negative relationship and NA indicates not assessed. Table adapted from Johnson *et al.* 1996.

Author	Ecosystem	Diversity/Productivity relationship	Diversity/Stability relationship
McNaughton, 1993	California annual grassland	plants (-)	plants (-)
McNaughton, 1993	New York Old fields	plants (-)	plants (+)
McNaughton, 1977	Serengeti	NA	plants (+)
Frank and McNaughton, 1991	Yellowstone grasslands	NA	plants (+)
Dodd *et al.* 1994 and Silvertown *et al.* 1994	British grasslands	plants (-)	plants (-) (Silvertown *et al*) plants (+) (Silvertown *et al* and Dodd *et al*)
Tilman and Downing, 1994 and Tilman, Wedin and Knops, 1994	Minnesota grasslands	plants (-) (Tilman and Downing) plants (+) (Tilman, Wedin and Knops)	plants (+) (Tilman and Downing) NA (Tilman, Wedin and Knops)
Naeem *et al.* 1994	Ecotron	plants (+)	NA

Why these experiments exhibit such a range of contradictory results is unknown. It is possible that species interact differently under different environmental (in the case of natural ecosystems) and management conditions (in the case of developed pastures). These relationships have not been defined in hill pasture ecosystems. New Zealand hill pastures are “man-made”, but have adapted over time to become naturalised. Therefore, they are different from most other natural grassland systems in which the relationship between diversity and productivity has been studied, making this research unique. The contradictory results from other research (Table 2.1) suggest that the relationship between species diversity, stability and productivity is particularly complex. Regardless of whether these relationships do exist, and what they might be, the importance of other non-productivity related benefits of biodiversity previously mentioned remains.

2.5 Functional Groups

It is difficult to predict the response of vegetation to environmental or management changes because of the complexity of interactions between plants and their environment (Korner, 1994). Simplification of these complex systems, to groups of species with similar functions in the system is required, hence reducing the total number of components being studied. Functional groups therefore can be defined as sets of plants exhibiting similar responses to environmental conditions and having similar effects on dominant ecosystem processes (Walker, 1992).

Functional groups can be formed at any level of organization and for any function. As the aim of functional groups is to simplify the system, the level of organization chosen, needs to be a balance between ecological applicability and experimental “safety”. By using functional groups rather than individual species, some degree of “control” of experimental conditions is lost, but this needs to accepted if functional groups are to be useful (Korner, 1994).

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There are many different ways of grouping species into functional groups (Grime, 1974; Whittaker, 1975; Smith and Huston, 1989; Korner, 1994; Solbrig, 1994; Chapin *et al.* 1996; and Diaz and Marcelo, 1997). Choosing functional groups is a subjective process (Korner, 1994). The experimenter must decide at which level of organization to form the functional groups and what grouping criteria to use. The same collection of individual species may be classified into quite different functional groups depending on the researchers objectives and the grouping criteria used.

In terms of the relationship between species diversity, stability and productivity, it has been postulated (Holmes, 1998) that species rich plots may produce more and be more stable, not because of the number of species in itself, but because they contain representatives of key functional groups. This leads to the hypothesis that functional group richness rather than individual species richness is more important for ecosystem function. Tilman *et al*. (1997) found that plots containing three functional groups were more productive than those containing two functional groups. Plots containing additional species in each functional group did better still, but the gain was minor compared to that of adding an additional functional group (Holmes, 1998). Similarly, Vitousek and Hooper (1994) found that the functional groups present, strongly determined productivity. Which functional groups were present was found to be more important than the number of functional groups.

Very few vegetative studies carried out in New Zealand have involved the use of functional groups (Campbell *et al*. 1996; Wardle *et al.* 1997) and none have dealt with the role of functional groups or techniques for defining them in hill pasture systems. Because of the steep nature of hill pastures, they are unable to be improved by conventional methods such as mechanical tillage and re-sowing. Other techniques must be used to maintain pasture productivity at a sustainable level because hill pastures are such a major contributor to the New Zealand economy. A greater understanding of hill pasture community dynamics, with the use of such tools as functional groups, will enable opportunities for pasture improvement using management techniques such as fertiliser application and grazing, to be identified.

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3. Biodiversity of New Zealand Hill Pastures

3.1 Introduction

Biodiversity can be defined at three levels. The first level is genetic diversity within species, which contributes both to short term success of individuals and populations by enhancing fitness and to species' long term capacity for adapting to environment change. The second level is species diversity which deals with the number of species present and which is influenced by resource availability and disturbance. The third level is ecological or community diversity which can be influenced by human activity, resource status and disturbance. This study deals specifically with the second level of diversity, that of the diversity of plant species contributing directly to biomass of North Island, New Zealand hill pastures. Other species (e.g. trees and soil fauna) do play an important role in the hill pasture ecosystem (Lambert *et al.* 1996), but were beyond the scope of this hill pasture survey. The term species richness is used to describe the diversity of species, and in this study refers to the number of pasture species present. Other indices of diversity (e.g. Shannon's diversity index), take into account the abundance of species as well as their presence.

There are three reasons why the maintenance of biodiversity is thought to be important both in natural ecosystems and agricultural systems (Ehrlich and Wilson, 1991). The first is for ethical and aesthetic reasons. Some believe that farmers should be responsible for the stewardship of the land they farm, the preservation of organisms on the land and the visual appearance of the land to others in the community. The second reason is for direct economic benefits. There is potential for economic benefits from the manipulation of species diversity in New Zealand hill pastures to improve production and to reduce costs by minimising fluctuations in production. Thirdly, there are a range of essential services provided by plant ecosystems in which a diverse range of species take part (e.g. generation and maintenance of soils and maintenance of atmospheric composition) and it is difficult to quantify these benefits. These are all factors which highlight the potential importance of studying biodiversity in New Zealand agriculture, particularly hill pastures.

Hill pastures are an ecological system of importance to New Zealand agriculture in which the role of biodiversity is unknown. Ballantrae Hill Research Station is typical of how these pastures (based on exotic species) were established in New Zealand, and gives an indication of the relative diversity of hill pasture composition compared to other pastoral systems in New Zealand. Ballantrae Hill Research Station was originally podocarp forest which was cut and burnt in the 1890's. In the 1930's secondary growth was cleared, and the land intensively subdivided and stocked. In the 1940's the land was re-cleared (to remove reverted secondary growth) and was oversown and topdressed with superphosphate (Grant and Brock, 1974). A typical oversowing mix for hill pastures included perennial ryegrass (*Lolium perenne*), white clover (*Trifolium repens*), browntop (*Agrostis capillaris*), crested dogstail (*Cynosurus cristatus*), chewings fescue (*Festuca rubra*) and danthonia (*Rytidosperma* spp.) (Hilgendorf, 1936). In addition to this, seed dispersed by wind, birds, stock, hay and resident native species contributed to species in the pasture.

North Island hill pastures in general are intermediate in the continuum between low (e.g. South Island native tussock grassland) and high (e.g. dairy pastures) rates of inputs. The botanical composition of hill pastures is typically more complex than those of lowland pastures (e.g. approximately 20 species at Ballantrae (Lambert *et al.* 1986a) compared with approximately 10 on a sheep grazed lowland pasture near Palmerston North (Matthew *et al.* 1988)). There are many factors contributing to these differences in species richness, including environmental factors such as topography, climate, soils, pests and diseases, and management factors such as species sown, fertiliser applied and grazing management imposed. In lowland pastures, most of these factors can be controlled to the extent that a uniform pasture is produced, with a managed mix of relatively few species coexisting together in the sward. In hill pastures, however, the effects of very variable topography, micro-climate and patchiness of grazing, result in a heterogeneous pasture with many different niches in which species are required to survive. Therefore, hill pasture species richness may be important to maintain production in a wide range of micro-environments. It is not known how many species are needed to maintain production on all these microsites, or whether there is some degree of redundancy (Lawton, 1994). This study sets out to clarify some of the questions about the role of biodiversity in hill pastures.

Research has shown that in some ecosystems (Naeem *et al.* 1996), increased plant species richness resulted in increased production and in smaller fluctuations in production. There are perhaps potential production improvements to be made from a better understanding of this relationship in New Zealand hill pastures. Because of the relatively low cost structure of hill farming systems (compared to high input dairy farming systems for example), any improvements in production and the continuity of production that could be achieved without increased physical inputs (e.g. fertiliser), but through management changes that alter pasture composition, could be of economic benefit. Fothergill *et al.* (1994) were able to induce large changes in pasture composition of upland British pastures within one growing season by altering grazing management and inputs. At this stage it is unknown whether hill pastures are meeting their full production potential from the pasture composition that is present.

3.2 Materials and Methods

3.2.1 Sites

Ten data sets were collected from six sites for this experiment. Two data sets were collected in 1968-69 and the remaining eight based on measurements taken between 1996 and 1998 (Table 3.1). The number of samples taken in each data set varied depending on site conditions.

The two sites from which the 1968-69 data were collected were located on Ballantrae Hill Research Station, a low fertility North Island hill country farm situated near Woodville, New Zealand. The soil at the first site, LM Ballantrae, comprised Ngamoka silt loam derived from loess and sandy silt stone. The area was predominantly sheep grazed. The second site, LM Morgans, comprised Mangamaku steepland soil derived from silty sandstone, and was grazed predominantly by cattle.

Three of the remaining sites were also located at the AgResearch Hill Country Research Station, Ballantrae. Soils are yellow brown earths and related steepland soils formed from tertiary sediments and sedimentary drift material. Part of this research station has been divided up into four 7ha farmlets, each having had different management regimes for the last 23 years. Three of these four farmlets were used in this experiment, and were called Low/Moist (LM), Medium/Moist (MM) and High/Moist (HM), with the first part of the name indicating general level of fertility and the second part the type of summer rainfall, in this case, summer moist. These farmlets were established in 1973 and, prior to that, very little fertiliser had been applied. From 1973 through until 1993 the Low/Moist farmlet had 1250 kg/ha superphosphate applied, the Medium/Moist farmlet had 4000 kg/ha superphosphate applied and the High/Moist farmlet had 8875 kg/ha superphosphate applied (Lambert *et al.* 1996). The Medium/Moist site (surveyed in 1996-97) was relocated on the identical plots as for the LM Ballantrae site (surveyed 28 years earlier, in 1968-69).

The last of the six sites was located on the Massey University Riverside Farm which is situated in the foothills of the Tararua ranges on the Opaki Plains, 15 km north-west of Masterton. This site was termed Low/Dry (LD) indicating that it was low fertility and summer dry. Though the average rainfall at Riverside was similar to that at Ballantrae, it was extremely variable from year to year (Hobson, 1996) and unevenly distributed within years.

Table 3.1 Site information for the 10 data sets collected. The first letter in the site name indicates the general fertility of the site (H=high, M=medium and L=low fertility). The second letter of the name indicates whether the site was summer dry (D) or summer moist (M). Spring and summer indicate in which season the data were collected. The historical sites, Ballantrae and Morgans, were both surveyed in spring.

Site Name	Year Surveyed	Average Olsen P (mgP/g soil)	Average hill slope (degrees)	Average stocking rate (su/ha)	Average summer rainfall (mm/3months)	Site location
HM spring	1996	64	27	14.8	368	Southern Hawkes Bay
HM summer	1997	64	27	14.8	368	Southern Hawkes Bay
MM spring	1996	24	24	13.8	368	Southern Hawkes Bay
MM summer	1997	24	24	13.8	368	Southern Hawkes Bay
LM spring	1996	21	26	8.3	368	Southern Hawkes Bay
LM summer	1997	21	26	8.3	368	Southern Hawkes Bay
LD spring	1997	16	27	10	254	Wairarapa
LD summer	1998	16	27	10	254	Wairarapa
LM Ballantrae	1968	2	24	5	368	Southern Hawkes Bay
LM Morgans	1968	3	29	5	368	Southern Hawkes Bay

3.2.1.1 1968-69 Data

The measurements on the LM Ballantrae and LM Morgans sites were carried out in spring and summer 1968-69. The two sites were approximately 20 m^2 and within each were 200 randomly placed microsites. In late September 1968 slope and Olsen P were measured at each of these microsites. Also, at each of the 200 microsites, 20, 5 cm diameter turf plugs were taken from which the percentage cover of each species present was calculated on a tiller basis. In November 1968, 40 of the 200 microsites (which included a full range of hill slopes) were used to calculate species growth rate. A 0.04 m^2 quadrat cut to ground level, was taken at each of the 40 microsites. For each of these microsites an adjacent area with a similar pasture composition and biomass was then selected and a grazing exclusion cage placed over it until early January 1969, when it was cut to ground level and the herbage collected. The species composition data collected from the microsites were then used to determine the growth rate of individual species over that period.

3.2.1.2 1996-97 and 1997-98 Data

The LM, MM and HM sites were measured in September-October 1996 and in January-February 1997. At both the LM and HM sites, two areas of 10 m^2 were chosen and 10 microsites within each randomly placed. At the Medium/Moist site, the exact 40 microsites used for the growth rate calculations in the 1968 LM Ballantrae survey were used. The exact microsites were re-identified using photographic and slope records. An area 20 m^2 was fenced to exclude grazing.

A 0.11 m^2 quadrat was cut to ground level at each of the microsites and the herbage was dissected and dried to determine the percentage composition and yield of individual species. Slope and Olsen P were measured at each microsite. An adjacent area at each microsite with similar composition and biomass to that cut for dissection was then selected and tagged with painted nails. Grazing animals were excluded from the site with a netting fence for a period of one month. Approximately one month later, these tagged areas at the microsites were re-identified, the herbage cut to ground level and total dry matter calculated. The percentage cover data for species determined at each microsite from the first herbage cut were then used to determine percentage composition in the second cut and from this the growth rate of individual species was calculated.

The same set of measurements was carried out at the LD site in September-October 1997 and January-February 1998. Two adjacent areas, both 16 m^2, were fenced and 20 microsites in each randomly placed for measurements.

3.2.1.2.1 Cumulative biomass

Cumulative biomass curves for addition of species in order of abundance were constructed for each data set. Parameters for the cumulative biomass curves were estimated using SAS (SAS Institute Inc., 1995). Data were plotted and fitted to the negative exponential equation:

$$y = a(b - e^{-cx})$$

where x = species in order of abundance and y = cumulative biomass
and a, b and c are constants

The parameter c (curvature) was used to compare the curves between sites.

3.2.1.2.2 Diversity indices

A series of randomly placed quadrat samples were taken to determine species composition. The Shannon diversity index (Shannon and Weaver, 1963; Pielou, 1966) was calculated for each quadrat and is based on the proportional abundance of species.

$$\mathrm{SDI} = \sum_{x=1}^{n} (x_i \text{-}\log x_i)$$

where x = % abundance of each species n = total number of species

Pielou's pooled quadrat method (Pielou, 1966) was used to determine the population diversity. The quadrats were pooled in random sequence and the cumulative diversity calculated using Shannon's index of diversity (Shannon and Weaver, 1963). Shannon cumulative diversity was plotted against the number of quadrats used. The point at which the resultant curve flattened was used to estimate the population diversity (Magurran, 1988).

3.3 Results

3.3.1 Pasture Cover

A total of 25 plant species were identified in the survey of the sites. There were 10 grasses, 4 legumes, 2 native herbs, moss (*muscii* spp.), 3 flatweeds (*Plantago lanceolata*, *Hypochaeris radicata* and *Leontodon taraxacoides*) and other species (*Achillea millefolium*, *Cirsium vulgare*, *Cirsium arvense*, *Ranunculus repens* and *Cerastium glomeratum*).

Dead matter was the main contributor to biomass, especially in summer (Table 3.2). The highest proportion of dead matter was at the LM Morgans site.
A. capillaris was the most abundant species, (accounting for 19.2% of biomass on average), except at the LM Ballantrae, LM spring and LD spring sites. At

these three sites *Muscii* spp. (20.2%), *Anthoxanthum odoratum* (28%) and *L. perenne* (17.5%), respectively, were the most abundant species. *A. capillaris* was present in greater abundance in spring than summer. On average, *L. perenne* was the second most abundant species. *L. perenne* was less abundant in summer than spring, with the exception of the LM sites where this pattern was reversed. Very low percentages of *L. perenne* were present on the LM Ballantrae and LM Morgans sites (0.1% and 0.8% respectively).

The most abundant legume was *T. repens* (5% on average). This species was most abundant in spring, with the exception of the HM sites where *T. repens* was more abundant in summer. The highest percentage of *T. repens* occurred on the HM sites with low percentages at the remaining sites.

Muscii spp. were more abundant in spring than summer. *Muscii* spp. were the greatest contributors to biomass on the LM Ballantrae site. The most common plant species over all the sites (>5% of average dry matter) were, *A. capillaris*, *A. odoratum*, *C. cristatus*, *L. perenne*, *T. repens*, flatweeds and *Muscii* spp. The least common species (<1%) included *Dactylis glomerata*, *F. rubra*, *Poa pratensis*, *T. dubium*, *T. subterraneum*, *Lotus pedunculatus*, *Centella uniflora* and *Nertera setulosa*.

Table 3.2 Summary of % cover of plant species for six sites (10 data sets) on hill pastures in the southern North Island, New Zealand. Sites are arranged from highest to lowest fertility from left to right.

	HMspring	HMsummer	MMspring	MMsummer	LMspring	LMsummer	LDspring	LDsummer	LMMorgans	LMBallantrae	**Average**
Agrostis capillaris	19.3	19.4	24.6	22.6	12.5	22.6	13.2	18.0	26.0	13.6	**19.2**
Lolium perenne	19.3	13.1	15.7	10.7	2.3	13.0	17.5	7.7	0.8	0.1	**10.0**
Anthoxanthum odoratum	6.3	4.5	5.0	4.8	28.0	3.8	3.8	3.9	4.2	6.3	**7.1**
Cynosurus cristatus	5.8	4.9	5.2	9.6	4.3	4.1	9.0	6.8	1.9	2.3	**5.4**
Rytidosperma spp.	2.1	1.0	0.9	1.5	2.7	7.4	2.9	4.0	1.8	2.1	**2.6**
Holcus lanatus	1.8	4.1	2.7	3.0	2.1	1.3	0.9	0.7	1.4	1.0	**1.9**
Poa annua	5.4	1.8	4.8	1.7	1.4	1.1	1.6	0.8	0.4	0.2	**1.9**
Festuca rubra	0.5	0.8	1.4	0.8	0.8	2.1	0.0	0.0	0.2	2.4	**0.9**
Dactylis glomerata	0.0	0.0	0.2	0.1	5.0	0.0	0.0	0.0	0.3	0.0	**0.6**
Poa pratensis	0.3	0.1	0.0	0.0	1.0	0.1	0.2	0.6	0.0	0.0	**0.2**
Trifolium repens	9.2	11.0	4.5	3.7	3.7	2.5	5.3	2.5	4.6	2.9	**5.0**
Trifolium dubium	2.7	0.4	0.5	0.3	0.8	0.3	1.4	0.0	0.1	0.1	**0.7**
Trifolium subterraneum	0.0	0.0	0.1	0.0	0.0	0.0	2.6	0.0	0.1	0.1	**0.3**
Lotus pedunculatus	0.1	0.7	0.1	0.0	0.7	2.5	0.0	0.0	0.1	0.1	**0.4**
Centella uniflora	0.1	0.3	0.3	0.3	0.0	0.2	0.0	0.0	0.0	0.7	**0.2**
Nertera setulosa	0.5	0.8	1.3	0.5	0.1	0.1	0.0	0.0	0.3	2.5	**0.6**
Flatweeds	2.2	1.2	7.9	4.4	8.6	3.9	9.9	15.8	0.0	7.0	**6.1**
Other species	0.9	0.7	0.8	0.4	1.5	0.8	0.8	0.8	5.3	1.3	**1.3**
Muscii spp.	3.7	0.5	11.7	2.1	1.4	0.2	7.7	1.0	5.8	20.2	**5.4**
Dead Matter	19.8	34.7	12.0	33.5	23.3	33.8	23.3	37.3	46.9	37.1	**30.2**

3.3.2 Species richness and standing green biomass.

Varying relationships between the number of species present and standing green biomass existed for the 10 data sets (Table 3.3). Only 5 data sets, HM summer, MM spring, MM summer, LM spring and LM Morgans, showed a significant relationship between the number of species present and standing green biomass. Two of these sites (LM Morgans and MM spring) showed a positive relationship, whereas the other three showed a negative relationship between number of species present and standing green biomass.

Table 3.3 Linear regression of species richness and standing green biomass

Site	Regression Slope	R2 value (%)	Prob>F
HM spring	-	13	0.1199
HM summer	-	47	0.0009
MM spring	+	10	0.0476
MM summer	-	10	0.0471
LM spring	-	34	0.0071
LM summer	-	2	0.5962
LD spring	+	0	0.9024
LD summer	-	2	0.4357
LM Morgans	+	12	0.0001
LM Ballantrae	+	1	0.2509

3.3.3 Species richness, standing green biomass and slope.

3.3.3.1 Biomass and slope

HM summer, MM summer, LD spring and LD summer followed similar patterns of decreasing biomass with increasing slope class (Figure 3.1). LM Ballantrae and LM Morgans showed increasing biomass to slope class 21-30° then a decreased biomass at greater slopes. Sites HM spring and LM spring had a reasonably even distribution of biomass over all slope classes, with HM spring having slightly higher biomass at lower slope classes and LM spring on higher slope classes. The MM spring site had increasing biomass with increasing slope class. There appeared to be no pattern between biomass production and slope class on the LM summer site. Biomass increased from 0 to 20°, decreased from 21 to 40°, and then increased at >41°.

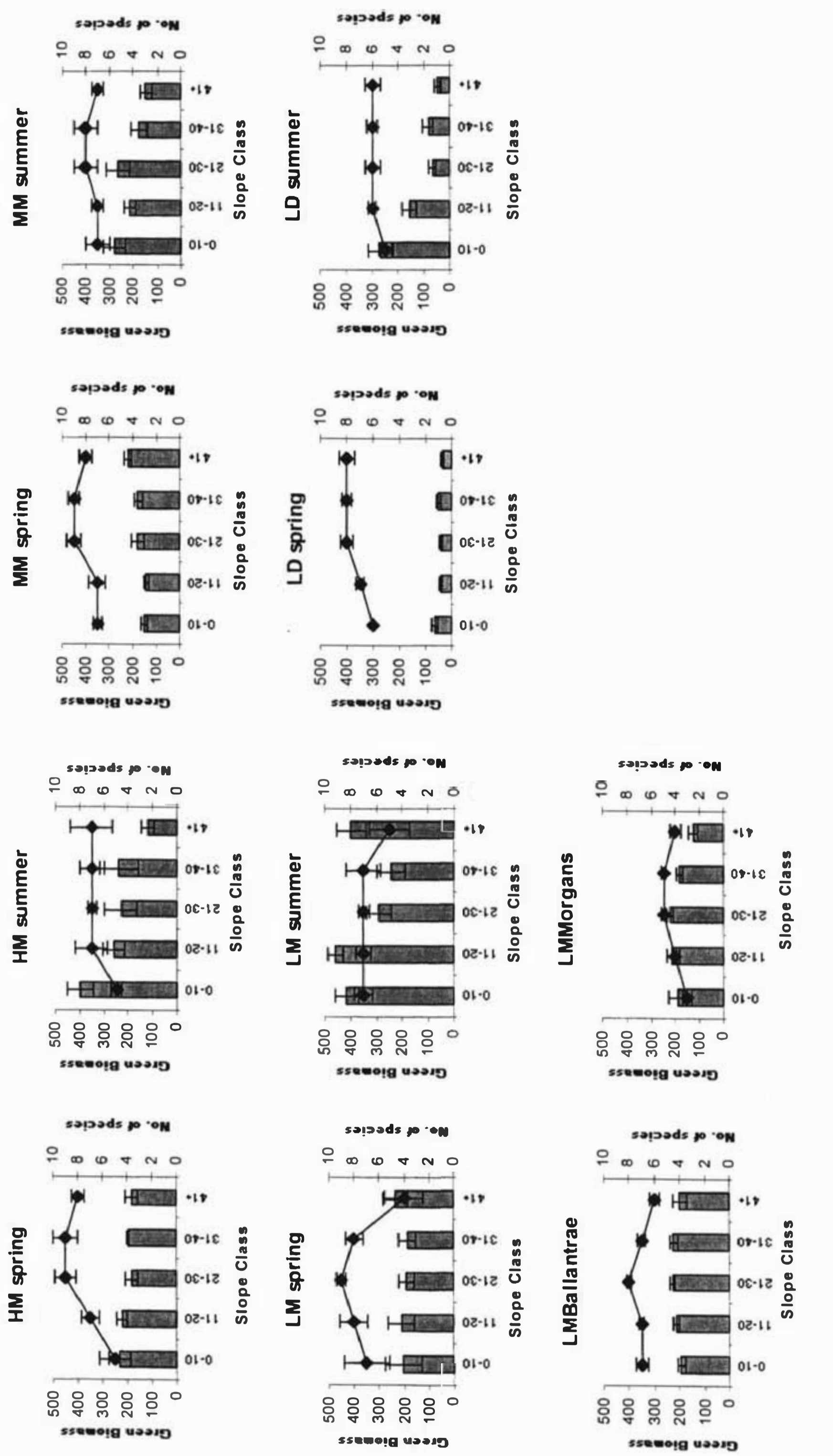
3.3.3.2 Species richness and slope

HM spring, MM spring, MM summer, LM spring, LM Ballantrae and LM Morgans all followed the same pattern of increasing species richness up to slope class 21-30° (i.e. peak richness at this slope class), then decreasing richness at steeper slopes (Figure 3.1). The HM summer, LD spring and LD summer sites all exhibited initial increases in species richness with increasing slope, then the richness stabilised. HM summer remained at 7 species and LD summer at 6 species from slope class 11-20° upwards. Site LD spring remained at 8 species from slope class 21-30° upwards. LM summer was the only site that stayed at 7 species from 0-40° slope, then decreased to 5 species at slopes greater than 41°.

3.3.3.3 Biomass, species richness and slope

At the LM Ballantrae and LM Morgans sites both biomass and species richness increased up to slope class 21-30° and then decreased on greater slopes (Figure 3.1). The MM summer site, with the exception of slope class 0-10° followed a similar pattern. MM summer had a relatively high biomass on the 0-10° slope class. The three sites that had decreasing biomass as slope

Figure 3.1 Green biomass (gDM/m^2) (bars) and number of species present/0.11m^2 plots (symbols) on five slope classes for each data set.



increased, MM summer, LD spring and LD summer, were also the sites where the number of species stabilised. The two sites which had a relatively even distribution of biomass over all slope classes, LM spring and HM spring, both had a similar pattern of species richness. That is, increased species richness to slope class 21-30°, then a decrease on steeper slopes. Although species richness at the MM spring site also increased to slope class 21-30° and then decreased on the steeper slopes, the biomass increased as slope increased. At the LM summer site, species richness did not follow the same pattern as biomass. At slopes greater than 41°, species number decreased and biomass increased.

3.3.4 Cumulative biomass

The cumulative biomass curves (Figure 3.2) show the rate of increase of biomass with the addition of species in order of abundance. The order of the species on the *x* axis of the cumulative biomass curves rank the species by abundance, and these rankings differ between sites. Parameter *c,* which is a measure of the curvature, was compared for each curve (Figure 3.3).

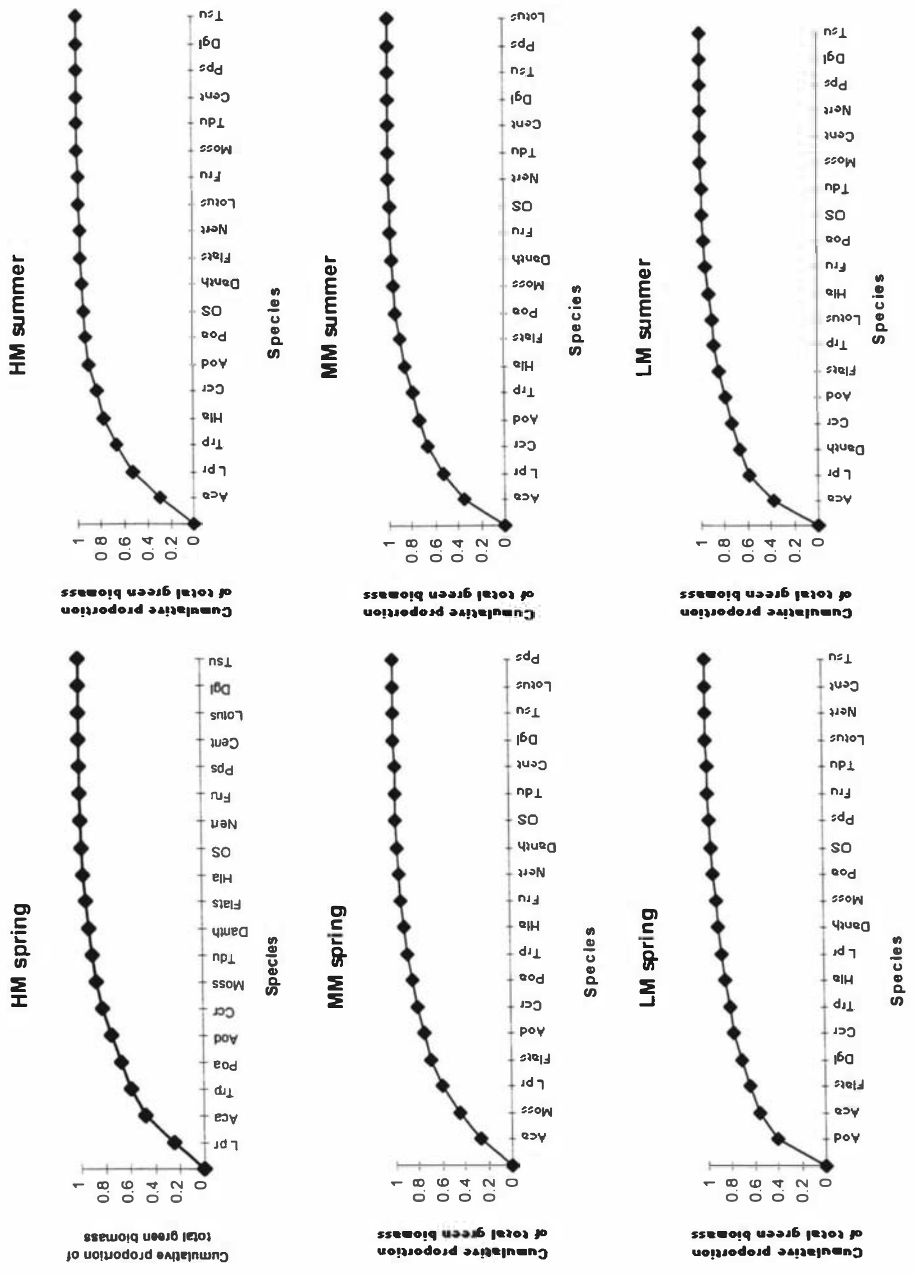
All the spring sites were significantly lower for the curvature coefficient (*c*) than the summer sites with the exception of the LD spring and summer sites which did not differ significantly (Figure 3.3). Using the 95% confidence interval as a measure of error, the LM Ballantrae and LM Morgans sites differed significantly. The HM summer and LM Morgans sites had significantly higher curvature coefficients than any other site. This indicated that at these sites, the cumulative biomass curves were steeper and that a few species dominated the sward. The MM spring and LM Ballantrae sites curvature coefficient differed significantly. The MM spring and LM spring sites had the lowest curvature coefficients, but not significantly lower than LD spring. The low curvature coefficient at these sites indicated that the cumulative biomass curves were flatter and that there was less dominance by the most abundant species

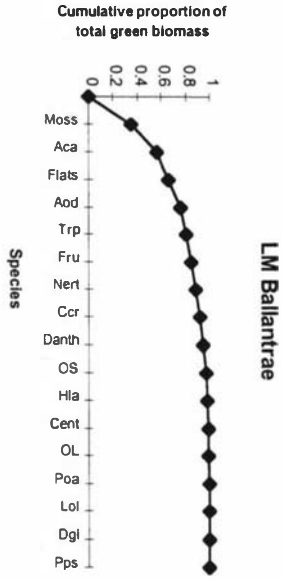
3.3.5 Species contributing to 50% of standing green biomass

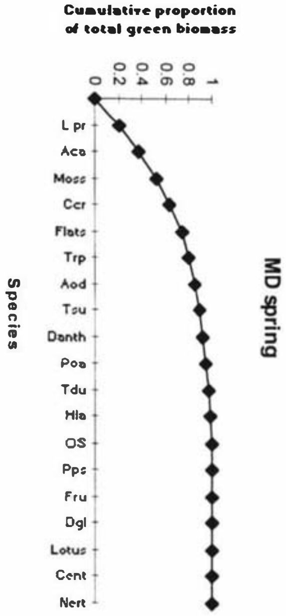
Regardless of total species richness, there were never more than 3 species contributing to 50% of green biomass at any site (Figure 3.2). LM Morgans had one species, LM Ballantrae, HM summer, MM summer, LM spring, and LM summer had two species and HM spring, MM spring, MD spring and MD summer had 3 species contributing to 50% of green biomass. The most common species contributing to 50% of green biomass were *A. capillaris* and *L. perenne*. One or both of these species were among the species contributing to 50% of green biomass at all sites. Other species contributing to 50% of green biomass tended to be site specific. Moss was the other main contributing species at the LM Ballantrae, MM spring and LD spring sites. *T. repens* was the other main contributor at the HM spring site, flatweeds at the LD summer site, and *A. odoratum* at the LM spring site.

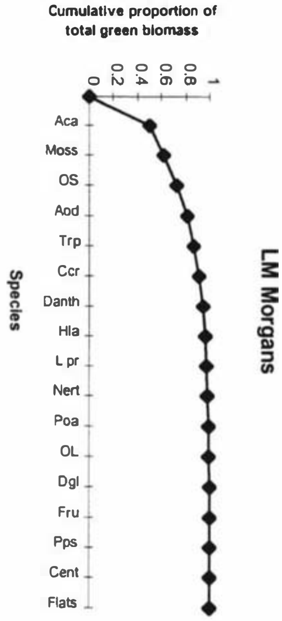
Figure 3.2 Cumulative standing green biomass presented as a proportion of total standing green biomass, for the 10 data sets.

(Aca = *A. capillaris*, Aod = *A. odoratum*, Cent = *C. uniflora*, Ccr = C. cristatus, Danth = *Rytidosperma* spp., Dgl = *D. glomerata,* Flats = Flatweeds, Fru = *F. rubra*, Hla = *H. lanatus*, Lpr = *L. perenne*, Lotus = *L. pedunculatus*, Moss = *Muscii* spp., Nert = *N. setulosa*, OS = other species, Poa = *Poa* spp., Pps = *P. pratensis*, Tdu = *T. dubium*, Trp = *T. repens*, Tsu = *T. subterraneum*)




LM Ballantrae
Cumulative proportion of total green biomass
0
0.2
0.4
0.6
0.8
1
Species
Moss
Aca
Flats
Aod
Trp
Fru
Nert
Ccr
Danth
OS
Hla
Cent
OL
Poa
Lol
Dgl
Pps


MD spring
Cumulative proportion of total green biomass
0
0.2
0.4
0.6
0.8
1
Species
L pr
Aca
Moss
Ccr
Flats
Trp
Aod
Tsu
Danth
Poa
Tdu
Hla
OS
Pps
Fru
Dgl
Lotus
Cent
Nert


LM Morgans
Cumulative proportion of total green biomass
0
0.2
0.4
0.6
0.8
1
Species
Aca
Moss
OS
Aod
Trp
Ccr
Danth
Hla
L pr
Nert
Poa
OL
Dgl
Fru
Pps
Cent
Flats

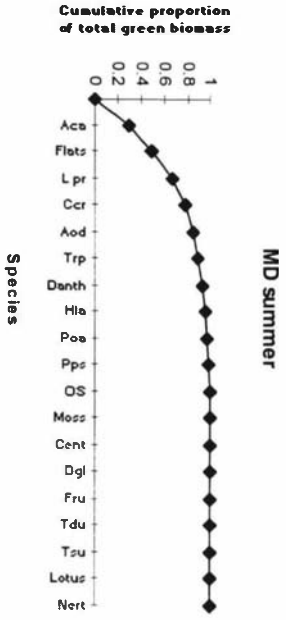
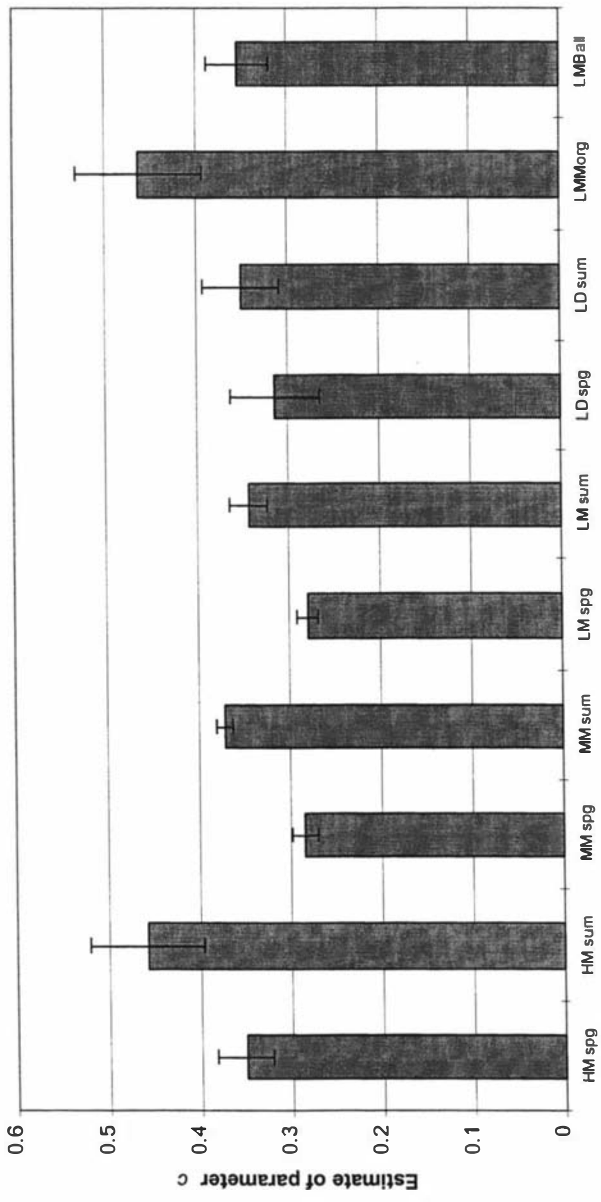

MD summer
Cumulative proportion of total green biomass
0
0.2
0.4
0.6
0.8
1
Species
Aca
Flats
L pr
Ccr
Aod
Trp
Danth
Hla
Poa
Pps
OS
Moss
Cent
Dgl
Fru
Tdu
Tsu
Lotus
Nert

Figure 3.3 Comparison of the curvature parameter (*c*) of the cumulative biomass curves. Error bars indicate the 95% confidence interval.



3.3.6 % contribution of the most abundant species and species richness.

All sites with the exception of HM summer, LD spring and LD summer, showed a significant ($P<0.05$) negative relationship between the % contribution of the most abundant species and species richness (Table 3.4). That is, the contribution of the most abundant species decreased (became less dominant) as species richness increased. There was no significant positive or negative relationship between % contribution of the most abundant species and species richness at the HM summer, LD spring and LD summer sites, and no increase or decrease in the dominance of the most abundant species as species richness increased.

3.3.7 Population diversity, average Shannon diversity and green biomass.

The population diversity calculated using Pielou's pooled quadrat method, was consistently higher than average Shannon diversity (Table 3.5). With the exception of the HM spring site, the Pielou index tended to decrease with decreasing fertility level. Again, with the exception of the HM spring site, the Pielou index was greater in spring than summer. For spring and summer at the LM site, the Pielou index values were similar. At all sites where spring and summer surveys were taken, average Shannon index was greater in spring than summer. Average Shannon index did not follow the same pattern as the Pielou index, that is, it did not decrease with decreasing fertility. The site with the highest Pielou index (HM summer), did not have the highest average Shannon index (which was at the LD spring site). The site with the lowest Pielou index (LM Morgans) did, however, have the lowest average Shannon index. The Morgans site had significantly lower Pielou and average Shannon indices than any other site, but did not have significantly less standing green biomass. Standing green biomass did not appear to be related to either the Pielou index or average Shannon index.

Table 3.4 Significance of regression between % contribution of the most abundant species and species richness.

Site	Regression Slope	R^2 value (%)	Prob > F
HM spring	-	30	0.0001
HM summer	-	10	0.1661
MM spring	-	31	0.0002
MM summer	-	10	0.0450
LM spring	-	58	0.0001
LM summer	-	28	0.0155
LD spring	-	18	0.0585
LD summer	-	6	0.1357
LM Morgans	-	39	0.0001
LM Ballantrae	-	15	0.0001

Table 3.5 Population diversity, average Shannon diversity and green biomass for each data set. Population diversity is an index of diversity for the whole data set, average Shannon diversity is based on average diversity of each plot surveyed, and standing green biomass is the dry matter standing when the samples were taken, less dead matter.

Site Name	Average Population diversity	std error	Average Shannon index	std error	Average green biomass (g DM/m^2)	std error
HM spring	2.18	0.10	1.55	0.09	203	12
HM summer	2.59	0.23	1.47	0.06	249	30
MM spring	2.12	0.07	1.58	0.04	174	8
MM summer	2.38	0.08	1.53	0.04	217	18
LM spring	2.00	0.14	1.40	0.11	203	19
LM summer	2.00	0.12	1.37	0.08	350	25
LD spring	2.28	0.06	1.65	0.05	44	3
LD summer	1.92	0.07	1.40	0.06	99	13
LM Morgans	1.98	0.04	1.38	0.02	218	6
LM Ballantrae	1.68	0.04	0.95	0.03	198	8

3.4 Discussion

3.4.1 Pasture composition

The 25 plant species identified from the six sites in the pasture survey had all been identified previously in southern North Island pasture surveys (Rumball and Esler, 1968; Grant and Brock, 1974; Lambert *et al.* 1986a). The most abundant species on average over all the sites was *A. capillaris*. This was confirmed in the Grant and Brock (1974) survey of pastures in the same area, before intensive improvements were made to the pasture through oversowing and fertiliser application. The abundance of *A. capillaris* in summer was slightly greater than spring, which might be due to its reasonable stress tolerance (Grime *et al.* 1988) compared to other species in the sward. Both *T. repens* and *L. perenne* were more abundant at the higher fertility sites. This same pattern was noted by Lambert *et al.* (1986a) in fertiliser trials conducted at Ballantrae Hill Research Station, where 8 of the 10 data sets were collected. In higher fertility sites (specifically high Olsen P sites) legume content was higher and was associated with a greater abundance of *L. perenne*. The occurrence of greater levels of *L. perenne* associated with increased legume content (specifically *T. repens*) is possibly due to the increased levels of N contributed to the soil by the legume.

The abundance of individual species has been shown to be influenced by topography, which encompasses slope, aspect and fertility; grazing management, which includes defoliation frequency and intensity; and fertiliser application (Rumball and Esler, 1968; Grant and Brock, 1974 and Lambert *et al.* 1986a). Only slope, fertility and seasonal differences were examined here, though the LM Morgans site was cattle grazed compared with all the other sites which were sheep grazed.

Luscombe e*t al.* (1981) identified the following composition in easy sloping (3-10°), low fertility (Olsen P of 3) hill country: 31% *A. capillaris*, 23% weed species, 10% *C. cristatus*, 8% clover (mainly *T. repens*), 6% other species, 4%

A. odoratum and 4% *L. perenne*. When compared to the LM Morgan site (also Olsen P of 3) (Table 3.2), there was more *A. capillaris*, *C. cristatus*, *L. perenne,* weeds and legumes in the Luscombe *et al.* (1981) survey, less other species and the same abundance of *A. odoratum.*

Dead matter contributed to 30% of total dry matter on average and was therefore the most abundant contributor to biomass. Lambert *et al.* (1986a) identified approximately 10% of biomass contributed by dead matter. This large difference may be attributable to two factors. Lambert's pasture cuts to determine biomass were not cut to ground level, as they were in this experimental work and calculations were based on six herbage dissections taken throughout the year, whereas the samples which gave 30% dead matter were taken in spring and summer. The average contribution of dead matter in the summer samples was higher than in the spring samples, probably due to under-utilisation of spring pasture growth, resulting in a build up of dead matter in summer (Lambert *et al.* 1986a). Leaf death rates also tend to increase with increasing soil temperature (Woodward, 1998) and rates of decay in summer tend to slow due to the low rainfall and low relative humidity (Cayley *et al.* 1980). The LM Ballantrae and LM Morgans sites were surveyed in spring, but both had high levels of dead matter present, particularly the LM Morgans site. Again this was most likely due to poor utilisation of the spring pasture flush. The LM Morgans site had 46.9% dead matter, which was probably due to the site being cattle grazed. Cattle grazing usually results in higher post grazing pasture levels in spring and summer, hence a greater build up of dead matter in the sward base.

The two data sets, LM Ballantrae and MM spring, collected at the same location but 28 years apart, illustrate the effect of management changes on pasture stability. The same species were present in both data sets, but the abundance of certain species changed with time, and with the management imposed during that time. In particular, the percentage of dead matter, flatweeds and moss decreased and of *A. capillaris*, *L. perenne* and *T. repens* increased. These changes are indicative of a general increase in fertility over time (Olsen P from 2 to 24 mg P/g soil) and improvements in grazing management (indicated by the decrease in dead matter content). That the same species were present in the sward after 28 years of changing management suggests that the species mix was reasonably stable. The species mix was able to absorb perturbations due to management and/or climate by adjusting the abundance of various species rather than species becoming extinct and new species migrating into the system. These results indicate that the role of farm management is in changing species abundance rather than botanical composition in order to try and improve pasture production. Genetic drift may also have occurred in some species, enabling them to absorb changes in management and environmental conditions and maintain a similar pasture composition (Barker, pers comm.).

There were several species present on most sites, that on average contributed to <5% of total dry matter. The role of some of these species can be suggested. For example, *F. rubra* and *Rytidosperma sp*. become greater contributors to biomass under dry conditions or in dry niches, and *P. annua*, *T. dubium* and *T. subterraneum* are all annual species that contribute mainly in late winter and spring, particularly when there are gaps in the sward. Other species, however, such as *C. uniflora* and *N. setulosa*, two native herbs, play an undefined role in hill pastures and their presence appears to have been largely ignored in the past.

3.4.2 Diversity and production.

The relationships between species richness and standing green biomass were variable and only 5 of the data sets showed significant relationships, two positive and the other three negative (Table 3.3). There have been many attempts to define the relationship between species richness and productivity. McNaughton (1994) carried out two grassland experiments where the results suggested that productivity (as measured by the change in total community standing crop) was inversely related to species richness. McNaughton's explanation for this phenomenon was that the production of individual species in more diverse vegetation is more evenly spread through the growing season. He stated that when the phenological differences of species were taken into account, there was no evidence that biodiversity and productivity were related. In the survey at Ballantrae, phenological differences between species would have been minor. The surveys were carried out in spring and early summer when all the species, which included perennials and summer annual plants, would have been actively growing. This may be one explanation why no definite relationship existed between species richness and production.

Tilman (1993) theorised that there was a greater loss of diversity on more productive sites. His theory was that as productivity of a vegetation patch changed, rates of colonisation and extinction changed, resulting in changes in species richness. His results suggested that it was the increased litter layer associated with productive sites, that altered species ability to colonise the site and caused extinction from the species present at the site, resulting in decreased richness. This theory may be suited to natural ungrazed or lightly grazed, grassland ecosystems, but under grazed pasture systems the theory is unlikely to apply because grazing animals minimise accumulation, and maintain similar biomass on both productive and unproductive sites. Also, hill pastures consist predominantly of perennial species, which on productive sites, are very competitive against colonising species.

Alternatively, Naeem *et al.* (1996) suggested that on average, species poor assemblages were less productive than species rich ones. They found that intra-specific competition was greater than inter-specific, so, in a species rich assemblage of similar density to a species poor assemblage, the effects of intra-specific competition are going to be greater in the species poor assemblage, hence lower productivity than the species rich one. Though Naeem *et al*'s experimental work showed this result, it does not appear to be applicable to the 10 data sets, as only 2 of these, LM Morgans and MM spring showed this relationship to a significant level. The LM Morgans site differed from the others in that it was cattle grazed. This may have altered the effects of inter and intra-specific competition in such a way as to result in a significant positive relationship between species richness and productivity. The MM spring site, however, was sheep grazed like all the other sites in the survey.

Unlike many other plant biodiversity experiments the 10 data sets were not from unmanaged and ungrazed grassland ecosystems, but were subject to controlled grazing management. McNaughton's (1994) work was carried out on grazed, but unmanaged natural Serengeti grassland, Tilman's (1993) work was carried out on lightly grazed, unmanaged natural and old-field grasslands and Naeem *et al*'s (1996) work was a pot experiment in a glasshouse.

Net above ground biomass (or the total biomass pool) was used as the measure of productivity in these experiments. In the surveys reported here, however, green biomass (which takes into account fluxes through the pool e.g. tissue turnover rates) was used as the measure of productivity as it is what is of value to the grazing animal. This may have also resulted in no clear relationship existing between productivity and diversity due to the added complication of different rates of tissue turnover for different species.

Though Naeem *et al*. (1996) obtained significant evidence in their experimental work to suggest that productivity increased with diversity, they emphasised that to state the converse is not necessarily true. Naeem *et al*. (1996) stated that "within ecosystems, reductions in species richness are just as likely to decrease productivity as increase it". This indicates that the relationship between productivity and species richness is complex and variable, and perhaps differs for different ecosystems, hence the variable results reported from this survey.

The relationship between green biomass production and species richness in North Island, New Zealand hill pastures is not straight forward. There appear to be underlying confounding factors such as fertility, moisture and grazing animal behaviour that are involved in the relationship. When an analysis of variance was carried out using Olsen P as a covariate, the LM Ballantrae (P = 0.0099), LM Morgans (P = 0.0694) and MM summer (P = 0.0216) data sets all showed a significant relationship between biomass production and species richness. Hence fertility (Olsen P) is a confounding factor in the relationship between biomass production and species richness for these three data sets.

3.4.3 Environmental effects.

One of the major environmental factors influencing hill pastures is hill slope. The effects of slope are indirect and act coincidentally through soil moisture availability, fertility, radiation interception and stock behaviour (Rumball and Esler, 1968; Gillingham, 1973).

3.4.3.1 Slope and production

There were several conflicting relationships between standing green biomass and slope class among sites and seasons. On flatter slopes, fertility and moisture levels tend to be high and species present on these slopes tend to be high fertility responsive species adapted to the levels of these resources (Lambert *et al.* 1986a). The positive influence of moisture on biomass production on flatter slopes compared to steep slopes was more apparent in summer than spring. Greater biomass was accumulated on the flatter slopes (HM and LD spring, HM, MM and LD summer), but more intensive grazing also occurred there due to the physical ease of grazing and the presence of high fertility responsive species (Figure 3.1). Growth on the flatter slopes may be inhibited by excess moisture in combination with animal treading. Constant standing green biomass levels occurred on some spring sites (HM, LM and LD spring) and may be attributed to a combination of intensive grazing on the flatter slopes and less intensive grazing on the steeper slopes with water being less of a limiting factor on steep sites in spring.

Peak biomass at slope class 21-30° occurred on several sites (MM summer, LM Morgans and LM Ballantrae). This pattern appeared to be associated with dominance by one or two species (e.g. *A. capillaris*). The specific fertility, moisture and grazing intensity was conducive for such dominants to produce large amounts of biomass at this slope class. At sites where the peak occurred, the flatter slopes tend to have biomass limited by intensive grazing and the steeper sites are limited by moisture deficiency, fertility and poorer producing species being present.

3.4.3.2 Slope and species richness

Species richness appeared to be influenced by slope effects (moisture, fertility and grazing intensity) in a similar manner to biomass. On flat and very steep slopes, there tended to be fewer species present (e.g. HM, MM, LM, and LD spring; LM Morgans, LM Ballantrae and HM and LD summer) (Figure 3.1). On the flatter sites this was probably due to high levels of competition between species for the abundant resources. On such sites, species that were good competitors (e.g. *L. perenne* and *A. capillaris*) were found in abundance, but few other species were present. On steep sites, stress tolerance rather than competitive ability possibly became the most important factor, particularly in summer when moisture availability was limited. There were few species adapted to the conditions present on a very steep site, hence species richness was low (e.g. LM summer).

Most sites exhibited peak species richness at slope class 21-30°, the same slope class where maximum biomass production occurred at several sites. At this slope class there may be a certain combination of moisture, fertility, grazing pressure and light that allows many species (from competitors through to stress tolerators) to co-exist, resulting in high species richness.

3.4.3.3 Slope, species richness and production

The sites (Figure 3.1) that had biomass increasing to a peak at 21-30° slope also had species richness following the same pattern (MM summer, LM Ballantrae and LM Morgans). Species richness and biomass production did not seem to be directly related and cannot be viewed as cause and effect variables. There were many factors involved in a pastoral system that determine both species richness and biomass produced. Some of these factors include fertility, moisture, aspect, grazing intensity, competition and colonisation or extinction of pasture species.

The three sites with distinct decreases in biomass as slope increased (HM summer, LD spring and LD summer), all showed the same pattern of species richness, that is, initial increases followed by stabilisation. This pattern suggested that on flatter slope classes, higher levels of competition for resources occurred, a few productive species were dominating, which in turn resulted in high biomass production. As slope increased, species richness remained the same, but biomass decreased, indicating that the poorer producing species were increasing in abundance as slope class increased.

Three of the other sites (HM spring, MM spring and LM spring) all showed the same pattern of species richness, but the MM spring site showed increasing biomass with increasing slope and the other two showed fairly even biomass production over all slope classes. The availability of water over all slope classes (because it was spring) may have had a bigger influence on the biomass produced, than species richness. The MM spring site may have been particularly wet resulting in suppression of growth on the flatter slopes.

The LM summer site did not show any definable relationship between species richness and standing green biomass. Biomass on the >41° slope class was probably high due to lack of control of spring pasture growth by sheep grazing (Lambert *et al.* 1983), rather than being attributable to the decrease in species richness. Sheep preferentially graze more productive flatter slopes resulting in an accumulation of biomass on steeper slopes. Sheep also tend to avoid grazing very steep slopes because of the physical difficulties of doing so. If the relationship between slope, biomass and species richness is to be identified, then pasture on all slopes would need to be cut to the same level. This would provide controlled conditions, but would not provide an indication of what happens in grazed hill pastures. Species richness declined at the >41° slope class because of the harsh environmental conditions present, resulting in fewer species being able to survive.

3.4.4 Species dominance.

Two species in particular, *A. capillaris* and *L. perenne*, played a particularly dominant role in the contribution of biomass at all sites (Figure 3.2). When species other than these two dominants contributed to the first 50% of standing green biomass, they were site specific, with *T. repens* contributing on a high fertility site, flatweeds on a low fertility dry site and moss and *Anthoxanthum odoratum* on a low fertility moist site.

Differences between the curvature of the cumulative biomass curves indicated that species response differed due to site factors, such as season and fertility. That all the spring sites differed from the summer sites (with the exception of the LD site) indicated that soil moisture also played a role. In general, flatter curves indicated less dominance and a more even contribution of species to biomass whereas steeper curves indicated dominance by a few species.

The dominance of both *A. capillaris* and *L. perenne* could be explained through studies carried out by Harris and Brougham (1968) and Kershaw (1958) in New Zealand hill pastures, where they identified that *L. perenne* and *A. capillaris* showed a significantly negative association. That is, *L. perenne* is found in relatively highly trodden, high fertility sites, and *A. capillaris* is found in less trodden, low fertility sites. Therefore, these two species tend to complement each other at a site where fertility and treading damage is heterogeneous. They are not competing for exactly the same niche, therefore can co-exist, and each dominate its own niche. The type of grazing animal can also have an influence on which species dominate in the sward. Clark *et al.* (1984) found that under goat grazing at Ballantrae Hill Research Station the dominant pasture species were *H. lanatus* and *T. repens,* compared with *L. perenne* and *A. capillaris* under sheep grazing.

The effect of species dominance on community structure, species richness and production has been widely studied (Grime, 1977; Reed, 1977; Chapin *et al.* 1986; Tilman, 1987; Gurevitch and Unnasch, 1989). Reed (1977) and Tilman (1987) observed that increasing soil fertility in herbaceous plant communities can lead to an increase in productivity, a reduction in species richness and an increase in the dominance of a few species. These changes in community composition have commonly been attributed to the exclusion of other species by competitively superior dominants where soil nutrients are high and rapid growth is possible. As mentioned earlier, *L. perenne* and *A. capillaris* were very dominant on flat sites, where fertility and soil moisture were relatively high.

Under resource poor conditions, there are two theories as to why dominance occurs. Tilman (1982) stated that species dominate because they are superior competitors under those environments. Grime (1977) postulated that competition was diminished in resource poor environments and it was the ability to withstand poor conditions, rather than competitive superiority that allowed certain species to dominate. Gurevitch and Unnasch (1989) stated that in general, the ability for a species to dominate a site is poorly understood and controversial, as the conflicting theories of Grime (1977) and Tilman (1982) showed. Gurevitch and Unnasch (1989) found that competition with dominant species limited other species in the community, and that the removal of the dominant resulted in increased species richness and evenness. Competition from the dominant species was more important in structuring the community when resource levels were high, and that the biomass of the first and second most abundant species were found to be good predictors of the number of species present (Gurevitch and Unnasch, unpublished data).

3.4.5 Diversity indices and pasture production.

Population diversity was greater than average Shannon diversity at all sites, as would be expected because of the patchiness of the vegetation being sampled (Pielou, 1966). That spring population diversity was greater than summer population diversity might indicate that the environmental conditions occurring in summer restricted the presence of some species, annuals in particular (Nicholas, unpublished data). The highest Shannon diversity occurred with maximum species richness and maximum evenness, and the reduction in summer population diversity may have been caused by changes in species richness or in the occurrence of dominance of certain species. Population diversity tended to decrease with decreasing fertility, though this was not a significant relationship. In contrast, studies (Reed, 1977; Bakelaar and Odum, 1978; Silvertown, 1980; and Tilman, 1987) found increased soil fertility resulted in a dramatic reduction in species richness.

Similarly to population diversity, average Shannon diversity was greater in spring than summer. The average Shannon index, however did not decrease with decreasing fertility. The effects of high evenness on the high fertility sites and high diversity on the low fertility sites may have cancelled out with averaging to result in no overall change in average Shannon diversity with fertility.

In agreement with the lack of relationship observed for species richness and standing green biomass, neither population, nor average Shannon diversity appeared to be related to standing green biomass in the pastures surveyed. Again, this would suggest that the relationship between plant species diversity and biomass production was not straightforward, and more work needs to be done in New Zealand hill pastures to better define the relationship.

3.5 Conclusions

There were 25 species identified in pasture surveys of six sites. These species were present on all sites, but the abundance of individual species varied due to environmental conditions. In the surveys carried out 18 years apart, the species present did not change, only the abundance. *A. capillaris* and *L. perenne* were consistently dominant contributors to biomass, but other species such as *T. repens*, flatweeds, *A. odoratum* and moss varied greatly depending on site factors such as fertility, slope and moisture.

T. repens was present in greater than 5% abundance only on the sites with high Olsen P levels (HM spring and summer). This indicates that increased Olsen P levels result in increased abundance of *T. repens.* As legumes, particularly *T. repens*, are the major source of nitrogen in hill pastures, Olsen P levels need to be kept relatively high to maintain the proportion of *T. repens* in the sward. The dominance of *L. perenne and A. capillaris* in the sward would also result in decreased levels of *T. repens* due to the competitive ability of these two grasses.

No direct relationship between species richness and green biomass production in hill pastures was found. It appeared that slope, which influences fertility, moisture availability and grazing animal behaviour, was a key factor in this complex relationship. The relationship between species richness, green biomass production and slope appeared to be influenced by season and management history of the site being surveyed. It was found that peak species richness occurred most often on slope class 21-30°.

From the results and discussion presented here, it was apparent that the role of species richness in North Island New Zealand hill pastures is complex. While hill pastoral systems are relatively stable in terms of the number of species present, it is clear that *A. capillaris* and *L. perenne* dominate and contribute to a large proportion of green biomass produced.

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4. Functional Groups

4.1 Introduction

It is difficult to predict the response of vegetation to environmental or management changes because of the complexity of interactions between plants and their environment (Korner, 1994). Simplification of these complex systems, to groups of species with similar functions in the system is required, hence reducing the total number of components being studied. Functional groups therefore can be defined as sets of plants exhibiting similar responses to environmental conditions and having similar effects on dominant ecosystem processes (Walker, 1992).

Both morphological and physiological traits are commonly used to classify species into functional groups (Grime, 1974; Whittaker, 1975; Smith and Huston, 1989; Korner, 1994; Solbrig, 1994). Korner (1994) identified five principles on which functional groups can be based. The first is the morphotype which is based on simple morphological characteristics (e.g. leaf type or obvious broad grouping criteria such as tree, vine, or shrub). The second basis is the investment type which groups species on the proportions in which carbon and nutrients are invested in plant structures (e.g. tap roots). The third basis, the physiotype, is the physiological characteristics such as sun/shade species and species that use a specific photosynthetic pathway (C3, C4 or CAM). There are problems with this grouping criteria in that many plants with vastly different morphology's can fall into the same physiotype group, and often morphology can have a greater influence on how plants succeed and survive in competitive environments, than physiological traits (Korner, 1994). The fourth basis, the physiomorphotype, overcomes this problem by combining morphological and physiological features. This is the most widely used grouping criterion (Korner, 1994). The final basis is life strategy and in comparison with the other grouping criterion mentioned, is more persistence-than growth-oriented. This is a difficult criteria to use because discrete boundaries are often not present, and survival strategies can change with changing environmental conditions.

There are many different methods for forming functional groups (Grime, 1974; Whittaker, 1975; Smith and Huston, 1989; Korner, 1994; Solbrig, 1994), and there is no quantitative basis for preferring any one of these methods. The groups chosen depend on the researchers specific interests (Davis and Heywood, 1963). For example, if a researcher is interested in the vegetation response to increased fertility at a site, factors that indicate plants responses to changes in fertility (e.g. root length, leaf area, nutrient content) will be used to group plant species into functional groups. One set of plant species may be able to form many different functional groups depending on the selection criteria used.

Because the formation of functional groups is subjective, a hierarchical approach was used to identify useful functional groups for hill pastures. This approach began with broad categories, which were then refined using a number of statistical approaches and classification factors.

4.2 Defining functional groups

The most common groupings for a hill country pasture are grasses, legumes, flatweeds and other species. This is a broad categorisation since other species includes species such as native *Centella uniflora* and *Nertera setulosa*, *Muscii* spp. and weed species such as *Achillea millefolium*. The broad groupings above suggest something is known about the species in the system. For example, that grasses and legumes are agronomically important, that flatweeds differ greatly in morphology, and that "other species" are an agronomically unimportant group.

Due to the nature of hill pastures (e.g. 20 plant species in North Island, New Zealand hill pastures (Nicholas, unpublished data) compared with 132 plant species in unmanaged rangelands in Minnesota (Tilman, 1993)), these groupings are reasonably descriptive, and interpreting the proportions of these functional groups gives some indication of the general resource status of the environment in which they are growing.

The first method used to define functional groups in hill pastures was an objective approach. Pasture composition was measured at a number of sites at the AgResearch Hill Research Station, Ballantrae, in 1968/69 and in 1996/97 (refer to methods, Chapter 3). The objective grouping of species into functional groups was carried out using a SAS cluster analysis on the standardised Ballantrae data. The PROC CLUSTER command and the average method were used (SAS Institute Inc., 1995). The inputs into the cluster analysis for each species were: yield (kg DM/ha), % cover, growth rate (kg DM/ha/day) and the regression slope of the relationship between growth rate and Olsen P, growth rate and hill slope and yield and Olsen P. The first three factors were standardised by ranking (Grime, 1997) and the last three were standardised by allocating a 3 to those species with a positive regression and 1 to those with a negative regression. The following seven groups were identified from the cluster analysis:

- *Trifolium dubium, Lotus pedunculatus,* and *Centella uniflora;*
- *Trifolium subterraneum and Poa pratensis;*
- *Anthoxanthum odoratum, Trifolium repens, Cynosurus cristatus* and *Muscii* spp.;
- *Holcus lanatus, Poa annua, Rytidosperma* spp.;
- flatweeds, *Festuca rubra* and *Nertera setulosa;*
- *Lolium perenne* and
- *Agrostis capillaris.*

These groupings were expected considering the inputs that were used in the cluster analysis, many of which were based on yield or abundance factors. Species that were similar in abundance have been grouped together. For example, *T. dubium, L. pedunculatus*, and *C. uniflora* yielded 15, 16 and 14 kg DM/ha, respectively; *T. subterraneum* and *P. pratensis* both 3 kg DM/ha; *A. odoratum, T. repens, C. cristatus* and *Muscii* spp. 152, 151, 148 and 196 kg DM/ha, respectively; *H. lanatus, P. annua, Rytidosperma* spp. and flatweeds 95, 100, 88 and 115 kg DM/ha, respectively; *F. rubra* and *N. setulosa,* 45 and 32 kg DM/ha, respectively, and finally *L. perenne,* 340 kg DM/ha and *A. capillaris,* 680 kg DM/ha. The usefulness of these groups as functional groups would be limited, as they are based on abundance, rather than function.

As the above objective approach did not result in the formation of groups of species based on function, another cluster analysis was carried out based on information about each species derived from literature. The variables used included ability to respond with increased growth to increased P levels; nitrogen fixing ability; ability to grow well on slopes; low growth habit; and tolerance to above average treading, grazing and drought levels. The cluster analysis resulted in six functional groups which have been named using the nomenclature of Lambert *et al.* (1986a):

- low fertility tolerant grasses,
- high fertility responsive grasses,
- other legumes,
- *T. repens*,
- flatweeds
- other species (in this pasture including *C. uniflora, N. setulosa* and *Muscii* spp.).

The cluster analysis based on literature derived variables (Hilgendorf, 1939; Struik, 1967; Grime *et al.* 1988; Davis *et al.* 1994; Nicholas *et al.* 1997) resulted in similar groups to those defined by Lambert *et al.* (1986a), but with some minor differences (Table 4.1). The low fertility tolerant grasses defined by Lambert *et al*. (1986a) were the same as those that formed the first group: *C. cristatus, Rytidosperma* spp., *F. rubra, A. capillaris* and *A. odoratum*. The high fertility responsive grasses (Lambert *et al.* 1986a) were the same as the second group of *L . perenne, H. lanatus* and *P. annua.* Lambert *et al.* (1986a) had *L. perenne* as a functional group on its own as it is more responsive to high fertility than either *H. lanatus* or *P. annua* (Grime *et al.* 1988). The two remaining functional groups defined by Lambert *et al.* (1986a) were legumes and other species. In the literature based analysis, all the legumes (*T. dubium, T. subterraneum* and *L. pedunculatus*) grouped together except for *T. repens* which was in its own functional group. Flatweeds also formed a functional group, but this was because they were the only weed species present. There were other species present in the pasture such as *C. uniflora, N. setulosa* and *Muscii* spp., but they were removed from the cluster analysis due to missing data. More would need to be known about the grazing tolerance of these species to group them correctly. That these species are indigenous suggests they would not be tolerant of sheep grazing and would therefore form their own functional group separate to flatweeds. The key functional differences between groups in this analysis appeared to be grazing tolerance and response to fertility. This would be expected as three of the inputted variables were related to fertility and three to grazing avoidance/tolerance. These are important variables from a pastoral perspective.

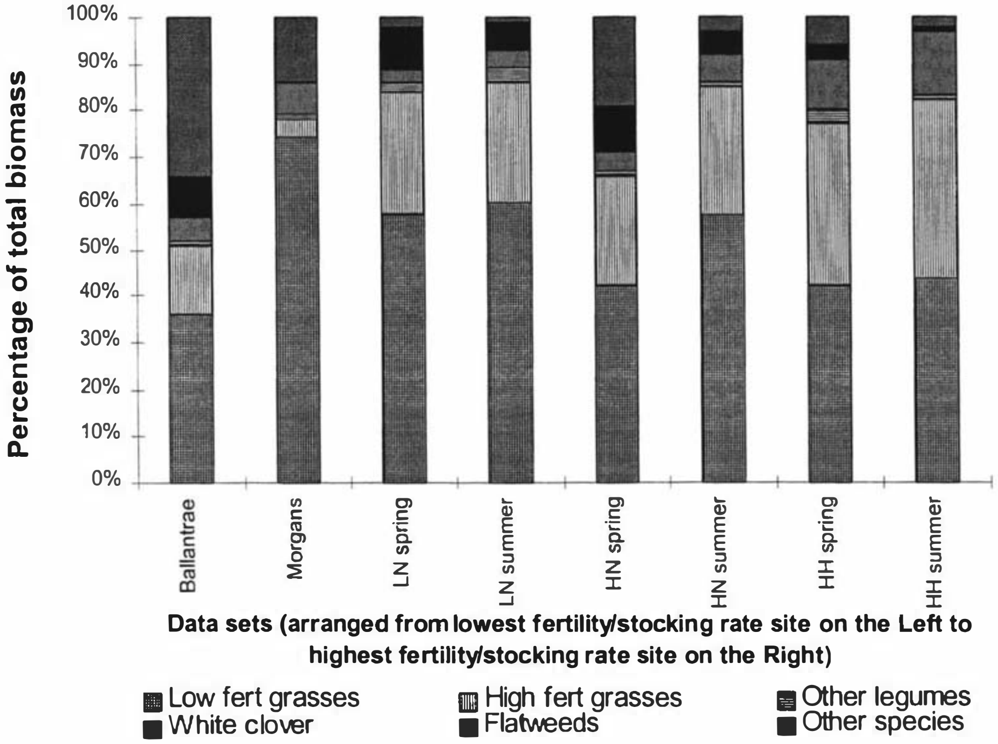
Table 4.1 Summary of the differences between the functional groups defined by Lambert *et al.* (1986a) and those defined in this study using literature derived variables.

Lambert *et al.* (1986a) Groupings	Literature derived Groupings
- High fertility responsive grasses e.g. *H. lanatus*, *Poa* spp.	- High fertility responsive grasses e.g. *L. perenne* , *H. lanatus*, *Poa* spp.
- Low fertility tolerant grasses e.g. *A. capillaris, A. odoratum, C. cristatus, Rytidosperma* spp., *F. rubra*	- Low fertility tolerant grasses e.g. *A. capillaris*, *A. odoratum, C. cristatus, Rytidosperma* spp., *F. rubra*
- *L. perenne*	- *T. repens*
- Legumes e.g. *T. repens*, *T. dubium*, *T. pratense*	- Legumes e.g. *T. subterraneum*, *T. dubium*, *T. pratense*, *L. pedunculatus*
- Other species e.g. *Hypochaeris radicata*, *Leontodon taraxacoides*, *Plantago lanceolata*, *Muscii* spp., *N. setulosa*, *Cerastium glomeratum*	- Other species e.g. *C. uniflora*, *N. setulosa*, *Muscii* spp.
	- Flatweeds e.g. *Hypochaeris radicata*, *Leontodon taraxacoides*, *Plantago lanceolata*

The relative contribution to biomass production of the six functional groups in response to soil fertility and grazing management history (Figure 4.1) showed (with the exception of the Ballantrae site) that low fertility responsive grasses decreased as fertility increased. Similarly, high fertility responsive grasses increased with increasing fertility. This suggested a functional response of these two groups to a fertility/grazing management gradient. The Ballantrae site had a low occurrence of all grasses and the highest occurrence of other species. Perhaps at this low fertility level, the function of the other species was more suited to the environment than that of low fertility responsive grasses. There did not appear to be any noticeable pattern over the fertility range for the other legumes functional group, though the occurrence of these legumes was greater in spring due to the low incidence of annual species in summer. The occurrence of white clover increased with increasing fertility, with the exception of the Ballantrae and Morgans sites. It appeared to be equally abundant on the two sites with the lowest fertility. Flatweeds appeared to occur more frequently on the lower fertility sites, with the exception of the Morgans site.

The literature-derived clusters clearly separated the pasture species into useful functional groups, but further refinement was needed to identify the most abundant species in the sward. It is important to identify these species as any changes to them, caused by changes in management or the environment, will have a large effect on total pasture production and perhaps pasture stability.

Figure 4.1 Relative contribution of 6 functional groups (defined from the literature) to biomass in the 8 data sets.



As a further refinement of the literature derived functional groups, two different measures of abundance were entered into a SAS cluster analysis (SAS Institute Inc., 1995) to see which produced the most useful separation of abundant species. The other data in the cluster analysis was that used in the literature derived cluster analysis. The first measure of abundance used was % cover. This clustering method resulted in more functional groups being formed, each with only 1, 2 or 3 species. The main difference in these cluster results was that three species, *A. capillaris*, *L. perenne, T. repens,* and flatweeds, formed their own functional groups. The low fertility tolerant grass group was divided into abundant (*A. odoratum* and *C. cristatus*) and scarce species (*Rytidosperma* spp. and *F. rubra*). The high fertility responsive grasses (*H. lanatus* and *Poa* spp.) were still grouped together, but *L. perenne* was removed to a group of its own because of its greater abundance. *T. repens* remained in a group of its own, but *L. pedunculatus* was removed from the other legumes group because of its inability to grow on steep slopes and to cope with drought, hence it was less abundant than the other legumes. *C. uniflora*, *N. setulosa* and *Muscii* spp. remained grouped together due to their overall negative response to the managed pasture environment.

The second measure of abundance used was ranking. The least abundant species was ranked 1 and species with the same % cover, were given the same ranking number. The results of this grouping did not appear to be as useful functionally as those described above. *A. capillaris* for example, which was the most abundant species was grouped with *A. odoratum*, which while being a low fertility tolerant (LFT) grass, was on average 80% less abundant than *A. capillaris.* Another unusual result was that *F. rubra* formed a group on its own. In other cluster analyses, this species was associated with other LFT grasses. Its ranking in this analysis did not suggest that it was greatly different from the other LFT grasses. *T. repens* and flatweeds were grouped together in this analysis. Functionally this separation was not useful, with *T. repens* being a legume and flatweeds having no nitrogen fixing ability and a very distinct growth habit. *L. pedunculatus* was also separated into a group of its own in this analysis.

Refining the literature derived functional groups using % cover data resulted in functionally useful groups being produced. As the objective of using functional groups is to simplify the system being studied, the following changes were made to the groups produced in the refined literature analysis (that included a measure of species abundance).

1. *L. pedunculatus* was grouped with *T. dubium* and *T. subterraneum* to form a group called other legumes. These species make a very small contribution to total cover, and it would make little contribution to the understanding of the system to study them individually.

2. The two groups of low fertility tolerant grasses (abundant and scarce) were grouped together to form a low fertility tolerant grass functional group. All these species (*A. odoratum, C. cristatus, Rytidosperma* spp. and *F. rubra*) were quite similar in terms of their response to slope, fertility and drought and because *Rytidosperma* spp. and *F. rubra* were reasonably scarce species (2.6 and 0.9% of total cover respectively), they did not warrant a group on their own.

Therefore, the functional groups that were defined using the hierachical approach described above were:

- *Agrostis capillaris*
- *Lolium perenne*
- High fertility responsive grasses - *Holcus lanatus*, *Poa* spp.
- Low fertility tolerant grasses - *Anthoxanthum odoratum*, *Cynosurus cristatus*, *Rytidosperma* spp., *Festuca rubra*
- *Trifolium repens*
- flatweeds
- Other legumes - *Trifolium dubium*, *Trifolium subterraneum*, *Lotus pedunculatus*
- Other species - *Centella uniflora*, *Nertera setulosa*, *Muscii* spp.

Using this hierarchical development approach, eight functional groups have been defined to represent approximately 20 species commonly found in North Island hill pastures. That eight functional groups have been defined suggests a range of functions are carried out by hill pasture species, however, in this study, a maximum of only three species form each functional group. These functional groups will be used in following chapters to describe pasture botanical changes.

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5. Management effects on pasture composition

5.1 Introduction

Hill country pastures are more difficult to manage than lowland pastures because they are heterogenous and diverse (Harris, 1994). This diversity is caused by climate (temperature and rainfall), edaphic factors (soil moisture and fertility) and biotic factors (grazing animals and management). These factors are further complicated by different aspects, slopes, microtopography and altitude (Harris, 1994). These variations not only occur at the whole farm level, but also within paddocks making application of management to achieve a desired pasture composition very difficult. Fencing is frequently used on hill farms to separate areas of different aspect or slope class, and this removes some variability within a paddock, but there are still many more acting to create a diverse pasture.

Harris (1994) suggested that successful hill pasture management involves balancing the three determinants of pasture composition and production derived by Grime (1973), competition, stress and disturbance. Using Grime's (1973) triangular ordination, species important in New Zealand hill pastures (e.g. *L. perenne*, *A. capillaris*, *T. repens*, *C. cristatus* and *A. odoratum* etc.) occur where there is a balance of competition, stress and disturbance. Disturbance is defined as any environmental stress that directly limits plant growth and survival; and competition, as plant interactions that may be beneficial by reducing environmental stress, but are more often competitive where adjacent plants interfere with each others growth and survival. Stress is defined as a factor such as cultivation or grazing which modifies interactions among plants (Harris, 1994). Harris (1994) also stated that if any one of these three factors is dominating, pasture composition will be simplified. Pasture composition, therefore, may be a useful tool for determining the health of a pasture and could be used successfully in combination with indicator species or functional groups.

Environmental effects, competition and management can all act to modify pasture composition (Kemp and Dowling, 1993). Each species and genotype of species responds to these external stimuli morphologically and physiologically. Just how each species responds and how they interact together determines pasture composition.

The objectives of this study are to identify the effects of imposed management conditions on the botanical composition and production of a North Island, New Zealand hill pasture.

5.2 Method

5.2.1 Turf removal

36 blocks of intact turf and soil were removed from Ballantrae Hill Research Station in early November 1996. The turves were 1 m long, 0.5 m wide and 0.4 m deep. 12 turves were removed from each of three sites, which had varied management history (Lambert *et al.* 1996). The high fertility (HH) site had 37.5 kg P/ha/year applied as superphosphate since 1973, the second (HN) site had the same level of fertiliser applied until 1980, when fertiliser application was stopped, and the third site (LN) had a low rate of fertiliser (12 kg P/ha/year) until 1973 and then fertiliser application ceased in 1980.

The turves were removed from the sites using cutting apparatus dragged by a tractor (Newton *et al.* 1994) (Plate 5.1). The apparatus consisted of a cutting tool and a turf bin. The cutting tool was mounted on the tractor and the bin in turn attached to the cutting tool. A hole was initially dug in the soil deep enough to fit the cutting tool and a bin flush with the soil surface. Water was pumped from the cutting apparatus on to the sides of the bin to aid movement of the soil through it. Wheels on the cutting apparatus controlled the depth of the turf. Once the turf bin was full, the turf was cut off using a spade. The bin was then lifted out of the channel using a second tractor, and a new bin attached to the cutting apparatus. This procedure was repeated until 12 turves were obtained. Due to physical constraints, the turves were removed from relatively flat areas at the sites rather than slopes, but stock camps and tracks were avoided.

The turves were removed over a period of approximately two weeks and were transported to the Plant Growth Unit at Massey University, Palmerston North. The turves remained outside for approximately one week during which time, the ends of the turves were tidied using a spade and sheet metal ends attached to the bins, so that no bare soil was showing. They were also hand-watered during this time. The turves were then randomly allocated within a 25 x 12.5 m glasshouse, with three rows of 12 turves (Plate 5.2). The turves were watered for approximately fifteen minutes nightly with overhead sprinklers.

5.2.2 Treatments

Treatment application began on 3 December 1996. The three management histories of the sites from which the turves were removed comprised levels of one factor. The second factor was cutting height. The turves were trimmed approximately once a week to maintain standard sward heights of 20 mm (short) and 75 mm (tall). The third factor was simulated sheep treading, consisting of treading (T) or no treading (NT). The simulated treading was applied using a studded roller that applied an average pressure of 1.28 Mg m^{-3} to the soil surface (Awan, 1995) (Plate 5.3). Each turf was trodden with 10 passes of the roller after each cutting.

5.2.3 Measurements

5.2.3.1 Dry matter harvests

Approximately once a week (from 3 December 1996 to 13 May 1997) the turves were trimmed using an electric hand-piece to the standard heights of 20 mm and 75 mm to simulate intense and lax, respectively, defoliation by grazing animals. A bracket was attached to the hand-piece onto which different sized guide wheels could be attached to achieve the required cutting height. All material removed from the turves during cutting was collected using a vacuum cleaner, dried and weighed to determine dry matter production.

5.2.3.2 Leaf extension

Leaf extension measurements were made on five of the most common and agronomically important species identified in the turves. These species were: *L. perenne, A. capillaris, H. lanatus, A. odoratum* and *T. repens.* Leaf extension was monitored for 5 days in February, March, April and May 1997. On each turf, one tiller of each species was tagged with an identifying colored piece of wire. The length of the youngest leaf was measured and then over subsequent days was re-measured. If the leaf died or ceased growing over this 5 day period, then the new leaf that appeared was measured.

5.2.3.3 Cover analysis

A specially designed point quadrat apparatus with 10 needles 0.05 m apart was used to non-destructively determine pasture composition of the turves. In December 1996 and April 1997, 100 points were sampled on each turf. In both February and March, 30 points were sampled on each turf. The point quadrat apparatus was used on a first hit basis. Only the first species hit by the needle was identified (Levy and Madden, 1933) and the percentage of hits (cover) for each species was calculated.

5.2.3.4 Tiller counts

On each turf, the tillers or growing points in three 0.025 m^2 samples were counted. The three samples were then averaged. This measurement was taken in January, February, March, April and May 1997.

5.2.3.5 Botanical composition

Four herbage dissections were carried out on samples cut from the turves. A 0.01 m^2 quadrat was cut from four areas near the corners of the turves in January, February, March and April 1997 respectively, and was dissected into component species and dead material. Dissected samples were then dried and weighed to determine the proportion of each species present.

5.2.3.6 Dry matter harvest dissections

The herbage removed from the turves on 3 March 1997 was collected and dissected into the following categories, *L. perenne*, other grasses, other species, *T. repens* and dead matter. This measurement was taken to determine species composition in the upper strata of the sward, above the standard cutting heights of 20 mm and 75 mm.

5.2.3.7 Root weight and length

In January 1997 four, 300 mm deep, soil cores (332 cm^3) were removed from each turf (one near each corner), discarded, and the holes back-filled with clean dry sand. Thirty days later, in February, the sand-filled cores were re-cored and the roots were removed by hand. Root length and root weight of the roots grown in one month were then determined. In March, after 60 days re-growth, the remaining two cores were removed and root length and root weight were determined.

5.2.3.8 Soil nutrients

Soil was sampled in December 1996, to a depth of 100 mm, and pH and the concentration of the following nutrients determined for each turf: Ca, K, P, Mg, Na, S.

5.2.4 Statistics

The experimental design was a 3 × 2 × 2 factorial, with 3 replicates. Due to an error in application of the factors, the design was unbalanced with treatments having a range of 1 to 6 replicates, however, only two treatments had 1 replicate. Type 3 sums of squares were used instead of type 1, due to their more conservative nature. The 5% level of significance was used to indicate significant differences between treatments.

5.3 Results

5.3.1 Measurement results

5.3.1.1 Soil nutrients

Calcium levels were significantly different between sites (P = 0.0010, Table 5.1). The HH turves had significantly higher calcium levels than the LN and HN turves. There were no significant differences in the potassium levels between sites. Olsen P level was significantly higher on the HH turves (P = 0.0001) than the HN and LN turves. At the 5% level of significance, magnesium, sodium and pH levels did not differ significantly between sites. Sulphur levels were significantly higher on the HH turves than the HN or LN turves (P = 0.0001).

There were no significant cutting height or treading effects on soil nutrient status.

5.3.1.2 Soil roots

Site effects significantly influenced root length in January (P = 0.0156) and root weight in March (P = 0.0392) (Table 5.2). In January, root length was significantly greater on the HH turves. Root length for the HN turves and the LN turves was similar. In March, root weight was significantly lower on the HN turves than the HH and LN turves, which did not differ significantly.

Cutting height and treading had no significant influence on root weight or length in either January or March.

Table 5.1 Soil nutrient status of turves in December 1996. Samples taken to a depth of 100 mm. Units for Ca, K, P, Mg, Na and S are mg/g of soil.

Soil		Sites			
parameters	LN	HN	HH	SEM	Prob>F
Ca	463	438	600	37.5	0.0010
K	86	118	118	14.0	0.2592
P	6	7	20	1.3	0.0001
Mg	99	97	88	6.5	0.1188
Na	30	39	53	6.0	0.0508
S	3	5	26	2.4	0.0001
pH	5.4	5.2	5.4	0.05	0.1853

Table 5.2 The effect of (a) site, (b) cutting height and (c) simulated treading on root length (m/m^3) and weight (g/m^3) in February (after 4 weeks re-growth) and March (after 8 weeks re-growth) 1997. Cores taken to a depth of 30 cm.

a)

	LN	HN	HH	SEM	Prob > F
February	(4 weeks re-growth)				
Weight	181	120	211	21.1	0.1051
Length	52980	44250	78266	6020.5	0.0156
March	(8 weeks re-growth)				
Weight	241	120	211	30.1	0.0392
Length	78266	43046	65322	12040.9	0.1016

b)

	Short (20 mm)	Tall (75 mm)	SEM	Prob > F
February	(4 weeks re-growth)			
Weight	151	181	18.1	0.1294
Length	48465	68332	5117.4	0.0575
March	(8 weeks re-growth)			
Weight	181	211	30.1	0.3925
Length	51776	72547	9331.7	0.1051

c)

	Treading	No treading	SEM	Prob > F
January	(4 weeks re-growth)			
Weight	151	181	18.1	0.9107
Length	55990	61108	5117.4	0.8601
March	(8 weeks re-growth)			
Weight	181	211	30.1	0.5786
Length	56893	67429	9331.7	0.3936

5.3.1.3 Dry matter accumulation

In December, dry matter accumulation was significantly higher on the HH treatment turves than the LN and HN turves (P = 0.0016, Table 5.3a). In March, the sites ranked HH > LN ≥ HN (P = 0.0001) and in May they ranked HH > LN ≥ HN (P = 0.0046) for their influence on dry matter accumulation.

Cutting height significantly influenced dry matter accumulation in all months with the short cutting height turves having significantly greater dry matter accumulation than the tall cutting height turves (Table 5.3b).

Treading did not significantly influence dry matter accumulation in any month (Table 5.3c). Trodden turves produced slightly more dry matter in December 96 (P = 0.3653) and May 97 (P = 0.9686). In January (P = 0.9766), February (P = 0.1329), March (P = 0.4839) and April 97 (P = 0.3388), the untrodden turves accumulated slightly more dry matter than the trodden turves.

5.3.1.4 Tiller density

Tiller density was significantly influenced by site in February, March, April and May 1997 (Table 5.4a). In February the sites ranked HH > HN ≥ LN for their influence on tiller density (P = 0.0064). In March, April and May the sites ranked HH > LN ≥ HN for their influence on tiller density (P = 0.0117, 0.0472, and 0.0071, respectively).

Cutting height significantly influenced tiller density in all months (Table 5.4b). In all months tiller density was significantly higher for the short cutting height than the tall cutting height.

The effect of treading only significantly influenced tiller density in May 97 when the untrodden turves had significantly greater tiller density than trodden turves (P = 0.0165) (Table 5.4c). From January to April, the untrodden turves had greater tiller density than trodden turves, but not significantly so.

Table 5.3 Summary of dry matter accumulation rate (kg DM/ha/day) for (a) site, (b) cutting height and (c) treading treatment.

a)

Month	LN	HN	HH	SEM	Prob>F
Dec 96	36.6	32.2	42.9	2.5	0.0016
Jan 97	34.6	28.2	26.3	3.0	0.0764
Feb	22.6	20.3	24.0	2.0	0.2490
Mar	29.1	24.4	34.4	1.3	0.0001
Apr	12.6	12.6	15.3	1.1	0.1236
May	7.4	6.9	10.9	1.1	0.0046

b)

Month	Short (20 mm)	Tall (75 mm)	SEM	Prob > F
Dec 96	43.3	31.2	2.0	0.0003
Jan 97	38.8	20.7	2.4	0.0001
Feb	27.6	17.0	1.5	0.0001
Mar	32.3	26.3	1.1	0.0003
Apr	15.6	11.7	0.9	0.0018
May	10.1	6.6	0.9	0.0162

c)

Month	Treading	No treading	SEM	Prob > F
Dec 96	38.9	35.5	2.0	0.3653
Jan 97	29.6	29.9	2.4	0.9766
Feb	20.9	23.7	1.5	0.1329
Mar	29.0	29.6	1.1	0.4839
Apr	13.2	14.0	0.9	0.3388
May	8.51	8.25	0.9	0.9686

Table 5.4 Summary of tiller density (tillers/m^2) for (a) site, (b) cutting height and (c) treading treatment.

a)

Month	LN	HN	HH	SEM	Prob>F
Jan 97	23235	21186	26756	2300	0.4248
Feb 97	18811	20515	25804	1300	0.0064
Mar 97	21056	18818	26406	1500	0.0117
Apr 97	18606	16189	23261	1500	0.0472
May 97	14728	13727	18170	900	0.0071

b)

Month	Short (20 mm)	Tall (75 mm)	SEM	Prob > F
Jan 97	27885	19567	1800	0.0004
Feb 97	25829	17591	1000	0.0001
Mar 97	25246	18941	1200	0.0004
Apr 97	22253	16451	1200	0.0012
May 97	17800	13284	900	0.0001

c)

Month	Treading	No treading	SEM	Prob > F
Jan 97	23042	24409	1800	0.7055
Feb 97	20190	23230	1000	0.0778
Mar 97	21366	22821	1200	0.4233
Apr 97	17637	21067	1200	0.0795
May 97	14109	16974	800	0.0165

There was a significant interaction between site and cutting height in February (P = 0.0007), March (P = 0.0001) and April (P = 0.0058). In all months, tiller density was significantly greater on HH site turves with a short cutting height.

5.3.1.5 Leaf extension

Site only had a significant influence on leaf extension in April and May 97 (Table 5.5a). In April the sites ranked HH = HN > LN for their influence on leaf extension (P = 0.0076), and in May the sites ranked HH ≥ HN > LN (P = 0.0001).

Cutting height significantly influenced leaf extension in February, March and May (Table 5.5b). In all those months, leaf extension was significantly greater on the tall cutting height turves (P = 0.0005, P = 0.0001 and P = 0.0001 respectively). In April, leaf extension was still greater on the tall cutting height turves, but not significantly so (P = 0.1375).

There was no significant difference in leaf extension between trodden and untrodden turves (Table 5.5c).

Leaf extension was significantly influenced by factor interactions in February and May. In February, there was a cutting height by species interaction (P = 0.0153), with greater leaf extension rates occurring for *L. perenne* on tall cutting height turves. In May, a treading by species interaction occurred (P = 0.0474) with lower leaf extension rates occurring for *T. repens* on both trodden and untrodden turves.

Table 5.5 Summary of leaf extension rates (mm/day) for (a) site, (b) cutting height and (c) treading treatment.

a)

Month	LN	HN	HH	SEM	Prob>F
Feb 97	3.9	4.5	5.0	0.4	0.0984
Mar 97	3.1	3.1	3.4	0.3	0.0991
Apr 97	2.5	3.2	3.2	0.2	0.0076
May 97	2.6	3.1	3.5	0.2	0.0001

b)

Month	Short (20 mm)	Tall (75 mm)	SEM	Prob > F
Feb 97	3.7	5.2	0.3	0.0005
Mar 97	2.6	3.7	0.2	0.0001
Apr 97	2.9	3.1	0.2	0.1375
May 97	2.7	3.5	0.2	0.0001

c)

Month	Treading	No treading	SEM	Prob > F
Feb 97	4.4	4.6	0.3	0.8417
Mar 97	3.2	3.2	0.2	0.7509
Apr 97	3.2	2.8	0.2	0.2443
May 97	3.1	3.1	0.2	0.9086

5.3.1.6 Dry matter harvest dissection

The abundance of *L. perenne*, other grasses and other species was significantly different between sites (Table 5.6a). The sites ranked HH ≥ HN > LN for their influence on *L. perenne* abundance (P = 0.0041), HH > LN > HN for their influence on other grasses abundance and HN ≥ LN > HH for their influence on other species abundance (P = 0.0289). *T. repens* abundance was greatest for the LN turves, but not significantly greater than the HN and HH turves. Dead matter abundance was greatest on the LN turves and least abundant on the HH turves, but not significantly so.

Cutting height significantly influenced the abundance of other grasses and other species (Table 5.6b). Other grasses were significantly more abundant on the short cutting height turves (P = 0.0001) as were other species (P = 0.0002). There was very little difference (< 1kg DM/ha) between the abundance of *L. perenne*, *T. repens* and dead matter on short and tall cutting height turves.

Treading significantly reduced the abundance of other grass species (P = 0.0352) (Table 5.6c) on the turves.

A significant interaction occurred between the cutting height and treading factors (P = 0.0182). *L. perenne* was more abundant on tall cutting height, untrodden turves and on short cutting height turves with treading.

Table 5.6 Summary of dry matter harvested (on 11 March 1997) above standard cutting heights (of 20 and 75 mm) which was then dissected (kg DM/ha) into 5 categories for (a) site, (b) cutting height and (c) treading treatment.

a)

	LN	HN	HH	SEM	Prob>F
L. perenne	12.4	20.6	25.7	2.8	0.0041
Other grasses	91.6	65.1	138.1	8.0	0.0003
Other species	39.9	41.0	18	7.0	0.0289
T. repens	3.6	1.8	1.8	1.1	0.5223
Dead matter	10.3	7.7	4.1	1.1	0.0683

b)

	Short (20 mm)	Tall (75 mm)	SEM	Prob > F
L. perenne	19.0	20.2	2.0	0.6506
Other grasses	120.6	76.0	7.0	0.0001
Other species	51.4	14.5	6.0	0.0002
T. repens	2.2	2.6	1.0	0.8327
Dead matter	7.6	7.2	2.0	0.6863

c)

	Treading	No treading	SEM	Prob > F
L. perenne	18.6	20.6	2.2	0.6052
Other grasses	86.0	110.6	6.6	0.0352
Other species	33.8	32.1	5.8	0.9667
T. repens	2.3	2.4	0.9	0.7869
Dead matter	7.8	6.9	1.8	0.9585

5.3.1.7 Botanical composition

In January (Table 5.7), the abundance of *C. uniflora* and dead matter was significantly influenced by site effects. *C. uniflora* was more abundant on HN turves than HH turves (P = 0.0197). No *C. uniflora* was present on the LN turves. Dead matter was significantly more abundant on the LN turves (P = 0.0014) than both the HN and HH turves, which did not differ.

In May, the abundance of *C. uniflora*, flatweeds, *L. perenne*, *Muscii* spp., *N. setulosa* and *Poa* spp. was significantly influenced by site. The sites were ranked HN ≥ HH > LN for their influence on *C. uniflora* abundance (P = 0.0001), LN > HN ≥ HH for their influence on flatweed abundance (P = 0.0330) and HN > HH ≥ LN for their influence on *L. perenne* abundance (P = 0.0088). The abundance of *Muscii* spp. was influenced by the sites in the following order LN = HN > HH (P = 0.0414). *Muscii* spp. were not present on the HH turves. The sites were ranked HH > HN ≥ LN for their influence on *N. setulosa* abundance (P = 0.0490) and HH ≥ HN > LN for their influence on *Poa* spp. abundance (P = 0.0124).

In January (Table 5.8), cutting height significantly influenced the abundance of *A. capillaris*, *A. odoratum* and *L. perenne*. These three species were all significantly more abundant on tall cutting height turves (P = 0.0309, 0.0001 and 0.0018, respectively). In May, cutting height significantly influenced the abundance of *A. capillaris* (P = 0.0269), *A. odoratum* (P = 0.0008), dead matter (P = 0.0304), *L. perenne* (P = 0.0283) and *T. repens* (P = 0.0045). In all cases, these species were significantly more abundant on the tall cutting height turves.

Table 5.7 Summary of pasture botanical composition (kg DM/ha) for sites taken one month after treatment application began (January) and at the end of the experiment (May)

Species		Jan	97				May	97		
	LN	HN	HH	SEM	Prob	LN	HN	HH	SEM	Prob
A. capillaris	23	18	20	3.5	0.4725	6	5	6	1.8	0.3475
A. odoratum	8	9	7	1.8	0.4177	3	3	3	1.3	0.6018
C. cristatus	1	2	2	0.7	0.7402	0.6	0.6	0.3	0.3	0.5306
C. uniflora	0	2	0.5	0.4	0.0197	0	5	4	0.8	0.0001
Dead matter	31	18	18	4.0	0.0014	20	15	16	6	0.7286
F. rubra	0.1	0	0	0.04	0.3954	0.1	0.04	0	0.05	0.4516
Flatweeds	6	7	1	2.8	0.1968	21	9	0.3	5	0.0330
H. lanatus	3	1	7	1.3	0.1379	3	1	7	1	0.1233
L. perenne	2	6	5	1.5	0.0729	2	5	3	0.7	0.0088
L. pedunculatus	0.1	0.4	0	0.4	0.5809	0.03	1	0.2	0.4	0.0739
Muscii spp.	3	2	0	1.0	0.1099	1	1	0	0.4	0.0414
N. setulosa	0	2	2	1.1	0.3432	0.3	3	7	1.7	0.0490
Other species	2	3	1	1.2	0.1174	1	6	1	3	0.1420
Poa spp.	0	1	2	0.7	0.0593	0.1	2	3	1	0.0124
T. dubium	0	5	0	0.2	0.0848	0.02	0.02	0.02	0.02	0.7533
T .repens	4	2	5	2.2	0.1513	2	1	1	0.7	0.7817

Table 5.8 Summary of pasture botanical composition (kg DM/ha) for cutting height taken one month after treatment application began (January) and at the end of the experiment (May). Short = 20 mm cutting height and tall = 75 mm cutting height

	Jan 97				May 97			
	Short	Tall	SEM	Prob>F	Short	Tall	SEM	Prob>F
A. capillaris	17	24	2.8	0.0309	4	7	1	0.0269
A. odoratum	3	13	1.4	0.0001	0.2	5	1	0.0008
C. cristatus	1	3	0.6	0.1762	0.6	0.4	0.2	0.6800
C. uniflora	0.5	1	0.3	0.5369	2	4	0.7	0.5170
Dead matter	22	23	3.2	0.7329	7	26	5	0.0304
F. rubra	0.1	0	0.03	0.1804	0	0.1	0.05	0.0722
Flatweeds	2	7	2.2	0.0862	7	12	4	0.1098
H. lanatus	3	5	1.0	0.6614	2	5	0.8	0.3329
L. perenne	2	6	1.2	0.0018	2	4	0.5	0.0026
L. pedunculatus	0.3	0	0.3	0.2943	0.2	0.6	0.4	0.6660
Muscii spp.	2	2	0.9	0.6460	0.7	0.5	0.3	0.6141
N. setulosa	3	0.2	0.9	0.0998	5	3	1	0.2343
Other species	3	2	0.9	0.4398	3	2	2	0.3567
Poa spp.	1	1	0.6	0.9757	0.6	2	0.7	0.0283
T. dubium	0.1	0.2	0.2	0.8238	0.04	0.01	0.02	0.1660
T. repens	3	5	1.8	0.1544	0.3	2	0.5	0.0045

Treading did not significantly influence the abundance of any species in January (Table 5.9). In May 97, the abundance of *C. uniflora* (P = 0.0102), *F. rubra* (P = 0.0459), *H. lanatus* (P = 0.0108) and *L. perenne* (P = 0.0309) was significantly negatively influenced by treading.

Significant interactions between factors occurred in all months in which pasture dissections were carried out. In January, *Rytidosperma* spp. production was increased by site by treading (HN by T and HH by NT) interactions (P = 0.0016) which resulted in yields of 0.09 and 0.07 kg DM/ha respectively. *H. lanatus* production was increased by a site by treading (HH by NT) interaction (P = 0.0346) which resulted in a yield of 11 kg DM/ha. In February, *H. lanatus* production was increased by a site by cutting height (HH by tall) interaction (P = 0.0026), a site by treading (HH by NT) interaction (P = 0.0093), a cutting height by treading (tall by NT) interaction (P = 0.0315) and a site by cutting height by treading (HH by tall by NT) interaction (P = 0.0001) which resulted in yields of 26, 23, 18 and 45 kg DM/ha, respectively. *L. perenne* production was increased by a cutting height by treading (tall by NT) interaction (P = 0.0070) which resulted in a yield of 12 kg DM/ha. *Muscii* spp. production was increased by a site by cutting height by treading (LN by tall by NT) interaction (P = 0.0355) which resulted in a yield of 4 kg DM/ha. Dead matter was increased by site by treading (HN by T and LN by NT) interactions (P = 0.0009) which resulted in yields of 38 and 31 kg DM/ha, respectively. In April, *C. cristatus* production was increased by a site by cutting height by treading (LN by tall by NT) interaction (P = 0.0362) which resulted in a yield of 1.4 kg DM/ha. *T. repens* production was increased by a cutting height by treading (tall by T) interaction (P = 0.0422) which resulted in a yield of 3 kg DM/ha. *N. setulosa* production was increased by a site by cutting height (HN by short) interaction (P = 0.0013), a site by treading (HN by T) interaction (P = 0.0009) and a site by cutting height by treading (HN by short by T) interaction (P = 0.0004) which resulted in yields of 17, 15 and 29 kg DM/ha respectively.

In May, *H. lanatus* production was increased by a site by treading (HH by NT) interaction (P = 0.0261) and a site by cutting height by treading (HH by tall by NT) interaction (P = 0.0229) which resulted in yields of 11 and 18 kg DM/ha. *L. perenne* production was increased by a cutting height by treading (tall by NT) interaction (P = 0.0010) and a site by cutting height by treading (HN by tall by NT) interaction (P = 0.0481) which resulted in yields of 7 and 10 kg DM/ha respectively. *C. uniflora* production was increased by a cutting height by treading (tall by NT) interaction (P = 0.0327) and a site by cutting height by treading (HH by tall by NT) interaction (P = 0.0241) which resulted in yields of 6 and 12 kg DM/ha respectively.

5.3.1.8 Point analysis

5.3.1.8.1 Change in average pasture cover over time

The cover of *C. uniflora*, flatweeds and other species increased during the experimental period (Table 5.10) whereas *L. perenne* and *T. repens* cover tended to decrease. The cover of all other species identified remained reasonably static from December 1996 to May 1997.

Table 5.9 Summary of pasture botanical composition (kg DM/ha) for treading treatments taken one month after treatment application began (January) and at the end of the experiment (May). T = treading and NT = no treading.

	Jan 97				May 97			
	T	NT	SEM	Prob>F	T	NT	SEM	Prob>F
A. capillaris	21	20	2.8	0.4042	7	4	1	0.0983
A. odoratum	8	9	1.4	0.6932	3	3	1	0.8940
C. cristatus	2	2	0.6	0.6313	0.5	0.5	0.2	0.7162
C. uniflora	0.8	0.6	0.3	0.5327	1	4	0.7	0.0102
Dead matter	23	22	3.2	0.9574	12	21	5	0.2151
F. rubra	0.1	0	0.03	0.0763	0	0.1	0.05	0.0459
Flatweeds	5	4	2.2	0.6291	15	5	4	0.0785
H. lanatus	3	5	1.0	0.2218	2	5	0.8	0.0108
L. perenne	4	4	1.2	0.8789	2	4	0.5	0.0309
L. pedunculatus	0.3	0.0	0.3	0.6062	0.05	0.8	0.4	0.1439
Muscii spp.	1	2	0.9	0.2724	0.5	0.7	0.3	0.6711
N. setulosa	1	2	0.9	0.6760	2	5	1	0.1237
Other species	3	2	0.9	0.3524	1	5	2.7	0.3325
Poa spp.	1	1	0.6	0.8782	1	2	0.7	0.5871
T. dubium	0.3	0.1	0.2	0.2857	0.01	0.03	0.016	0.4833
T. repens	6	2	1.8	0.2721	2	1	0.5	0.2469

Table 5.10 Changes in pasture species cover (by point analysis) averaged over all turves for each month

Species	Dec 1996/ Jan 1997	Feb 1997	Mar 1997	Apr 1997/ May 1997
A. capillaris	14	18	14	14
A. odoratum	16	20	21	12
Bare	0	0	0	1
C. cristatus	12	4	6	8
C. uniflora	2	4	5	5
Dead matter	5	7	5	7
F. rubra	0	0	0	0
Flatweeds	10	11	12	12
H. lanatus	7	10	9	9
L. perenne	18	12	12	12
L. pedunculatus	1	1	2	1
Muscii spp.	0	0	0	1
N. setulosa	2	3	1	4
Other species	2	4	7	8
Poa spp.	1	1	1	2
Rytidosperma spp.	0	0	0	0
T. dubium	1	0	0	0
T. repens	8	5	5	3

5.3.1.8.2 Effect of site on the cover of individual species.

In December/January and February, seven species were significantly influenced by site effects, in March five species and in April/May, nine species (Table 5.11 and Figure 5.1). *A. capillaris* was significantly influenced by site effects in December/January, February and April/May. In December/January, *A. capillaris* had significantly more cover on the LN turves (LN > HH ≥ HN), in February and April/May on the HH turves (HH > LN > HN and HH > LN ≥ HN, respectively). *H. lanatus* cover was significantly influenced by site effects in December/January, March and April/May. In all these months, *H. lanatus* had significantly more cover on the HH turves (HH > LN > HN). *L. perenne* cover was significantly influenced by site effects in all months. *L. perenne* had significantly more cover on the HH turves in all months, and less cover on the LN turves, but the LN turves were only significantly less than the HN turves in December/January and April/May. *Poa* spp. cover was significantly influenced by site effects in February and April/May. In February, *Poa* spp. had significantly more cover on HH turves (HH > HN ≥ LN). In April/May, *Poa* spp. had significantly more cover on HH than LN turves, with HN turves intermediate. *L. pedunculatus* was significantly influenced by site effects in February and March. In both months, *L. pedunculatus* had significantly more cover on the HN turves (HN > LN ≥ HH). *C. uniflora* was significantly influenced by site effects in all months. *C. uniflora* had the most cover on the HN turves in all months, but only significantly more than the HH turves in December/January, February and April/May. *C. uniflora* had the least cover on the LN turves, but only significantly less in December/January, March and April/May. *N. setulosa* cover was significantly influenced by site effects in December/January and April/May. In December/January, *N. setulosa* had significantly more cover on HH turves than LN turves, with HN turves intermediate. In April/May, *N. setulosa* again had the most cover on HH turves, but not significantly more than HN turves (HH ≥ HN > LN). Flatweeds were also significantly influenced by site effects in all months. Flatweeds had significantly more cover on LN turves and significantly less on HH turves, with HN turves intermediate. Other species cover was significantly influenced by site effects in February and April/May. In both February and April/May, other species had significantly more cover on HN turves (HN > HH ≥ LN and HN > LN ≥ HH, respectively).

Bare soil was only present in April/May, and had significantly greater cover on the HH turves (HH > LN ≥ HN).

5.3.1.8.3 Effect of cutting height on the cover of individual species.

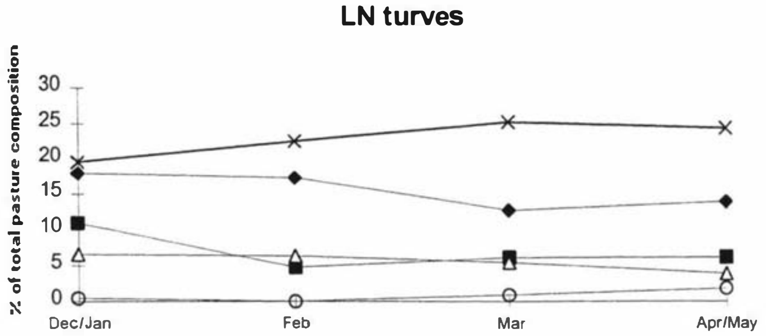
In December/January, the cover of three species was significantly influenced by cutting height; in February and March, six species were affected; and in April/May, nine species (Table 5.12 and Figure 5.2).

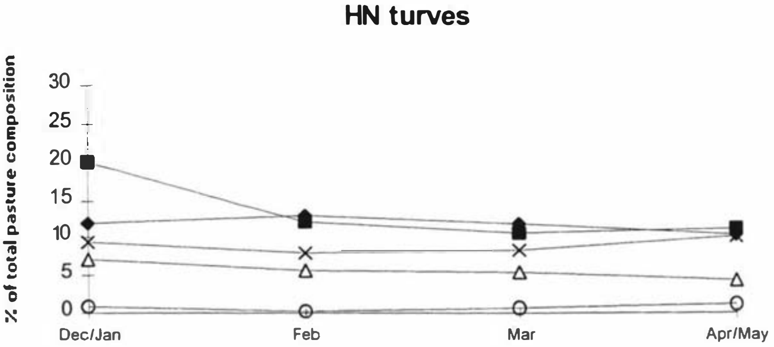
A. odoratum cover was significantly influenced by cutting height in February, March and April/May. In all these months, *A. odoratum* had significantly greater cover on the tall cutting height turves. *C. cristatus* cover was only significantly influenced by cutting height in March, when there was significantly more *C. cristatus* cover on the short cutting height turves. *H. lanatus* cover was significantly influenced by cutting height in February and April/May. In both periods, *H. lanatus* had more cover on the tall cutting height turves. *T. repens* cover was significantly influenced by cutting height in February, March and April/May. In all months, *T. repens* had more cover on the tall cutting height turves. Flatweeds were significantly influenced by cutting height in April/May when more flatweeds were found on the tall cutting height turves. *C. uniflora* cover was significantly influenced by cutting height in December/January, February and April/May. In all months, *C. uniflora* had significantly more cover on short cutting height turves. *Muscii* spp. cover was significantly influenced by cutting height in December/January, March and April/May. In all months, *Muscii* spp. had more cover on the short cutting height turves. *N. setulosa* was significantly influenced in February, March and April/May. As with *Muscii* spp., it had more cover on the short cutting height turves. So too did other species, which were only significantly influenced in March and April/May.

Table 5.11 Summary of Prob>F values for site effects on cover (by point analysis) of each species for each month. A point in the table means that that species was not present.

Species	Dec1996/ Jan 1997	Feb 97	Mar 97	Apr 1997/ May 1997
A. capillaris	0.0372	0.0430	0.1932	0.0056
A. odoratum	0.5083	0.3134	0.3178	0.6381
Bare	.	.	.	0.0001
C. cristatus	0.1418	0.7889	0.5557	0.0752
C. uniflora	0.0001	0.0005	0.0007	0.0001
Dead matter	0.2736	0.0501	0.4862	0.1666
F. rubra	0.6339	.	.	.
Flatweeds	0.0001	0.0001	0.0001	0.0001
H. lanatus	0.0065	0.1051	0.0009	0.0002
L. perenne	0.0001	0.0022	0.0010	0.0001
L. pedunculatus	0.3182	0.0440	0.0051	0.0935
Muscii spp.	0.1884	0.4224	0.2341	0.0787
N. setulosa	0.0245	0.0842	0.1129	0.0031
Other species	0.0854	0.0422	0.0660	0.0141
Poa spp.	0.0587	0.0003	0.0612	0.0265
Rytidosperma spp.	0.4668	.	.	.
T. dubium	0.1009	.	0.4259	0.2623
T. repens	0.0632	0.2291	0.8360	0.5356

Figure 5.1 The effect of site on the % cover (by point analysis) of five categories of species. ◆ =*A. capillaris* ■ = *L. perenne* Δ=*T. repens* x = flatweeds O=*Muscii* spp.





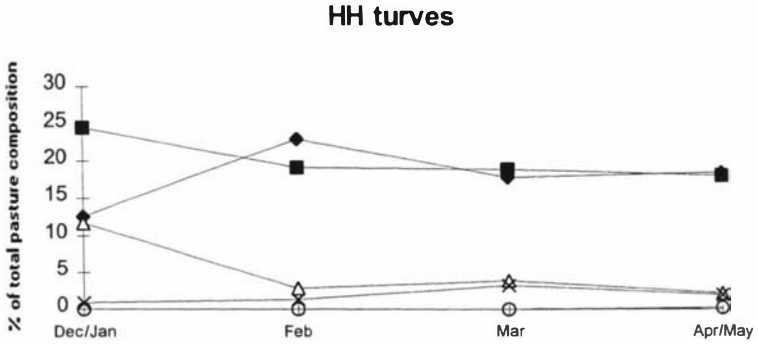
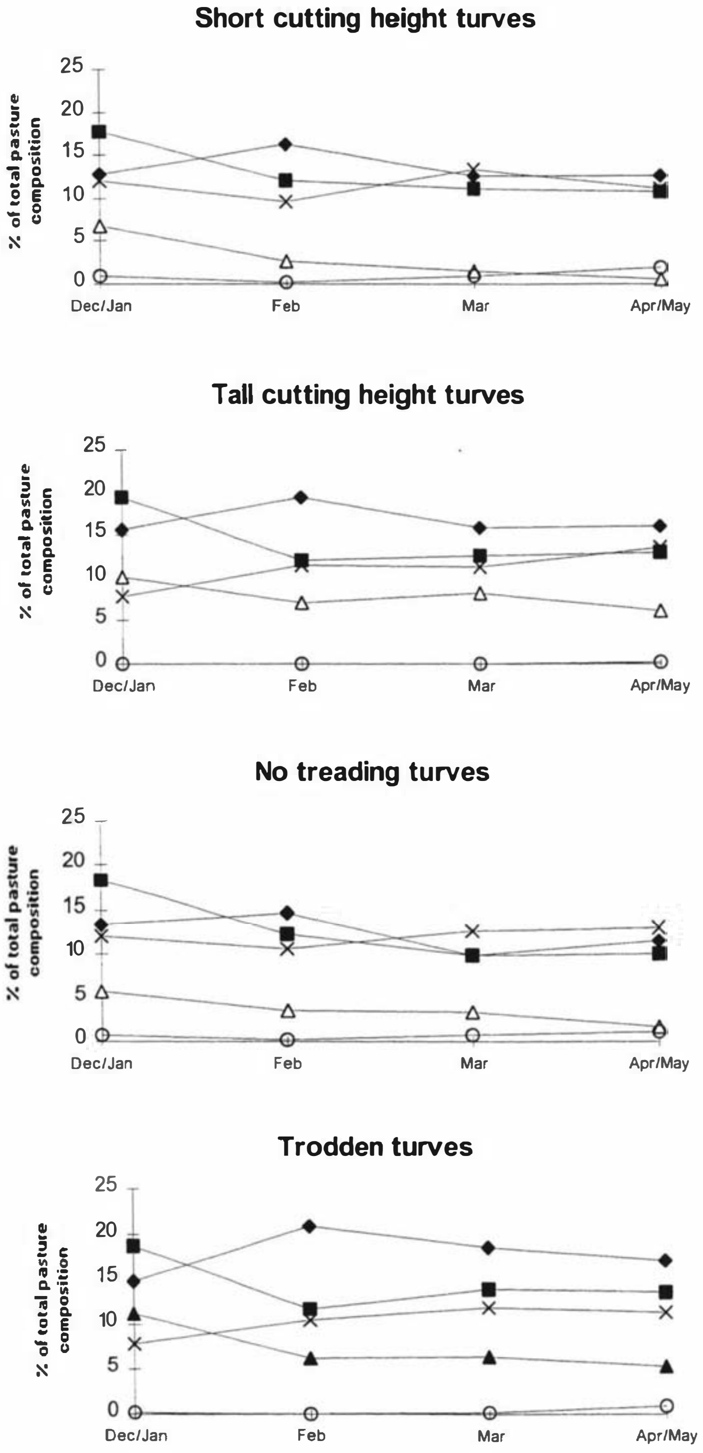


Table 5.12 Summary of Prob>F values for cutting height effects on pasture cover (by point analysis) for each species in each month

Species	Dec 1996/ Jan 1997	Feb 97	Mar 97	Apr 1997/ May 1997
A. capillaris	0.0899	0.3894	0.3647	0.1076
A. odoratum	0.0535	0.0347	0.0020	0.0001
Bare	.	.	.	0.0001
C. cristatus	0.2424	0.5927	0.0248	0.3739
C. uniflora	0.0041	0.0135	0.0610	0.0024
Dead matter	0.0101	0.0118	0.2477	0.2302
F. rubra	0.6473	.	.	.
Flatweeds	0.2858	0.0972	0.8905	0.0054
H. lanatus	0.5298	0.0097	0.9189	0.0045
L. perenne	0.9242	0.5976	0.9939	0.6069
L. pedunculatus	0.5637	0.1531	0.8745	0.0672
Muscii spp.	0.0331	0.3496	0.0438	0.0068
N. setulosa	0.8088	0.0342	0.0196	0.0023
Other species	0.1714	0.2025	0.0135	0.0036
Poa spp.	0.3210	0.4093	0.3194	0.2158
Rytidosperma spp.	0.3797	.	.	.
T. dubium	0.9741	.	0.4366	0.5682
T. repens	0.1530	0.0086	0.0073	0.0007

Figure 5.2 The effects of cutting height and treading on the % cover of five categories of species. ◆ =*A. capillaris* ■ = *L. perenne* Δ=*T. repens* x = flatweeds O=*Muscii* spp.



Short cutting height turves

Tall cutting height turves

No treading turves

Trodden turves

Dead matter cover was significantly influenced by cutting height in December/January and February when there was significantly more dead matter present on the short cutting height turves. Bare soil was only present in April/May and had significantly more cover on short cutting height turves.

In summary, those species whose cover was increased under the tall cutting height regime included *A. odoratum*, *H. lanatus*, *T. repens* and flatweeds. Those species whose cover was increased under the short cutting height regime included *C. cristatus*, *C. uniflora*, *Muscii* spp., *N. setulosa*, other species and dead matter.

5.3.1.8.4 Effect of treading on the cover of individual species.

The cover of two species was influenced by treading in February; three species in March and four species in April/May (Table 5.13).

A. capillaris was significantly influenced by treading in March, when *A. capillaris* had more cover on the trodden turves. *C. cristatus* was significantly influenced by treading in April/May, when *C. cristatus* also had more cover on the trodden turves. *H. lanatus* cover was significantly influenced by treading in February, March and April/May. In all periods *H. lanatus* had more cover on the untrodden turves. *C. uniflora* cover was significantly influenced by treading in March and April/May. In both periods, *C. uniflora* had more cover on untrodden turves. The appearance of bare soil only occurred in April/May, when there was significantly more bare soil present on the trodden turves. The cover of dead matter was significantly influenced by treading in February, when there was more dead matter present on trodden turves.

In summary, those species whose cover was increased under the treading regime included *A. capillaris* and *C. cristatus.* The cover of bare soil and dead matter also increased under this regime. Those species whose cover increased under the no treading regime included *H. lanatus* and *C. uniflora*.

Table 5.13 Summary of Prob>F values for treading treatment effects on pasture cover (by point analysis) for each species in each month

Species	Dec 1996/ Jan 1997	Feb 97	Mar 97	Apr 1997/ May 1997
A. capillaris	0.6189	0.3284	0.0205	0.1422
A. odoratum	0.9232	0.9141	0.5595	0.7302
Bare	.	.	.	0.0001
C. cristatus	0.7263	0.1165	0.5370	0.0158
C. uniflora	0.5026	0.5930	0.0295	0.0284
Dead matter	0.4761	0.0246	0.8456	0.8406
F. rubra	0.8322	.	.	.
Flatweeds	0.8484	0.2308	0.2704	0.3801
H. lanatus	0.1758	0.0032	0.0170	0.0002
L. perenne	0.2551	0.2602	0.7103	0.8297
L. pedunculatus	0.9947	0.9657	0.7977	0.3540
Muscii spp.	0.9376	0.6997	0.8026	0.2062
N. setulosa	0.9347	0.5768	0.3679	0.2891
Other species	0.3306	0.2566	0.1271	0.3227
Poa spp.	0.3256	0.4221	0.5288	0.6425
Rytidosperma spp.	0.7174	.	.	.
T. dubium	0.3733	.	0.5415	0.4832
T. repens	0.0845	0.1767	0.4778	0.0716

5.3.1.8.5 Significant factor interactions

In December/January, *C. uniflora* cover was increased by a site by cutting height (HN by short) interaction (P = 0.0342) which resulted in *C. uniflora* contributing to 6% of cover.

In February, *A. odoratum* cover was affected by site by cutting height by treading interactions (P = 0.0325). There was less *A. odoratum* on HN site by short cutting height by treading and HH site by short cutting height by no treading turves, which resulted in *A. odoratum* contributing to 1 and 9% of cover, respectively. *H. lanatus* cover was increased by a site by cutting height (HH by tall) interaction (P = 0.0029) and a site by treading (HH by NT) interaction (P = 0.0152) which both resulted in *H. lanatus* contributing to 27% of cover. Dead matter cover was decreased by site by treading (HN by NT and HH by NT) interactions (P = 0.0456) and increased by a short cutting height by treading interaction (P = 0.0359) which resulted in dead matter contributing to 1, 4 and 16% of cover, respectively.

In March, *H. lanatus* cover was increased by a site by treading (HH by NT) interaction (P = 0.0060), a cutting height by treading (tall by NT) interaction (P = 0.0428) and a site by cutting height by treading (HH by tall by NT) interaction (P = 0.0012) which resulted in *H. lanatus* contributing to 28, 18 and 41% of cover, respectively. Flatweeds cover was increased by site by cutting height by treading (LN by tall by NT, LN by short by T and HN by short by T) interactions (P = 0.0423), and by site by cutting height (LN by tall, LN by short and HN by short,) interactions (P = 0.0362) which resulted in flatweeds contributing to 38, 37, 33, 32, 26 and 21% of cover, respectively. Flatweeds cover was decreased by a short cutting height by treading interaction (P = 0.0177) which resulted in flatweeds contributing to 9% of cover. *C. uniflora* cover was increased by site by cutting height by treading (HN by short by NT and HH by tall by NT) interactions (P = 0.0418) which resulted in *C. uniflora* contributing to 20 and 14% of cover, respectively. *N. setulosa* cover was increased by a site by cutting height (HN by short) interaction (P = 0.0022) and a site by cutting height by treading (HN by short by T) interaction (P = 0.0181) which resulted in *N. setulosa* contributing to 6 and 10% of cover, respectively.

In April/May, *A. capillaris* had less cover on HN site by short cutting height turves (P = 0.0240) and more cover on tall cutting height by treading turves (P = 0.0135) resulting in *A. capillaris* contributing to 4 and 19% of cover, respectively. *H. lanatus* cover was increased by a site by treading (HH by NT) interaction (P = 0.0076) and a site by cutting height by treading (HH by tall by NT) interaction (P = 0.0157) which resulted in *H. lanatus* contributing to 21 and 29% of cover, respectively. *L. perenne* cover was increased by site by cutting height (HH by short, HN by tall and HH by tall) interactions (P = 0.0089) which resulted in *L. perenne* contributing to 20, 16 and 15% of cover, respectively. Flatweed cover was increased by a site by cutting height (LN by tall) (P = 0.0034) interaction, and a site by cutting height by treading (LN by tall by NT) interaction (P = 0.0396) which resulted in flatweeds contributing to 34 and 41% of cover, respectively. Flatweeds cover was decreased by a cutting height by treading (short by NT) interaction (P = 0.0137) which resulted in flatweeds contributing to 8% of cover. *C. uniflora* cover was increased by a site by treading (HN by NT) interaction (P = 0.0188) which resulted in it contributing to 16% of cover. *N. setulosa* cover was increased by site by cutting height (HN by short and HH by short) interactions (P = 0.0143), site by treading (HH by NT and HN by T) interactions (P = 0.0003) and site by cutting height by treading (HN by short by T and HH by short by NT) interactions (P = 0.0114) which resulted in *N. setulosa* contributing to 15, 14, 17, 12, 25 and 22% of cover, respectively. Dead matter cover was increased by a LN site by short cutting height interaction (P = 0.0071) which resulted in it contributing to 12% of cover. Bare soil was increased by a site by cutting height (HH by short) interaction (P = 0.0001), a site by treading (HH by T) interaction (P = 0.0001), a cutting height by treading (short by T) interaction (P = 0.0001) and a site by cutting height by treading (HH by short by T) interaction (P = 0.0001) which resulted in bare soil contributing to 5, 5, 4 and 10% of cover, respectively.

5.3.1.9 Functional Groups

5.3.1.9.1 Dry matter production from functional groups

A. capillaris production increased slightly from January to February, then decreased to a low of 6.53 kg DM/ha/day in May (Table 5.14). High fertility responsive grass production also increased from January to February, then decreased again in April. Low fertility tolerant grass production also increased from January to February, then decreased to a low of 3.91 kg DM/ha/day in May. *L. perenne* production followed the same pattern as low fertility tolerant grasses and reached a low of 2.74 kg DM/ha/day in May. Other legumes production decreased from January to April and then increased to higher than initial January levels in May (0.77 kg DM/ha/day). Other species production increased steadily from January through to May, *T. repens* production decreased from January to April and then increased again to 1.36 kg DM/ha/day. Flatweed production fluctuated, having peaks of dry matter production in February and May, with the greatest production of flatweed dry matter occurring in May.

5.3.1.9.2 Effect of site on functional groups

In January, the abundance of high fertility responsive grass and other species groups was significantly influenced by site (Table 5.15). High fertility responsive grasses were most abundant on HH turves (HH > LN ≥ HN) and other species were most abundant on HN turves (HN > LN ≥ HH). In February, the abundance of high fertility responsive grasses, *L. perenne*, other species and flatweeds were significantly influenced by site. High fertility responsive grasses were most abundant on HH turves (HH > HN ≥ LN), *L. perenne* was most abundant on HN turves (HN > HH ≥ LN), other species were most abundant on HN turves (HN > HH with LN intermediate), and flatweeds were most abundant on LN turves (LN > HN ≥ HH). In April, the abundance of other legumes, other species and flatweeds were significantly influenced by site effects. Other legumes abundance was greatest on HN turves (HN > LN ≥ HH), other species abundance was also greatest on HN turves (HN > HH > LN) and flatweeds were most abundant on LN turves (LN > HN > HH). In May, like February, the abundance of high fertility responsive grasses, *L. perenne*, other species and flatweeds was influenced by site effects. High fertility responsive grass abundance was greatest on HH turves (HH > HN ≥ LN), *L. perenne* abundance on the HN turves (HN > HH ≥ LN), other species abundance on the HN turves (HN ≥ HH > LN) and flatweeds on the LN turves (LN > HN > HH).

Table 5.14 Dry matter production (kg DM/ha/day) from functional groups. HFRG represents high fertility responsive grasses, LFTG represents low fertility tolerant grasses, OL represents other legumes and OS represents other species.

Functional group	January 97	February 97	April 97	May 97
A. capillaris	19.29	19.49	10.63	6.53
HFRG	4.22	7.34	5.04	5.27
LFTG	10.00	14.19	5.56	3.91
L. perenne	4.75	5.69	2.82	2.74
OL	0.60	0.58	0.38	0.77
OS	5.76	6.32	7.34	9.37
T. repens	4.86	2.29	0.98	1.36
Flatweeds	4.77	6.78	3.87	8.64
SEM	1.122	1.349	1.028	1.366
Prob > F	0.0001	0.0001	0.0001	0.0001

Table 5.15 Summary of Prob > F values (dry matter production (kg DM/ha/day)) for functional groups for 3 sites in 4 months.

Functional group	January 97	February 97	April 97	May 97
A. capillaris	0.4725	0.4171	0.2331	0.3475
HFRG	0.0160	0.0291	0.1691	0.0121
LFTG	0.3061	0.1408	0.9083	0.7498
L. perenne	0.0729	0.0483	0.1151	0.0088
OL	0.1955	0.2305	0.0446	0.0726
OS	0.0178	0.0182	0.0022	0.0022
T. repens	0.1513	0.2633	0.2974	0.7817
Flatweeds	0.1968	0.0002	0.0003	0.0330

5.3.1.9.3 Effect of cutting height on functional group abundance

In January, the abundance of *A. capillaris*, low fertility tolerant grasses and *L. perenne* was significantly influenced by cutting height (Table 5.16). Each of these three functional groups was more abundant on the tall cutting height turves. In February, the abundance of high fertility responsive grasses, low fertility tolerant grasses and *L. perenne* was significantly influenced by cutting height. Again, all three functional groups were more abundant on tall cutting height turves. In April, the abundance of *A. capillaris*, high fertility responsive grass, low fertility tolerant grass, *L. perenne* and *T. repens* functional groups was significantly influenced by cutting height. All five functional groups were more abundant on tall cutting height turves. The same functional groups were significantly influenced by cutting height in May. They too were more abundant on tall cutting height turves.

5.3.1.9.4 Effect of treading on functional group abundance

No functional groups were influenced by treading in January (Table 5.17). In February, the abundance of the high fertility responsive grass functional group was significantly influenced by treading. This group was more abundant on the untrodden turves. In April, the *T. repens* functional group was significantly more abundant on the trodden turves. In May, the high fertility responsive grass, *L. perenne* and other species functional groups were significantly more abundant on untrodden turves. The flatweeds functional group was most abundant on the trodden turves.

Table 5.16 Summary of Prob > F values (dry matter production (kg DM/ha/day)) for functional groups for 2 cutting heights in 4 months.

Functional group	January 97	February 97	April 97	May 97
A. capillaris	0.0309	0.0506	0.0184	0.0269
HFRG	0.6600	0.0099	0.0164	0.0288
LFTG	0.0001	0.0001	0.0001	0.0006
L. perenne	0.0018	0.0022	0.0001	0.0026
OL	0.4050	0.2905	0.7767	0.7119
OS	0.1298	0.7340	0.1451	0.0862
T. repens	0.1544	0.2247	0.0007	0.0045
Flatweeds	0.0862	0.6831	0.5918	0.1098

Table 5.17 Summary of Prob > F values (dry matter production (kg DM/ha/day)) for functional groups for 2 treading treatments in 4 months.

Functional group	January 97	February 97	April 97	May 97
A. capillaris	0.4042	0.6319	0.4016	0.0983
HFRG	0.2734	0.0127	0.0533	0.0472
LFTG	0.5879	0.1652	0.8531	0.9061
L. perenne	0.8789	0.3514	0.7038	0.0309
OL	0.9954	0.4786	0.8424	0.1374
OS	0.8775	0.9726	0.3775	0.0170
T. repens	0.2721	0.2886	0.0067	0.2469
Flatweeds	0.6291	0.8114	0.1791	0.0469

5.3.1.9.5 Significant interactions which influenced the abundance of functional groups

In February, high fertility responsive grass abundance was increased by the following interactions: HH site by tall cutting height (P = 0.0015), HH site by no treading (P = 0.0162), tall cutting height by no treading (P = 0.0189) and HH site by tall cutting height by no treading (P = 0.0006) which resulted in the high fertility responsive functional group contributing to 11, 12, 8 and 17% of cover, respectively. *L. perenne* functional group abundance was also increased by a tall cutting height by no treading interaction in February (P = 0.0070) which resulted in it contributing to 12% of cover. In April, the abundance of the *T. repens* functional group was increased by a tall cutting height by treading interaction (P = 0.0422) which resulted in it contributing to 3% of cover. In May, the abundance of the *L. perenne* functional group was increased by a tall cutting height by no treading interaction (P = 0.0010) and a HN site by tall cutting height by no treading interaction (P = 0.0481) which resulted in the *L. perenne* functional group contributing to 7 and 10% of cover, respectively.

5.3.1.10 Treatment effects on species richness

It was observed from the December/January and February point quadrat analyses, that there were significantly more species on the HN turves (P = 0.002). From the April/May quadrat analysis there were significantly fewer species present on the LN turves (P = 0.0027). The HN turves still had the greatest species richness, but not significantly greater than the HH turves.

The cutting height and treading factors did not significantly influence species richness.

5.3.1.11 Species richness versus dry matter accumulation

There was no significant relationship between species richness and dry matter accumulation when data was pooled over all months of the experiment and over all turves, nor when the relationship between species richness and dry matter accumulation was examined for each month.

5.3.1.12 Leaf extension and dry matter accumulation

Only the *T. repens* functional group showed a significant relationship between leaf extension and dry matter accumulation (P = 0.0150) (data averaged for February, April and May 1997). The relationship was negative (correlation coefficient = -0.4021). Of the remaining four functional groups tested for the relationship (low fertility tolerant grasses, high fertility responsive grasses, *A. capillaris* and *L. perenne*), the relationship was found to be positive, but non-significant.

Leaf extension was also regressed with dry matter accumulation for each functional group under each treatment to see if the relationship differed under the treatments. Significant relationships between leaf extension and dry matter accumulation were found for *T. repens* on the HN turves (P = 0.0314, R^2 = 38%), *T. repens* on the tall cutting height turves (P = 0.0064, R^2 = 38%) and *T. repens* on the trodden turves (P = 0.0285, R^2 = 27%).

5.3.1.13 Tiller number and dry matter accumulation

Relationships between tiller number and dry matter accumulation (Table 5.18) were only observed on the HH turves in April, HN turves in January, LN turves in January and February, tall cutting height turves in April and May, short cutting height turves in February and April, trodden turves in January, February and April and the untrodden turves in February and April.

In April, 5 of the 7 treatments showed a significant relationship between tiller number and dry matter accumulation. The HN and LN treatments were the two exceptions.

Table 5.18 Significance and fit of regression (R^2 and Slope) between tiller density and dry matter accumulation for 5 months for each treatment.

	Site			Cutting height		Treading	
	HH	HN	LN	Tall	Short	T	NT
January							
Prob > F	0.0522	0.0331	0.0054	0.1550	0.1565	0.0008	0.0671
R^2	33	38	56	12	12	51	19
Slope	+1.0	+1.5	+0.5	+0.4	+0.4	+0.7	+0.6
February							
Prob > F	0.0544	0.2247	0.0020	0.5004	0.0002	0.0154	0.0001
R^2	32	14	63	3	60	31	72
Slope	+0.5	+0.5	+0.9	+0.2	+0.9	+0.9	+0.8
March							
Prob > F	0.4211	0.5394	0.1911	0.3931	0.5007	0.1862	0.5433
R^2	7	4	16	5	3	11	2
Slope	-47.6	+61.0	-317.2	-31.5	+65.6	-109.6	-36.1
April							
Prob > F	0.0001	0.2051	0.0572	0.0117	0.0025	0.0003	0.0106
R^2	83	16	32	34	45	57	34
Slope	+0.9	+0.6	+1.0	+0.7	+0.6	+0.7	+0.7
May							
Prob > F	0.0819	0.2673	0.1273	0.0305	0.7832	0.0595	0.6881
R^2	27	12	22	26	0.5	20	1
Slope	-0.7	+0.7	+0.3	+0.5	+0.1	+0.4	-0.1

5.4 Discussion

5.4.1 Species responses to applied factors over time

5.4.1.1 Site factor

The soil nutrient concentration of the turves (December 1996) showed that the HH turves were significantly more fertile than either the LN or HN turves (Ca, Olsen P and S). Though fertility was generally slightly higher on the HN turves, they had similar fertility to the LN turves, despite having had different management imposed on them over the last 20 years, and as a result having quite different relative abundance's of individual species and plant structures.

The turves basically had the same species present, with a few exceptions. In the analysis of species richness there were significantly more species present at the start of the experiment on the HN turves and significantly fewer species present on the LN turves at the end of the experiment. The difference in species richness that made them significantly less or greater, was only a change in one or two species. On some turves some species were present in such small quantities, that they appeared to be absent from the sward in the botanical analyses. For example *C. uniflora*, *N. setulosa*, *Poa* spp. and *T. dubium* on the LN turves; *F. rubra* on the HN turves and *F. rubra*, *L. pedunculatus*, *Muscii* spp. and *T. dubium* on the HH turves.

The absence of these species described above on the particular treatment turves indicated they were either averse to the conditions present on the turves, or they were not present on the turves in great abundance at that time in the season. There may have been seasonal effects influencing the abundance of the annual *T. dubium*. It was present on all the turves in the May sample, but only on the HN turves in the January samples. That *C. uniflora* was not present on the LN turves at any time in the season indicated that the low fertility conditions and management that had been imposed on the LN turves were not conducive to *C. uniflora* growth. *Muscii* spp. showed the opposite pattern and were present on the LN and HN turves, but not the HH turves. Flatweeds showed the same pattern as *Muscii* spp., but in a more clearly defined manner because of the overall greater abundance of flatweeds. The abundance of flatweeds decreased markedly from LN to HH turves, with HN turves being intermediate. This group of species, with its very distinctive distribution, may be useful as an indicator species. To define exactly what the abundance of flatweeds is indicating is difficult, as there are not just fertility effects involved, though this may be a leading contributing factor. The remnant effects of the management (e.g. stocking rate and grazing system used) imposed could also affect the abundance of flatweeds. However, as a general indicator of nutrient status and intensity of grazing, flatweeds abundance may be of some use.

H. lanatus was significantly more abundant on the HH turves than either the LN or HN turves, but the HN turves had less *H. lanatus* than the LN turves. This would not be expected if the response was primarily due to fertility as the HN turves were slightly more fertile than the LN turves. Again this illustrates that the management factors rather than fertility alone were having an influence on the abundance of some species. There was a change in the abundance of *A. capillaris* as the season progressed. *A. capillaris* was much more abundant in the January pasture dissection than in May. This may have been due the ability of *A. capillaris* to increase in abundance in moist summer conditions (refer Chapter 6) and become dominant in the sward.

5.4.1.2 Cutting height factor

The cutting heights significantly influenced the abundance of *A. capillaris*, *A. odoratum* and *L. perenne* in January and *A. capillaris*, *A. odoratum*, dead matter, *L. perenne*, *Poa* spp. and *T. repens* after 4 months of treatment (May). That the abundance of more species were influenced by cutting height at the end of the experiment than the start, was probably due to the treatment requiring a long period of time for the individual species to respond to it.

L. perenne, *A. odoratum*, and *A. capillaris* were all found to be more abundant on the tall cutting height turves, and of these species, *A. capillaris* was most abundant. Studies carried out by Harris and Thomas (1972) comparing the growth of *L. perenne* and *A. capillaris* in differently grazed swards showed that under lax grazing (8 cm cutting height), *L. perenne* was always more abundant and more competitive than *A. capillaris*. *L. perenne* usually dominated *A. capillaris* in a sward by being much faster growing in the establishment phase and by having a tall erect growth habit which enabled *L. perenne* to intercept more light. The period of pasture establishment had passed in the turf swards and over time the management conditions imposed (usually short grazing by sheep) had favoured *A. capillaris* growth (Lambert *et al.* 1986a). This resulted in a greater abundance of *A. capillaris* than *L. perenne* in the sward, which remained when the cutting height treatments were imposed. The levels of *A. capillaris* and *L. perenne* in the sward were similar in the second pasture dissection in May and this may be indicative of *A. capillaris* being a winter dormant species. That 24 of the 36 turves had similar, low fertility levels (LN and HN turves had similar nutrient composition) may have influenced the comparison of *A. capillaris* and *L. perenne* abundance when averaged over all turves. *A. capillaris* is a low fertility tolerant grass species (Lambert *et al.* 1986a) and is capable of sustaining growth in low fertility environments, unlike *L. perenne* which is more responsive to high fertility situations (Lambert *et al.* 1986a). Because of the greater numbers of low fertility turves, it was likely that most would be *A. capillaris* dominant.

By the end of the experiment (May), dead matter was significantly more abundant on the tall cutting height turves. It appeared that the amount of dead matter on the short cutting height turves had decreased rather than dead matter on the tall cutting height turves increasing. In January, dead matter accounted for 22 and 23% of total cover on the short and tall cutting height turves, respectively. In May, dead matter accounted for 7% on the short cutting height turves and 26% on the tall cutting height turves. From the full pasture dissection, dead matter was found to be more abundant under the tall cutting height treatment, but from the point analysis, dead matter cover was greater under the short cutting height treatment. This conflicting result was probably a result of the point analysis technique for estimating the cover of particular pasture components. Most dead matter occurs in the base of a sward, hence if the pasture was short, live plant material was in the same strata in the sward as dead material, and its contribution to cover can be estimated. In taller swards, dead matter content is often underestimated because the needle rarely gets to a depth in the sward where most dead matter is present, without hitting a live plant specimen first. Therefore, the pasture dissection data was more likely to be representative of the amount of dead matter in the sward.

Abundance of *T. repens* was less in May than in January, but in May, the tall cutting height turves had significantly more *T. repens* dry matter than the short cutting height turves. The short cutting height resulted in significantly greater tiller numbers, resulting in a much denser sward than the tall cutting height turves. More open swards (as with the tall cutting height) enabled *T. repens* to colonize through lateral spread of stolons into gaps in the sward (Lambert *et al.* 1986a). Very tall swards are not entirely conducive to *T. repens* growth either, as more erect plants shade the prostrate *T. repens.*

The greater abundance of *Poa* spp. on the tall cutting height turves in May, may have been due to the same reasons as *T. repens* abundance. *Poa annua* requires gaps in the sward in order to establish (Grime *et al.* 1988) and on the short cutting height turves, the sward was probably too dense for this to occur. Also, *Poa* spp. have an erect growth habit (Grime *et al.* 1988) which enables them to compete well with lower growing species in the tall cutting height turves.

5.4.1.3 Treading factor

Treading had no significant influence on the abundance of any species in the January pasture dissection. This was most likely due to the treatment having been applied for only a short period of time and any influence of treading may not have been apparent at this stage. After 5 months of treading, *C. uniflora*, *F. rubra*, *H. lanatus* and *L. perenne* were significantly ($P<0.05$) less abundant than on the trodden turves.

H. lanatus was described by Grime *et al.* (1988) as being intolerant of close grazing and heavy trampling due the species having lax tillering and relatively few shoot buds. The shoots of *H. lanatus* were also erect, which when combined with the fact that the species has few shoot buds, makes them susceptible to treading damage. Hence its greater abundance under the no treading treatment. *H. lanatus* was the pasture species least tolerant of treading of the 10 tested by Edmond (1964).

C. uniflora abundance was negatively influenced by the treading treatment. Work has been carried out by Harrington and Rahman (1998) on *C. uniflora* resistance to herbicide and by Sykes and Wilson (1990) on the burial of the species in sand dunes, but relatively little is known about this species in pastures and how it responds to management changes. This experiment showed that it was more abundant on the untrodden turves, indicating that it is a treading intolerant species. This would be expected as it is a native species of New Zealand and has evolved in an environment of very little, if any, treading.

The negative effect of treading on *L. perenne* abundance was consistent with the results of work carried out by Edmond (1964). *L. perenne* is often described as being tolerant of trampling and grazing (Grime *et al.* 1988). This statement needs to be quantified somewhat. There are two main responses of plants to such a stress as treading. They are resistance to the treading and resilience. Resistance is the ability of a plant to keep functioning whilst being influenced by a stress and is synonymous with the term tolerance. Resilience on the other hand is the ability of a plant to recover after the stress has been removed. Davis *et al*. (1994) described *L. perenne* as being a resilient rather than resistant species under water stress. It appeared that the treading stress also reduced yield, indicating that *L. perenne* was not resistant to treading. The recovery of *L. perenne* following the treading stress is discussed in more detail in Chapter 6.

5.4.1.4 Factor interactions

Species that showed significant interaction effects in the months where full pasture dissections were carried out (January, February, April and May) included *Rytidosperma* spp., *H. lanatus, L. perenne* , *Muscii* spp., dead matter, *C. cristatus, T. repens, N. setulosa and C. uniflora.* *H. lanatus* showed significant interactions in three of the four months and *L. perenne* in two of the four months. All other species interactions were specific to one month.

H. lanatus consistently showed the same interactions. The abundance of *H. lanatus* was promoted on HH by no treading, HH by tall cutting height, tall cutting height by no treading and HH by tall cutting height by no treading treatments. From this information we can surmise that *H. lanatus* growth was most suited to an environment of high fertility, moderate defoliation height and no treading. This is supported by Grime *et al*. (1988) who stated that *H. lanatus* was not tolerant of close grazing or heavy trampling.

L. perenne abundance was increased on turves where both the tall cutting height and no treading occurred. These conditions suited *L. perenne* because of its erect growth habit. It was able to dominate in a tall sward and increase light interception at the expense of other species. Absence from treading preserved tiller numbers and leaves were not physically damaged, hence light interception and photosynthesis were maximized. A three way interaction between HN by tall cutting height by no treading also occurred. Grime *et al.* (1988) describe *L. perenne* as having high nutrient requirements, and as being highly productive on fertile soils. From this, the ideal conditions for *L. perenne* would be expected to be HH by tall cutting height by no treading, but this does not appear to be the case for the turves.

In January, *Rytidosperma* spp. were more abundant on HN by trodden and HH by untrodden turves. This indicated that under low fertility conditions (HN site), treading increased abundance and under high fertility conditions, *Rytidosperma* spp. abundance was greater when there was no treading. *Rytidosperma* spp. are low fertility tolerant grass species (Lambert *et al*. 1986a), hence they were capable of growth on the HN turves. Treading may have caused enough gaps in the sward to reduce competition from other species and allowed *Rytidosperma* spp. to increase in abundance. Under high fertility conditions (HH), tillering of *Rytidosperma* spp. probably increased. Absence from treading meant that tiller numbers were not reduced through direct damage to the plant, hence abundance of *Rytidosperma* spp. was increased.

Muscii spp. were responsive to a three way interaction (LN by tall cutting height by no treading), which increased their abundance. In earlier hill pasture surveys (see Chapter 3), *Muscii* spp. were found to be most abundant under low fertility conditions. Due to their low growth habit, a tall defoliation height meant that only a small proportion of their biomass was removed at each cut. Treading would have created gaps in the sward and allowed other more competitive species to grow into these gaps, hence reducing the abundance of *Muscii* spp.

Dead matter was most abundant on the HN by treading and LN by no treading turves in February. This difference in the effects of treading is difficult to explain as the HN and LN turves had similar fertility. One explanation could be that it was not a fertility by treading interaction but a past history by treading interaction. The histories imposed on the HN and LN sites may have resulted in different species compositions developing. A combination of species that were not tolerant to treading may have developed on the HN turves and those tolerant to treading on the LN turves.

In April, *C. cristatus* was most abundant on LN, un-trodden turves. Lambert *et al.* (1986a) described *C. cristatus* as being a low fertility tolerant grass, and

Grime *et al.* (1988) stated that it had a marked restriction to heavily grazed short turf, indicating that was relatively intolerant of treading. *T. repens* abundance was greater on the tall cutting height and trodden turves. The tall cutting height meant that *T. repens* was defoliated very little, due to its prostrate growth habit. Treading enhanced the abundance of *T. repens* in the sward by creating gaps which *T. repens* stolons could colonize (Lambert *et al.*1986a).

N. setulosa was most abundant in April on HN by short cutting height, HN by trodden and HN by short cutting height by trodden turves. This indicated that the conditions most suitable for *N. setulosa* growth in April were low to moderate fertility, short defoliation height and treading. *N. setulosa* has a very prostrate growth habit and therefore very little material would be removed under short defoliation. The short cutting height would have removed more erect and competitive species allowing *N. setulosa* to intercept more light. The treading would allow *N. setulosa* to act in a similar manner to *T. repens*, by enabling it to colonize gaps in the sward.

In May, *C. uniflora* was most abundant under tall cutting height by no treading and HH by tall cutting height by no treading conditions. *C. uniflora* is a native species of New Zealand which has evolved under conditions with no grazing, hence it would be expected to be more abundant when treading was not present. *C. uniflora* also appeared to be a rather erect species and when left uncut, tended to grow reasonably tall, however most of the material under a lax cutting height would be stem rather than leaf. Little is known about the conditions conducive to *C. uniflora* growth. It is, however, commonly found in sand dunes which would tend to have low fertility. In this experiment it appeared that *C. uniflora* growth was responding to high fertility when combined with the effects of lax cutting height and no treading.

5.4.2 Dry matter accumulation

5.4.2.1 Sites

Dry matter accumulation on the turves was significantly different between sites in December, March and May. In these 3 months, the HH turves produced significantly more dry matter than any other. In March the HH turves produced the most, the HN turves the least and the LN turves were intermediate. The HN turves and LN turves were not significantly different in terms of chemical fertility, so some other factor must have been influencing dry matter accumulation in March. It may have been that different species were present on the LN and HN turves as a result of the management histories imposed on the sites for the last 20 years. There may have been conditions in March (e.g. hot weather) that favoured the species present on the LN turves. Another explanation could be that dead matter increased on the LN turves in March (due to summer conditions) which resulted in higher levels of dry matter accumulation.

The reason that HH turves produced the most dry matter was most likely to be their high level of fertility which would allow highly productive species such as *L. perenne* to grow uninhibited.

5.4.2.2 Cutting height

The short cutting height turves consistently accumulated more dry matter than the tall cutting height turves. This contradicted the many experiments summarized by Harris (1978) that showed more frequent and more intensive defoliation resulted in a reduction of herbage dry matter yield.

Cutting the pastures to 20 mm meant that prostrate species such as *L. pedunculatus*, *N. setulosa* and *Muscii* spp. became included in the harvested material, whereas with a tall cutting height, this would not occur. This result was illustrated in the dissection of the cut material harvested. On the short cutting height turves, other species contributed 51.4 kg DM/ha, but on the tall cutting height turves only 14.5 kg DM/ha was contributed by other species.

The tall cutting height would also result in the shading of less erect growing species, resulting in their decreased growth. This appeared to have occurred for some members of the other grasses group (all grass species present except *L. perenne*). For the tall cutting height treatment, other grasses contributed 79 kg DM/ha, but for short cutting, other grasses contributed 120.6 kg DM/ha. The other grass group may have been less competitive for the tall cutting height. Under short cutting there would have been more available light for all species in the sward strata to intercept hence increasing overall dry matter accumulation on the turves.

5.4.2.3 Treading

Treading did not significantly influence herbage accumulation in any month. Herbage accumulation rate was actually higher on the trodden turves in December and May, but less on the trodden turves in the remaining months. This result occurred because the treading treatment may not have been intense enough. A balance between competition restricting growth on the untrodden turves and increased gaps in the sward of the trodden turves in which species could colonize may have occurred resulting in similar herbage accumulation rates under both treatments.

5.4.3 Tillers

5.4.3.1 Sites

In all months of the experiment, except January, tiller numbers were significantly greater on the high fertility turves. Matthew *et al.* (1988) in a survey of lowland pasture found that tiller density of some species (e.g. *L. perenne*) increased with increasing fertility and the tiller density of other species (e.g. *A. odoratum*) decreased. Lambert *et al.* (1986b) noted that *L. perenne* tiller density was greater under high fertility than low fertility conditions, but tiller weight was less under high fertility conditions. Other grasses (e.g. *A. capillaris*, *A. odoratum*, *C. cristatus*, *F. rubra* and *Rytidosperma* spp. (low fertility tolerant grasses) and *H. lanatus* and *Poa* spp. (high fertility responsive grasses) (Lambert *et al.* 1986b) tillers were heavier in low fertility pasture than high fertility pastures. According to Bircham (1981) where tillers are large, there are usually fewer of them than for smaller tillers. That is, there is a negative relationship between tiller density and tiller weight. Lambert *et al.* (1986b) also found that density of other clover plants was greatest on low fertility pastures, as was moss. The density of *T. repens* nodes was greater under high fertility conditions. *A. capillaris* was the most abundant species present on the HH turves in January, hence its tillering response to fertility would contribute greatly to total tiller numbers on the HH turves.

5.4.3.2 Cutting height

Tiller density was significantly greater on the short cutting height turves throughout the experiment. Bircham (1981) found that at high herbage mass (e.g. as on the tall cutting height turves) tillers were large, but few. At low herbage mass (e.g. as on the short cutting height turves) tiller numbers were greater, but tillers were smaller. Tiller weight was not measured on the turves, but according to Bircham's (1981) findings it would have been less per tiller on the short cutting height turves. This size/density relationship for tillers is determined by the amount of light penetrating to ground level. Rate of leaf appearance and therefore rate of tiller development is strongly influenced by the amount of light reaching the base of grass tillers (Mitchell and Coles, 1955). In a short sward therefore, where light interception is high at the base of grass tillers, many tillers are produced, but competition between plants is strong hence their tillers are small (Smetham, 1994). Under tall cutting height treatment, shading reduced the amount of light penetrating to tiller bases, reducing tillering rates. The tillers that survived because they were tall, grew large due to reduced intra-plant competition for nutrients.

5.4.3.3 Treading

Treading only significantly influenced tiller density in May 1997 when tiller numbers were greater on the untrodden turves. Many species reduce growth rates or cease growing in the winter months, which might explain the decrease in tiller density per m^2 on both the trodden and untrodden turves in May. This reduction in growth rate would mean that any tillers damaged physically by the treading treatment would not be replaced, resulting in significantly fewer tillers on the trodden turves.

5.4.4 Tiller density and dry matter accumulation

The relationship between tiller density and dry matter accumulation was quite variable between months and treatments. For example, in March, none of the seven treatments exhibited a significant relationship between tiller density and dry matter accumulation, but in April, five of them did (HH site, tall and short cutting height and treading and no treading). There appeared to be no defined pattern as to which treatment exhibited a significant relationship between tiller density and dry matter accumulation. When it did occur significantly, it occurred most frequently on the trodden turves (in three of the five months). Treading had the effect of reducing tiller density by physically damaging plant growing points. This in turn reduced the amount of dry matter produced.

These results suggest in general, that management imposed on a pasture often results in changes in tiller density and dry matter accumulation and that the relationship between these two factors is positive. Management's imposed, therefore, need to take into account the effect on tiller density in order to maintain high levels of production. Treading, for example, was shown in this experiment to reduce tiller density, resulting in decreased dry matter accumulation. The compensatory effect of increased tiller size when tiller numbers are smaller also needs to be considered. In this experiment, the tall cutting height resulted in decreased tiller density, but according to Bircham's (1981) findings tiller size increases where tiller density is decreased. This may explain why there was a significant relationship between tiller density and dry matter accumulation on the tall cutting height turves in two months (April and May) but the relationship was quite weak (R^2 values of 34 and 26% respectively).

Tiller density was also significantly greater on the HH turves. A significant relationship between tiller number and dry matter accumulation only occurred on the HH turves in April. This suggested that perhaps there was a maximum tiller density beyond which dry matter accumulation was not increased because of the effects of increased competition. There may be a significant relationship between tiller number and dry matter accumulation up to a certain tiller density and then dry matter accumulation plateaus. In April, the tiller density on the HH turves may have been low enough to still be increasing dry matter accumulation, but why this only occurred in April is unknown.

5.4.5 Leaf extension rates

5.4.5.1 Sites

The site from which the turves were removed only had a significant effect on leaf extension rate in April and May. In April, leaf extension rate was significantly lower on the LN turves and in May leaf extension was lowest on the LN turves, highest on the HH turves and intermediate on the HN turves. The effect of sites may not have become apparent until April and May due to conditions in earlier months that may have over-ridden the site effects. Soil moisture in February and March may have been the factor controlling leaf extension rates, as there was no significant difference between sites in these months ($\alpha = 5\%$). Turner and Begg, (1978) stated that leaf extension rate was the most sensitive plant morphological response to water deficit. No difference between the leaf extension rate of the turves in the summer, suggested that soil moisture levels were similar on all the turves and resulted in all turves having similar average leaf extension rates. Shoot height was found by de Kroon and Knops (1990) to increase in graminoid species under higher levels of fertilization, indicating that leaf extension also increased under high fertility conditions. The response varied between species however, depending on their responsiveness to high levels of fertility in general. For example, high fertility responsive grasses (Lambert *et al.* 1986a) would be likely to respond in a different manner to low fertility tolerant species.

5.4.5.2 Cutting height

Cutting height had a significant influence on average leaf extension rate in February, March and May. In these months, leaf extension was greater on the tall cutting height turves. Cutting pastures to 20 mm resulted in more green leaf material being removed, hence photosynthetically active material was reduced. This meant that the plant was not accumulating photosynthates as quickly, hence leaf growth rate was reduced. On tall cutting height turves, only a small amount of leaf area was removed and enough photosynthetically active material was retained to allow plant growth. There must be an equilibrium point between the degree of shading that occurs in a tall cutting height sward and the amount of leaf material available to intercept incident radiation. In short swards, interception of light would be high, but there may not be enough leaf material present to utilize the light.

5.4.6 Species abundance over time

5.4.6.1 Sites

There were three species whose abundance was significantly influenced by site effects in all months. These species were *L. perenne*, flatweeds and *C. uniflora*. *L. perenne* was most abundant on HH turves and least abundant on LN turves, *C. uniflora* was most abundant on HN turves and least abundant on LN turves and flatweeds were most abundant on LN turves and least abundant on HH turves.

These results provide more information about the native species *C. uniflora*. It was significantly more abundant on the HN turves, which suggested that the management and fertility on the HN site provided better conditions for *C. uniflora* growth than either the LN or HH sites. It was unlikely that it was simply a fertility factor as the LN turves had a very similar chemical fertility to the HN turves, but the LN turves had the least *C. uniflora*. It may have been that the area from which the HN turves were removed had environmental conditions that suited *C. uniflora* growth more than the HH and LN sites.

Besides having their abundance influenced by fertility, flatweeds also grew better than many other species in dry environments because they possess a taproot. Hence the presence of flatweeds may be an indication of the site being low fertility or dry, or a combination both factors.

L. perenne abundance has been shown to increase with increasing fertility, although this is not the only factor that increases its abundance. *L. perenne* was particularly resilient to treading events (Edmond, 1964) hence its abundance is likely to increase over time in trodden swards.

The use of these species as indicators of certain environmental conditions therefore is somewhat limited because their presence or absence was not just determined by one factor.

5.4.6.2 Cutting height

The abundance of three species was significantly influenced by cutting height over the experimental period. Unlike the site effects which influenced certain species significantly in all months (December/January through to April/May), cutting height effects were only significant in three months (February, March and April/May). The most likely cause of this occurrence was that it took longer for the cutting height, which began in December, to have an effect on the turves, unlike the site effects which were always present.

The species significantly affected by cutting height effects were *T. repens*, *N. setulosa* and *A. odoratum*. Both *T. repens* and *N. setulosa* are prostrate species that were identified earlier to be more abundant on short cutting height turves. Under these conditions, *T. repens* and *N. setulosa* were able to receive enough light for photosynthesis to occur, unlike in tall swards where their prostrate growth habit meant they were shaded by more erect species.

A. odoratum was the only grass species to be significantly influenced by the cutting height. Again, earlier measurements indicated that its abundance was negatively influenced under short cutting heights. This was supported by Grime *et al.* (1988) who stated that *A. odoratum* was sensitive to defoliation. This inability of *A. odoratum* to persist under the 20 mm cutting height may be due in part to its limited capacity for tillering and it relatively slow growth rate (Grime *et al.* 1988).

5.4.6.3 Treading

Only the abundance of *H. lanatus* was significantly influenced by treading over time. As with the cutting height treatment, the effect was only significant from February through until April/May as the treading treatment took time to take effect.

H. lanatus abundance was significantly reduced in these months. *H. lanatus* is intolerant to treading due to the fact that it exhibits lax tillering and has relatively few shoot buds.

It is interesting to note that only this species was significantly influenced by the treading treatment over time as there were other species in the sward (i.e. *C. uniflora* and *N. setulosa*) which did not evolve under grazed conditions and would therefore be assumed to be intolerant of treading. This does not appear to be the case however as these species appeared to be unaffected by the treading treatment from the results of the point analysis.

5.4.7 Functional groups

5.4.7.1 Dry matter production

Of the eight functional groups defined (Chapter 4), two of them (*A. capillaris* and low fertility tolerant grasses (LFTG)) contributed significantly more to dry matter production than any other in the months of January and February. In April and May, the emphasis moved away from the *A. capillaris* and LFTG groups producing the most dry matter to the OS and flatweeds functional groups being dominant. This shift may be due to several factors. As the experiment progressed, the factors applied (treading and short or tall defoliation height) may have changed the sward characteristics such that many of the prostrate and spreading species present in the OS group were favoured over the grass species in the *A. capillaris* and LFTG groups. The treading treatment for example would have opened up gaps in the sward, and reduced tillering of the grass species, enabling species such as *N. setulosa* and *C. uniflora* to colonize gaps. The short cutting height would have reduced the competitive advantage of LFTG and *A. capillaris* functional groups by keeping their leaves short and not allowing them to shade the more low growing species.

5.4.7.2 Sites

Only the HFRG, OS and flatweeds functional groups were significantly influenced by site effects in three or more of the four months in which functional group abundance was measured.

That the HFRG functional group was significantly more abundant on HH turves suggested that to encourage high fertility responsive grasses into hill country swards, management similar to that imposed on the HH site would be required. The economic costs of imposing such management (e.g. high fertiliser application) on hill pasture farms may not balance with profitable increased production and this needs to be considered.

The flatweeds functional group was significantly more abundant on the LN turves which suggested in order to remove these species from the pasture, management and fertility needs to be altered to be more like that of the HN and HH sites turves. As mentioned previously, it may not be economically practical to change management and fertility to that of the HH turves, just to remove flatweeds from the sward.

The OS functional group was significantly more abundant on the HN turves in all months. The value of these species to pasture stability and to animal feeding value is unknown. That they were all very low growing species suggested that they did not form a major part of the grazing animal's diet, however they may have a role in pasture stability.

5.4.7.3 Cutting height

All the functional groups containing grass species (*A. capillaris,* HFRG, LFTG and *L. perenne*) and *T. repens* were significantly influenced by cutting height. The abundance of all these functional groups was promoted under the tall cutting height regime. Under the tall cutting height regime, the more erect growing grass species were able to gain a competitive advantage by maintaining a larger photosynthetically active leaf area than if they were cut short.

It was unusual that the abundance of the *T. repens* functional group increased under the tall cutting height. *T. repens* has a prostrate growth habit and would therefore be expected to be shaded under a tall cutting height regime. One explanation for this occurrence may be the decrease in tiller density under the tall cutting height regime, which resulted in a less dense sward (refer section 5.4.1.2).

These results suggested that to encourage more favorable functional groups such as all those containing grass species and *T. repens*, a tall defoliation height is required. The cutting height used in this experiment (75 mm) has proven to increase the abundance of the grass containing functional groups and the *T. repens* functional group, under glasshouse conditions. Whether this occurs in the field is unknown. At taller cutting heights the result is likely to differ, especially in spring and summer when feed quality will decrease as the grass species become reproductive.

5.4.7.4 Treading

Four of the eight functional groups were significantly influenced by treading effects (OS, *T. repens,* flatweeds and HFRG functional groups).

The HFRG group was positively influenced by the no treading treatment. Under treading conditions, damage can occur to individual plants (refer section 5.4.1.3) resulting in decreased tillering and growth. The abundance of the OS functional group was also greater when no treading was present. The species that made up this group were predominantly native and therefore have not evolved to be treading tolerant.

The abundance of both the *T. repens* and flatweeds functional groups was increased under the treading treatment. *T. repens* is a species which is able to rapidly colonize gaps in the sward that are cause by treading. The treading treatment also acted to reduce the vigor of some grass species, enabling *T. repens* to compete for light resources. The abundance of the flatweeds functional group may have increased by new plants developing in gaps in the sward created by the treading treatment. There may also have been reduced competition by high fertility responsive grasses for light resources under treading conditions.

5.4.8 Testing functional group definition

The functional groups used in this experiment were defined using a range of responses to environmental and management factors (see Chapter 4) including response to fertility/management history, defoliation height, treading and moisture. Only three of these factors, which simulate farm management practices, were imposed in this experiment (fertility/management history, defoliation height and treading).

The functional groups defined in Chapter 4 were high fertility responsive grasses (HFRG), low fertility tolerant grasses (LFTG), *L. perenne* , *A. capillaris*, other species (OS), other legumes (OL), flatweeds and *T. repens*.

The HFRG group separated from the *L. perenne*, LFTG and *A. capillaris* functional groups because of its negative response to treading. The HFRG and *L. perenne* groups separated from the LFTG group and the *A. capillaris* group because of their response to the site treatment. Both *L. perenne* and HFRG responded positively to the HN and HH sites, while LFTG and *A. capillaris* groups were unresponsive.

The LFTG and *A. capillaris* groups did not appear to separate using the management factors imposed. They were both unresponsive to site effects, positively influenced by a tall cutting height and neither were influenced by treading. The *A. capillaris* functional group however, was significantly more abundant than the LFTG group (Table 5.14) in all months. As such, the *A. capillaris* functional group would have a larger influence on the entire sward than the LFTG group and though these two groups do not differ significantly in terms of their response to these management factors, they may in response to other factors such as moisture.

The flatweeds and OS functional groups did not separate particularly well under these management factors either. Both were highly responsive to the site and treading treatments and neither were responsive to defoliation height. Because of the morphology of species in the flatweeds functional group however, they are likely to respond differently to the OS functional group under other imposed factors, such as moisture. This is dealt with in Chapter 6. The OL and *T. repens* functional group separated by *T. repens* being positively influenced by a tall cutting height and treading and being unaffected by the site effects. The OL functional group was not influenced by either treading or defoliation height and was positively influenced on the HN site turves.

The functional groups, therefore, did respond to the imposed management factors as predicted in the definition of the functional groups. These functional groups can be used to help simplify the hill pastoral system and aid pasture managers in identifying pasture status. As the response of the functional groups to several imposed management factors is known, pasture composition can be altered to achieve a more desirable sward through farm management.

5.4.9 The role of pasture management

There are practical difficulties associated with managing hill pastures (e.g. diverse range of aspects, slope, microtopography) (White, 1994). Understanding the effects of environmental and management perturbations is necessary so that a desirable botanical composition can be achieved and maintained in hill country pastures. In trying to alter pasture composition using management it is important for producers to understand the complex pastoral system they are working with, and be able to identify species and their abundance. A greater abundance of undesirable species may give the farmer an indication of underlying resource base problems. For example, the presence of a high percentage of low fertility tolerant grasses may indicate that that soil fertility is low and fertiliser application is required. A high abundance of *A. capillaris*, *L. perenne*, *T. repens*, *T. dubium* and bare soil, and a low abundance of *C. cristatus*, flatweeds and *L. pedunculatus*, may indicate that the pasture has been heavily trodden. The presence or absence of a species and the abundance of those species present can be used as an indication of the state of the pasture.

Kemp (1991) developed the State and Transition model (Westoby *et al*. 1989) to a useful management tool for land managers called the pasture management envelope. The envelope works by defining upper and lower boundary requirements for stable pastures and optimal animal production (Kemp, 1991). Defining these upper and lower boundaries makes it easier for land managers to identify the state of their pastures. The results of this experiment go part way in defining what these upper and lower boundaries may be in North Island New Zealand hill pastures.

The development of these sorts of management tools for New Zealand hill pastures would be valuable. They would enable farmers to identify the state of their pastures in terms of composition and production and in turn implement management strategies to achieve a more desirable stable state. These tools may also be useful to identify pasture degradation during an extreme environmental event such as a drought and allow farmers to act early before a permanent change of state occurs. Reversing a change in state may be costly since the inputs required to return the pasture to pre-stress levels, might not be proportional to the resulting yield response.

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Plate 5.1 Turf removal from the summer moist, low fertility farmlet (LM) at Ballantrae Research Station, November 1996. The water tanks and pump on the cutting apparatus were used to lubricate the turf bin.

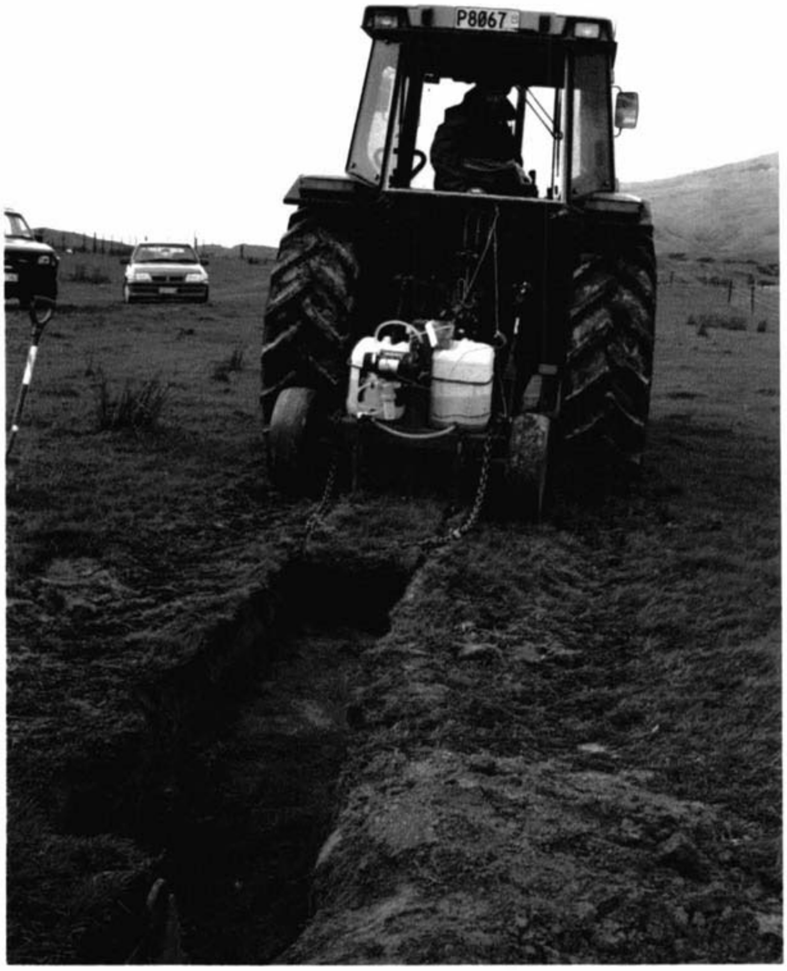


Plate 5.1 Turf removal from the summer moist, low fertility farmlet (LM) at Ballantrae Research Station, November 1996. The water tanks and pump on the cutting apparatus were used to lubricate the turf bin.

Plate 5.2 Turves arranged in the glasshouse at the Plant Growth Unit, Massey University, prior to the commencement of the first experiment.

Plate 5.3 Apparatus used to apply the simulated sheep treading treatment in both the first and second turves experiments. The instrument was rolled over the turf surface.

6. Environmental effects on pasture composition

6.1 Introduction

Hill pastures are variable, and this variability is caused by both environmental and management factors (White, 1994). As discussed in previous chapters (Chapter 5), environmental factors that influence pastures include temperature, rainfall, soil type, slope and aspect, whilst management factors include animal type, stocking rate, fertiliser application and grazing strategy. The interactions between management and environmental factors need to be considered carefully, as farmers are unable to control environmental conditions. Therefore, they must adjust their own management to maintain a desired hill pasture in terms of both productivity and composition.

Aspect and slope are two environmental factors that have a significant influence on moisture availability in hill pastures. Steep northerly faces are much drier than sheltered, flatter, southerly faces. This effect of aspect on soil moisture availability results in changes in pasture composition. On sunny slopes, perennial grass species such as *Rytidosperma* spp. and *D. glomerata* exist along with annual grasses and legumes (White, 1994). On shady slopes, species composition has been described as being more diverse, including species such as *A. capillaris*, *A. odoratum* , *C. cristatus*, *H. lanatus*, *L. perenne* and *T. repens* (White, 1994). Annual pasture production can also vary between aspects, depending on whether moisture or temperature is the dominating factor (White, 1994). Studies by Lambert and Roberts (1978) on aspect effects showed that pasture composition differences were also related to topography and its affects on stock management, animal behaviour and nutrient transfer, which illustrates the importance of considering the interactions between environment and management.

Soil moisture and animal treading are both influenced by the slope and aspect variability of hill country, soil moisture directly and animal treading through the effects of topography on animal behaviour. These two stresses can act individually, or interact to have physical effects on plant growth such as leaf extension and tillering, and on pasture composition, and both these stresses influence herbage production. Species have different mechanisms to cope with both environmental and management stresses, but most species in hill pastures either have the ability to tolerate the stresses or the ability to recover from the stresses.

The general objectives were to improve the ability of land managers to understand the interactions between environmental and management stresses which will enable them to prevent damage to pastures from management stresses, and will minimize damage from environmental stresses. The specific objectives were to identify the effects of an environmental stress (i.e. moisture stress) and its interaction with a management stress (i.e. treading), on botanical composition and production of a North Island, New Zealand hill pasture.

6.2 Materials and Methods

6.2.1 Method

This experiment used the same turves described in Chapter 5 (see Chapter 5 for turf removal details). The turves were rested for 3 months between experiments, during which time they were watered daily and trimmed weekly to a standard height of 50 mm. Fertiliser was applied at the beginning of the 3 month rest period to replace S, P and N removed from the turves in herbage harvested. The total amount of herbage harvested during the first turves experiment was calculated, the content of S, P and N in the removed herbage was approximated and superphosphate and urea were applied to replace those nutrients removed.

The turves maintained their original differences in fertility that were developed at the sites at Ballantrae. There were 12 each of the high, medium and low fertility turves with Olsen P levels of 13.3, 8.2 and 6.3, respectively. Moisture and treading treatments were applied over these fertility treatments. The experiment comprised the treatment phase (2 months) and the recovery phase (2 months).

Three moisture and two “treading” treatments were applied between September 1997 and 18 November 1997. The three moisture treatments were established on the turves using an automated watering system, and polythene shields placed between adjacent turves to prevent water crossing between the water treatments. Eighteen turves had heavy watering applied, 9 received control levels of watering and 9 received no water. The heavy watering treatment involved maintaining the turves at a soil volumetric moisture content of approximately 60% as determined by Time Domain Reflectometry. The control turves were maintained at a soil moisture content of approximately 40% and the dry turves during this phase were unwatered, and dried from a soil moisture content of 60% to an average of approximately 10%.

The second treatment was simulated treading, using a studded roller that applied an average pressure of 1.28 Mg m^{-3} to the soil surface (Awan, 1995). The turves were trodden with 10 passes of the roller applied after each cutting. This treatment was applied to half of the heavily watered turves. It was not applied to the control or dry treatments due both to the lack of replication that would result (as the number of turves were limited), and to the method of treading having very little impact on the hard soil developed in the dry treatment.

In summary there were four treatments each applied to 9 turves in phase one:

- wet (W)
- wet and treading (WT)
- control (C)
- dry (D)

In phase two, (from 18 November 1997 to 31 January 1998) the wet treatment turves were allowed to dry until they reached the control level of soil moisture (approximately 40%), and the dry treatment turves were wet up to the control levels of moisture. Both treatments took approximately 10 days to reach control moisture levels. The treading treatment ceased on the WT treatment turves.

During both phases, the sward was maintained by weekly cutting to a height of 50 mm.

6.2.2 Measurements

The 10 sets of measurements taken in this experiment are described below.

6.2.2.1 Botanical composition.

The contribution of all species to herbage mass (kg DM/ha) was determined for a 0.01 m^2 area (cut to ground level) at the centre of each turf. Two dissections that separated all species present were carried out. The first was taken at the start of phase one of the experiment in September 1997. The same technique was used at the end of phase two of the experiment in February 1998, but a 0.11 m^2 quadrat was used as the turves were not required for further experimentation.

6.2.2.2 Dry matter harvests

Once a week the turves were trimmed with electric shears to a height of 50 mm to simulate defoliation by grazing animals. Herbage was collected using a vacuum cleaner, dried and weighed to determine pasture growth rate (kg DM/ha/day) over that period.

6.2.2.3 Leaf extension

Leaf extension rate (mm/day) was measured on the most common and agronomically important species present. These species were: *L. perenne, A. capillaris, H. lanatus, A. odoratum and T. repens.* Leaf extension was monitored over a period of 5 days each month. On each turf, one tiller of each species was tagged with an identifying coloured piece of wire. The length of the youngest leaf was measured from the collar of the most recently fully expanded leaf to the tip, and then over the subsequent days was re-measured. If the leaf died or ceased growing over this 5 day period, the new leaf that appeared was measured instead.

6.2.2.4 Point analysis

A specially designed point quadrat apparatus with 10 needles 50 mm apart was used to non-destructively determine pasture composition of the turves. At the beginning of phase one and end of phase two, 100 points were sampled per turf. During the rest of the experiment, 30 points per turf were measured each month. The point quadrat apparatus was used on a first hit basis to measure cover. Only the first species in the plant strata hit by the needle was identified, not every species hit by the needle as it passed down through the strata (Levy and Madden, 1933). The percentage of hits on each species was calculated to estimate the cover of each species. Only the first hit species were identified due to both time constraints and the swards being reasonably short, and hence the plant strata were narrow.

6.2.2.5 Soil nitrogen

In late November 1997, early in the recovery phase, soil samples were removed from each turf and a 2M KCl-extractable nitrate procedure (Blakemore, Searle and Daly, 1987) used to determine the concentration of NH_4^+ and NO_3^- (ppm). Soil cores were taken to a depth of 75 mm and core diameter was 25 mm.

6.2.2.6 Tiller counts

On each turf, the tillers or growing points were counted in three 0.025 m^2 samples and then averaged (tillers/m^2).

6.2.2.7 Soil nutrients

Soil samples were taken from the turves at the beginning of the experiment to identify if any major changes had occurred in fertility between the first and second experiments. P, S and pH were measured for all 36 turves.

6.2.2.8 Root weight and length

Two root samples were taken, one in each phase. In early September 1997, two 30 cm deep soil cores (332 cm^3) were removed from each turf, discarded, and the holes backfilled with clean dry sand. At the end of phase one (17 November 1997) the sand filled cores were removed and the roots removed by hand and washed. Root length and root weight of the roots grown in this phase were then determined.

Two more cores were taken at the end of the second phase (4 February 1998) and the same method used to determine the length and weight of roots.

6.2.2.9 Soil temperature

Soil temperature measurements were made weekly on each turf using a 0.1 m soil temperature probe in five fixed positions in each turf, and then averaged for the turf.

6.2.2.10 Soil moisture

Soil moisture was measured using Time Domain Reflectometry (TDR). Two 0.2 m probes were permanently placed in the centre of each turf and monitored twice weekly.

6.3 Statistical analysis

Basic ANOVA was carried out on all data using the PROC GLM command of the SAS program (SAS Institute Inc. 1995). Manova's were carried out on species specific data to identify the differences between species. Canonical correlation analysis was used to determine the correlation between point analysis and full herbage dissection to determine botanical composition. Regression analysis was used to identify relationships between species richness and dry matter production. Coefficient of variation was used to identify the variation in abundance of functional groups over the experimental period.

6.4 Results

6.4.1 Background results

6.4.1.1 Soil moisture

From September 1997 through to 18 November 1997, the stress treatments resulted in significantly different soil moisture contents (Table 6.1). In September, volumetric soil moisture content of the D treatment turves was significantly less than that of the WT, W and C treatment turves. In October, the WT and W treatment turves were significantly greater than C turves, which were still significantly greater than the D treatment turves. The same pattern occurred in the first half of November (November A). From the second half of November (November B) 1997 through to January 1998, none of the turves had significantly different soil moisture content.

Site had an effect (P = 0.0894) on soil moisture content in all months except December 1997 and January 1998. In the months when site was significant, the sites from highest soil moisture to lowest were LN, HH and HN, with the exception of November A, when the sites were ranked LN, HN and HH from highest soil moisture to lowest.

There were no site by stress treatment interactions for soil moisture content.

6.4.1.2 Soil temperature

In all months, soil temperatures were significantly different in the stress treatments (Table 6.2). In September 1997, the D treatment turves had significantly higher soil temperatures than the other treatments. In October and the first half of November, C and D treatment turves had significantly higher soil temperatures than the W and WT treatment turves. In the second half of November, the W treatment turves were significantly warmer than the other treatments, and the WT and C treatment turves were similar. The D treatment turves were significantly colder than the other treatment turves. In December 1997, W and D treatment turves were both warmer than WT and C treatment turves, which were not significantly different. In January 1998, W treatment turves had the highest temperature and W and D were not significantly different. D, WT and C treatment turves were not significantly different.

Table 6.1 Summary of volumetric soil moisture content (%) data for stress treatments. C = control, D = dry, W = wet and WT = wet and treading.

		Stress Treatments				
Month	C	D	W	WT	SEM	Prob>F
Sept 97	58.7	45.1	59.0	59.4	1.6911	0.0001
Oct 97	50.7	25.8	63.1	62.5	1.3564	0.0001
Nov A 97	39.2	13.1	60.7	59.5	1.2401	0.0001
Nov B 97	37.7	39.0	42.8	42.0	1.5960	0.1121
Dec 97	41.2	39.4	43.8	38.3	2.2120	0.3490
Jan 97	39.2	36.9	38.4	36.5	1.9180	0.7335

Table 6.2 Summary of soil temperature (°C) data for stress treatments. C = control, D = dry, W = wet and WT = wet and treading.

		Stress Treatments				
Month	C	D	W	WT	SEM	Prob>F
Sept 97	14.3	14.6	14.3	14.0	0.0970	0.0028
Oct 97	16.6	16.6	16.0	15.8	0.1070	0.0001
Nov A 97	16.6	17.0	16.1	16.0	0.0719	0.0001
Nov B 97	19.0	17.4	19.4	19.1	0.0938	0.0001
Dec 97	19.3	19.5	19.8	19.3	0.1798	0.0205
Jan 98	20.9	20.9	21.1	20.9	0.0735	0.0852

In all months, with the exception of December 1997 and January 1998, site did not have a significant influence on soil temperature. In December 1997, site had a significant effect (P = 0.0101) and HH had the highest temperature, but it was not significantly higher than LN. LN and HN sites were not significantly different. In January 1998, HH had the highest soil temperature, but was not significantly different to LN. HN turves had the lowest soil temperature, which was significantly lower than HH and LN.

There were no site by treatment interactions for soil temperature.

6.4.1.3 Soil nutrients

Soil pH was significantly different among sites (P = 0.0471) (Table 6.3) and the sites were ranked LN ≥ HN ≥ HH. Stress treatments did not have a significant effect on soil pH and there were no site by stress treatment interactions.

Sulphur (ppm) was significantly different between sites (P = 0.0001) and the sites were ranked HH > LN ≥ HN. Stress treatments did have a significant effect on sulphur (P = 0.0827). The stress treatments were ranked C ≥ WT ≥ D ≥ W for their influence on sulphur levels. C treatment turves had significantly greater levels of sulphur than W treatment turves, with WT and D treatment turves intermediate. There were no site by stress treatment interaction effects.

Olsen P (ppm) was significantly different between sites (P = 0.0001) and the sites were ranked HH > HN ≥ LN. There were no stress treatment effects or site by stress treatment interactions.

Nitrogen in the soil in the form of NH_4^+ (ppm) was found to differ between treatments (P = 0.0981) and the stress treatments were ranked W ≥ C ≥ WT ≥ D. The W treatment turves had significantly higher levels of NH_4^+ than D treatment turves, with C and WT treatment turves intermediate. There were no site or site by stress treatment interactions. NO_3^- did not differ significantly between sites or stress treatments.

Table 6.3 Summary of soil nutrient measurements (ppm) for each site taken August 1997. LN = low fertility and input farmlet, HN = medium fertility and input farmlet and HH = high fertility and input farmlet.

	Sites				
	LN	HN	HH	SEM	Prob>F
pH	5.68	5.62	5.57	0.0471	0.0312
Sulphur	13.5	10.3	26.5	1.6642	0.0001
Olsen P	6.3	8.2	13.3	0.9292	0.0001

6.4.1.4 Roots

In phase 1 of the experiment, root weight did not differ significantly between sites or stress treatments. Root length was significantly different between stress treatments (P = 0.0194). Root length was greatest in the W treatment turves (95,560 m/m^3), but was not significantly different to the C treatment turves. D treatment turves had the lowest root length (51,110 m/m^3), but did not differ significantly from WT and C treatment turves.

In phase 2, stress treatments had a significant effect on root weight (P = 0.0394) and the stress treatments were ranked C (152 g/m^3) > D (64 g/m^3) with W (125 g/m^3) and WT (117 g/m^3) treatment turves intermediate.

Both site (P = 0.0015) and stress treatments (P = 0.0175) had a significant effect on root length. The sites were ranked LN (58,750 m/m^3) ≥ HH (53,167 m/m^3) > HN (28,333 m/m^3) for their effect on root length. The stress treatments were ranked C (59,353 m/m^3) ≥ WT (49,556 m/m^3) ≥ W (49,333 m/m^3) > D (28,778 m/m^3) for their influence on root length.

6.4.2 Measurement results

6.4.2.1 Dry matter accumulation

In all months, except the first and second half of November, site had a significant influence on dry matter accumulation (Table 6.4a). From August through to October, the HH turves accumulated the highest levels of dry matter, followed by the HN turves and the LN turves were the lowest producing. In December, the difference in dry matter accumulation from the different sites was marginal (P = 0.0910). In January, the sites were ranked HH ≥ LN ≥ HN for dry matter accumulation.

Stress treatment effects did not become significant until October 1997, and they remained significant for the rest of the experimental period (Table 6.4b). In October 1997, the stress treatments ranked W and C > WT and D, with the W treatment turves accumulating the most dry matter and the D treatment turves the least. In November A, the stress treatments ranked W > WT and C > D for dry matter accumulation. In November B, the W treatment turves still produced significantly higher levels of dry matter (12.2 kg DM/ha/day) and WT and C treatment turves did not differ significantly again. The lowest producing turves were again D treatment turves, but they were not significantly lower than C treatment turves. In December 1997, the stress treatments ranked D ≥ W > C ≥ WT for dry matter accumulation. The same order of production occurred in January 1998 as December 1997. D treatment turves produced the most dry matter (32.6 kg DM/ha/day) and WT turves the least (20.4 kg DM/ha/day). The stress treatments ranked D ≥ W ≥ C ≥ WT for dry matter accumulation.

An interaction between site and stress treatment occurred only in November A. For the C and WT treatments, all sites accumulated very similar levels of dry matter (C 6.65 ± 0.11 kg DM/ha/day; WT 6.69 ± 0.13 kg DM/ha/day). The D treatment turves showed a slight decrease in dry matter accumulation as the fertility of the sites increased. The D by LN turves produced the most, followed by D by HN, and D by HH produced the least. The W treatment turves showed the greatest interaction. The W by LN turves (9.97 kg DM/ha/day) produced approximately half as much dry matter as the W by HN (15.4 kg DM/ha/day) and W by HH (17.4 kg DM/ha/day) turves.

Table 6.4 Summary of dry matter production (g DM/m^2/day) for (a) sites and (b) stress factors.

(a)

		Sites			
Month	LN	HN	HH	SEM	Prob>F
Aug 97	0.88	1.03	1.37	0.0990	0.0062
Sept 97	1.06	1.18	1.65	0.0728	0.0001
Oct 97	0.86	0.96	1.24	0.0686	0.0026
Nov A 97	0.70	0.79	0.84	0.0651	0.3297
Nov B 97	0.61	0.68	0.79	0.1004	0.4773
Dec 97	2.49	2.01	2.45	0.1620	0.0910
Jan 97	2.73	2.33	3.14	0.2040	0.0327

(b)

		Stress Treatments				
Month	C	D	W	WT	SEM	Prob>F
Aug 97	1.16	1.10	1.09	1.02	0.1143	0.8428
Sept 97	1.20	1.32	1.36	1.31	0.0841	0.5598
Oct 97	1.15	0.74	1.32	0.88	0.0792	0.0001
Nov A 97	0.67	0.34	1.43	0.67	0.0751	0.0001
Nov B 97	0.55	0.30	1.22	0.71	0.1160	0.0001
Dec 97	1.62	3.33	2.83	1.48	0.1871	0.0001
Jan 97	2.48	3.26	3.16	2.04	0.2356	0.0038

6.4.2.2 Tillers

Site significantly influenced tiller number in all months (Table 6.5a). HH turves produced significantly more tillers than either the HN or LN turves, which did not differ significantly.

In October and November 1997, the stress treatments had a significant effect on tiller number (Table 6.5b) with both the WT and D treatments negatively affecting tiller number. In October, the stress treatments ranked W ≥ C > D ≥ WT for tiller number and in November, the stress treatments ranked W ≥ C ≥ WT > D for tiller number (Table 6.5b).

There were no site by stress treatment interactions.

6.4.2.3 Leaf extension

Site effects did not begin to have a significant effect on leaf extension until November 1997, they then remained significant until the end of the experiment (Table 6.6a). The HH turves consistently had the highest rate of leaf extension (not significantly higher than HN turves in any month), HN turves had the second highest rate of leaf extension and LN turves the slowest (significantly slower than HN only in December 1997) in every month where site effects were significant.

Treatment effects became significant from October to the end of the experiment (Table 6.6b). In October 1997, the effects of stress treatments on leaf extension ranked W ≥ WT ≥ C > D. In November, after re-wetting, D treatment turves had significantly faster rates of leaf extension (7.7 mm/day) than any other treatment. C treatment turves had the slowest rate of leaf extension (2.3 mm/day) but not significantly slower than WT treatment turves. In December, the stress treatments ranked D > W, WT and C for their influence on leaf extension. In January, D treatment turves again had the fastest rate of leaf extension (7.9 mm/day), but not significantly faster than WT treatment turves. C, W and WT treatment turves did not differ significantly.

There were no site by stress treatment interactions.

On the C treatment turves, the leaf extension rates of *A. capillaris* and *H. lanatus* decreased slightly from September to November (Figure 6.1). The petiole extension rate of *T. repens* remained relatively constant from September to December. The general trend of *L. perenne* leaf extension was decreasing from September to November and *A. odoratum* leaf extension was relatively static from September to November, then increased. The leaf extension rates of all species increased from December to January.

Table 6.5 Summary of tiller density (tiller no./m^2) for (a) sites and (b) stress factors.

(a)

		Sites			
Month	LN	HN	HH	SEM	Prob>F
Sept 97	12378	11511	15733	805	0.0030
Oct 97	11967	11244	16189	815	0.0006
Nov 97	11433	11500	15200	662	0.0006
Dec 97	11478	12033	18700	911	0.0001
Jan 97	13111	13167	20533	1470	0.0019

(b)

		Stress Treatments				
Month	C	D	W	WT	SEM	Prob>F
Sept 97	12548	12874	14859	12548	929	0.2609
Oct 97	14444	11333	16059	10696	941	0.0014
Nov 97	13956	9274	15807	11807	765	0.0001
Dec 97	12711	14089	15096	14385	1053	0.4562
Jan 98	14385	15274	13689	19067	1698	0.1444

Table 6.6 Summary of leaf extension data (mm/day) for (a) sites and (b) stress factors.

(a)

		Sites			
Month	LN	HN	HH	SEM	Prob>F
Sept 97	3.1	3.1	3.6	0.3	0.4634
Oct 97	3.0	2.8	3.3	0.3	0.2771
Nov 97	3.7	4.7	5.8	0.5	0.0542
Dec 97	3.1	4.2	4.8	0.4	0.0050
Jan 97	5.3	6.0	7.4	0.5	0.0251

(b)

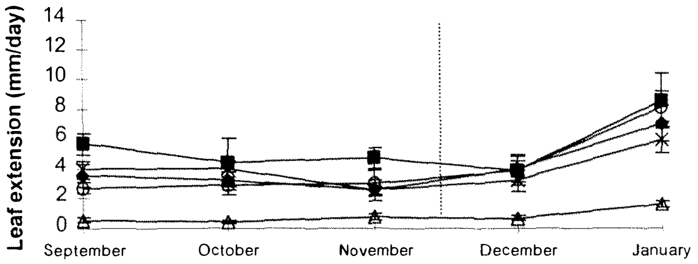
		Stress Treatments				
Month	C	D	W	WT	SEM	Prob>F
Sept 97	3.7	3.1	3.2	3.2	0.3	0.5972
Oct 97	3.1	0.4	4.7	4.0	0.4	0.0001
Nov 97	2.7	7.7	4.7	3.9	0.5	0.0001
Dec 97	3.1	5.8	4.2	3.0	0.4	0.0001
Jan 98	5.4	7.9	5.2	6.4	0.6	0.0118

Figure 6.1 Summary of leaf extension rates (mm/day) for each species measured and for each factor over the experimental period.

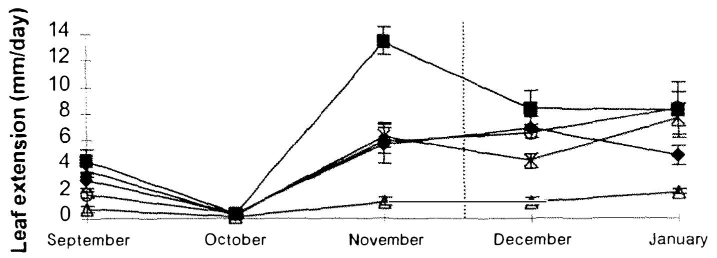
…………… **Change over of treatments - 18 November 1997.**

◆ =*A. capillaris* ■= *L. perenne* Δ=*T. repens* x = *H. lanatus* O=*A. odoratum*

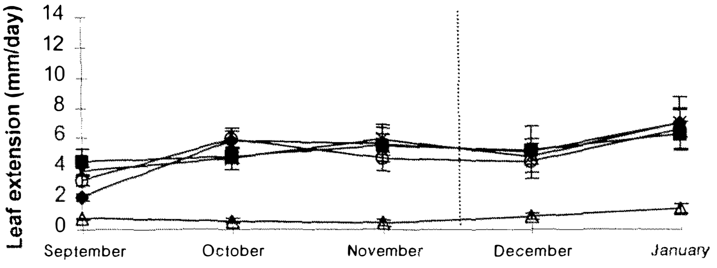
Control Turves



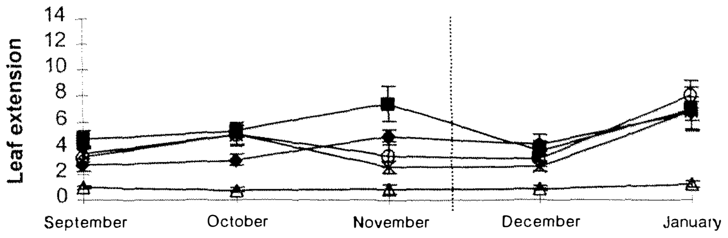
Dry Turves



Wet turves



Wet and Treading turves



On the D treatment turves, the leaf extension rates of all species decreased to 0 mm/day between September and October (Figure 6.1). On re-wetting, *A. capillaris*, *H. lanatus* and *A. odoratum* leaf extension rates increased from 0 mm/day in October to approximately 6 mm/day in November. The leaf extension rate of *L. perenne* on re-wetting was more than double that of any other species (13 mm/day). *T. repens* petiole extension rates increased from 0 mm/day to 2 mm/day in November and December, with a slight increase in January to 3 mm/day. From November to January, *L. perenne* leaf extension rates decreased and *A. odoratum* and *H. lanatus* rates increased resulting in all 3 species having similar leaf extension rates in January (8 mm/day). *A. capillaris* leaf extension rate increased until December, then decreased to approximately 5 mm/day in January.

On the W treatment turves, leaf extension rates, (except at the start of treatment application in September) were very similar for all the grass species measured (within 2 mm/day) (Figure 6.1). There was a slight increase in leaf extension from September to October, then no change until January when there was an increase. *T. repens* petiole extension rate remained relatively static from September to December, followed by a slight increase in January.

On the WT turves, *A. capillaris* and *L. perenne* leaf extension rates increased from September to November, then decreased in December followed by another increase in January (Figure 6.1). *A. odoratum* and *H. lanatus* leaf extension increased from September to October then decreased through to December. There was an increase in the leaf extension rates of *A. odoratum* and *H. lanatus* in January. The petiole extension rate of *T. repens* remained constant (1 mm/day) through the experimental period.

6.4.2.4 Botanical composition

In the September 1997 quadrat cut and dissection, there were no significant site or stress treatment effects on total dry matter removed from the turves. The sites ranked HN ≥ LN ≥ HH and the stress treatments ranked W ≥ D ≥ C ≥ WT for their influence on total dry matter removed in the quadrat cut. There were significant species effects on total dry matter removed. Flatweeds contributed to significantly more dry matter than any other species (276 kg DM/ha). Dead matter was the next largest contributor (214 kg DM/ha). *P. annua*, *A. capillaris* and *H. lanatus* were the next greatest contributors to dry matter, but they did not differ significantly from one another. *H. lanatus*, *C. uniflora, C. cristatus, N. setulosa,* other species, *A. odoratum, T. repens, Muscii* spp., *L. perenne, L. pedunculatus, T. dubium* and *F. rubra* did not differ significantly in contribution to dry matter. *F. rubra* contributed the least to dry matter production (0.27 kg DM/ha) in September 1997.

Species that were significantly influenced by site effects (Table 6.7a) included *A. odoratum, L. perenne, P. annua, L. pedunculatus*, flatweeds, *C. uniflora* and *N. setulosa*. *A. odoratum* was found in significantly greater quantities on the HN turves (HN > LN and HH). *L. perenne, P. annua* and *N. setulosa* were found in greatest abundance on HH turves (HH ≥ HN ≥ LN). *L. pedunculatus* was found in greatest abundance on the HN turves (HN ≥ LN). There was no *L. pedunculatus* on the HH turves. Flatweeds were most abundant on LN turves (LN ≥ HN). No flatweeds were found on HH turves. *C. uniflora* was most abundant on HN turves, (HN ≥ HH). *C. uniflora* was not found on LN turves.

Species that were significantly influenced by stress treatment (Table 6.7b) effects included *C. cristatus, L. perenne, C. uniflora* and dead matter. *C. cristatus* was most abundant on the WT treatment turves (WT ≥ C and W ≥ D) and *L. perenne* was most abundant on the C treatment turves (C ≥ W and WT ≥ D). *C. uniflora* was significantly more abundant on D treatment turves (D

> W, C and WT) and dead matter was most abundant on W treatment turves (W ≥ D and C ≥ WT).

Table 6.7a Summary of pasture species dissection data (kg DM/ha) for sites.

Species		Sept	1997				Feb	1998		
	LN	HN	HH	SEM	Prob	LN	HN	HH	SEM	Prob
A. capillaris	125	128	139	37	0.9648	117	163	350	42	0.0019
A. oderatum	13	49	9	8	0.0025	23	34	26	7	0.5662
C. cristatus	56	59	58	14	0.9895	33	33	12	8	0.1470
C. uniflora	0	114	86	23	0.0059	1	297	213	57	0.0038
Dead matter	189	271	182	47	0.3494	262	295	425	89	0.4071
F. rubra	0	1	0	0.3	0.1593	0	1	0	0.2	0.0504
Flatweeds	574	254	0	115	0.0071	432	194	37	38	0.0001
H. lanatus	116	25	119	36	0.1347	96	7	60	11	0.0001
L. perenne	9	18	29	6	0.0904	10	27	31	6	0.0587
L. pedunculatus	20	32	0	10	0.0958	24	112	0	25	0.0100
Muscii spp.	26	35	1	12	0.1474	17	37	5	16	0.3964
N. setulosa	0	25	125	40	0.0846	0	14	160	22	0.0001
Other species	39	62	9	18	0.1317	28	98	83	26	0.1604
Poa spp.	0	152	261	52	0.0069	0	24	55	11	0.0096
T. dubium	0	11	0	6	0.3840	0	0	0	0	.
T. repens	23	30	13	8	0.3631	21	27	12	5	0.1080

Table 6.7b Summary of botanical composition (kg DM/ha) for stress factors.

		Sept	97					Feb	98			
Species	C	D	W	WT	SEM	Prob	C	D	W	WT	SEM	Prob
A. capillaris	129	106	140	149	43	0.9038	194	188	235	222	49	0.8880
A. odoratum	20	23	27	25	9	0.9546	27	32	19	33	8	0.6000
C. cristatus	61	22	63	84	17	0.0910	34	12	15	45	10	0.0700
C. uniflora	34	157	61	14	27	0.0057	152	222	155	151	65	0.8352
Dead matter	178	204	341	135	55	0.0734	374	246	528	162	103	0.0945
F. rubra	0	0	0	1	0.4	0.1435	0	0.7	0	0	0.2	0.0347
Flatweeds	343	268	307	186	133	0.8558	216	321	211	136	44	0.0535
H. lanatus	69	132	84	62	42	0.6428	60	41	80	38	13	0.1081
L. perenne	31	4	25	16	7	0.0645	14	38	11	27	7	0.0489
L. pedunculatus	17	20	30	3	12	0.4641	68	1	89	24	28	0.1407
Muscii spp.	9	14	36	23	14	0.5452	44	10	24	2	19	0.4359
N. setulosa	7	91	96	6	46	0.3291	25	56	109	42	25	0.1227
Other species	25	29	70	24	20	0.3411	129	50	59	42	30	0.1856
Poa spp.	218	122	90	121	60	0.4839	34	13	27	33	13	0.6655
T. dubium	0	14	0	0	7	0.4114	0	0	0	0	0	0.0000
T. repens	20	13	19	35	10	0.4309	26	12	10	31	6	0.0413

There was a significant interaction between site and stress treatment for *C. uniflora* and "other species", though there were no significant main effects for "other species". *C. uniflora* was approximately three times more abundant on HN by D turves, than any other combination of treatments.

In the February 1998 quadrat cut and full dissection, there were significant site and stress treatment effects on total dry matter removed from the turves. There were no significant site by stress treatment interactions. The HH turves produced the most dry matter of the sites (HH ≥ HN ≥ LN) and the W treatment turves produced the most dry matter (W ≥ C ≥ D ≥ WT) of the stress treatments.

Dead matter contributed to dry matter significantly more than any species (327 kg DM/ha). *N. setulosa, A. capillaris* and flatweeds contributed the next greatest amount to dry matter, though they did not differ significantly. *Muscii* spp., *C. uniflora, F. rubra, L. pedunculatus, A. odoratum, C. cristatus, L. perenne, H. lanatus, P. annua,* other species and *D. glomerata* did not differ significantly in their contribution to dry matter. *D. glomerata* was the least abundant species (0.18 kg DM/ha) in February 1998.

Species that were significantly influenced by site effects included *A. capillaris, F. rubra, H. lanatus, L. perenne, P. annua, L. pedunculatus*, flatweeds, *C. uniflora* and *N. setulosa* (Table 6.7a). *A. capillaris* was significantly more abundant on HH turves (HH > HN ≥ LN), *F. rubra* was significantly more abundant on HN turves (HN > HH ≥ LN) and *L. perenne* and *P. annua* were both most abundant on HH turves (HH ≥ HN ≥ LN). *L. pedunculatus* was significantly more abundant on the HN turves (HN > LN). No *L. pedunculatus* was present on HH turves. Flatweeds were significantly more abundant on LN turves (LN > HN > HH), *C. uniflora* was most abundant on HN turves (HN ≥ HH > LN) and significantly greater amounts of *N. setulosa* were found on HH turves (HH > HN). No *N. setulosa* was present on LN turves.

Species significantly influenced by stress treatment included *C. cristatus, F. rubra, L. perenne, T. repens*, flatweeds and dead matter (Table 6.7b). *C. cristatus* was most abundant on the WT treatment turves (WT ≥ C ≥ W ≥ D), *F. rubra* was only present on D treatment turves and in small quantities (0.7 kg DM/ha) and *L. perenne* was most abundant on D treatment turves (D ≥ WT ≥ C ≥ W). *T. repens* was most abundant on WT treatment turves (WT ≥ C ≥ D ≥ W). Flatweeds were most abundant on D treatment turves (D ≥ C ≥ W ≥ WT). Dead matter was most abundant on W treatment turves (W ≥ C ≥ D ≥ WT).

Species exhibiting significant site by stress treatment interactions included *F. rubra, H. lanatus* and *C. uniflora*. *F. rubra* only appeared on HN by D turves. Relatively large amounts of *H. lanatus* were present on the HH by W (137 kg DM/ha) and LN by C (141 kg DM/ha), compared with the next most abundant site, LN by W, which produced 98 kg of *H. lanatus* DM /ha. Relatively high levels of *C. uniflora* were present on the HN by D turves (620 kg DM/ha). This was almost 200 kg DM/ha greater than the next most abundant treatment combination, HH by WT (422 kg DM/ha). The HH by D (43 kg DM/ha) and the HN by WT (30 kg DM/ha) turves had relatively less *C. uniflora* than any of the other HH or HN turves, but not less than the LN turves, on which *C. uniflora* only appeared in combination with the D treatment, and which still only had 3 kg of *C. uniflora* DM/ha.

6.4.2.5 Point analysis

6.4.2.5.1 Changes in pasture composition over time

The cover of *A. capillaris* and *H. lanatus* decreased from August to October, but increased in November (Table 6.8). Bare soil, *C. cristatus*, *Muscii* spp. and dead matter had increasing cover to October, and then in November this declined to pre-treatment levels. Flatweeds showed increasing cover through to December, followed by a decrease in January. *A. odoratum* and *Poa* spp. cover continually decreased throughout the experiment and *C. uniflora* and *L. pedunculatus* continually increased. *F. rubra* cover increased from August to

September, then in October and November, no *F. rubra* was present. In December, *F. rubra* was 1% of cover (similar to September) and this declined to 0.3% of cover in January (similar to August). The cover of *L. perenne, N. setulosa*, other species, *T. dubium* and *T. repens* remained relatively constant over the experimental period.

Table 6.8 Summary of average pasture composition (%) over all months of the experiment, taken from point quadrat data.

Species	Aug 1997	Sept 1997	Oct 1997	Nov 1997	Dec 1997	Jan 1998
A. capillaris	17	11	11	17	20	24
A. odoratum	7	7	3	4	3	4
Bare soil	0	0	3	1	1	0.1
C. cristatus	7	5	8	4	6	4
C. uniflora	3	6	5	5	6	10
Dead matter	4	4	13	9	4	3
F. rubra	0.3	1	0	0	1	0.3
Flatweeds	19	17	22	23	23	17
H. lanatus	12	12	8	10	13	12
L. perenne	4	5	4	4	3	3
L. pedunculatus	1	2	2	3	5	5
Muscii spp.	1	2	2	1	0.4	0.1
N. setulosa	2	3	3	2	3	4
Other species	6	7	6	4	6	7
Poa spp.	13	15	6	6	1	2
T. dubium	1	0.4	1	1	1	0
T. repens	4	4	4	4	5	5

6.4.2.5.2 The effect of applied stress factor on the cover of individual species

The effect of the stress treatments was apparent from the number of species significantly influenced by the stress treatments in each month (Table 6.9). The number of species significantly influenced increased from two in August to eight in November when the stress treatments were at their peak. The number of species affected decreased to 7 in December and 4 in January.

A. capillaris was only significantly affected at the peak of the stress treatments (November), with the WT treatment having significantly more *A. capillaris* cover than any other treatment. *A. odoratum* was only significantly affected in the recovery phase (December and January), when the W turves had the least *A. odoratum* cover, though not significantly less than the other treatments. *C. cristatus* was significantly affected by stress treatments in September, October and November, and in the first month of the recovery phase (December). The WT turves had the most *C. cristatus* cover in each month, but only significantly more in December. *F. rubra* was not significantly influenced by stress treatments in any month, though it was not present in October and November. *H. lanatus* was significantly affected by stress treatments in October, November and January. In October, *H. lanatus* had significantly more cover on W and C turves, in November W turves and in January, W and C turves. *L. perenne* was significantly affected by stress treatment only in October, when it had the most cover on the W treatment turves, but not significantly more than the WT turves. *L. pedunculatus* was significantly influenced by stress treatments in November and December (marginal in December). In November, *L. pedunculatus* had significantly more cover on W treatment turves and in December there was no *L. pedunculatus* on the dry turves and only 1% on WT turves, compared with 8 and 10% on the C and W turves respectively. *T. dubium* was significantly influenced by stress treatments in November, when there was no *T. dubium* on the W and D treatment turves. The WT and C treatment turves did no differ significantly in terms of the cover of *T. dubium*.

Table 6.9 Summary of Prob>F values for stress factor main effects on pasture cover (by point analysis) for each species in each month of the experiment. A point in the table indicates the species was not present.

Species	Aug 1997	Sept 1997	Oct 1997	Nov 1997	Dec 1997	Jan 1998
A. capillaris	0.3362	0.1432	0.7287	0.0067	0.4668	0.1490
A. odoratum	0.2857	0.2818	0.1188	0.6196	0.0839	0.0239
Bare	.	.	0.0001	0.0001	0.0696	0.4114
C. cristatus	0.8333	0.0869	0.0526	0.0707	0.0032	0.8590
C. uniflora	0.0008	0.0419	0.4367	0.4076	0.3060	0.0645
Dead matter	0.3905	0.0383	0.0001	0.0001	0.0050	0.0324
F. rubra	0.4311	0.4114	.	.	0.4114	0.5120
Flatweeds	0.9167	0.6226	0.1473	0.0207	0.0830	0.6814
H. lanatus	0.5913	0.7780	0.0013	0.0037	0.1803	0.0582
L. perenne	0.6639	0.2518	0.0061	0.3540	0.8488	0.9051
L. pedunculatus	0.0987	0.2838	0.2167	0.0161	0.0947	0.1221
Muscii spp.	0.9367	0.4964	0.4687	0.8458	0.7452	0.4114
N. setulosa	0.0006	0.3614	0.3546	0.3046	0.5516	0.8070
Other species	0.5584	0.9431	0.1107	0.4466	0.2203	0.4466
Poa spp.	0.6196	0.7918	0.1785	0.6049	0.3767	0.3407
T. dubium	0.3539	0.2107	0.4491	0.0903	0.4211	.
T. repens	0.0387	0.4023	0.0075	0.1661	0.0819	0.0117

T. repens was significantly influenced by stress treatments in August, October, December and January. In August and October, *T. repens* had significantly more cover on the WT treatment turves, but not significantly more than C, D and W treatment turves in December and January, respectively. Flatweeds became significantly influenced by stress treatments in November and December. In these months the W and WT turves had the lowest cover of flatweeds, but only WT turves were significantly lower than C and D turves. *Muscii* spp., *N. setulosa,* other species and *Poa* spp. were not significantly influenced by stress treatments in any month. *C. uniflora* was significantly influenced by stress treatments in August and September. In these months, there was significantly more *C. uniflora* on the dry treatment turves.

Bare soil only became significantly affected by stress treatments in October and remained so in November and December. The WT turves had significantly more bare soil in October and November, and still had the most bare soil in December, but not significantly so.

The abundance of dead matter was significantly influenced by stress treatments from September through to January. In September there was significantly less dead matter on W turves, in October and November, there was significantly more dead matter on D turves, in December D and C turves and in January D and W turves.

6.4.2.5.3 The effects of site on the cover of individual species

A. capillaris was significantly influenced by site in October, November, December and January (Table 6.10). In October and January, *A. capillaris* had the most cover on HH turves (HH ≥ LN ≥ HN). In November and December, *A. capillaris* had significantly more cover on HH turves. *A. odoratum* was significantly influenced by site in October and January. In these months, *A. odoratum* had the most cover on HH turves, but not significantly more than HN turves. *C. cristatus* was significantly influenced by site in November when it had the most cover on HN turves, but not significantly more than HH turves. *F.*

rubra was not significantly influenced by site in any month, no *F. rubra* was found in October and November. *H. lanatus* was significantly influenced by site in all months. In August, October and January, *H. lanatus* had significantly more cover on LN turves. In September, *H. lanatus* had the most cover on LN turves but not significantly more than HH turves. In November and December, *H. lanatus* had the most cover on HH turves, but not significantly more than LN turves. *L. perenne* abundance was also significantly influenced by site in all months. *L. perenne* had the most cover on HH turves, but only significantly more in November and January. In other months the cover of *L. perenne* on HH turves was not significantly greater than on HN turves. *Poa* spp. cover was significantly influenced by site in all months except January. From August to November, *Poa* spp. had significantly more cover on HH turves. In December *Poa* spp. still had the most cover on HH turves, but not significantly more than HN turves.

The cover of *T. dubium* was significantly influenced by site in August and October, in both months having significantly more cover on HN turves. No *T. dubium* was present in January. *T. repens* cover was significantly influenced by site in October and January. In both months *T. repens* had the most cover on LN turves, but not significantly more than HN turves. The cover of *L. pedunculatus* was significantly influenced by site in all months. *L. pedunculatus* had significantly more cover on HN turves in August, October and November. In September, December and January, it still had the most cover on HN turves, but not significantly more than LN turves.

The cover of *C. uniflora* was significantly influenced by site in all months. In August and January, *C. uniflora* had significantly more cover on HN turves. In September, October and November, *C. uniflora* had the most cover on HN turves, but not significantly more than HH turves. In December this was reversed with the HH turves having the greatest cover of *C. uniflora*. *N. setulosa* was significantly influenced by site in all months except December. In August, September and January, *N. setulosa* had significantly more cover on

HH turves. It had the most cover on HH turves in October and November also, but not significantly more than HN turves. Other species cover was significantly influenced by site in all months except September. In October, November, December and January, other species cover was significantly greater on HN turves. In August it still had the most cover on HN turves, but not significantly more than LN turves. Flatweeds were significantly influenced by site in all months. In all months, flatweeds had significantly more cover on LN turves, and in all months except December, significantly less cover on HH turves. In December there was no significant difference in the cover of flatweeds on HN and HH turves. The cover of *Muscii* spp. was significantly influenced by site in November, with no *Muscii* spp. being present on the HH turves and the cover of *Muscii* spp. on the HN and LN turves differing significantly.

The cover of dead matter was significantly influenced by site in September, December and January. In September, dead matter had the most cover on HH turves, but not significantly more than HN turves. In December, dead matter had significantly more cover on HH turves and in January the most cover on HH turves, but not significantly more than LN turves.

Table 6.10 Summary of Prob>F values for site main effects on pasture cover (by point analysis) for each species in each month of the experiment.

Species	Aug 1997	Sept 1997	Oct 1997	Nov 1997	Dec 1997	Jan 1998
A. capillaris	0.1394	0.2163	0.0716	0.0051	0.0034	0.0188
A. odoratum	0.3044	0.4892	0.0473	0.8376	0.5809	0.0845
C. cristatus	0.9455	0.7470	0.3185	0.0789	0.2034	0.3638
C. uniflora	0.0001	0.0021	0.0074	0.0043	0.0054	0.0001
Dead matter	0.1600	0.0862	0.2898	0.1037	0.0030	0.0895
F. rubra	0.4114	0.3840	.	.	0.3840	0.1673
Flatweeds	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
H. lanatus	0.0023	0.0451	0.0001	0.0054	0.0052	0.0001
L. perenne	0.0228	0.0043	0.0086	0.0309	0.0785	0.0060
L. pedunculatus	0.0049	0.0803	0.0307	0.0057	0.0640	0.0312
Muscii spp.	0.1257	0.2863	0.4662	0.0872	0.8574	0.3840
N. setulosa	0.0106	0.0033	0.0990	0.0555	0.5717	0.0019
Other species	0.0335	0.2644	0.0179	0.0322	0.0334	0.0257
Poa spp.	0.0001	0.0001	0.0001	0.0002	0.0524	0.1213
T. dubium	0.0188	0.4782	0.0185	0.8450	0.1346	.
T. repens	0.1194	0.3424	0.0503	0.6185	0.1346	0.0298

6.4.2.5.4 Effects of site by stress factor interactions on individual species cover

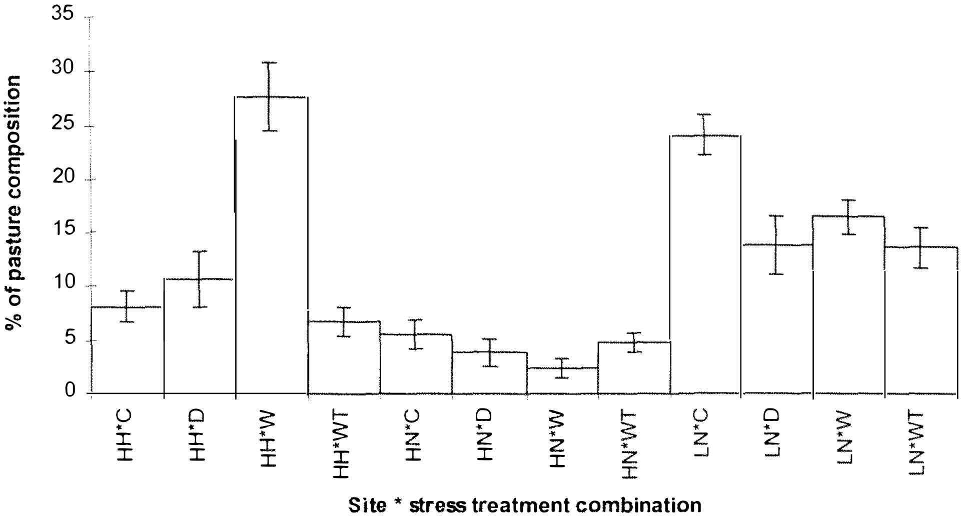
The only species that showed significant site by stress treatment interactions were bare soil, *C. uniflora*, dead matter, *H. lanatus*, *L. perenne*, *L. pedunculatus*, other species and *T. dubium* (Table 6.11). The % of bare soil was significantly influenced by a site by stress treatment interaction in November. Bare soil was only present on the WT turves, and there was five times more bare soil on the HN by WT turves (5%) than the HH by WT or LN by WT turves. There was a significant site by stress treatment interaction effect for *C. uniflora* in August, September and January. In August, the cover of *C. uniflora* on HN by D turves was approximately five times greater (16%) than that present on any other turves. In September there was almost three times more *C. uniflora* on HN by D turves (21%) and in January there was two times more *C. uniflora* on HN by D turves (42%). Dead matter cover was significantly influenced by a site by stress treatment interaction in September. There was approximately eight times more dead matter on HH by C (9%) and HH by WT (8%) turves than HH by D (1%) and HH by W (1%) turves. On the HN turves, there was no dead matter on HN by W turves and two times more dead matter on HN by D turves (7%) than HN by C (2%) and HN by WT (3%) turves.

H. lanatus cover was significantly influenced by site by stress treatment interactions in all months except September (Figure 6.2). In August, HH by D and HH by W turves had three times more *H. lanatus* (20% and 18% respectively) than HH by C and HH by WT turves (6% and 4% respectively). In October, HH by W and LN by C turves had approximately two times more *H. lanatus* (21% and 20% respectively) than any others. In November, the HH by W (35%), LN by W (20%) and LN by C (20%) turves had more than twice the cover of *H. lanatus* than any other turves. In December, HH by W turves had three times more *H. lanatus* (38%) than any other HH turves. LN by C turves had twice as much *H. lanatus* (29%) as LN by W (14%) and LN by WT (13%), and LN by D turves were approximately half as much (8%). In January, HH by W turves had twice as much *H. lanatus* (27%) than any other HH turf. There was no *H. lanatus* on HN by D turves. Figure 6.2 illustrates the effect of the treatment interaction (averaged over all months) that significantly influenced the cover of *H. lanatus* on HH by W and LN by C turves.

Table 6.11 Summary of Prob>F values for site by stress factor interaction effects for pasture cover (by point analysis) in each month of the experiment

Species	Aug 1997	Sept 1997	Oct 1997	Nov 1997	Dec 1997	Jan 1998
A. capillaris	0.8394	0.6670	0.9339	0.6099	0.8222	0.8216
A. odoratum	0.3389	0.6958	0.1010	0.5960	0.7607	0.4757
Bare	.	.	0.1808	0.0013	0.9678	0.4500
C. cristatus	0.3997	0.3286	0.7076	0.9941	0.3183	0.8543
C. uniflora	0.0004	0.0765	0.2148	0.2146	0.3352	0.0074
dead matter	0.8773	0.0066	0.6730	0.3034	0.3751	0.1508
F. rubra	0.4226	0.4500	.	.	0.4500	0.5868
Flatweeds	0.3431	0.8598	0.2329	0.3850	0.3018	0.8048
H. lanatus	0.0885	0.2964	0.0006	0.0308	0.0335	0.0800
L. perenne	0.7222	0.2309	0.0376	0.7297	0.5018	0.7991
L. pedunculatus	0.0781	0.5524	0.5215	0.0708	0.2120	0.5379
Muscii spp.	0.7182	0.4837	0.7127	0.1026	0.3489	0.4500
N. setulosa	0.3056	0.3441	0.2714	0.2661	0.3413	0.4336
other species	0.7011	0.3461	0.0348	0.1331	0.1999	0.0459
Poa spp.	0.9642	0.7533	0.3079	0.8032	0.7093	0.7121
T. dubium	0.4657	0.6066	0.9627	0.8394	0.0819	.
T. repens	0.9248	0.4463	0.1536	0.9306	0.4484	0.9204

Figure 6.2 Average *Holcus lanatus* abundance over all months, for each factor combination.



L. perenne cover was significantly influenced by a site by stress factor interaction in October. There was nearly four times more *L. perenne* on HN by W turves than any other HN turves and there was nearly two times more *L. perenne* on HH by W (8%) and HH by WT (9%) turves than other HH turves.

L. pedunculatus cover was significantly influenced by a site by stress factor interaction in August and November. HN by C turves had the greatest cover of *L. pedunculatus* (5%), followed by HN by W (3%). Only 3 other site by stress factors had any *L. pedunculatus*, HN by D (1%), LN by D (1%) and LN by W (2%). The cover of other species was significantly influenced by a site by stress treatment interaction in October and January. In October, HN by W turves had greater than four times more other species present than any other factor combination and in January greater than three times more. The cover of *T. dubium* was significantly influenced by a site by stress factor interaction in December, when HN by C and LN by W turves had twice as much *T. dubium* (2%) than any other factor combination. The only other treatment combinations where *T. dubium* was present were HN by WT and LN by WT turves.

6.4.2.5.5 Change in the cover of five species groups over time

On the C treatment turves (Figure 6.3), the cover of flatweeds increased steadily from August (17%) to peak at 30% in November. After the treatment change over, flatweeds cover decreased to approximately 20% in January. *A. capillaris* cover fluctuated from August to November, but with a general downward trend from 16% to 10%. After the treatment change over, *A. capillaris* cover increased to approximately 22% and then decreased in January to 20%. *Muscii* spp., *L. perenne* and *T. repens* cover remained relatively constant throughout the experimental period.

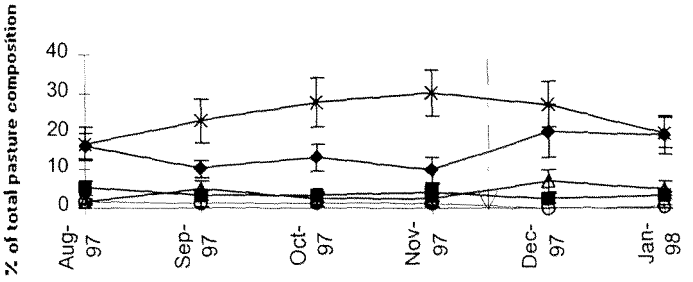
On the D treatment turves (Figure 6.3), the cover of flatweeds steadily increased from 20% in August to approximately 27% in December. A peak of flatweeds cover occurred after the treatment change over date, then cover decreased in January to below pre-treatment level (16%). *A. capillaris* increased from August to September (13 to 15%) and then decreased again in October (10%). From October to January, *A. capillaris* cover increased to peak at 25% in January. *L. perenne* cover decreased slightly as the D treatment became more severe in October and November, and then increased again on re-wetting to pre-treatment levels. The cover of *Muscii* spp. and *T. repens* remained consistently low throughout the experiment.

On the W treatment turves (Figure 6.3), the cover of flatweeds remained relatively constant throughout the experimental period, but with a slight decrease of approximately 5% in January. *A. capillaris* cover decreased from August to October (17% to 9%) and then increased from November to January, to peak in January at 17%. *L. perenne* cover increased slightly (by 3%) from August to September. *L. perenne* cover remained constant into October, then decreased to reach a low in January of 4%. *Muscii* spp. followed a similar pattern of cover to *L. perenne*. *T. repens* cover fluctuated from month to month.

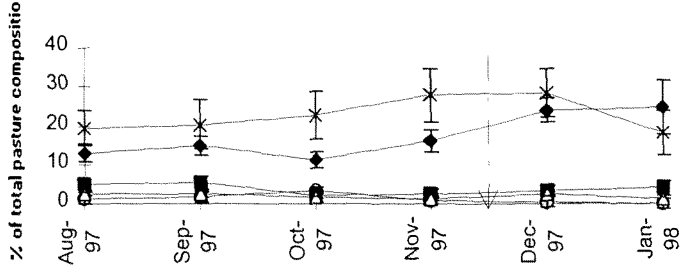
On the WT turves (Figure 6.3) the cover of flatweeds increased from August to September (20 to 26%), then decreased to a low of approximately 13% in December. In January, cover increased again to 15%. *A. capillaris* cover dropped by 12% from August to September, then increased to a peak in November (27%). There was another decrease to 22% in December, then an increase in January to a peak of 33%. *T. repens* cover increased slightly (by 3%) over the entire experimental period, with peak cover occurring in October (12%). *L. perenne* cover fluctuated very little over the experimental period. *Muscii* spp. accounted for only 1% of composition in all months except September when it was 5% of total composition.

Figure 6.3 The effects of stress factors on the % abundance of five species groups. The arrow indicates the treatment change over date.
◆ =*A. capillaris* ■ = *L. perenne* △=*T. repens* x = flatweeds O=*Muscii* spp.

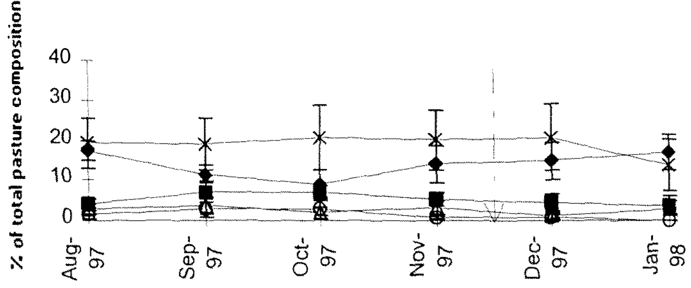
Control turves



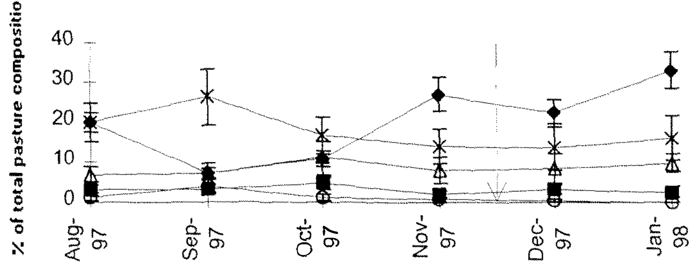
Dry turves



Wet turves



Wet and Treading turves

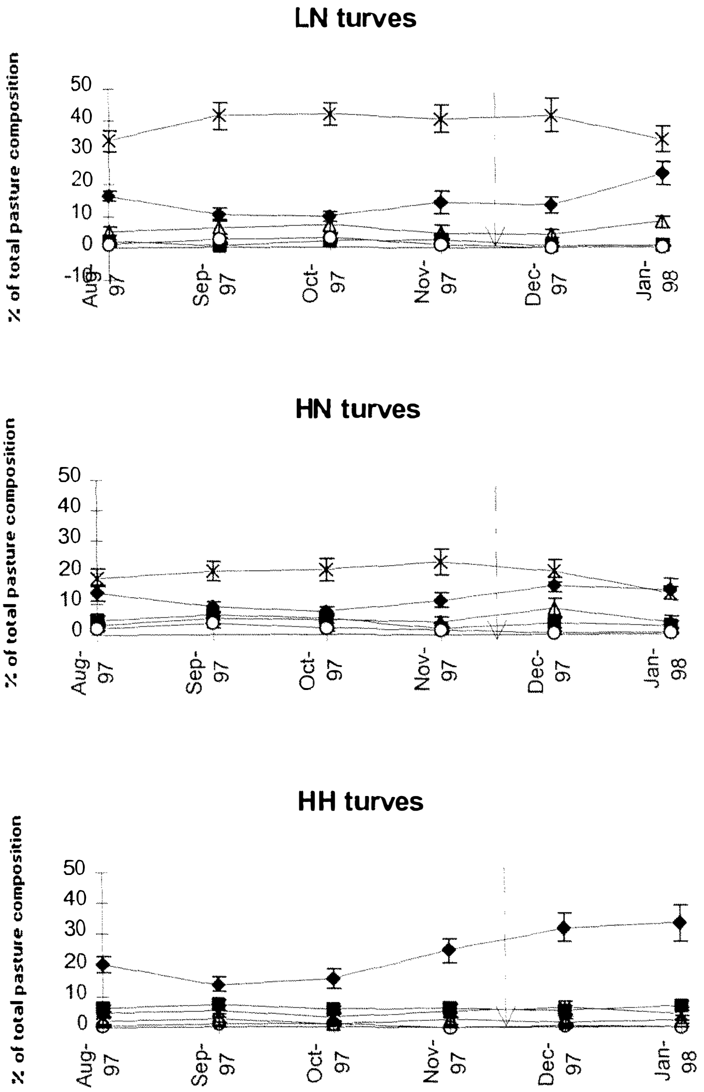


On the LN turves (Figure 6.4) the cover of flatweeds increased from 33 to 40% from August to September and then remained relatively constant until January, when it decreased to approximately 37%. *A. capillaris* cover decreased from 17% to 10% from August to September, remained static in October and then slowly increased to peak at 23% in January. *T. repens* cover fluctuated by only 2% throughout the experimental period, and *L. perenne* and *Muscii* spp. cover fluctuated very little.

On the HN turves (Figure 6.4) flatweeds cover peaked in November at 25% and was lowest in January (11%). *A. capillaris* cover decreased from 15% in August to 6% in October. *A. capillaris* cover then increased to peak at 15% in December and decreased slightly in January (14%). The cover of *L. perenne, T. repens* and *Muscii* spp. fluctuated very little, and all three species followed a similar pattern when changes did occur. A slight increase in cover occurred for all species in September. *T. repens* cover increased to 10% in December.

On the HH turves (Figure 6.4), *A. capillaris* cover decreased from August to September (20 to 13%). From September to January, *A. capillaris* cover increased, but at a decreasing rate, to peak in January at 33%. The cover of the remaining species varied relatively little over the experimental period. *L. perenne* and flatweeds were very similar in their pattern of cover, as were *Muscii* spp. and *T. repens*.

Figure 6.4 The effects of site on the % abundance of five species groups. The arrow indicates the treatment change over date.
◆ =*A. capillaris* ■ = *L. perenne* Δ=*T. repens* x = flatweeds O=*Muscii* spp.



6.4.3 Advanced data analysis

6.4.3.1 MANOVA of point quadrat and pasture dissection data

The results of the point quadrat analysis (Table 6.12) indicated that block was a significant effect in October, site in all months of the experiment, stress factors in September, October, November and December and site by stress factor interactions in September and October.

MANOVA on the full dissection data (Table 6.13) indicated that block was not a significant effect in either September or February, site and stress factors were significant effects in September and February, and the site by stress factor interaction was not significant in either month.

6.4.3.2 Canonical correlation for comparison of the point quadrat analysis with full pasture dissection as a technique for predicting pasture composition

In September the canonical correlation coefficient for the comparison of pasture composition using point analysis and full dissection was 0.77 (Table 6.14). This was a significant correlation (P = 0.0003). The canonical correlation coefficient for the data collected in February was 0.36 which was not a significant correlation (P = 0.1471).

Table 6.12 MANOVA test on point analysis data to determine pasture composition, using Wilks' Lambda criteria for the null hypothesis of no overall effect.

Month	Block	Site	Stress treatment	Site by Stress treatment
August 97	0.0314	0.0004	0.1397	0.1340
September 97	0.4398	0.0186	0.0777	0.0892
October 97	0.0304	0.0001	0.0001	0.0485
November 97	0.1168	0.0013	0.0065	0.6746
December 97	0.8452	0.0003	0.0914	0.1274
January 98	0.7818	0.0001	0.2069	0.1974

Table 6.13 MANOVA test on pasture dissection data to determine botanical composition, using Wilks' Lambda criteria for the null hypothesis of no overall effect.

Month	Block	Site	Stess treatment	Site by Stress treatment
September 97	0.1070	0.0001	0.0033	0.1887
February 98	0.1898	0.0002	0.0984	0.1554

Table 6.14 Canonical correlation analysis to compare the use of point analysis as an estimate of pasture composition with full pasture dissections carried out in September 1997 and February 1998 .

Month	Canonical Correlation Coefficient	Prob >F Wilks Lambda statistic
September 97	0.7678	0.0003
February 98	0.3672	0.1471

6.4.3.3 Shannon Diversity Index and species richness - differences between treatments and months

For sites, both species richness and Shannon diversity were highest for the HN turves, followed by HH turves and then LN turves which had the lowest diversity (Table 6.15a). There was a highly significant difference between sites based on both Shannon diversity and species richness.

The stress factors were significantly different for both Shannon diversity and species richness (Table 6.15b). Both diversity indices were highest on the C turves, followed WT, W then the D turves.

Over time, Shannon diversity and species richness followed the same pattern (Table 6.15c). Species richness decreased from 9.9 species per 100 point quadrat hits in August, to 6.7 species per 100 point quadrat hits in December. In January species richness increased slightly to 6.8 species per 100 point quadrat hits. There was a highly significant difference between months based on both Shannon diversity index and species richness.

6.4.3.4 Species richness and dry matter production

The R^2 values for the relationship between species richness and dry matter production, for all months, were very low, ranging from R^2=2% in August and December to R^2=7% in October. The relationship between species richness and dry matter production was only significant in October ($P = 0.0683$).
A significant relationship between dry matter production and species richness only occurred on LN turves in September (R^2=27%) and January (R^2=18%) and on HN turves in November (R^2=33%) (Table 6.16). No other main effects showed a significant relationship between species richness and dry matter production.

Site and stress factor combinations (when pooled over the experimental period) that showed a significant relationship between dry matter production and species richness included LN by W (R^2=12%), LN by WT (R^2=12%) and HN by W (R^2=22%) (Table 6.16).

Table 6.15 Shannon Diversity Index and Species Richness for (a) site, (b) stress factors and (c) months.

(a)

Diversity Index	LN	HN	HH	SEM	Prob>F
Richness	6.4	8.8	7.6	0.2	0.0001
Shannon	1.43	1.77	1.61	0.03	0.0001

(b)

Diversity Index	C	D	W	WT	SEM	Prob>F
Richness	8.1	7.2	7.5	7.6	0.2	0.0086
Shannon	1.67	1.51	1.59	1.64	0.03	0.0039

(c)

Month	Shannon	Richness
Aug 97	1.83	9.9
Sept 97	1.71	7.7
Oct 97	1.54	7.3
Nov 97	1.50	7.2
Dec 97	1.49	6.7
Jan 98	1.56	6.8
SEM	0.04	0.2
Prob>F	0.0001	0.0001

Table 6.16 Significant relationships between species richness and dry matter production (kg DM/ha/day) identified on treatments applied.

Treatment	Month	Slope	R^2	Prob>F
LN	Sept 97	+	27	0.0485
	Jan 98	+	18	0.0928
HN	Nov 97	+	33	0.0305
LN by W	pooled over all months	+	12	0.0884
LN by WT	pooled over all months	+	12	0.0907
HN by W	pooled over all months	+	22	0.0283

6.4.3.5 Dry matter accumulation from functional groups

In August and September (Table 6.17), high fertility responsive grasses produced the most dry matter when averaged over all turves (25.3 and 25.8 kg DM/ha/day, respectively). Other legumes produced the least dry matter in August and September (both 1.8 kg DM/ha/day). In October, November and December, flatweeds produced the most dry matter (22, 23.1 and 22.6 kg DM/ha/day, respectively). In October, other legumes again produced the least dry matter (2.2 kg DM/ha/day) and in November, December and January, *L. perenne* produced the least dry matter (3.6, 3.4 and 3.4 kg DM/ha/day, respectively). In January, the *A. capillaris* functional group produced the most dry matter.

The contribution of the *A. capillaris* functional group (Table 6.17) to dry matter production decreased from August to September and October, and then increased from November to January. The high fertility responsive grasses group contribution to dry matter generally decreased as the experiment progressed, though there was a slight increase in November (from 14.4 to 15.7 kg DM/ha/day). The *L. perenne* group contribution remained relatively static in August, September and October, and then decreased by 1 kg DM/ha/day in November and remained at that level in December and January. The contribution of other legumes to dry matter production generally increased over time with a slight decrease of 0.5 kg DM/ha/day in January. Other species contribution generally increased over time except for a decrease of 4.5 kg DM/ha/day in November. Other species contribution to dry matter continued to increase in December and January. *T. repens* contribution remained relatively constant throughout the experiment with only a slight decrease in dry matter produced in November (from 4.4 to 3.8 kg DM/ha/day). The contribution of flatweeds increased from August to November, then in December and January, decreased.

Table 6.17 Dry matter accumulation rate (kg DM/ha/day) for functional groups. HFRG = high fertility responsive grasses and LFTG = low fertility tolerant grasses.

Group	Aug 1997	Sep 1997	Oct 1997	Nov 1997	Dec 1997	Jan 1998
A. capillaris	16.7	11.0	11.0	16.8	20.4	23.5
HFRG	25.3	25.8	14.4	15.7	14.1	13.9
LFTG	14.3	11.1	11.2	8.5	9.7	8.3
L. perenne	4.4	4.8	4.4	3.6	3.4	3.4
other legumes	1.8	1.8	2.2	3.9	5.3	4.8
other species	5.9	15.5	15.2	10.7	15.0	20.9
T. repens	3.6	4.6	4.4	3.8	4.8	4.7
Flatweeds	18.9	22.1	22.0	23.1	22.6	16.9
SEM	1.2	1.5	1.3	1.4	1.7	1.7
Prob>F	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

6.4.3.6 The effect of site on functional group cover

Functional groups that were significantly influenced by site in all months included high fertility responsive grasses, *L. perenne*, other legumes, other species and flatweeds (Table 6.18). The low fertility tolerant functional group was not significantly affected by site in any month. The high fertility responsive functional groups had the most cover on the HH site, but only significantly so in August, September, October and November. In December and January, the HH turves did not have significantly more high fertility responsive grasses than LN turves.

The *L. perenne* functional group also had the most cover on the HH turves in every month, but only significantly so in August, November and January. In September, October and December, there was no significant difference between HH and HN turves. The other legumes functional group had the most cover on HN turves in all months, but only significantly more than the LN turves in August, October and November. The other species functional group also had the most cover on the HN turves, but only significantly more than the HH turves in August, November and January. The flatweeds functional group had significantly more cover on the LN turves in all months and significantly less cover on the HH turves in all months. The cover of the low fertility tolerant grass functional group was only significantly influenced by site in October, and this was only a marginal influence ($P = 0.0949$). The cover of the *A. capillaris* functional group was significantly influenced by site in October, November, December and January. In all months the *A. capillaris* functional group had the most cover on the HH turves, but only significantly more in November and December. The cover of the *T. repens* functional group was only significantly influenced by site in December and January. In December, the *T. repens* group had the most cover on the HN turves, but not significantly more than LN turves, and in January it had more cover on the LN turves, but not significantly more than the HN turves.

Table 6.18 Summary of Prob>F values for pasture cover of functional groups for sites over all months

Functional group	Aug 1997	Sept 1997	Oct 1997	Nov 1997	Dec 1997	Jan 1998
A. capillaris	0.1394	0.2109	0.0716	0.0051	0.0034	0.0188
HFRG	0.0003	0.0009	0.0001	0.0001	0.0031	0.0007
LFTG	0.5842	0.7065	0.0949	0.6726	0.6616	0.1183
L. perenne	0.0228	0.0040	0.0086	0.0309	0.0785	0.0060
other legumes	0.0010	0.0949	0.0067	0.0077	0.0377	0.0312
other species	0.0019	0.0022	0.0090	0.0007	0.0616	0.0001
T. repens	0.1194	0.3691	0.0503	0.6185	0.0670	0.0298
Flatweeds	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001

6.4.3.7 The effect of stress factors on functional group cover

The stress factors did not have a significant effect on functional group cover until October and no functional groups were significantly influenced by a stress factor for more than three months (Table 6.19). The *A. capillaris* functional group was only significantly influenced by stress factors in November, at which time it had significantly more cover on the WT turves than any other. The high fertility responsive functional group was significantly influenced by the stress factors in October and November. In both months the high fertility responsive group had the most cover on the W treatment turves (but not significantly so), followed by the C, WT and D turves.

The cover of the low fertility tolerant grass group was only significantly influenced by stress factors in October and December, when the low fertility tolerant group had significantly more cover on the WT turves. The *L. perenne* functional group was significantly influenced by stress factors in October when it had the most cover on the W turves, but not significantly more than the WT turves.

The other legumes functional group was significantly influenced by stress factors in November and December. In both months, the other legumes functional group had the most cover on the W treatment turves, but not significantly more than the WT or C turves. The other species functional group was significantly influenced by stress factors only in October. It had the most cover on the W treatment turves, but not significantly more than the C or D turves. The *T. repens* functional group was significantly influenced by stress factors in October, December and January. In October, the *T. repens* group had significantly more cover on the WT turves. In December and January, it still had the most cover on the WT turves, but not significantly more. The flatweeds functional group was only significantly influenced by stress factors in November and December. In November, it had the most cover on the C turves, but not significantly more than D turves. In December, the flatweeds functional group had the most cover on the D turves, but not significantly more than C turves.

Table 6.19 Summary of Prob>F values for pasture cover of functional groups for stress factors.

Functional group	Aug 97	Sept 97	Oct 97	Nov 97	Dec 97	Jan 98
A. capillaris	0.3362	0.1389	0.7287	0.0067	0.4668	0.1490
HFRG	0.3166	0.9031	0.0184	0.0031	0.3826	0.2718
LFTG	0.1500	0.0973	0.0119	0.8517	0.0034	0.1611
L. perenne	0.6639	0.2558	0.0061	0.3540	0.8488	0.9051
other legumes	0.1060	0.4142	0.1300	0.0735	0.0659	0.1221
other species	0.1136	0.3069	0.0855	0.3009	0.0777	0.1895
T. repens	0.0387	0.4088	0.0075	0.1661	0.0819	0.0117
Flatweeds	0.9167	0.6295	0.1473	0.0207	0.0830	0.6814

6.4.3.8 The effect of site by stress factor interactions on functional group cover

Significant effects of site by stress treatment interactions on functional group cover only occurred for high fertility responsive grasses, *L. perenne*, other legumes and other species (Table 6.20). Significant interactions were observed in October, November and December for the high fertility responsive grass functional group. In October and November, the high fertility responsive grass functional group accounted for approximately twice as much cover on the HH by W turves than any other turves. In December, the high fertility responsive grass functional group accounted for twice as much cover on HH by W turves than on any other turves, with the exception of LN by C turves. The cover of the high fertility responsive functional group on the LN by C turves was approximately one and a half times that on any other turves.

The *L. perenne* functional group was significantly influenced by a site by stress factor interaction in October. There were relatively high levels of the *L. perenne* functional group on HN by W, HH by W and HH by WT turves. The other legumes functional group was significantly influenced by a site by stress factor interaction in August. The cover of the other legumes group on HN by C and HN by W turves was relatively high. The other species functional group was significantly influenced by a site by stress factor interaction in December, when the cover of the other species functional group was twice as great on HN by W turves than any other site by stress factor combinations.

Table 6.20 Summary of Prob>F values for pasture cover of functional groups for site by stress factor interactions

Functional group	Aug 97	Sept 97	Oct 97	Nov 97	Dec 97	Jan 98
A. capillaris	0.8394	0.6347	0.9339	0.6099	0.8222	0.8216
HFRG	0.5991	0.9147	0.0285	0.0203	0.0575	0.1084
LFTG	0.6525	0.1375	0.3769	0.7814	0.5997	0.8804
L. perenne	0.7222	0.2642	0.0376	0.7297	0.5018	0.7991
other legumes	0.0932	0.4979	0.4708	0.1824	0.1116	0.5379
other species	0.6808	0.5998	0.2203	0.3656	0.0672	0.4503
T. repens	0.9248	0.4249	0.1536	0.9306	0.4484	0.9204
Flatweeds	0.3431	0.8502	0.2329	0.3850	0.3018	0.8048

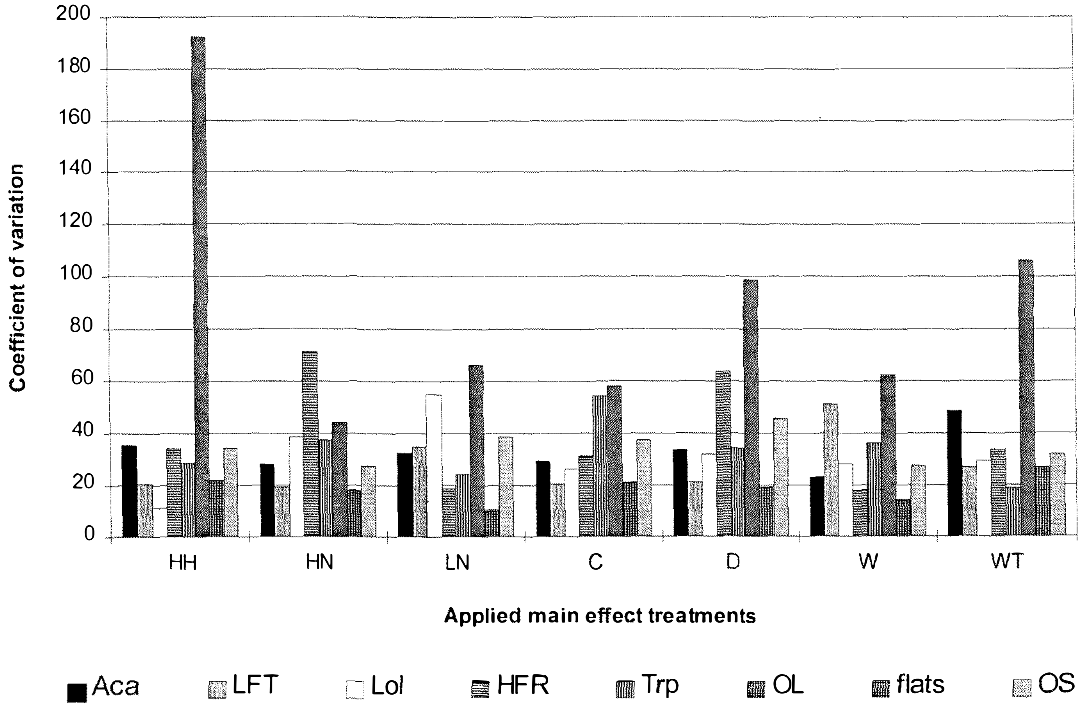
6.4.3.9 The variation in the cover of functional groups over time

The cover of the *A. capillaris,* the low fertility tolerant grass, the flatweeds and the other species functional groups over time was reasonably stable over all treatments, with a few exceptions (Figure 6.5). On the WT turves the variation in the cover of the *A. capillaris* group was greater than any other treatment. The variation in the cover of the low fertility tolerant grass group was relatively higher on the LN and W turves. Flatweeds had a slight decrease in the amount of variation on the LN turves. The variation in the cover of the other species functional group was slightly higher on the D turves.

The variation in the cover of the *L. perenne* group was low on the HH turves and high on the LN turves compared with the other treatments. The variation in the cover of the high fertility responsive grass functional group was high on HN and D turves and low on LN and W turves. The variation in the cover of the *T. repens* functional group was high on C turves and relatively low on WT, LN and HH turves. The variation in the cover of the other legumes functional group was variable. This was difficult to interpret because very large coefficients of variation were created by other legumes not being present on some turves.

Figure 6.5 Coefficient of variation of the cover of the functional groups over the experimental period.

Aca=*A. capillaris*, LFT=low fertility tolerant grasses, Lol=*L. perenne*, HFR=high fertility responsive grasses, Trp=*T. repens*, OL=other legumes, flats=flatweeds and OS=other species .



6.4.3.10 Growth flush in the recovery phase

There appeared to be a flush of growth in the recovery phase (Figure 6.6) and the rate of herbage accumulation in that flush differed between treatments.
The regression slopes of the herbage accumulation curves over the entire recovery period showed that the D turves had the greatest herbage accumulation rate, followed by the C turves, the W turves and the WT turves (Table 6.21a). Only the D and the WT turves differed significantly in terms of herbage accumulation rate.

In the first part of the recovery phase (days 3 - 24 after change over), where the herbage accumulation curves appear the steepest (Figure 6.6), the regression slopes of the curves showed that the D turves had a significantly higher herbage accumulation rate than all other treatments. The W turves had a significantly higher herbage accumulation rate than the C and WT turves, which did not differ significantly (Table 6.21b).

In the second half of the recovery period (days 24 to 65) the regression slopes of the herbage accumulation curves indicated that there was no significant difference in the rates of herbage accumulation between treatments (Table 6.21c).

6.4.3.10.1 Effects of tillering on herbage accumulation flush

There were no significant relationships between tiller number and dry matter accumulation in late November, December and January (recovery phase), over all treatments and for each individual treatment.

Figure 6.6 Herbage accumulation rate for four pasture treatments (numbers at the top of the graph indicate the days into the recovery period).

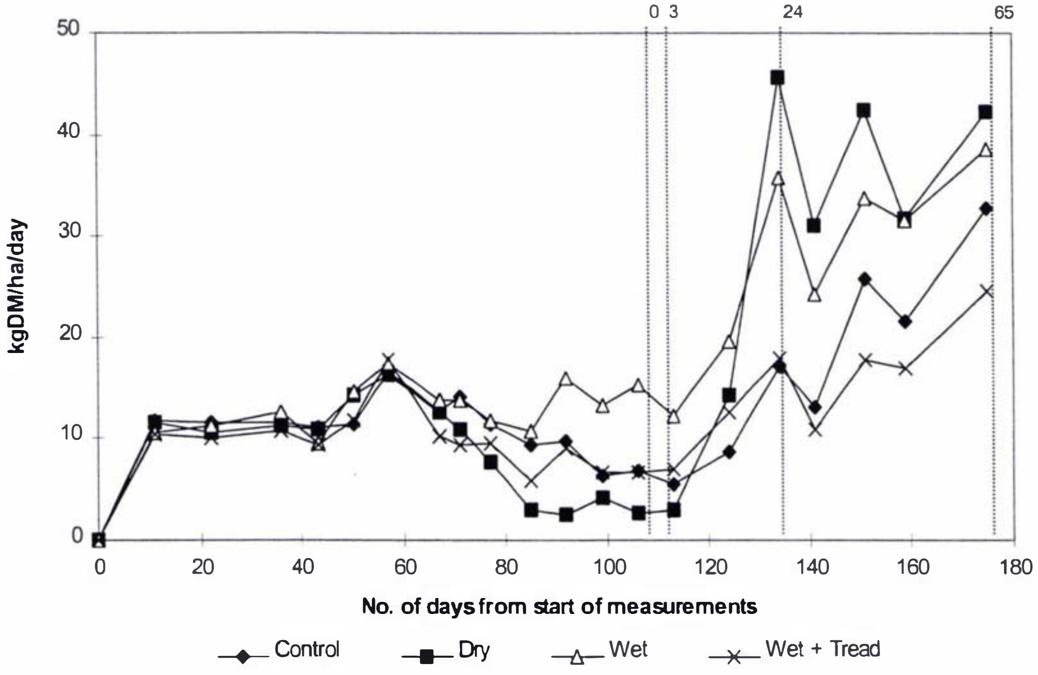


Table 6.21 Regression between herbage accumulation rate (kg DM/ha/day) and time (days) for each stress factor.

(a) For the entire recovery period (3 - 65 days after change over).

Treatment	Slope	R^2 (%)	SEM
C	+0.431	0.90	0.0647
D	+0.552	0.53	0.2305
W	+0.378	0.69	0.1121
WT	+0.235	0.74	0.0617

(b) For the first part of the recovery period (3 - 24 days).

Treatment	Slope	R^2 (%)	SEM
C	+0.547	0.92	0.1620
D	+2.016	0.92	0.6120
W	+1.115	0.95	0.2690
WT	+0.520	0.99	0.0103

(c) For the second part of the recovery period (24 - 65 days).

Treatment	Slope	R^2 (%)	SEM
C	+0.506	0.79	0.1826
D	+0.235	0.28	0.2665
W	+0.374	0.82	0.1243
WT	+0.378	0.91	0.0808

6.4.3.10.2 Effects of leaf extension on herbage accumulation flush

When leaf extension rate was averaged over all 5 species and regressed with dry matter accumulation in the recovery phase (late November, December and January), the C turves showed significant relationships in November and December (P = 0.0433 and P = 0.0061, respectively), the W turves in November (P = 0.0039), the WT turves in December (P = 0.0024) and the D turves showed no significant relationship in any month.

When the relationship between leaf extension and dry matter accumulation was examined for each individual species on each treatment, there were several different significant relationships in each month (Table 6.22). In November, there were six combinations of species and treatment that showed a significant relationship between leaf extension and dry matter accumulation. Of these six, five showed a positive, and one (*T. repens* on the D treatment turves) showed a negative relationship (Table 6.22a). In December, there were seven species and site combinations that showed a significant positive relationship (Table 6.22b). In January, only two species by treatment combinations showed a significant relationship, one positive and the other negative (Table 6.22c).

Table 6.22 Species by treatment interactions exhibiting significant regressions between leaf extension (mm/day) and dry matter accumulation rate (kg DM/ha/day) for (a) November, (b) December and (c) January 1997.

(a)

Species	Treatment	R^2 (%)	Prob > F	Slope
A. capillaris	W	0.75	0.0024	+
A. odoratum	C	0.39	0.0708	+
A. odoratum	WT	0.40	0.0665	+
H. lanatus	C	0.64	0.0096	+
L. perenne	C	0.39	0.0732	+
T. repens	D	0.99	0.0060	-

(b)

Species	Treatment	R^2 (%)	Prob > F	Slope
A. odoratum	WT	0.49	0.0364	+
H. lanatus	C	0.39	0.0719	+
H. lanatus	WT	0.64	0.0174	+
L. perenne	C	0.54	0.0237	+
L. perenne	W	0.36	0.0865	+
T. repens	C	0.37	0.0842	+
T. repens	WT	0.56	0.0196	+

(c)

Species	Treatment	R^2 (%)	Prob > F	Slope
A. capillaris	D	0.37	0.0820	+
L. perenne	WT	0.37	0.0811	-

6.5 Discussion

6.5.1 Introduction

The physiological responses that occurred for both the moisture and treading treatments are discussed for each species. Botanical composition changes under each of the treatments are also discussed, as is the resistance and resilience of species to the imposed stresses.

6.5.2 Pasture responses to moisture

The moisture treatments applied to the turves were designed to create moisture deficit and excessive moisture. The results of the experiment indicated that moisture deficit (D treatment turves) had a far greater negative influence on pasture production than the wetting treatment (W treatment turves).

6.5.2.1 Morphological changes

Turner and Begg (1978) suggested that some morphological responses, such as leaf area development, tillering and root growth, are more sensitive to water deficits than some physiological processes, such as photosynthesis and respiration. No measures of physiological changes with moisture stress were taken in this experiment, but several morphological measurements were: tiller counts, leaf extension rates, dry matter accumulation rates and root growth.

6.5.2.1.1 Tillers

Tillering on the D treatment turves was reduced, though not significantly, as the intensity of the water deficit increased from September to peak moisture deficit of approximately 13% volumetric soil moisture content in November. A regression of soil volumetric moisture content and tiller number, over the period September to November, resulted in a positive relationship between tiller number and soil moisture (Slope=0.009, R^2=96%). This reduction in tiller number with increasing moisture deficit may have been brought about by two mechanisms. The first is the increased rate of tiller death under drought conditions. Sheehy *et al.* (1975) found that when the leaf water potential of *L. perenne* was allowed to fall to 1.5 MPa, the weight of dead tillers increased to

50% of total dry weight. The other mechanism is through reduction in new tiller growth. Perry and Larson (1974) showed in *Medicago sativa* that the reduction of soil water to 50% of field capacity reduced both the number of primary shoots and the regrowth of shoots after defoliation. Both these mechanisms are designed to reduce total plant leaf area from which evapotranspiration can occur, hence reducing water loss from the plant.

During recovery, D treatment turves exhibited an increase in tiller numbers and tiller number was greater at the end of the recovery period than at the start of the experiment in September. Such compensatory growth is proposed to come from rapid expansion of cells which had continued to divide during water deficit (Turner and Begg, 1978).

6.5.2.1.2 Leaf extension

Leaf extension rate decreased significantly in the stress phase on the D treatment turves compared to the control turves. In the recovery phase however, leaf extension rates on the D treatment turves showed a compensatory effect, by having higher than initial leaf extension rates and higher leaf extension rates than any of the other treatments.

Cell growth or expansion is the most sensitive of the plant processes to water stress, due to its dependence on turgor pressure (Hsiao and Acevedo, 1974). High turgor pressure is required for cell expansion because the structural characteristics of the cell wall do not permit extension when turgor pressure falls below a threshold value. This threshold value varies between species, but Turner and Begg (1978) suggest that leaf extension for most pasture species will be markedly decreased at leaf water potentials below 0.4 MPa. The range of turgor pressures allowing cell expansion can be narrow (Boyer, 1973), which makes leaf extension sensitive to moisture fluctuations. Most species for example, will cease leaf elongation completely at leaf water potentials of -1 MPa (Turner and Begg, 1978). This range also varies for different species

(Turner and Begg, 1978) and is one of the mechanisms different species use to cope with water deficit situations.

In this experiment, the species responded quite differently to the water deficit treatment, particularly in the recovery phase when *L. perenne* leaf extension was greater than that of any other species (Figure 6.1). Leaf extension ceased for all species as the D treatment turves approached maximum water deficit of approximately 13% volumetric soil moisture content. Which species ceased leaf elongation first was not apparent in this case as measurements were only taken at monthly intervals. In an experiment (Davis, 1995) on the effects of moisture deficit on hill pasture species, leaf elongation ceased the earliest in *L. perenne*. Other species such as *A. capillaris* and *H. lanatus*, were found to be slower than *L. perenne* to show signs of leaf extension ceasing. *T. repens* petiole extension did not cease entirely in the Davis (1995) experiment.

During the recovery phase, *L. perenne* showed the fastest and greatest increase in leaf extension. This compensatory leaf extension may be due to cell division continuing to occur once leaf extension stopped (Hsiao and Acevedo, 1974). In Figure 6.1, a large increase in the leaf extension rate of *L. perenne* occurred on the D treatment turves after re-wetting. In the Davis (1995) experiment, *A. capillaris* and *H. lanatus* did not recover at all from severe water stress. In this experiment, however, they did recover, along with *A. odoratum*, to a leaf extension rate of 6 mm/day (more than half that of *L. perenne*). Towards the end of the recovery period, leaf extension rate slowed for *L. perenne* and increased slightly for *A. odoratum* and *H. lanatus* which resulted in these 3 grass species having similar leaf extension rates at the end of the experimental period. The slowing of leaf extension rate for *L. perenne* was probably due to cell division and expansion rates returning to normal after the initial flush in the recovery period. The increase in extension rate for *A. odoratum* and *H. lanatus* may have been due to cell division levels returning to pre-stress levels. Leaf extension rate did not appear to be affected on the W treatment turves as there was sufficient moisture for leaf extension to proceed unhindered.

6.5.2.2 Herbage accumulation rate

The herbage accumulation rate on the turves was significantly influenced by the moisture treatments.

Rates of herbage accumulation were slow to differentiate between the treatments, probably due to the high soil moisture levels at the beginning of the experiment. All turves were fully watered at the start of the experimental period (approximately 40% VSMC). Over the 60 day period before a differentiation in herbage accumulation rate became apparent, volumetric soil moisture content will have altered according to the treatment applied, the pasture species will have recognised that moisture levels had changed, and cellular processes will have occurred with the primary aim of ensuring plant survival. As the moisture deficit increased towards the end of the stress phase, these morphological changes increased resulting in suppressed herbage accumulation rates on the D turves.

From 85 days to the end of the stress period (approximately 110 days) the W turves had the highest herbage accumulation rates. The most likely explanation for this was that the control turves had enough plant available water to ensure plant survival and to maintain levels of herbage accumulation, but on the W treatment turves where volumetric soil moisture content was approximately 60%, the extra water available may have been utilized by the plants for increased rates of leaf extension, the rate of which is directly affected by soil moisture (Hsiao and Acevedo, 1974). This effect may have been accentuated in the glasshouse as the experiment proceeded due to the approach of summer and temperatures both outside and inside the glasshouse were increasing. Having a volumetric soil moisture content of 60% may have alleviated some heat stress that could have occurred on the turves with the lower volumetric soil moisture content of 40% (control turves). The effects of

heat stress on the plants were not measured, however, nor was the change in temperature in the glasshouse as the season progressed. Soil temperatures were higher in the second phase of the experiment than the first (Table 6.2).
In the recovery phase, the release of the turves, particularly the D treatment turves, from the applied moisture stress resulted in increased rates of herbage accumulation. The recovery period had two phases. The first was the initial flush of growth that occurred immediately following the removal of the moisture stress. This period lasted for approximately 25 days after the stress removal. D and W treatments showed the greatest increase in herbage accumulation. In addition to the removal of the moisture stress itself, NH_4^+ and NO_3^- can be released upon re-wetting of dry soil, which can also result in a flush of growth. Concentrations of these were measured in the soil approximately one month after the change-over period and no differences in the levels of these nutrients were found between treatments. It is possible that the release of these nutrients had occurred and had been absorbed by the plants or soil organisms by the time the soil tests were carried out. Twenty four days into the recovery period, the rates of herbage accumulation were beginning to slow, indicating that the effect of the cause of the growth flush was diminishing.

The flush of growth on the W treatment turves may have been contributed to by a release of plant available nitrogen with removal of excess moisture, resulting in increased herbage accumulation rates, but again, the soil N tests may have been too late to pick up any differences. An increase in soil temperature also occurred on the W treatment turves in the recovery phase of the experiment (Table 6.2) and may have contributed to increased herbage accumulation rates. The drying out of the turves may also have resulted in improved oxygenation of the soil which could also contribute to increased plant growth. Eccles *et al.* (1990) noted that water-logging caused decreased leaf extension rates and increased senescence rates in *Bromus willdenowii* and Trought and Drew (1980) noted similar symptoms in water-logged wheat. Trought and Drew (1980) stated that the reduction in leaf extension rate in water-logged plants may result from reduction in water uptake associated with low oxygen concentrations around the roots. The removal of the excess water would result in improved oxygenation and associated increased leaf extension rates. This process is likely to be partially responsible for the flush of growth seen on the W treatment turves in the recovery phase.

The second phase of the recovery period occurred from approximately 25 days to 65 days after stress treatment ceased. In this phase, herbage accumulation rates slowed on all treatment turves and the rates of herbage accumulation were very similar amongst treatments. The D turves still produced the most herbage, probably because they maintained the productive advantage developed in the first part of the recovery phase. Over time however, the herbage accumulation rates of all treatments would be expected to approach a common value, or stable production level. Though they did not differ significantly, the slope of the herbage accumulation graph for the D turves was less than that of any other treatment, indicating that herbage production was moving back to some long term “stable” level. The slope of the WT herbage accumulation curve was steeper than that of the W turves which could indicate that the effects of treading were lessening and the herbage production was also moving back to a long term stable state.

The relationship between herbage accumulation rate and leaf extension rate was investigated for each species on each treatment (Table 6.22). It appeared that leaf extension rates and herbage accumulation rates were related, particularly on the C and WT turves, and that the mechanism of leaf extension strongly contributed to the increase in herbage accumulation in the recovery phase.

In summary, excess moisture enhanced herbage accumulation and moisture deficit resulted in considerably depressed herbage accumulation in this experiment. The removal of the moisture deficit stress resulted in a much larger compensatory flush of growth than the removal of the excess moisture treatment, though the removal of that treatment did still result in an increase in herbage accumulation.

Overall, when deficits from the stress phase and flushes of growth from the recovery phase are taken into account, herbage production was greatest on the W treatment turves, followed by the D treatment turves and then the control turves. Thresholds must exist, which are undefined in this experiment, beyond which the moisture stress (be it water-logging or water deficit) results in a marked depression in herbage accumulation. These thresholds may be reached through duration of the stress or intensity of the stress and it would be helpful for pasture managers to know what these limits are in order to develop a contingency plan to cope with such events.

6.5.2.3 Species composition responses to moisture

That only 7 of the 15 species present on the turves showed a significant response to the moisture treatment illustrates the differing abilities species have to deal with stress. Significant influences of water stress on the turves occurred mainly in the late stress phase (October and November) and early recovery phase (November and December), when plant strategies for survival and recovery from moisture stress conditions were most pronounced. The species that were most influenced were *A. capillaris*, *C. cristatus*, flatweeds, *H. lanatus*, *L. perenne*, *T. repens* and *L. pedunculatus.* If these species were grouped in terms of function (see Chapter 3), there were 7 functional groups represented (*A. capillaris*, low fertility tolerant grasses, flatweeds, high fertility responsive grasses, *L. perenne*, *T. repens* and other legumes). To simplify the response of each functional group to the moisture treatments they were classified as increasers, decreasers (Dyksterhuis, 1948) or static (in terms of their cover), in both the peak stress and early recovery phase. Noy-Meir *et al.* (1989) described the response of species to grazing stress in this way and likened these groupings to the plant strategies of competitors, stress tolerators and ruderals which Grime (1979) described in relation to stress and disturbance.

At peak stress on the D treatment turves, *A. capillaris*, low fertility tolerant grasses and flatweeds were increasers, high fertility responsive grasses, *T. repens* and other legumes were decreasers and *L. perenne* was static. In this case, the increasers could be described as stress-tolerators or the species that survive by functioning normally, with the expectation that moisture will increase in a relatively short period of time. They could be described as being resistant to the stress (Davis, 1995). If the moisture deficit was only short term, these species have not lost any competitive advantage they may have had before the water deficit occurred. If however, the water deficit was prolonged, often these species did not recover due to cellular damage and depletion of plant resources from trying to function normally under adverse conditions. The decreasers in the stress phase could be described as survival strategists. They begin to shut down cellular processes relatively early to conserve moisture and basically cease growing, with the focus on survival. These decreaser functional groups were all increasers in the recovery phase and could be described as being resilient to the moisture stress. Cellular processes begin again as soon as adequate moisture is available and these species are normally associated with rapid recovery, which enables them to take advantage of gaps in the sward to establish a competitive advantage.

At peak stress for the W treatment turves, *A. capillaris*, high fertility responsive grasses, *T. repens* and other legumes were all increasers, low fertility tolerant grasses and *L. perenne* were decreasers and flatweeds abundance remained static. The W treatment did not appear to have induced as much stress in the pasture species present. Four functional groups were increasers under the W treatment, but only 3 under the D treatment. It was interesting to note that the decreasers in the stress period under the D treatment, were increasers for the W treatment (high fertility responsive grasses, *T. repens* and other legumes) and low fertility tolerant grasses which were increasers under dry conditions are decreasers under wet conditions. *L. perenne* was static under dry conditions, but became a decreaser under wet conditions indicating that perhaps it was more intolerant of water-logged conditions than dry conditions. Flatweeds were increasers under dry conditions, but were static on the W treatment turves. This indicated that flatweeds were more tolerant of dry conditions.

In the recovery phase on the W turves, only *A. capillaris* and other legumes increased in abundance. Low fertility tolerant grasses, high fertility responsive grasses, *L. perenne* and *T. repens* decreased, and flatweeds remained static. The increase in abundance of the other legumes group may be a seasonal effect, as the abundance of *L. pedunculatus* (a member of the other legumes functional group) increased as summer progressed. *A. capillaris* increased in abundance under all treatments in the recovery phase. The control turves followed the W treatment turves more closely than the D treatment turves in terms of the functional groups that were decreasers. Low fertility tolerant grasses, high fertility responsive grasses and *L. perenne* were decreasers on both the control and wet turves. Flatweeds became decreasers on the control turves and *T. repens* increasers when compared to the wet turves.

From this information it can be deduced that these functional groups can be divided up further with regard to their response to the moisture treatments. *A. capillaris* was in a group of its own, as it showed increased abundance in all phases except the peak stress phase on the control turves. This may have occurred due to competition from more vigorously growing functional groups (e.g. *L. perenne*). Work by Harris and Brougham (1968) and Kershaw (1958) showed that *L. perenne* and *A. capillaris* were significantly negatively associated in swards. *L. perenne* and *A. capillaris* were negatively associated on all treatment turves in both the stress and recovery phases, except the D treatment recovery phases. In this instance, all species were on an even competitive level as they had all been under moisture deficit stress and all responded with increased leaf extension rates on release from the stress. Long term, it would be most likely that only one of these species would eventually dominate in the sward.

Low fertility tolerant grasses also appeared to be in a group of their own. The abundance of this group was positively influenced by dry conditions and negatively influenced by water-logged conditions. This was most likely because its constituent species (*A. odoratum*, *C. cristatus* and *F. rubra*) were all intolerant to water-logging (Grime *et al.* 1988).

High fertility responsive grasses, *T. repens* and other legumes were intolerant of dry conditions, and their growth was promoted under moist conditions (of the level seen in this experiment).

Flatweeds and *L. perenne* appeared to be rather plastic in their response to drought and water-logging. Flatweeds were generally more responsive to dry conditions, and *L. perenne* to moist conditions, but the abundance of both species was not negatively affected under the opposite extreme of moisture.

6.5.3 Pasture responses to treading

Brown and Evans (1973) divided the effects of treading on individual plants into two areas. The indirect effects on plants through changes in soil and direct effects on plants.

6.5.3.1 Indirect effects on plants through changes in soil.

The two main effects of treading on soil likely to affect plant growth are soil compaction and pugging. In experiments carried out on *L. perenne*, it was found that compaction had very little effect on plant yield, in fact, yield increased as compaction increased (Edmond, 1958b). Though compaction was not measured in the turves experiment, it is unlikely that the mechanical treading would have had as much influence on plant growth as animal treading because the downwards force (determined largely by animal weight in the field) used to “tread” the turves would not have been as great.

Root weight and length on the WT turves were not significantly different to the W or C turves, hence the treading and subsequent effects on the soil, did not affect root growth. Edmond (1958a) found in one experiment that treading was insufficient to limit root growth, but in another experiment with very heavy rates of treading (Edmond, 1962), root growth was limited.

Pugging is the other main effect of treading on soil and plants and is a particular problem when the soil is wet. Pugging results in reduced drainage of soils by breaking down large soil pores. Betteridge *et al.* (1999) stated that pore damage resulting from a short duration treading event, can rapidly recover through the action of earthworm and plant root growth. Edmond (1958b) found that pugging of the soil significantly reduced *L. perenne* yields. The pugging effect influences plant growth by inhibiting gaseous diffusion, and through this, plants growing in these soils suffer from lack of oxygen. Chlorosis of plant tissue can be a symptom of lack of oxygen, but this was not observed on the turves.

Pugging occurs when a soil reaches its plastic limit (Betteridge *et al.* 1999) and the volumetric soil moisture content at which this occurs, varies between soil type. In a treading trial carried out on the same farm from which the turves were removed, the plastic limit of the soil was approximately 40 to 50% volumetric soil moisture content. This soil moisture content was less than that at peak moisture on the WT turves (60%) hence pugging would have been expected to occur. Plastic deformation of the soil like that described by Betteridge *et al.* (1999) did not appear to occur on the turves however. This may be explained by the treading events usually taking place several hours after watering, during which time excess surface water had been absorbed.

Other influences of treading on wet soil, which in turn may affect plant growth, included mud on the leaves, microbial activity in buried litter, loss of soil structure, lack of earthworms and anaerobic soil conditions (Edmond, 1962). These factors are all thought to be important on wet and heavily trodden soils.

6.5.3.2 Direct effects of treading on pasture plants

Edmond (1962) observed that treading of pasture resulted in crushed and bruised leaves (particularly on dry, hard soils) and direct root damage, plant displacement, plant burial and films of mud on leaves. The crushing and bruising of leaves acts by reducing photosynthetic area and breaking plant vascular structure. The burial of plants in mud and films of mud being present on leaves results in reduction of photosynthesis and restriction or cutting off of transpiration and gaseous diffusion due to stomata being blocked (Brown and Evans, 1973). Previous work (Edmond, 1962) stated that while bruising and tearing of leaves does occur under treading of wet soils, the effects of plant burial and leaves being covered in mud are greater. In the turves experiment, the mechanical treading treatment used appeared to cause quite a lot of bruising and tearing of leaves, which was clearly visible after each treatment application. A reasonable amount of plant burial appeared to take place, but from observation, it did not appear that films of mud being present on leaves would have had a great affect on plant growth. When treading treatments were applied there were no surface puddles of water, hence no slurried mud with which to cover leaves.

Tillering was found to be negatively affected by treading in all experiments by Edmond (1958a, 1962, 1964, 1974) on pasture species, as it was in this experiment. Tillering was significantly reduced on the WT turves in the stress phase when compared to the W treatment turves. Both tiller number and tiller vigour are thought to be affected by treading (Edmond, 1962) and species respond differently according to the position of their growing points in the sward. For example, Apanui cocksfoot (*Dactylis glomerata*) (which has a similar leaf tensile strength to Ruanui ryegrass (*L. perenne*) was less tolerant to treading due to its elevated growing points (Edmond, 1964). Edmond (1958a, 1958b) noted that pasture plant growth form tended to change from erect to prostrate under heavy grazing. This indicated that more plastic species were avoiding the effects of treading by having their growing points closer to the ground where they were less susceptible to damage.

There appeared to be a compensatory tillering effect on the WT turves in the recovery phase, though this did not become apparent until approximately one month into the recovery phase. Edmond (1958a) also noted the rapid recovery of buried and damaged tillers after treading. Brougham (1956) explained this occurrence by stating that in similar pasture, rate of plant growth per unit area increases until all light energy is intercepted. Growth therefore on an untrodden or lightly trodden pasture would be approximately constant. In open, trodden swards, where there is less competition for light, pasture plants can develop rapidly. The delay of one month between the end of the treading treatment and the apparent tillering flush may be explained by a reduction in plant vigour caused by the treading rather than a reduction in growing point numbers. This apparent loss of vigour may have been due to damage to surviving plant units and to the replacement of older tillers with young less productive tillers. Until the younger tillers had developed and the damaged plants recovered, tiller numbers were suppressed.

Leaf extension was not as influenced by treading as it was by the moisture treatment, in particular the leaf extension rates between the W and WT turves did not differ significantly. The wetting treatment turves had higher leaf extension rates than control turves, and this suggested that the positive effects of water outweigh any negative effect that treading may have on leaf extension. From the results of the leaf extension and tillering data, it appeared that the moisture treatment had a greater influence on leaf extension and the treading treatment a greater effect on tillering.

Herbage accumulation rate was negatively influenced on the WT turves compared with the W and C turves. Similar results were found by Edmond (1958a, 1962, 1964 and 1974), Carter and Sivalingam (1977), Witschi and Michalk (1979), Sheath and Carlson (1998) and Betteridge *et al.* (1999) in treading trials on pasture. The mechanisms for this decrease are described in previous sections and include reduction in tiller number and vigour, physical damage to plants causing a decrease in photosynthetic area, and reduced transpiration and gaseous diffusion rates.

Herbage accumulation on the WT turves was the lowest of any treatment in the recovery phase. This indicated that even on cessation of the treading treatment, herbage accumulation was suppressed by the effects of treading. The rate of herbage accumulation on the WT turves increased in the second half of the recovery period so that it was slightly greater than that on the W turves. This late increase in herbage accumulation rate on the WT turves is most likely to be associated with the increase in tiller numbers observed at this time.

Edmond (1958a, 1964) noted that treading altered pasture composition and that the long term affects of altered composition needed to be considered as well as short term decreases in production caused by direct plant damage. Similarly in this experiment the abundance of some species (*A. capillaris*, *L. perenne*, *T. repens* and *T. dubium*) increased under treading, as did the occurrence of bare soil. The abundance of other species (*C. cristatus*, flatweeds and *L. pedunculatus*) decreased under treading and the abundance of some was unaffected (*A. odoratum*, *C. uniflora*, *H. lanatus*, *Muscii* spp., *N. setulosa*, *Poa* spp. and other species). These changes in composition were caused by the variable tolerance of species to treading. Factors that determine treading tolerance include the tensile strength of leaves, the positioning of growing points in the sward and the ability to alter morphology to avoid damage under prolonged treading (Edmond, 1964; Brown and Evans, 1973).

Experiments were carried out (Evans, 1964; Edmonds, 1964) to test the varying tensile strengths of pasture species leaves, after the suggestion of Edmond (1960) that *L. perenne* was better able to tolerate treading than any other pasture species because of the high tensile strength of its leaves. Both experiments showed that *L. perenne* leaves consistently had the highest and *H. lanatus* the lowest tensile strength. The abundance of *L. perenne* was positively influenced under treading, but the abundance of *H. lanatus* was not negatively influenced in the turves experiment. Species such as *A. capillaris* and *T. repens* were intermediate in strength, but their actual order between experiments differed quite markedly, indicating different strengths in the different experiments. Both *A. capillaris* and *T. repens* were positively influenced by the treading treatment in the turves experiment. These results lead Evans (1964) to conclude that while leaf strength appeared to have some connection to treading tolerance, other factors were also important. Edmond (1967) also suggested that the length of the pasture could affect its treading tolerance. It was proposed that long, tough *L. perenne* leaves acted as a cushion to protect their own, and other species growing points.

The position of growing points on plants may also affect their ability to tolerate treading. Edmond (1964) found that even though *L. perenne* and *D. glomerata* had similar leaf strengths, *D. glomerata* was less treading tolerant, probably because of the elevated position of its growing points. Though *D. glomerata* was not present on the turves, this is an example of how different plant morphology can have an influence on treading tolerance. All the grass species present on the turves were described by Grime *et al.* (1988) as tufted, but shoot orientation ranged from erect or spreading shoots (*C. cristatus*, *A. odoratum*, *Poa* spp., *F. rubra* and *L. perenne*), erect or ascending shoots (*H. lanatus*), procumbent or ascending stems (*T. dubium*) to creeping stems (*T. repens*). This indicated that the position of growing points on these species differs and could confer differing tolerances to treading.

The ability of a species to be plastic, in the sense that they are able to adjust their morphology when subjected to a stress such as treading, enables them to become tolerant of that stress over time. Edmond (1958a) noted that round tufted plants tended to become elliptical under treading and that growth form changed from erect to prostrate. The plasticity of *L. perenne* for example was apparent when Edmond (1964) and Matthew *et al*. (1989) noted that it occasionally took on the growth form of *A. capillaris* (i.e. produced stolons and some rhizomes) under treading.

Of the species whose abundance was unaffected by treading, 3 of them were native species or native species groups (*C. uniflora*, *N. setulosa* and *Muscii* spp.). Native species of New Zealand have not evolved under intensive grazing and hence it would be assumed that they have developed none of the defense mechanisms of plants that have evolved under grazing. The reasons for these species ability to tolerate treading are therefore unknown, but they were all low growing, prostrate species which may by default make them treading tolerant. Their growing points are likely to be very close to the soil surface and therefore somewhat protected from hoof damage.

6.5.4 Resistance and resilience

In order to manage a pasture successfully and to know the thresholds (May, 1977) beyond which species cannot be pushed, it is necessary to understand individual species responses to natural (e.g. moisture stress) and imposed stresses (e.g. grazing).

Pasture species can be separated into those that are resistant to the stress and those that are resilient. Resistance (sometimes referred to as inertia (Westman, 1978)) is defined as the ability of the plant to maintain function when exposed to a stress (Davis *et al*. 1994), and is characteristic of the stress tolerator type from Grime's (1973) plant strategy theory. Resilience is the rate of recovery after stress removal (Davis *et al.* 1994) and is consistent with the competitive type in Grime's (1973) plant strategy theory. Westman (1978) described resilience as being the function of elasticity (time for the plant to recover to pre-stress levels), amplitude (the threshold beyond which a plant will not recover), hysteresis (whether the paths of alteration due to disturbance and recovery are the same) and malleability (similarity of stable state before and after recovery).

In the turves experiment and from other experimental work, leaf extension was identified to be the most sensitive indicator of moisture stress, hence was a good indicator of the resistance and resilience of species exposed to water stress. It was not possible to identify which species ceased leaf extension first in this experiment, but Davis (1995) showed that *L. perenne* ceased leaf elongation earliest and *T. repens* petiole extension did not cease at all. Other hill pastures species tested such as *A. capillaris* and *H. lanatus* were intermediate. Therefore, *L. perenne* could be described as having low resistance to stress and *T. repens* as being stress tolerant or having high resistance to water deficit stress. This is supported by the recovery phase of the turves experiment, where *L. perenne* exhibited the fastest and greatest increase in leaf extension, and the rate of petiole extension for *T. repens* remained relatively constant. This result was indicative of *L. perenne* being a resilient species or a competitive type (Grime, 1973) and *T. repens* being a resistant species or a stress tolerator type (Grime, 1973). *A. capillaris, A. odoratum* and *H. lanatus* appear to be intermediate.

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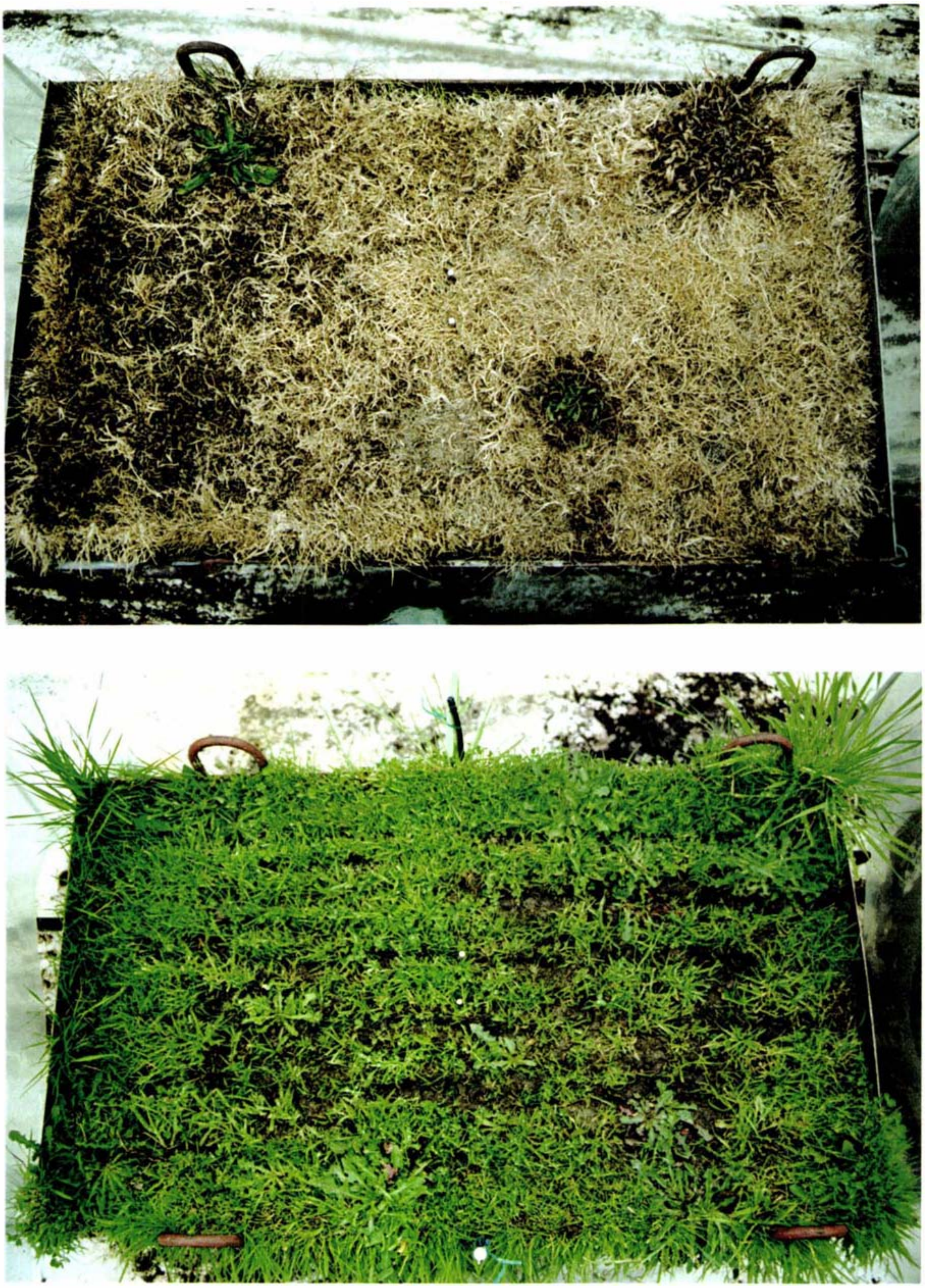
Plate 6.1 The visual effects of the moisture deficit (D) (top) and excess moisture and treading (WT) treatments (bottom) on the turves at the peak of the stress period, early November 1997.



7. General Discussion

7.1 Introduction

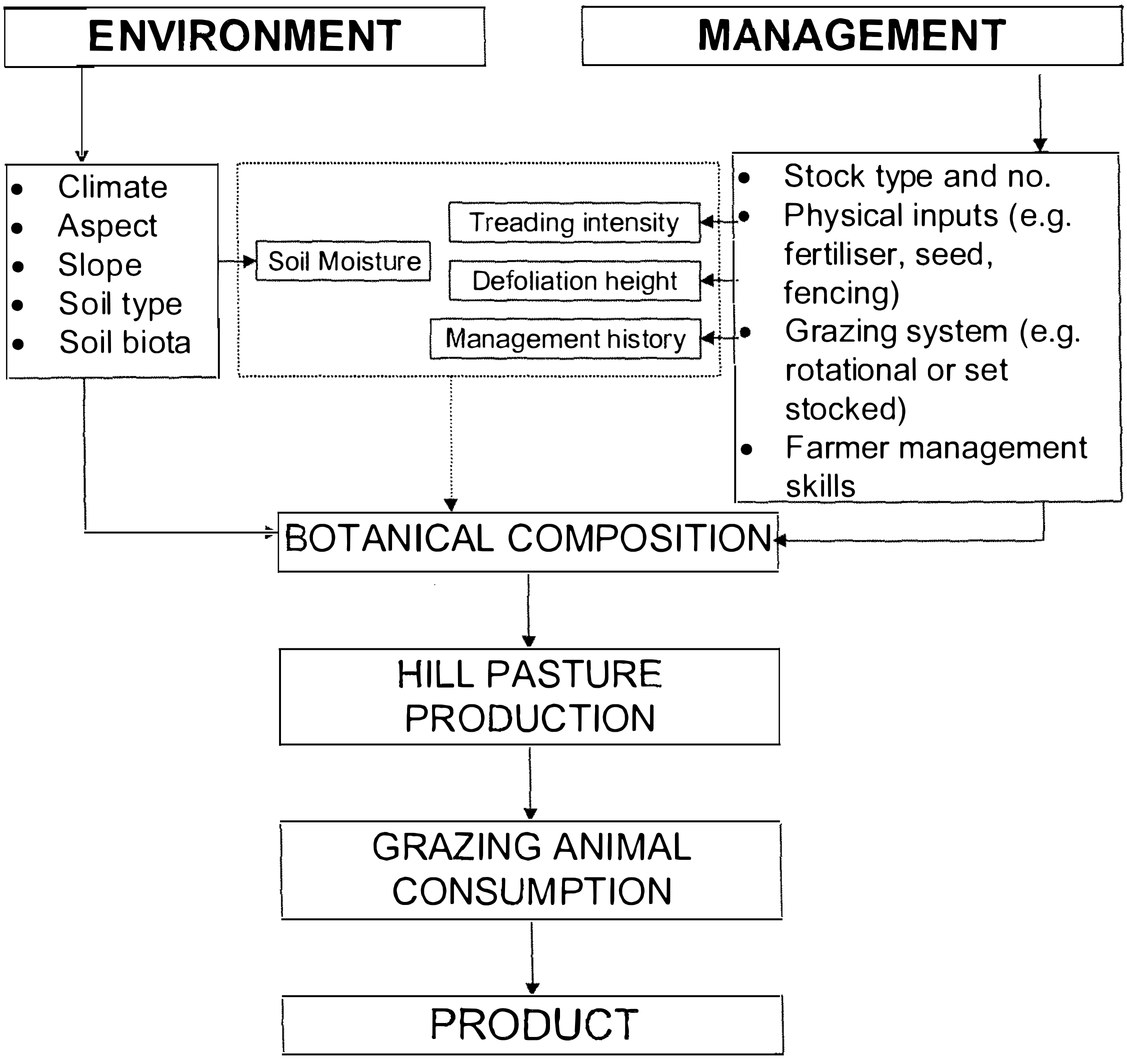
The objectives for this thesis were to identify how hill pasture management and the environment affect pasture composition. Figure 7.1 illustrates the role of management and environmental conditions in determining hill pasture botanical composition. Other objectives were to develop useful functional groups to simplify the study of the hill pasture ecosystem, and to identify the relationship between species diversity and productivity in “man-made” and subsequently naturalised hill pastures, an ecosystem in which studies of this type had not previously been carried out.

7.2 Botanical Composition

Botanical composition of hill pastures was surveyed at Ballantrae Research Station and was more diverse than the lowland pastures reported by Matthew *et al.* (1988). Twenty-five species were identified over the six sites compared to only 10 in a lowland pasture with an equivalent fertility level and stocked with sheep. The species identified in the survey had all been identified in previous surveys (Rumball and Esler, 1968; Grant and Brock, 1974 and Lambert *et al.* 1986a). *A. capillaris* was the most abundant species and its abundance was greater in summer than spring. *T. repens* and *L. perenne* were associated with high fertility sites and this supports the findings of others (Lambert *et al.* 1986a). On average, dead matter was the greatest contributor to biomass (approximately 30%). This was greater than the 10% previously observed (Lambert *et al.* 1986a) and was most likely a result of the differing experimental techniques used to determine composition.

The composition of the hill pastures surveyed was found to be relatively stable over time. The same species were found in the two data sets collected from the same site, but 28 years apart. However, the abundance of some of these

Figure 7.1 The role of environmental and management factors in determining the botanical composition of North Island, New Zealand hill pastures. The factors within the dotted lines were examined in this thesis.



species changed over time. The contribution of flatweeds, *Muscii* spp. and dead matter decreased over time and the abundance of *A. capillaris*, *T. repens* and *L. perenne* increased. This shift from poor quality, low producing pasture species to more agronomically important species (in terms of feed quality, pasture production and soil improvement), may be a result of increased soil Olsen P (from 2 to 24 mgP/g of soil over the 28 year period) and more intensive grazing management. The increase in the abundance of *T. repens* is of importance, as this species is the major provider of nitrogen in hill pastures. An increase in *T. repens* abundance usually results in an increase of grass species, such as *L. perenne,* as soil nitrogen levels increase (Lambert *et al.* 1986a).

That pasture composition did not change significantly over the 28 year period, in which management varied quite considerably, suggested that hill pastures are stable. MacArthur (1955) defined stability in ecosystems as the temporal constancy of population numbers. As the same number of species were identified in both data sets, the hill pasture ecosystem matches this criterion for stability. Johnson *et al.* (1996) defined stability in terms of the ability of a community to resist change in its ability to maintain ecosystem function (resistance) and to recover to normal levels of function after disturbance (resilience). Again, the hill pastures surveyed meet these criteria, as pasture ecosystem function (production of biomass for grazing animal consumption) was maintained over the 28 year period.

The hill pasture system exhibited plasticity, in that the component species in the sward adjusted their abundance to absorb environmental and management events that occurred, with no subsequent loss of production. This readjustment of species abundance, rather than extinction of species and replacement with new species, illustrated that the species mix was stable. The role of management in hill pastures appears to be in changing pasture species abundance to result in a more desirable composition, rather than changing the species that make up the pasture, to maximize production. That the same number of species were present regardless of production level, tends to favour the Rivet Popper (Ehrlich and Ehrlich, 1981) or the Redundancy (Walker, 1992) hypotheses, with reference to the relationship between diversity, stability and production.

The observation that the same species were present throughout hill pastures, and just their abundance differed, was further examined in the turves experiments. It was observed that essentially the same species were present on the turves from the different farmlets, with some exceptions. There was no *F. rubra* present on the HH turves at any time in the first or second turves experiments. *F. rubra* was identified as being present on the HH farmlet in the hill pasture survey carried out at Ballantrae, but only in very small quantities (<1%). Other species such as *C. uniflora* and *Muscii* spp. appeared to be absent from the LN and HH turves, respectively, but their presence became apparent later in the second turves experiment. These results suggested that indeed all the species were present on all farmlets, but the sampling method resulted in some species being missed in one or more of the experiments.

From the hill pasture survey, *A. capillaris* was on average the most abundant species on all farmlets and this is supported by the findings of Grant and Brock (1974). The next most abundant species were flatweeds on the LN farmlet, flatweeds and *C. uniflora* on the HN farmlet and *L. perenne*, *H. lanatus* and *T. repens* on the HH farmlet. *A. capillaris* was consistently the most common species, regardless of season, but the abundance of the next most abundant species often changed with season.

In the hill pasture survey, *L. perenne* was also found to be a dominant species, and this was also reported by Grant and Brock (1974) and Sheath and Boom (1985). However, it was not apparent in the turves experiments. This may be a result of the location from which the turves were removed on the farmlets (flat areas with no stock camps or tracks). The hill pasture survey results therefore are more representative of average hill pasture composition than the turves results.

The effect of species dominance on community structure, species richness and production has been studied (Grime, 1977; Reed, 1977; Chapin *et al.* 1986; Tilman, 1987 and Gurevitch and Unnasch, 1989). Under high resource conditions, competitively superior species dominate (Reed, 1977; Tilman, 1987). Under poor resource conditions, species that are able to tolerate the poor conditions dominate (Grime, 1977). Which of these mechanisms results in the dominance of *A. capillaris* and *L. perenne* in hill pastures is unknown, but hill pastures could be described as being intermediate between resource rich and resource poor. Both *A. capillaris* and *L. perenne* are relatively competitive species and the reason for both being able to dominate may be explained by studies carried out by Harris and Brougham (1968) and Kershaw (1958), which showed that *A. capillaris* and *L. perenne* were negatively associated. *A. capillaris* is found more on untrodden, low fertility sites and *L. perenne* more on higher fertility, trodden sites. Due to the variability of hill country topography (White, 1994), there are enough suitable microsites in which each of these species can dominate, and in turn, on average, dominate hill pasture composition.

7.3 Pasture species diversity and productivity

The relationship between pasture species diversity and pasture production was determined from data collected in both the hill pasture survey and in the two turves experiments. In the hill pasture survey, species richness was defined as the number of species present at one point in time in a given area, and production was defined as the standing green biomass in that given area at the same time.

Of the ten data sets collected in the hill pasture survey, only five exhibited a significant relationship between species diversity and pasture production. The LM Morgans and MM spring data sets showed the relationship to be positive, while the HM summer, MM summer and LM spring data sets exhibited a negative relationship. Why only 5 of the 10 data sets showed a significant relationship between species diversity and pasture production is unclear, but it is possible that both season and farmlet acted separately and interacted to influence the relationship. Of the 3 data sets collected from a low fertility site in spring, two of these (LM Morgans and LM spring) exhibited significant relationships between species diversity and production, though the relationship was positive for the LM Morgans site and negative for the LM spring site. The remaining data set collected at a low fertility site in spring (LM Ballantrae) exhibited a significant positive relationship when Olsen P was used as a covariate. The data also indicated that slope had an influence on both biomass production and species richness, but the exact nature of its influence on the diversity/productivity relationship requires further experimentation. Previous studies of grasslands (McNaughton, 1994; Naeem *et al.* 1994; Tilman and Downing, 1994; Vitousek and Hooper, 1994) also showed the relationship between species diversity and productivity to be variable.

That the LM Morgans and MM spring data sets (which were both collected in spring, at the same site, but 28 years apart) both showed a significant positive relationship between species diversity and production is important. The management of this site changed considerably over the 28 year period, with Olsen P increasing from 2 to 24 mg P/g soil. This suggested that the environmental conditions present at the site, rather than the management imposed on the pasture, resulted in the positive relationship.

The results indicated that the relationship between pasture species diversity and pasture production, if it does exist, is variable. The data also suggested that the Diversity-Stability hypothesis (MacArthur, 1955) did not hold in North Island New Zealand hill pastures. Certain seasonal and management conditions resulted in the relationship occurring in some circumstances, but it was not present under most conditions. In section 7.1 it was noted that the same 25 species were present throughout the hill farm surveyed, only the abundance differed. This suggested that pasture species diversity (measured as number of species) was also the same throughout the farm. Therefore, the variable that was changing in the diversity and production relationship, was production. Environmental effects such as aspect and slope, and management effects such as stock type, grazing management and fertiliser application, all have a strong influence on production (Figure 7.1). The influence of these factors on production, have possibly overridden any effect of species diversity on production. Other diversity indices (e.g. the Shannon diversity index), which take into account species abundance as well as species presence (Magurran, 1988), can be used instead of the number of species present, for determining the relationship between diversity and production. This was examined using the hill pasture survey data, and no significant relationship between the Shannon diversity index and pasture production was identified.

In both the first and second turves experiments, on average over all the treatments, no significant relationship between dry matter accumulation and species richness was observed. In the second turves experiment, when individual treatments were tested, a significant positive relationship between diversity and productivity existed on the LN turves in two months and on the HN turves in one month. When data were pooled over all months, significant relationships between diversity and productivity were observed on turves with the following treatments: LN farmlet with watering, LN farmlet with watering and treading and the HN farmlet with watering. From this information it appeared that there was an interaction between farmlet (both the LN and HN farmlets had similar low fertility levels) and moisture that resulted in a significant relationship between species diversity and productivity.

7.4 Functional groups

Functional groups were developed in Chapter 3 to simplify the study of hill pasture ecosystems. Using functional groups simplifies the study of a plant ecosystem by reducing the number of units being studied (i.e. reduction from individual species to functional groups). Many other studies have also developed methods for grouping species into functional groups (Grime, 1974; Whittaker, 1975; Smith and Huston, 1989; Korner, 1994; Solbrig, 1994; Chapin *et al*. 1996 and Diaz and Marcelo, 1997).

The functional groups derived using a hierarchical approach were:

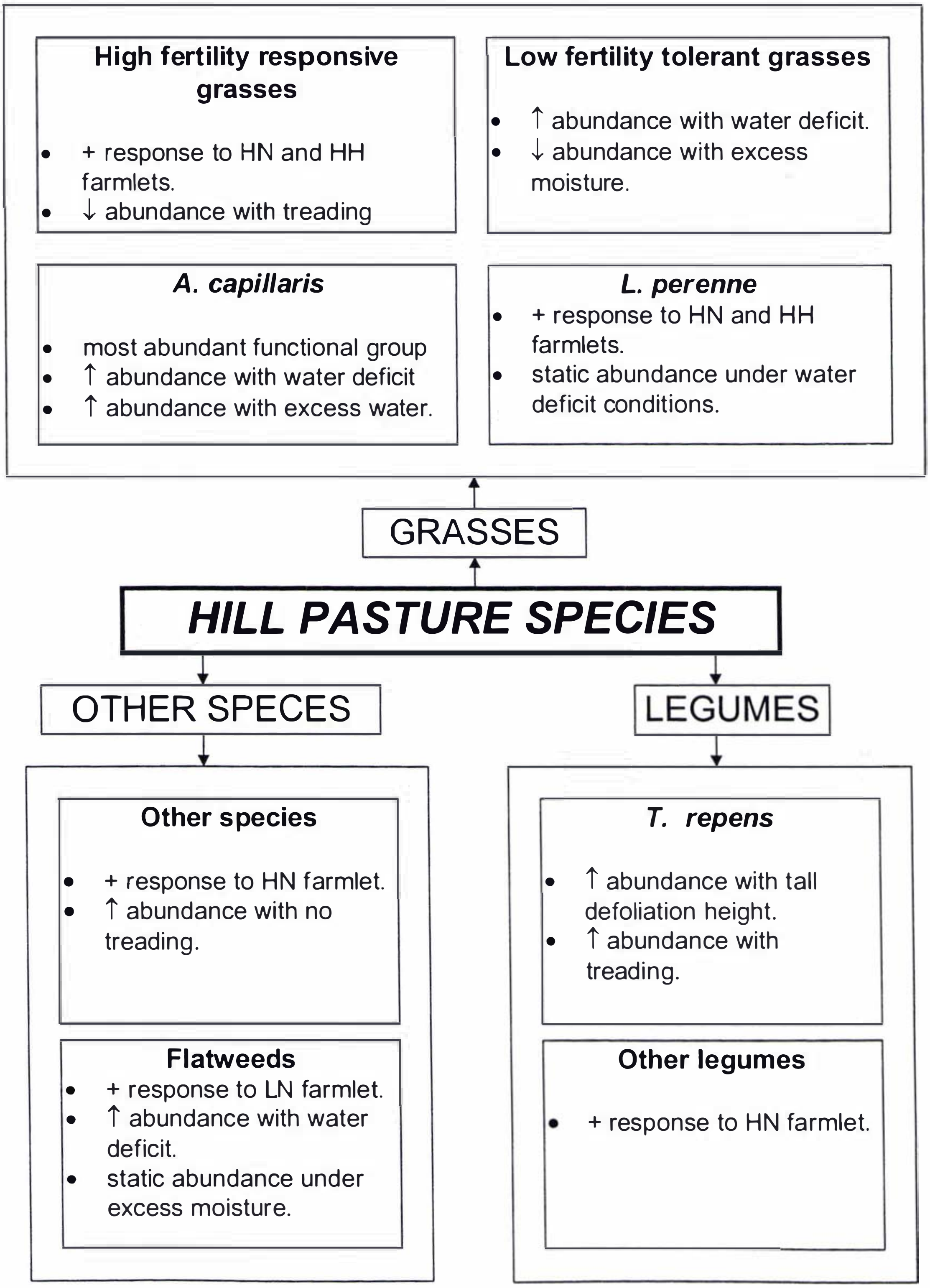
- *A. capillaris*
- *L. perenne*
- high fertility responsive grasses (including *H. lanatus* and *Poa* spp.)
- low fertility tolerant grasses (including *A. odoratum*, *C. cristatus*, *Rytidosperma* spp. and *F. rubra*)
- *T. repens*
- flatweeds
- other legumes (including *T. dubium*, *T. subterraneum* and *L. pedunculatus*)
- other species (including *C. uniflora*, *N. setulosa* and *Muscii* spp.)

In the turves experiments, dry matter accumulation from functional groups and the effects of farmlet, cutting height, treading and moisture on functional group abundance were determined. In the first turves experiment (averaged over all treatments), for the first two months the *A. capillaris* and low fertility tolerant grass functional groups were dominant. As the experiment progressed and defoliation height and treading effects became more pronounced, there was a shift in functional group dominance, with the other species and flatweeds functional groups becoming dominant. This is an important shift from a management perspective. The *A. capillaris* and low fertility tolerant grass functional groups are important for hill pasture herbage production for grazing animal consumption. The treatments imposed on the turves and perhaps the effects of the glasshouse and season, resulted in a shift towards “weedy” species. A similar shift in functional group dominance occurred during the second turves experiment. The high fertility responsive grass and flatweeds functional groups were dominant early in the experiment. As the experiment progressed the abundance of the flatweeds functional group remained relatively constant, the abundance of the high fertility responsive grass functional group declined and the abundance of the other species and *A. capillaris* functional groups increased. Again, this is important from a management perspective as high fertility responsive grasses, which provide leafy green herbage, have declined and been replaced by lower quality “weedy” species such as those present in the other species functional group. The abundance of flatweeds remaining stable is also worthy of note as management practices that decrease their presence, in favour of more desirable functional groups (e.g. those containing grasses and legumes), are preferred.

The treatments applied in the two turves experiments were also used to verify the functional groups developed in Chapter 3 and refine them where necessary. In Chapter 3, information derived from the literature on the response of species to factors such as increased fertility, treading, drought and defoliation, was used to group species commonly identified in the Ballantrae hill pasture survey. Figure 7.2 shows the resulting functional groups, and within each functional group describes a response, or responses, to the treatments applied during the turves experiments, which illustrates the separation of each functional group from the others.

The functional groups defined using information from literature and a hierarchical process of development, have proven to be appropriate for the study of the effects of farmlet management, treading, defoliation height and moisture treatments on hill pasture systems. Each functional group was shown to have a unique response to the imposed treatment, hence they had different functions in the hill pasture ecosystem.

Figure 7.2 Summary of functional groups derived in Chapter 3 (boxes) and the responses of the functional groups to the treatments applied in the turves experiments (information in boxes), which verify the differences between functional groups.



High fertility responsive grasses

- + response to HN and HH farmlets.
- ↓ abundance with treading

Low fertility tolerant grasses

- ↑ abundance with water deficit.
- ↓ abundance with excess moisture.

A. capillaris

- most abundant functional group
- ↑ abundance with water deficit
- ↑ abundance with excess water.

L. perenne

- + response to HN and HH farmlets.
- static abundance under water deficit conditions.

GRASSES

HILL PASTURE SPECIES

OTHER SPECES

LEGUMES

Other species

- + response to HN farmlet.
- ↑ abundance with no treading.

Flatweeds

- + response to LN farmlet.
- ↑ abundance with water deficit.
- static abundance under excess moisture.

T. repens

- ↑ abundance with tall defoliation height.
- ↑ abundance with treading.

Other legumes

- + response to HN farmlet.

7.5 The effects of management on hill pasture botanical composition.

The aim of hill pasture management is to achieve a sward with a high clover and green leaf content and a low dead matter content (White, 1994). Due to the variable nature of hill land topography, this is not an easy task to achieve, as blanket management strategies cannot be applied to the whole farm. Different management strategies, using grazing management and external inputs, need to be developed for different types of hill land (e.g. different aspects, slopes and soil types).

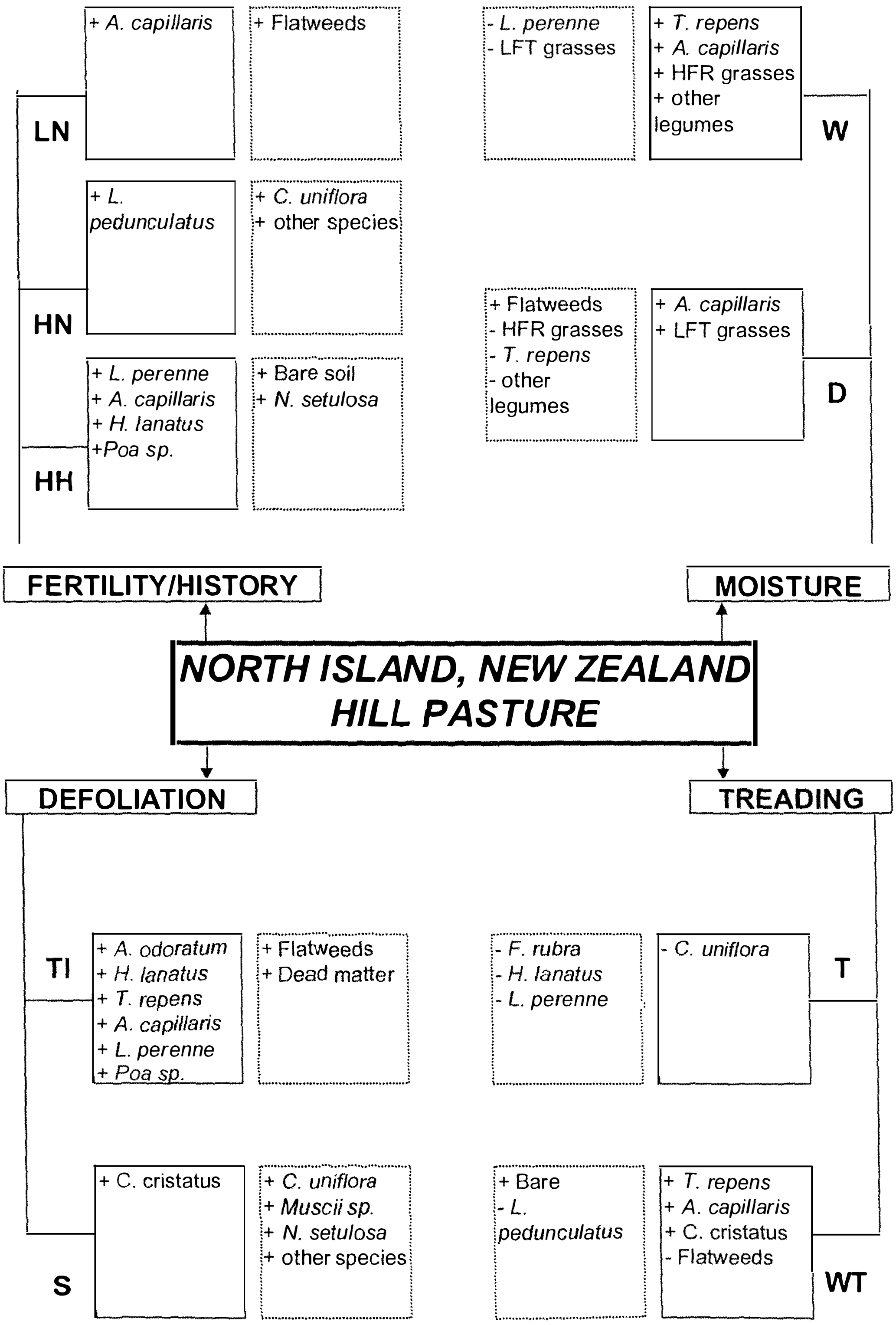
The two management factors that resulted in changed pasture composition in the first turves experiment were treading and defoliation height (Figure 7.3). These two factors can be easily controlled by farm managers through stock type, grazing duration and stocking rate, on a paddock by paddock basis. The abundance of *A. capillaris*, *A. odoratum*, *L. perenne, T. repens* and *Poa* spp. increased with the tall defoliation height. This was a positive effect from a composition perspective as the abundance of several grass species (which provide the desired leafy green component of swards) and *T. repens* was increased. The abundance of *L. perenne* and *T. repens* was reported by Sheath and Boom (1985) to decrease under lax grazing, though they were studying the effect of lax grazing at specific times of the year. The increase in abundance of annual species such as *Poa* spp. under lax grazing was confirmed by Sheath and Boom (1985).

There were negative effects associated with the tall cutting height. At the end of the experimental period, the abundance of dead matter was greater under the tall cutting height treatment (26%) than the short cutting height treatment (7%). Another trade-off that could occur using a lax defoliation height to alter pasture composition, is that lower stocking rates or a shorter grazing duration would be required to leave the desired 7.5 cm height residual. This may result in a shortening of the rotation over the whole farm, which in turn may have other effects on botanical composition and production. For example, the occurrence of treading events would be increased and this was shown in the turves experiment to reduce the abundance of *H. lanatus*, *F. rubra* and *L. perenne*. A compromise needs to be made to determine a defoliation height between 2 and 7.5 cm, where the benefits from favorable composition changes occur, whilst minimizing associated negative effects.

In the first turves experiment, the treading treatment significantly reduced the abundance of *F. rubra*, *H. lanatus* and *L. perenne.* In the second turves experiment, the treading treatment in combination with moist soil (Figure 7.3) resulted in *a* decrease in the abundance of flatweeds and *L. pedunculatus* and an increase in the abundance of *A. capillaris*, *C. cristatus*, *T. repens* and bare soil. That the species affected by treading differed between the two turves experiments is likely to be due to an interaction between treading and soil moisture occurring in the second turves experiment. Therefore, pasture composition improvements occurred with treading, particularly in terms of the increase in *T. repens* abundance in moist environments. Detrimental effects include the decrease in abundance of *H. lanatus* and *L. perenne* and an increase in bare soil. *L. perenne* is reported in the literature as being tolerant to treading (Edmond, 1962). It is probably more appropriate from the results of this experiment to say that it is resilient to treading. The abundance of *L. perenne* decreased whilst treading was occurring, but it was able to recover quickly once treading was removed. The increase in the amount of bare soil in the sward may have both positive and negative effects. It would reduce the competition for light between grasses and *T. repens*, and also provide conditions conducive for weed seed germination.

The key to improving hill pasture composition and production is to increase the abundance of *T. repens*. This species is the primary source of nitrogen in hill pastures and drives the growth potential of desirable grass species such as *L. perenne* and *A. capillaris*. As seen in the turves experiments, lax grazing (to 7.5 cm) and treading will increase the abundance of *T. repens*. Lambert *et al.* (1986b) stated that an adequate Olsen P status is also required to ensure unlimited *T. repens* growth. In the first turves experiment, *T. repens* abundance

Figure 7.3 The response of North Island, New Zealand hill pasture to imposed management and environmental factors. The solid boxes represent desired botanical composition changes and the broken boxes represent negative botanical composition changes. W=wet, D=dry, LN, HN and HH are the low, med and high input farmlets respectively, Tl=tall cutting height, S=short cutting height, T=treading and WT=wet and treading.



was greater at the start of the experiment on the HH turves, which had an Olsen P of 20 mg P/g soil, but not significantly greater than the other farmlets. At the end of the experiment, there was more *T. repens* present on the LN turves, which had an average Olsen P of 6 mg P/g soil. In the second turves experiment, *T. repens* was consistently less abundant on the HH turves, which had an average Olsen P of 13 mg P/g soil at the time. *A. capillaris* which was a prolific species on the turves throughout both experiments may have been responsible for this phenomenon occurring. Studies by Jackman and Mouat (1972b) concluded that *A. capillaris* and *T. repens* directly compete for phosphorus in the top 2.5 cm of top-dressed soil, and because grass decreases phosphorus availability by increasing soil moisture tension, these two effects together adversely affect white clover growth and abundance. Also, because it is such a densely tillered species, *A. capillaris* has the effect of suppressing *T. repens* growth. The treading treatment increased the abundance of *T. repens* by creating more bare areas that allowed *T. repens* stolon spread.

From the turves experiments and other studies (Sheath and Boom, 1985; Lambert *et al*. 1986a), it appears that management imposed on hill pastures to increase the abundance of desirable species is often associated with negative changes also, such as an increase in the abundance of undesirable species and dead matter. A balance needs to be achieved to minimize these negative effects. The exact balance is going to vary from farm to farm, and often paddock to paddock, depending on environmental conditions such as climate and soil type and other management constraints such as stock availability. It may be that the use of management techniques to manipulate functional groups, rather than individual species, is more important. Species within a functional group, by definition, play the same role in pastures and more than one species in a functional group provides insurance in the event of the removal of the main species. As we have seen, a management technique that positively influences the abundance of desirable species such as *A. capillaris*, *T. repens* and *L. perenne* (which all form their own functional groups), may also decrease the abundance of another desirable species (e.g. *C. cristatus*).

If, however, the functional group containing *C. cristatus,* (low fertility tolerant grasses), is represented by another species (e.g. *A. odoratum*), and that species is not detrimentally affected by the management imposed, then overall function of the pastoral ecosystem is not changed. This is consistent with the Redundancy hypothesis developed by Walker (1992).

The role of less abundant species in hill pasture swards, such as *C. uniflora* and *N. setulosa*, is unknown. These species have little value in terms of animal feed, but may be useful as a ground cover to prevent soil loss. These minor species were consistently present in all botanical compositions taken in both the hill survey and the turves experiments. In no environment and under no management treatment imposed, were these species made extinct. This suggested that they were either highly resistant to disturbance, or had a function which relates to the general stability of the sward and supports either the Rivet popper (Ehrlich and Ehrlich, 1981) or the Redundancy (Walker, 1992) hypotheses regarding the relationship between diversity, stability and production.

7.6 The role of soil moisture and its interaction with treading in determining hill pasture botanical composition.

Soil moisture is an environmental factor over which hill country farmers have no control. It is an important aspect of hill farming because soil moisture levels usually vary widely over a farm due to the variation in hill slope and aspect. Much research has been carried out looking at the suitability of various species for different hill aspects (Lancashire, 1984; Charlton and Belgrave, 1992). North facing aspects are usually much drier than south facing ones, hence species are required that are suited to these conditions in order to maintain production throughout the year.

The second turves experiment was designed to investigate how a period of moisture deficit and excess moisture, by itself and in combination with treading, affected botanical composition and then on removal of the stress, how the sward recovered.

For the reasons presented in section 7.4, the response of functional groups, rather than individual species was analysed. Over the soil moisture deficit period of approximately two and a half months, the abundance of the *A. capillaris*, low fertility tolerant grass and flatweeds functional groups increased, the abundance of the high fertility responsive grass, *T. repens* (also observed by Lancashire (1974)) and other legumes functional groups decreased and the *L. perenne* functional group abundance remained the same. In the recovery period from the moisture deficit, the abundance of the *L. perenne* and *A. capillaris* functional groups increased, the flatweeds functional group abundance decreased and *T. repens* abundance remained the same. The increase in abundance of the *L. perenne* and *A. capillaris* functional groups is important since they were key contributors to the green leafy component of the sward. That *T. repens* abundance did not increase on removal of the water deficit stress was also significant as this is a key component of the sward. It may be that the rapid recovery of the two vigorous grass species (*A. capillaris* and *L. perenne*) suppressed *T. repens* recovery, or that *T. repens* recovery is slower than that of other species.

In the period of excess soil moisture, the abundance of the *A. capillaris*, the high fertility responsive grass, the *T. repens* and the other legumes functional groups increased, the abundance of the low fertility tolerant grass and the *L. perenne* functional groups decreased and the abundance of the flatweeds functional group remained stable. In the recovery period, the abundance of the *A. capillaris* and the other legumes functional groups kept increasing, the abundance of the low fertility tolerant grass, the high fertility responsive grass, the *L. perenne* and the *T. repens* functional groups decreased and the abundance of the flatweeds functional group remained static. The results of most significance were that many of the grass containing functional groups and the *T. repens* functional group decreased in abundance in the recovery period.

This is not conducive to maintaining a green leafy, *T. repens* containing sward. That *A. capillaris* and other legumes abundance increased was some consolation as there was still some nitrogen fixation occurring and the prolific tillering ability of *A. capillaris* provided some leafy green material.

The herbage accumulation rate was reduced by the combination of wet soil and treading treatments and was suppressed even after the removal of the treatment. This suggested that the treading treatment had a residual effect on herbage accumulation, as no suppression of herbage accumulation was observed for the wet treatment alone. Tillering was also reduced by the wet soil and treading treatment in the stress phase, and though compensatory tillering did occur, it did not begin until a month after the removal of the stress treatment. This time delay before tiller number recovered was most likely due to physical damage that was inflicted on existing tillers having to repair, before new tillers could develop (Edmond, 1962). The compensatory tillering effects under the dry and wet soil treatments occurred immediately after removal of the stress treatment. Under the wet soil and treading treatment, the abundance of *A. capillaris*, *L. perenne*, *T. repens* and *T. dubium* increased, whilst the abundance of *C. cristatus*, flatweeds and *L. pedunculatus* decreased. This result was important from a management perspective because the abundance of species which provide green leafy material and legumes increased. That the abundance of flatweeds decreased is also important as flatweeds are unable to be grazed for long periods through the year and cover quite a large area of ground, hence reducing the cover of other more valuable species.

The functional groups that were decreasers under the moisture deficit treatment were increasers under the excess moisture treatment (high fertility responsive grass, *T. repens* and other legumes) and vice versa (low fertility tolerant grass). Thus it was possible to further define the functional groups by adding their response to moisture deficit and excess moisture. This may be useful from a management perspective as land managers will know which functional groups are suited to dry areas and which are suited to wetter areas. Managers may also be able to use a combination of factors such as defoliation height and treading to shift the composition of a pasture to contain functional groups that maintain production in an area that is susceptible to drought or water-logging.

7.7 Conclusions

This thesis set out to test the objectives presented in Chapter 1. Objectives 1, 4 and 5 were to identify the effects of hill pasture management and environmental conditions on hill pasture composition. It was found that the same species were observed under all conditions and only the abundance of those species changed, depending on their functional response to imposed conditions. Pasture species abundance was manipulated with the use of treading, defoliation and moisture treatments. In order to improve the abundance of leafy green grasses and legumes (particularly *T. repens*) whilst minimising any significant increase in the abundance of undesirable species, the following management and environmental conditions are recommended:

- Lax defoliation height (7.5 cm) to increase the abundance of *L. perenne*, *T. repens*, *A. capillaris*, *H. lanatus*, *Poa* spp. and *A. odoratum.*
- High fertility and management history similar to that on the HH farmlet, to increase the abundance of *L. perenne, A. capillaris*, *H. lanatus* and *Poa* spp.
- When treading occurs, more desirable changes in composition occur when soil is moist rather than dry. When treading occurs on moist soils, the abundance of *T. repens*, *A. capillaris* and *C. cristatus* is increased and the abundance of flatweeds is decreased.
- Moist, but not water-logged, conditions will result in an increase in the abundance of *T. repens*, *A. capillaris*, high fertility responsive grasses and other legumes.

The hill pasture system was relatively resilient and able to return to its normal function on removal of the imposed management or environmental factor. This indicated that hill pasture composition was stable and that in order to maintain desirable changes in pasture composition, inputs need to be continuous. The apparent stability of one species in particular, *A. capillaris*, is worthy of note. None of the imposed management factors (i.e. defoliation height, treading, excess moisture and moisture deficiency) reduced the abundance of this species significantly. This would indicate that *A. capillaris* is particularly well adapted to hill country conditions. Removal of *A. capillaris* in favour of species such as *L. perenne* might be associated with a decrease in stability of production as the abundance of *L. perenne* was decreased in wet conditions and under treading.

In fulfillment of objective 3, eight functional groups were identified as being useful for predicting vegetation change under the different management and environmental conditions imposed in hill pastures.

Objective 2 was to identify the relationship between pasture species diversity and productivity in North Island, New Zealand hill pastures. There appeared to be no direct relationship between species diversity and productivity. Hill slope, soil fertility, season and farm management all appear to be co-variates in the relationship. The Rivet Popper hypothesis (Ehrlich and Ehrlich, 1981) or the Redundancy hypothesis (Walker, 1992) appear to be more likely to be occurring in hill pastures, with regard to the relationship between diversity, stability and productivity, than the Diversity-Stability (MacArthur, 1955) or the Idiosyncratic (Lawton, 1994) hypotheses.

Changes in the botanical composition of hill pasture can be achieved through management, and management in combination with prevailing environmental conditions. In order to achieve the greatest benefits (in terms of production and stability of production) from using management to alter pasture composition, it is apparent that the management needs to be environment specific. That is, areas with different aspects, slopes and fertility status need to managed separately so that a botanical composition ideal for those particular conditions is achieved.

From the results of this research, it is apparent that botanical composition is a key factor in the productivity and stability of North Island hill pastures in New Zealand.

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Appendices

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Production, Stability and Biodiversity of North Island, New Zealand Hill Pastures.

P. K. Nicholas[1], P. D. Kemp[1], D. J. Barker[2], J. L. Brock[2] and D. A Grant[3]

[1] Department of Plant Science, Massey University, Private Bag, Palmerston North, New Zealand.

[2] Grasslands Division, AgResearch, Private Bag 11008, Palmerston North, New Zealand.

[3] Farms Administration, Massey University, Private Bag, Palmerston North, New Zealand.

Abstract

The relationship between pasture biomass and pasture stability, with species diversity was derived for two low fertility, hill land sites. At one site, pasture production increased with an increased number of species contributing to biomass. The coefficient of variation in biomass, however, decreased with higher numbers of species. At a second site, pasture biomass was also found to increase with increasing species diversity, but the relationship between yield stability and species diversity was not as strong as at the first site. This suggested there were other factors that influenced the stability of pastures, which could include the substitution effect between species or the greater contribution of particular species to yield and stability.

Keywords: Hill land pastures, low fertility, production, stability, species diversity.

Introduction

There has been continued debate about the hypothesis that diversity begets stability, within plant communities (Tilman, 1996). Elton (1958) suggested that decreased diversity would lead to decreased ecological stability and functioning while others (May, 1973) showed that population dynamics were more stable as the number of species decreased. In long term studies on rangeland pastures, Tilman (1996) found that biodiversity stabilised plant community and ecosystem processes, but not plant population processes. Species rich plots were found to have less variation in annual yield (i.e. more stable) when subjected to a major perturbation (e.g. drought) or year to year variation in climate, but year to year variability in species abundance was not stabilised by plant species richness. In order to test Tilman's findings, data was collected from two low fertility North Island hill pastures. It was hypothesised from the results of Tilman (1996), that sites with more species present would have a higher green yield than those with low species diversity and that there would be less variability in the yield (i.e. greater stability) of species rich sites.

Materials and Methods

In September and October 1968, a survey was carried out on two low fertility North Island, New Zealand hill country sites (175° 50′ E, 40° 19′ S), 500m apart and having an Olsen P of 3.4 and 1.9 μg P/g soil, respectively. The first site had an average north-west facing slope of 29°. It had been predominantly grazed by cattle and comprised a Mangamaku steepland soil derived from silty sandstone. The second site had an average west facing slope of 24° and had been predominantly grazed by sheep. It comprised a Ngamoka silt loam soil derived from loess and sandy siltstone. Herbage from 20 - 5 cm diameter turf plugs per plot was removed to ground level, from 200 plots randomly located within a 20×20 m area per site. Herbage was manually dissected into dead matter and all major species present, and subsequently dried. SAS was used to perform the regression analysis and the coefficient of variation for each number of species was calculated. The coefficient of variation for plots with 10, 11 and 12 species were bulked, as there were very few plots with these numbers of species.

Results and Discussion

The species found most commonly at sites included *Agrostis capillaris, Anthoxanthum odoratum, Cynosurus cristatus, Muscii* spp., *Trifolium repens, Lolium perenne, Dactylis glomerata, Poa* spp., *Festuca rubra, Rytidosperma* spp., *Nertera setulosa, Centella* spp., flatweeds (*Plantaginaceae* and *Asteraceae*), with rarer occurrences of other species (*Cirsium arvense* and *C. vulgare*) and other legumes (*T. subterraneum* and *T. dubium*). This botanical composition was similar to previous surveys (Suckling, 1954; Lambert, 1986; Grant and Brock, 1974).

Figure 1 shows the relationships between green biomass and the number of species contributing to green biomass for sites 1 and 2. The regression lines for the relationship were significant at both sites ($P<0.01$ and $P<0.05$, respectively), and showed increased biomass with increasing numbers of contributing species, in agreement with the results of Tilman (1996). The strength of the relationship varied between sites, probably due to more favourable environmental conditions on the first site (including higher fertility and less intense grazing). The lower mean yield on the second site may have been due to sheep rather than cattle grazing.

The coefficient of variation of green biomass for both sites showed a similar pattern of decreasing coefficient of variation with increasing species diversity, though the relationship appears to be more variable for the second site (Fig. 2). This result is of significance in agriculture as it suggests that with fewer species present there is the chance that a very low biomass yield could occur, whereas if there are more species present, there is a smaller chance of a very low yield occurring.

These results strongly suggest that in low fertility hill farmlands, biomass is increased with increasing species diversity. There was, however, variation in the strength of this relationship depending on factors yet to be determined. The site 1 data showed that the stability of pasture yield increased with increasing species diversity, the site 2 data did not show this relationship as clearly. This suggested that there are other, presently unknown factors which influence the stability of hill pastures, but which could include the substitution effect between certain species or the greater importance of certain species as yield contributors (e.g. *Agrostis capillaris*) (Lamont, 1995). The results presented here cannot be extended to higher fertility hill farmlands (i.e. Olsen P > 10) or other topographic classes without similar pasture surveys being conducted. The literature suggests (Suckling, 1959; Lambert, 1986) that under high fertility, fewer species might contribute to yield. The importance of carrying out such a survey and analysis as this on higher fertility hill farm lands should not be overlooked as the trend on New Zealand hill land farms is to increase fertility by fertiliser application and legume oversowing (Suckling, 1959). If relationships between species diversity, yield and pasture stability on higher fertility hill lands can also be identified, then more efficient use can be made of the hill land resource in its current fertility status.

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Figure 1 The relationship between green biomass and the number of species contributing to green biomass for two sites in North Island, New Zealand hill farm land (symbols are the means of 5-25 plots).

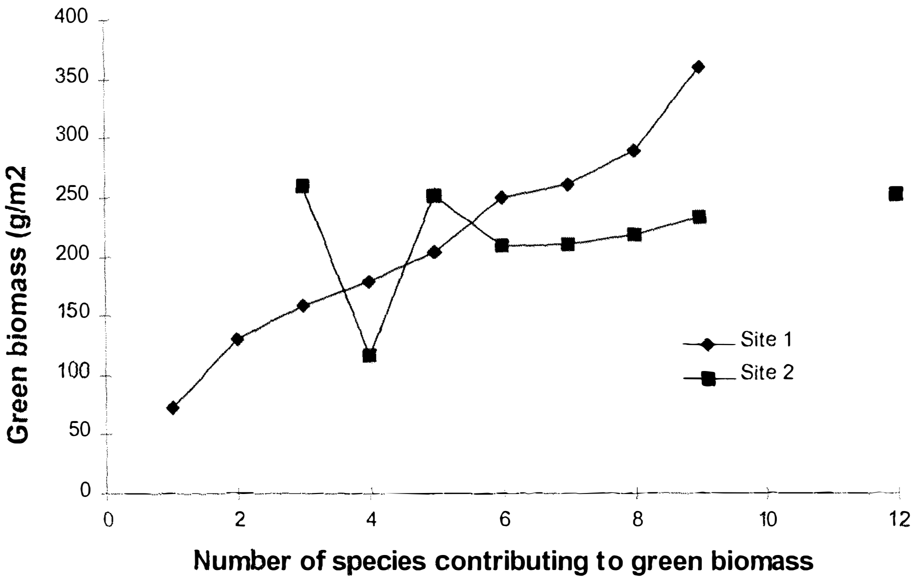
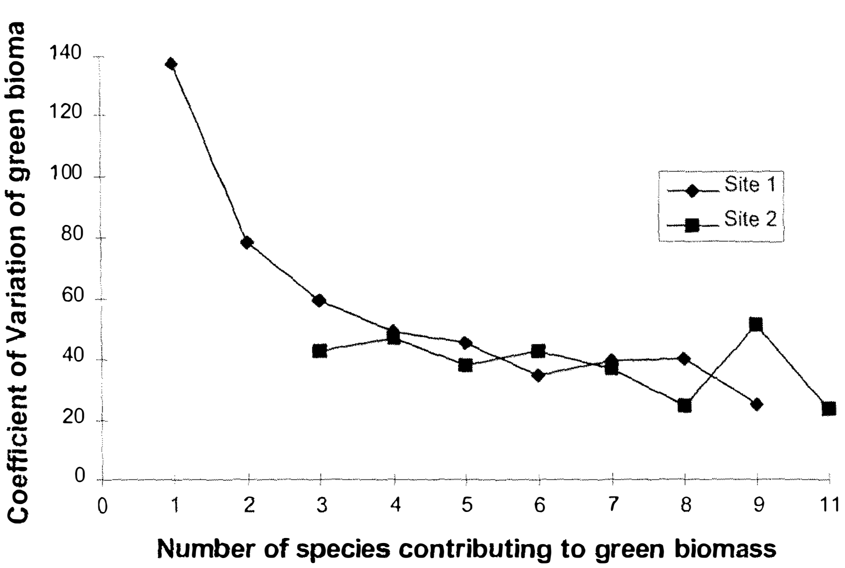


Figure 2 The coefficient of variation of green biomass in relation to the number of species contributing to green biomass for two sites in North Island, New Zealand hill farm land (symbols as for Fig. 1).



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Biodiversity, stability and pasture management - the role of functional groups

P. K. Nicholas[1], P. D. Kemp[1] and D. J.Barker[2]

[1] Plant Science Department, Massey University, Palmerston North, New Zealand
[2] AgResearch Grasslands, Palmerston North, New Zealand

Abstract

Data collected in 1968/69 and 1996/97 from a North Island, New Zealand hill research farm have been used to identify relationships between biodiversity, stability and production. These data sets have been collected at sites that have been subjected to different management regimes for approximately 20 years. It is proposed that the use of functional groups simplifies interpretation of changes in pasture composition and hence production, in the differently managed systems. Both the historical and new data are used to identify functional groups in the species present using a number of techniques. The effectiveness of these techniques is discussed as is the contribution of functional groups to the study of biodiversity, production and stability of production in North Island, New Zealand hill pastures.

Keywords: Hill land pastures Management Biodiversity Production Functional groups

Introduction

Functional groups are collections of species that have been grouped or clustered together based on sets of traits common to these species (*e.g.*

morphological, physiological, environmental responses). Functional groups are used to simplify ecological systems and are most commonly used to make predictions about the effects of environmental changes on vegetation (Chapin *et al.* 1996; Grime *et al.* 1997).

There are two ways of defining functional groups, objectively and subjectively. The objective definition of functional groups involves subjecting a range of data, collected from a population of plants, to statistical procedures that are able to analyse the data and group similar species together. Two problems exist with this method: 1) the resulting clusters are specific to the environment from which the data were collected; and, 2) the resulting functional groups can be biased by the data chosen as inputs (Chapin *et al.* 1996).

The second method of grouping species into functional types is to do so subjectively. Subjective grouping is based on knowledge about species in terms of their physiology, morphology and how they respond to environmental influences. No specific data sets are required. However, again clusters generated can be biased due to the factors chosen to be used for the clustering.

Specifically for North Island, New Zealand hill pastures, a method needs to be developed to best define functional groups. The use of these functional groups is in identifying the role of functional group biodiversity in hill pastures and how this responds to farm management.

Methods

In October 1968 and January 1969 a survey was carried out on two low fertility North Island hill pasture sites, 20 km NE of Palmerston North, New Zealand. These sites are described fully in Nicholas *et al.* (1997), but had average Olsen P values of 3.4 (Site 1) and 1.9 (Site 2) mg P/g of soil, respectively. The survey involved measuring botanical composition, species yield and growth rate, Olsen P and hill slope on 200 microsites at each of the sites.

The survey was carried out again on the same farm (now Ballantrae Hill Research Station) in October 1996 and January 1997. Spring and summer surveys were carried out to identify the effects of seasonality on abundance of species. The farm had been broken up into farmlets that have been subjected to different management for the last 20 years (Lambert *et al.* 1996). The resulting average Olsen P values of the sites were 50 (Site 3), 19 (Site 4) and 21 (Site 5) mg P/g soil. Site 1 in the 1968 survey and Site 4 in the 1996 survey were positioned at the same location.

Three methods were used to cluster the species present in this hill farm pasture (Nicholas *et al.* 1997) into functional groups. The first used groupings devised by Lambert *et al.* (1986a), developed particularly for North Island, New Zealand hill pasture species. The second method was the use of literature (Hilgendorf, 1936; Grime *et al.* 1988) to fill in a matrix of factors for each species, which was then put into a cluster analysis in SAS to identify clusters of species. The variables used included: ability to respond with increased growth to increased P levels; nitrogen fixing ability; ability to grow well on slopes; low growth habit; and tolerance to above average treading, grazing and drought levels. The third method used the Ballantrae data collected in 1968/69 and 1996/97 surveys which were averaged for each species over all 8 data sets. The data were standardised (using ranking and assigning standard numbers to identify relationships) and again put into a cluster analysis in SAS to identify clusters of species.

Results and discussion

The example of objective grouping of species into functional groups was carried out using a cluster analysis on standardised Ballantrae data. The inputs for each species were: yield (kg DM/ha), % cover, growth rate (kg DM/ha/day) and the regression slope of the relationship between growth rate and Olsen P, growth rate and hill slope and yield and Olsen P. The first three factors were standardised by ranking (Grime *et al.* 1997) and the last three were standardised by allocating a 3 to those species with a positive regression and 1 to those with a negative regression. The following 7 groups were identified from the analysis: 1) *Trifolium dubium, Lotus pedunculatus,* and *Centella uniflora;* 2) *Trifolium subterraneum and Poa pratensis;* 3) *Anthoxanthum oderatum, Trifolium repens, Cynosurus cristatus* and *Muscii* spp.; 4) *Holcus lanatus, Poa annua, Rytidosperma* spp. and 5) *Flatweeds; Festuca rubra* and *Nertera setulosa* and finally 6) *Lolium perenne* and 7) *Agrostis capillaris* in groups of their own. These groupings do not appear to have been made based on function. *T. repens* for example, a productive, grazing tolerant legume has been grouped with *A. oderatum* and *C. cristatus* (both grazing intolerant grasses that are usually associated with low fertility sites) and *Muscii* spp. which are a non-significant species in agricultural production, with little or no grazing tolerance. A similar pattern arises in the grouping of *H. lanatus, P. annua, Rytidosperma* spp. and flatweeds. *H. lanatus* and *P. annua* are similar in that they are associated with high fertility sites and both are intolerant of drought. *Rytidosperma* spp. are associated with low fertility sites and are drought tolerant, the opposite to *H. lanatus* and *P. annua.* Flatweeds are morphologically different from grasses, hence the grouping of these four species does not seem to be based on function.

It appears that these groupings have been biased by the inputs used in the clustering analysis. The variables used in the analysis are variables that would commonly be measured in a biodiversity study (yield, growth rate and % cover of each species). However, these are all measures of abundance. One of the factors in each of the regressions used to define the relationships with Olsen P and hill slope was either growth rate or yield, hence abundance factors have been incorporated into these relationships. It appears the cluster analysis has grouped according to species abundance.

This is demonstrated by the yields of the species that were grouped together in the cluster analysis. 1) *T. dubium, L. pedunculatus,* and *C. uniflora*, 15, 16 and 14 kg DM/ha respectively. 2) *T. subterraneum* and *P. pratensis* both 3 kg DM/ha. 3) *A. odoratum, T. repens, C. cristatus* and *Muscii* spp. 152, 151, 148 and 196 kg DM/ha respectively. 4) *H. lanatus, P. annua, Rytidosperma* spp. and Flatweeds 95, 100, 88 and 115 kg DM/ha respectively. 5) *F. rubra* and *N. setulosa* had 45 and 32 kg DM/ha respectively and finally *L. perenne* 340 kg DM/ha and *A. capillaris* 680 kg DM/ha. These results indicate that the cluster analysis has been based on the yield factor. If objective definition of functional groups is desired, then the data describing the species need to be based on the function of the species, not on common agronomic measures of abundance.

The cluster analysis based on the literature derived variables resulted in similar groups to those defined by Lambert *et al.* (1986a), but with some slight differences. The low fertility grasses defined by Lambert *et al.* (1986a) were the same as those that formed the first group: *C. cristatus, Rytidosperma* spp., *F. rubra, A. capillaris* and *A. odoratum.* The high fertility responsive grasses (1986a) were the same as the second group of *L .perenne, H. lanatus* and *P. annua.* Lambert *et al.* (1986a) had *L. perenne* as a functional group on its own as it is more responsive to high fertility than either *H. lanatus* or *P. annua*. The two remaining functional groups defined by Lambert *et al.* (1986a) were legumes and other species. In the literature based analysis all the legumes (*T. dubium, T. subterraneum* and *L. pedunculatus*) grouped together except for *T. repens* which was in its own functional group. Flatweeds also formed a functional group, but this was because they were the only weed species present. There were other species present in the pasture such as *C. uniflora, N. setulosa* and *Muscii* spp., but they were removed from the cluster analysis due to missing values. More would need to be known about the grazing tolerance of these species to group them correctly. That these species are indigenous suggests they are not tolerant of sheep grazing and would therefore form their own functional group separate to flatweeds. The key functional differences between groups in this analysis appear to be grazing tolerance and response to fertility. This would be expected as three of the inputted variables were related to fertility and three to grazing avoidance/tolerance. These are important variables from a pastoral perspective.

The cluster analysis resulted in 6 functional groups: low fertility responsive grasses, high fertility responsive grasses, other legumes, white clover, flatweeds and other species (in this pasture including *C. uniflora, N. setulosa* and *Muscii* spp.) The relative contribution to biomass production of the 6 functional groups in response to soil fertility and grazing management history is shown in Fig. 1. The trend, with the exception of the Ballantrae site is that low fertility responsive grasses decrease as fertility increases. Similarly, high fertility responsive grasses increase with increasing fertility. This suggests a functional response of these two groups to a fertility/grazing management gradient. The Ballantrae site has a low occurrence of all grasses and the highest occurrence of other species. Perhaps at this low fertility level, the function of the other species is more suited to the environment than that of low fertility responsive grasses. There does not appear to be any noticeable pattern over the fertility range with the functional group of other legumes, though the occurrence of these legumes in spring is greater due to annual species dying out in summer. The occurrence of white clover increases with increasing fertility, with the exception of the Ballantrae and Morgans sites. It appears to be equally abundant on the two sites with the lowest fertility. Flatweeds appear to occur more frequently on the lower fertility sites, with the exception of the Morgans site.

Conclusion

Functional groups can be formed from a group of species either objectively or subjectively. In either case, the inputs used to group the species together must be chosen carefully and be relevant to the environment that is being studied. Functional groups can usually be broken down into sub groups based on lower levels of function. However, in ecological studies the purpose of using functional groups is to simplify the system and a level of function must be chosen, below which the function is not of major importance to the system being studied. The functional groups chosen were shown to respond to fertility and management histories in a predictable manner and provide a basis for investigations into how management factors affect biodiversity, production and stability of North Island, New Zealand hill pastures.

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Figure 1 Relative contribution of 6 functional groups (defined from the literature) to biomass in the 8 data sets.