ECOLOGY OF PASTORAL COMMUNITIES IN A HETEROGENEOUS ENVIRONMENT

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Ignacio Fernando López
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ABSTRACT

A group of studies was conducted to examine environmental variables and pasture components and their relationships in heterogeneous hill country pasture. Four studies were conducted in relation to the hill country grassland ecosystem of New Zealand.

1. The effects of long-term fertiliser-stocking rate and hill country slope category (LS Low slope, 0-12°; MS Medium slope, 13-25°; HS High slope, >25°) on soil physical and fertility attributes and pasture production were examined. Field treatments, high fertility-high stocking rate (HH) and low fertility-low stocking rate (LN), have been applied to paddocks since 1975. Soil samples were taken from the slope categories of the two field treatments (microsites) and physical and fertility features were analysed. Dry matter production through the year was also measured from these units. The soil attributes that explained the largest percentage of the differences between microsites were water holding capacity (WHC), water conductivity (K_{unsat}), slope, soil compressibility (SC), bulk density (BD), Olsen-P, soil total nitrogen (Total-N) and soil rebound after compression (SR). Slope led to greater differences between soil features of microsites than fertiliser and stocking rate history. Dry matter production increased with increasing Total-N, Olsen-P, WHC and SC, and decreasing slope, K_{unsat}, BD and SR.

2. The presence of plant functional groups, species segregation and their relationship with soil features were analysed. The relationship between field condition and plant functional group was also examined. The evaluation was conducted in the same sites as the first study. The pasture botanical composition for each microsite was measured through the year and plant functional groups determined. The relationship between the presence of plant species and the soil attributes WHC, K_{unsat}, slope, SC, BD, Olsen-P, Total-N and SR (from the first study) and plant functional groups were studied, as well as the field condition-plant functional groups relationship. Seven functional groups were determined. High fertility grasses and *Lolium perenne* (Lp) were associated with LS and high availability of resources, while low fertility species were segregated to HS. Groups of species such as *Agrostis capillaris* (Ac) were indifferent to environmental changes. Functional groups proved to be good indicators of soil development. Field condition and plant functional groups were complementary concepts in grassland dynamic analyses.

3. Sheep grazing behaviour was examined in relation to slope category and plant species selection. The study was conducted in the same microsites as studies 1 and 2. Transects with marked tillers of *Anthoxanthum odoratum* (Ao), Ac and Lp were placed in the slope categories as follows: Ac and Lp in LS; Ac, Ao and Lp in MS; and Ac and Ao in HS. The evaluation was carried out during 4 weeks in each of Summer, Autumn, Winter and Spring, and records of grazed and ungrazed tillers were analysed. Pasture growth rates were calculated through the year. During Spring sheep grazed mainly the LS. With decreasing availability of pasture, sheep enlarged their grazing areas towards the HS. Species selection was only present during Winter when pasture availability was low. In Winter sheep also grazed in all slope categories and selected Lp over of Ac but showed no selection for Ao.

4. Ecotype segregation and plant phenotypic plasticity were examined. Plant material was collected from the extremes of the environmental gradient analysed in studies 1, 2 and 3 and grown in glasshouse conditions under five levels of phosphorus and three of nitrogen in the soil. The plants in each pot were cut on three occasions and total dry matter was calculated. Height, plant architecture, plant horizontal expansion and leaf growth were analysed for *Cynosorus cristatus* (Cc), *Holcus lanatus* (Hl), Ac, Ao and Lp. Morphological and physiological differences were present between genotypes of Lp whereas only physiological genotypic differences existed in Ao and Cc. Consistent differences were not found between Hl genotypes. Thus, Ao, Cc and Lp showed ecotype differentiation. Ac genotypes showed high plasticity with no ecotype differentiation.

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LIST OF ABBREVIATIONS

Ac	*Agrostis capillaris*
Al	Exchangeable aluminium
Al_{sat}	Aluminium saturation
Ao	*Anthoxanthum odoratum*
AP	Air permeability
BD	Bulk density
Ca	Exchangeable calcium
Cc	*Cynosorus cristatus*
Ctr	Control group
GDD	Growing degree days
FT	Field treatment
FVSM	Field volumetric soil moisture
HCS	*Lolium perenne* Hill Country Selection
HH	High-High
HH-HS	High high-High slope
HH-LS	High high-Low slope
HH-MS	High high-Medium slope
Hl	*Holcus lanatus*
HS	High slope
K	Exchangeable potassium
K_{unsat}	Unsaturated hydraulic conductivity
K_5	K_{unsat} at 5 mm of tension
K_{20}	K_{unsat} at 20 mm of tension
K_{40}	K_{unsat} at 40 mm of tension
K_{100}	K_{unsat} at 100 mm of tension
LL	Leaf length
LN	Low-No
LN-HS	Low no-High slope
LN-LS	Low no-Low slope
LN-MS	Low no-Medium slope

Lp	*Lolium perenne*
LS	Low slope
Mg	Exchangeable magnesium
MS	Medium slope
Na	Exchangeable sodium
NH_4-N	Ammonium-nitrogen
NO_3-N	Soil nitrate-nitrogen
P	Olsen-P
pH_{CaCl2}	pH $CaCl_2$
pH_w	pH water
SC	Soil compression
SLP	Slope
SN	*Lolium perenne* cv. Super Nui
SOM	Soil organic matter
SO_4-S	Soil sulphate
SP	Total soil porosity
SPP	Plant species
SR	Soil rebound after compression
SR:SC	Soil rebound-compression ratio
STB	Soil total bases
Total-N	Total soil nitrogen
VSM	Volumetric soil moisture
VSM_{10}	VSM at 10 cm of tension
VSM_{20}	VSM at 20 cm of tension
VSM_{50}	VSM at 50 cm of tension
VSM_{100}	VSM at 100 cm of tension
WHC	Water holding capacity

CHAPTER 1

Introduction

On a local scale, topography and soil attributes have been recognised as important variables that affect vegetation variability across landscape, exerting strong influences on plant distribution, growth and abundance (Archer and Smeins, 1991; Gastó *et al.*, 1993). In addition to topo-edaphic heterogeneity and annual climatic variability, plant community dynamics are affected by grazing animals (Archer and Smeins, 1991; Stuth, 1991; Archer, 1994; Archer, 1996). Therefore, grassland ecosystems are continuously changing over time (Pieper, 1994).

Environmental variables that constitute constraints in grassland ecosystems can promote changes in the botanical composition (Tilman, 1990; Díaz *et al.*, 1999). These changes can determine the placement of species within the sward and according to the plants' relationship with environmental variables (Tilman, 1990; López *et al.*, 1995; Inouye *et al.*, 1987).

This dynamic nature of grasslands can be utilised to assess field condition and plant functional groups allowing an interpretation of the structure and dynamics of plant species within a grassland. Field condition allows the state of an ecosystem in a particular moment to be evaluated (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973; Gastó *et al.*, 1993; Pieper, 1994) and it is possible to group plant species together as plant functional groups according to their use of resources or response to disturbances (Gitay and Noble, 1997).

The presence of ecotypes and phenotypic plasticity have been recognised as individual mechanisms of adaptation that plants may use to survive when changes occur in the level of environmental variables (Snaydon and Davies, 1982; Hutchings and Bradbury, 1986; Sultan, 1987).

The hill country of New Zealand has a heterogeneous environment (Lambert *et al.*, 1986; Lambert *et al.*, 2000), such that the microrelief of the faces of the hills in combination with soil moisture and soil nitrogen content are thought to be important constraints to pasture growth (Lambert and Roberts, 1978; Wedderburn and Pengelly, 1991). The slope of the microrelief of the hills can be classified into three categories: Low slope (0-12°), medium slope (13-25°) and high slope (>25°) (Lambert *et al.*, 2000). Sheep may increase field heterogeneity through redistributing nutrients between the slope categories (Saggar *et al.*, 1990). However, it is not clear whether sheep have any grazing pattern through the year in relation to slope category and botanical composition.

Hill country pasture has been shown to have high botanical composition heterogeneity (Lambert *et al.*, 1986). There is little information, however, about whether there is any relationship between environmental variables and the presence of hill country plant species. It is also unclear whether plant species have a pattern of distribution across hill country environmental gradients. If such a pattern exists, this may allow them to be grouped according to this pattern.

In relation to the presence of ecotypes in New Zealand, a collection of genotypes of *Agrostis capillaris* from contrasting sites has been studied previously but no differences were found between populations suggesting that *A. capillaris* survive through phenotypic plasticity (Rapson and Wilson, 1988). Genotypes of *Lolium perenne* from the hill country have also been studied and the presence of different types of plants was recognised (Wedderburn *et al.*, 1989; Wedderburn *et al.*, 1990; Wedderburn and Pengelly, 1991). However, in both cases the relationship between genotypes and environmental variables was not analysed.

Based on this background the main objective of this work was to evaluate ecotype segregation and plant species plasticity as responses to soil physical and fertility characteristics and selective grazing.

To reach this objective, studies were conducted:

- To evaluate the relationship between soil physical and fertility characteristics in contrasting environments on a micro-scale and their effect on pasture production.
- To analyse whether contrasting environments at a micro-scale have been colonised by plant functional groups and to analyse whether plant functional groups have been segregated in these microenvironments and whether soil variables have had a role in any segregation. Also to analyse whether there is any relationship between plant functional groups and field condition.
- To evaluate whether sheep selectively graze heterogeneous pasture in relation to landscape microrelief and/or plant species through the year.

- To evaluate whether environmental variables exert a selection pressure on field species causing segregation of ecotypes within plant species, or if species with similar genetic features have prospered under different selection pressures due to adequate plasticity, with no ecotype segregation.

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CHAPTER 2

Literature Review

INTRODUCTION

A grassland is a plant community dominated by grasses, herbaceous legumes and other herbaceous species (Thomas, 1980), in close relationship with the environment (Gastó *et al.*, 1993) and each other (Tilman, 1980; Tilman, 1982). All of these factors are constantly changing over time, thus, a grassland is highly dynamic (Huston and Smith, 1987). In a wide analysis, there are two types of grasslands, those that correspond to natural or climax grasslands and those grasslands that have been directly or indirectly generated by human activity. Both, however, represent merging fractions of an environmental spectrum (Tothill, 1976).

Perspectives to analyse the phenomena that occur in a grassland can be without the consideration of time, which means that the analysis is in a determined instant, (Gastó *et al.*, 1993) or may involve time, in which case it is a dynamic analysis that involves ecological successions of the plant species (Tilman, 1987; Gastó *et al.*, 1993). However, in both cases the botanical composition is a reflection of competition, stress and disturbance (Grime *et al.*, 1989).

The objectives of the present review are to discuss the literature related to the plant-environment relationship, and how this relationship affects plant biodiversity in the grassland ecosystem both amongst and within species.

PLANT SPECIES DIVERSITY WITHIN A GRASSLAND

Biodiversity has been defined as the variety of life (Taylor and Smith, 1997). Biodiversity can be measured as genetic diversity; that is the variety of genes in a particular population; as species diversity, that is the total number of species present in a determined area (Begon *et al.*, 1996), or ecological diversity, which corresponds to the number of different ecosystems or ecological processes in an area (Taylor and Smith, 1997). Between the genetic and species level, biodiversity can be analysed to the level of subspecies, subpopulations, ecotypes, or polymorphs (Begon *et al.*, 1996).

There is some evidence that biodiversity maintains stable productivity of ecosystems (Tilman and Downing, 1994). In grasslands a decrease in diversity has been associated with a decrease in productivity (Milton *et al.*, 1994; Tilman and Downing, 1994) and to ecosystem degradation processes (Milton *et al.*, 1994; Pieper, 1994). Therefore, diversity is an important factor in the analysis of the structure of a community.

There are indices that allow an analysis of biodiversity, which can take into account the relative abundances, biomasses or productivities of the coexisting species (Iwasa *et al.*, 1994; Begon *et al.*, 1996). In the case of a pasture, the Shannon-Weaver diversity index (H') and Simpson's index (D) weight the number of species according to production or abundance (Begon, 1996). McNaughton (1994) measured diversity as number of species corrected for differences in density. There are also techniques that can be used to evaluate the state of grassland ecosystems by analysing plant species composition and their dynamics, such as range condition (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973; Pieper, 1994), which is also termed field condition (Gastó *et al.*, 1993).

FIELD CONDITION, ECOLOGICAL TREND AND BOTANICAL COMPOSITION

Field condition is a comparative technique that allows the state of an ecosystem to be described at a particular moment (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973; Gastó *et al.*, 1993; Pieper, 1994). The state of the grassland is rated according to the state of the sward compared with the known or presumed climax (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973; Archer and Smeins, 1991) or in relation to the ideal state in a managed ecosystem (Gastó *et al.*, 1993). Field condition can be measured as the productivity of the field at a particular moment, in relation to the maximum potential productivity of the site (Gastó *et al.*, 1993; Pieper, 1994), with both measurements corresponding to two successional stages of the same sere (Gastó *et al.*, 1993). Therefore, field condition represents the state of the ecosystem in a particular moment expressed as a proportion of the absolute maximum (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973; Archer and Smeins, 1991; Gastó *et al.*, 1993). This relationship is usually based on the amount of dry matter produced (Noble, 1973; Gastó *et al.*, 1993).

Field condition originally evaluated the impact of grazing animals on grasslands (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973). The concept has, however, evolved and now includes environmental variables that at a local scale can became constraints (Gastó *et al.*, 1993). Soil fertility, available water, physical features of the soil and grazing animals are variables that affect field condition through changing plant species dynamics in the field (Gastó *et al.*, 1993; Archer, 1994; Milton *et al.*, 1994; Pieper, 1994), through fluctuation, retrogression and progression (Archer and Smeins, 1991; Gastó *et al.*, 1993). Fluctuation corresponds to reversible changes in dominance in a sward with a stable botanical composition, while progression and retrogression reflect an ecological trend through successional changes of plant species with direction (Rabotnov, 1974). When botanical composition and the proportion of the plant species deviate from the maximum potential productivity of the site, field condition declines, with this process termed retrogression (Barbour *et al.*, 1987). Loss of plant species diversity, pasture production and density of the sward are consequences of retrogression (Archer and Smeins, 1991). Successional changes that occur in the opposite direction to retrogression, and represent the recovery of the ecosystem structure after disturbance, are termed progression. Progression is characterised by an increase in plant diversity, pasture production and sward density through time (Archer and Smeins, 1991; Gastó *et al.*, 1993).

Ecological trend has been defined as the movement of the field condition of the ecosystem towards a new condition, where ecological trend is determined in relation to the more desirable condition (Archer and Smeins, 1991; Gastó *et al.*, 1993). Therefore the ecological trend indicates the direction of changes in ecological succession (Archer and Smeins, 1991; Gastó *et al.* 1993; Pieper, 1994). Ecological successions of plant species have been studied in relation to the variation of availability of soil nitrogen content (Inoye *et al.*, 1987; Tilman and Wedin, 1991a; Tilman and Wedin, 1991b) and different intensities of defoliation (Archer, 1994; Pieper, 1994).

Various theories have been hypothesised to explain the factors that lead to succession (Tilman, 1990; Tilman, 1994a). These include: a) the colonisation-nutrient competition hypothesis, b) the colonisation-light competition hypothesis, c) the nutrient:light ratio hypothesis, d) the maximal growth rate trade-offs, and e) the herbivore trade-offs.

The colonisation-nutrient competition hypothesis is applied to environments with low availability of resources. If there is a compromise between ability to compete for nutrients and ability to colonise, these can lead to successional changes, with the sward being firstly dominated by superior colonists. These would emphasise seed and/or vegetative spread, instead of nutrient competition. Later on, species that are poorer colonists but better nutrient competitors would replace the superior colonist species.

The colonisation-light competition hypothesis is applied to fertile soils. In these highly productive conditions, light competition is enhanced. In early stages better colonists would dominate the sward, but gradually light competitive ability would lead the progression of the succession.

The nutrient:light ratio hypothesis is relevant when succession begins in a low fertility environment. However, with time, nutrients may accumulate and the fertility of the soil rises. As a consequence of this change in fertility, sward production increases and competition for light becomes the limiting factor. Another possibility is that the fertility of the soil may decrease due to leaching. As the soil becomes more infertile, the concentration of plants in the sward decreases and the importance of light competition decreases.

The maximal growth rate trade-offs hypothesis argues that species from fertile soils have high vegetative growth rates but a low competitive ability. With a decrease in the availability of environmental resources, species with lower maximal growth rate but that are superior competitors would tend to dominate the sward.

The herbivore trade-offs hypothesis argues that in habitats where defoliation is a major limiting factor, there is a trade-off between susceptibility to defoliation and colonisation rate or between susceptibility to defoliation and the ability to compete for the available resources (nutrient or light). These trade-offs explain the ecological succession of the plant species as grazing intensity varies.

These hypotheses explain the dynamics of ecological successions in the field and thus explain the nature of changes of plant species from one field condition to the next.

Field condition classifies plant species into four main groups according to their relative dominance in the botanical composition in each type of field condition: decreasers, increasers, invaders and indifferents (Dyksterhuis, 1949; Noble, 1973; Gastó *et al.,* 1993). The presence of the plant species of each group in the field has been shown to be related, not only to grazing pressure, but also to the response of the plant species to the environmental constraints affecting the sward (Pieper, 1994). Thus, at a particular field condition, plant species may be grouped together with changes occurring in the sward due to the presence of the plant species within each group increasing, decreasing or remaining stable. However, the plant species within each group respond in a similar manner to environmental constraints and require similar environmental resources. This hypothesis needs further investigation, but links the functional groups concept that groups together, in functional groups or types, species with similar uses of resources (nitrogen, water, light etc.) or that respond in a similar manner to disturbances (such as grazing) (Gitay and Noble, 1997).

Thus, field condition is the reflection of complex processes that are involved in driving ecological successions. In this way, a progression of the field condition would be related to higher availability of resources in the soil and to plant species capable of taking soil resources faster. A retrogression of the field condition would be related to a progressive decay in the availability of the resources of the soil and, therefore, highly tolerant plants species would be expected to tend to dominate. However, in a pasture under degraded conditions the competition for resources between plant species should be high.

RELATIONSHIP BETWEEN ENVIRONMENTAL CONSTRAINTS AND BOTANICAL COMPOSITION

Before the relationship between environmental variables and the presence/abundance of a plant species of an ecosystem can be analysed, it is necessary to establish the scale on which the environment will be analysed. The scale of analysis determines which variable or filters should be considered in the analysis. For example the appropriate environmental variables at the regional scale would be different than those at paddock level (Gastó *et al.*, 1993; Díaz *et al.*, 1998).

Variables that affect plant development at local scale are features such as geomorphology and site, which are permanent environmental variables, and soil fertility, and water availability, which are continually changing (Gastó *et al.*, 1993). Environmental variables can constitute constraints depending on the result of the relationship between them and the species that are colonising that specific environment. In this way an environmental constraint has been defined as a factor that influences the fitness of organisms in a habitat (Tilman, 1994a).

Pastoral ecosystems are characterised by the presence of several plant species (Grime *et al.*, 1989; Schulze and Mooney, 1994) and species diversity is considered to be an important variable for the stability of the pastoral ecosystem (Pimm, 1984; Schulze and Mooney, 1994; Lawton and Brown, 1994; Tilman and Downing, 1994). Thus an ecosystem with high species diversity would have a higher probability of containing species that would survive under given environmental constraints (Pimm, 1984; Berendse, 1994; Lawton and Brown, 1994; Tilman and Downing, 1994). Grazing animals may be considered as one of the environmental constraints for the pasture, with grazing intensity promoting changes in the botanical composition (Dyksterhuis, 1949) and in density of tillers and plants (Briske, 1991).

Environmental Variables as a Source of Selection Pressure on Species

When an environmental variable becomes a constraint, it exerts a selection pressure on plant species and may cause a re-distribution of the plant species along the environmental gradient created by the constraints (Tilman, 1990; Milton *et al.*, 1994; Díaz *et al.*, 1999). This re-distribution of the plant species is determined by the level of compatibility between the plant species and environmental constraints (Vavra *et al.*, 1994; Díaz *et al.*, 1999). In a study at the regional scale, Díaz and Cabido (1997) showed that the presence and survival of groups of plant species in the field depend on their compatibility with climatic gradients. At a local scale environmental variables such as availability of soil resources, including water, light, germination sites (Tilman, 1990 and Tilman, 1994a) and intensity of defoliation are considered the most relevant environmental constraints for plant species (Tilman, 1990) and can cause segregation of species at the site or paddock level. López *et al.* (1995) reported that changes in slope and water availability among neighbouring naturalised swards in Western Patagonia, Chile, led to drastic changes in botanical composition. Inouye *et al.* (1987) showed that increasing nitrogen availability decreased local species richness and increased the presence of perennials and woody species. Tilman (1994b) reported that increasing soil nitrogen content promoted the succession of dominant species in the field and related this succession with the capacity of species to compete for the available resources. Kleyer (1999) studied the effect of resource availability on field plant species and related those to disturbance. Results showed that groups of plant species adjusted their growth according to the levels of resources available and disturbance intensities.

In New Zealand, the hill country presents a very heterogeneous environment (Lambert *et al.*, 1983; Lambert *et al.*, 1996). Low soil moisture and low soil nitrogen are two important constraints affecting botanical composition and the performance of the plants in this environment (Wedderburn and Pengelly, 1991). In the hill country, soil moisture is related to aspect and may become a relevant constraint, especially in combination with high slopes. In this manner, the aspect has a strong effect on botanical composition (Lambert and Roberts, 1978). For example, *Lolium perenne* and *Holcus lanatus* are more predominant in sites located on eastern aspects, as is the case with *Cynosorus cristatus*, although this species also colonises sites facing the south. However, species as *Agrostis capillaris* and *Anthoxanthum odoratum* seem to be indifferent to the aspect (Lambert and Roberts, 1978). Moreover, dry matter production is related to the aspect, where the south facing (shady) aspects are reported to produce more dry matter than north facing (sunny) aspects (White *et al.*, 1972; Radcliffe *et al.*, 1977; Lambert and Roberts, 1978).

A close relationship between fertility features of the site and botanical composition has been reported by Matthew *et al.* (1988) where changes in field botanical composition were related to fertility gradients. For example, *A. capillaris* dominated microsites with low fertility, whereas with increasing phosphorus levels, the prevalence of *L. perenne* increased. In general, soil fertility can become an important constraint for dry matter production, playing an important role in the botanical composition of a sward (Lambert *et al.*, 1996).

It is clear that the environmental factors that are constraining the sward growth are acting together and are interrelated. Generally, however, environmental factors are studied separately. In order to obtain a better understanding of their action over the field botanical composition, the effect of environmental factors on the botanical composition of the sward should be analysed together using multivariate statistical analyses (Wilson, 1999).

Selective Grazing: Another Source of Selection Pressure on Species

Grazing animals interact with soil and pasture species (Briske and Heitschmidt, 1991). Five hierarchical levels have been recognised regarding the process of animal diet selection by grazing animals: landscape, plant community, patch, feeding station and plant (Stuth, 1991). Plant palatability, animal preference, animal selection and accessibility of the various sward components are involved in this process (Hodgson, 1979; Stuth, 1991; Hodgson *et al.*, 1994). Palatability can be defined as agreeable to the taste (Hodgson, 1979) and is related to inherent features of the plants (Hodgson, 1979; Stuth, 1991). Grazing preference reflects the free choice of animals when all the components are freely available (Hodgson *et al.*, 1994), and is essentially behavioural (Stuth, 1991). When grazing animals remove some components of the sward or groups of components rather than other components, this is defined as selection (Hodgson, 1979).

The presence of individual species in a pasture in which animals have been grazing selectively is not even. Grazing selection may affect the botanical composition of the sward, inducing changes such that the decrease of the selected species (Briseño de la Hoz and Wilman, 1981), while the presence of non-selected species may increase (Brown and Stuth, 1993). For example, Silvertown *et al.*, (1994) reported that *Festuca rubra* was a bad competitor without grazing, however, when the sward was grazed, animals selected *L. perenne* rather than *F. rubra*, such that *F. rubra* increased its presence in the field whereas *L. perenne* did not.

Resistance mechanisms of plants species are based on tolerance and avoidance. "Tolerance" mechanisms are mechanisms that increase plant growth after defoliation whereas "avoidance" mechanisms are mechanisms that lower the probability of being grazed and the intensity of the grazing (Briske, 1991; Briske, 1996).

Late-successional dominant species depend more on tolerance strategies to resist grazing than early successional species (Davison, 1993). Late-successional species are characterised as being faster-growing species that are highly selected by grazing animals and grow in environments rich in resources (Coley *et al.*, 1985; Briske, 1996). In contrast early successional species have slower growth rates, colonise environments with lower availability of resources, invest more in avoidance mechanisms, such as having more biochemical defences (lignins, alkaloids, etc), and are less selected by grazing animals (Coley *et al.*, 1985; Briske, 1991; Briske, 1996). If animals remove biomass from plant species faster than the plants can replace it, tolerance mechanisms are less effective than avoidance mechanisms (Briske, 1996). This can provoke changes in plant species dominance in the field, such that faster-growing species actually decrease their presence and slow-growing species becoming dominant (Coley *et al.*, 1985; Briske, 1996). Because of this, selective grazing may start degradation processes in a grassland when animals over graze late-successional dominants (Milton *et al.*, 1994; Pieper, 1994; Briske, 1996). Therefore, when there is selective grazing, the competitive ability between plant species and the grazing resistance of the species may determine the final plant community composition (Pieper, 1994; Briske, 1996).

Several studies have shown that sheep have the ability to select species from the field, differentiating between legume and grass (Ridout and Robson, 1991; Penning *et al.*, 1997), between legume and grass species (Edwards et *al.*, 1993) and between grass species (Grant *et al.*, 1984; Silvertown *et al.*, 1994). For example, Parsons *et al.* (1994) reported that sheep preferred diets composed of about 70% *Trifolium repens* and 30% *L. perenne*. Penning *et al.* (1997) evaluated grazing preference by sheep and goats in mixed swards of *L. perenne* and *T. repens* and reported that there is a grazing preference by both types of animal for grazing one or the other species with sheep having a 70% preference for *T. repens* and goats a 52% preference for *T. repens*.

Grazing can also produce morphological differentiation between populations of grass species. Brock and Fletcher (1993) reported that plants of *L. perenne* that grew under set stocking had significantly shorter leaves, leaf sheathes and stems than plants grown under a rotational grazing system. However, Brock and Fletcher (1993) did not clarify whether these differences found in *L. perenne* were due to plasticity of the original material or because different types of *L. perenne* plants, within the entire initial sown population, had survived under each type of grazing management.

Selective grazing can have a double effect on botanical composition. The selected species can be over-grazed, such that their presence in the field can decrease with time. Selective grazing can also be an advantage for the non-selected species, because these species would have the opportunity of increasing their presence in the field. However, it is possible that selective grazing may genetically segregate different groups of individuals of the same species that initially were part of the same population. This could result in plants of the same species with differences in grazing resistance and/or competitive ability characteristics. This hypothesis requires investigation.

Environmental Constraints and Species Competition

Competition and resource availability have been a topic that had created disagreement in the past (Tilman, 1987; Thompson 1987; Grime, 1988; Tilman, 1989; Thompson and Grime, 1988). Grime (1974) has defined competition as "the attempt by neighbouring plants to utilise the same units of light, water, mineral nutrients or space". In this definition the concept of ‘competitor' is equivalent to a ‘resource capture specialist' (Grace, 1991). Thus, in a pasture with plant species competing for the available resources, the individual that is capable of taking the most resources over time would be the best competitor (Mooney, 1976).

On the other hand, Tilman (1990) defines successful competitor species as those that can reduce the concentration of the limiting resource to the lowest level and tolerate it at this level. Grace (1991) fully discussed the debate between Grime's and Tilman's hypotheses and made the reasonable conclusion that the theories were not contradictory. Grime's theory considers a wide range of features, all attributes that affect the colonisation process. Tilman's theory focuses on resource use characteristics and is less specific taking into account trade-offs related to colonisation ability (Grace, 1991).

Huston and Smith (1987) recognised that because resources are limited in a ecosystem, plants must compete for the resources in order to survive, but the level of the resources changes continuously, with these changes preventing any species from maximising its competitive ability under all circumstances.

In a grassland ecosystem the competition intensity changes according to the available resources with more intense competition when there are environmental resource shortages (Tilman, 1994a). That was reported to occur in a study by Plantenkamp and Foin (1990) where competition between species was more intense at the xeric site than at the mesic site. Tilman (1994b) measured the effects of competition on the ecological succession of plant species when the levels of available soil nitrogen varied. Plants that finally dominated under low available soil nitrogen were those that had high allocation to the root, low nitrogen content in the tissue, low allocation to seed or rhizome, low maximal growth rates and greater root longevity (Tilman, 1990). Therefore, neighbouring species constitute another source of constraint on individual plant development and exerts selection pressure (Turkington and Harper, 1979; Aarssen and Turkington, 1985).

FITNESS IN PLANT SPECIES

"Fitness" is the degree of adaptation of an individual to the environment, which is related to its relative success in survival and reproductive output (Sultan, 1987), i.e. its relative contribution to the gene pool of the next generation (Begon *et al.*, 1996).

Plant species colonising heterogeneous environments can reach fitness through ecotypes (Snaydon, 1970; Snaydon and Davies, 1982) or phenotypic plasticity (Hutchings and Slade, 1988; Hutchings *et al.*, 1997).

Biodiversity within Species

Environmental constraints may provoke adaptive evolution as a survival response from individual plants (Harper, 1977). Therefore, if a population of plants is facing an environmental constraint in a heterogeneous environment, selection for different genes will occur in each section of the environment, with phenotypic differences present within the populations (Antonovics, 1978). In plant populations the levels of the environmental constraint has to exert a constant selection pressure, both spatially and temporally for selective divergence to occur (Sultan, 1987). Examples include heavy-metal containing soils (Antonovics and Bradshaw, 1970; Symeonidis *et al.*, 1985), chill and freezing acclimation (Loick and Nobel, 1993) and altitudinal gradients with different flowering and fruiting (Clausen *et al.*, 1940; Clausen *et al.*, 1948; Clausen and Hiesey, 1958).

Plant populations may be genetically dynamic with gene flow occurring such that local specialised races may appear within the species (Begon et al., 1996). An ecotype is considered to be a subset of individual plants within a species, with genetically determined differences in growth characteristics or environmental tolerances between populations, that are reflected by their survival in particular environments (Begon *et al.*, 1996). The specific genotype that allows a particular genotype to perform better in a specific environment than in other environments may result in poorer performance in other environments (Plantenkamp and Foin, 1990).

Clausen *et al.* (1948) and Clausen and Hiesey (1958) have shown that at a geographic level, plants may genetically vary according to the survival requirements of the local environment. The survival requirements may provide selection pressures resulting in the generation of ecotypes. This phenomena can occur at a microsite scale (Antonovics, 1978). The degree of genetic drift (genetic disjunction or differentiation) between adjacent populations is a function of the relative magnitude of contrasting selection pressures in the two environments, and the genetic recombination within and between populations (Jain and Bradshaw, 1966). Therefore, a mosaic of populations of one species can diverge into types that are morphologically and physiologically adapted, in response to a mosaic of environmental heterogeneity (Snaydon, 1970; Snaydon and Davies, 1972).

Snaydon and Davies (1976) recognised that it is possible to obtain a rapid genetic differentiation between populations which are in close proximity to each other, through the interaction of environmental selection pressure, gene flow and recombination. If the populations are genetically less similar, this signifies that the selection pressures in both sites were more intense and/or there has been limited gene flow between the populations.

More evidence of genetic population differentiation, due to the action of environmental constraints over plant populations, has been provided by two populations of *A. odoratum* (Platenkamp, 1990; Platenkamp, 1991; Platenkamp and Shaw, 1992). In the two populations, reproductive output, growth and flowering time differed suggesting a difference in past selection between the populations according to the different environmental constraints (Platenkamp, 1991). This has also occurred in *A. odoratum* where differences in soil moisture have been reported to generate genetic divergence in the population by selecting according to flowering time (Platenkamp, 1990; Platenkamp and Shaw, 1992). Plants that survived in the site of origin (xeric environment) were early flowering, as were those present in another site (mesic), moreover these plants (ecotypes) had a higher reproductive output in the xeric site than in the mesic site (Platenkamp, 1990; Platenkamp and Shaw, 1992). Another difference between the two populations was that seeds that had a xeric origin had a lower level of dormancy than those from the mesic site (Platenkamp, 1991). *Bromus tectorum* shows local adaptation and genetic differentiation between an arid-saline site and a cool-mesic site (Rice and Mack, 1991a; Rice and Mack, 1991b).

Snaydon and Davies (1976) found that, because *A. odoratum* is a short-lived perennial, its persistence in the field is highly correlated to the amount of annual seed production. Therefore, a strong selection pressure is required to obtain genetic differentiation between two adjacent populations. Snaydon and Davies (1976) reported that morphological differentiation could occur between populations over distances of only 0.1 m, when the environmental constraints are sufficiently different between sites. The level of differentiation between populations will depend on the degree of change in environmental conditions, the effects of gene flow, and the duration and stability of the selection pressures involved (Snaydon and Davies, 1976; Sultan, 1987).

Other experiments with *A. odoratum* (Snaydon and Davies, 1982) have shown that genetic changes, that lead to population divergence, can occur over a short period of time, and that the magnitude of the divergence amongst populations varies from attribute to attribute. Some attributes where populations of *A. odoratum* have diverged were: plant height, plant posture, plant yield, seasonal pattern of growth, reproductive strategy, and disease susceptibility (Snaydon and Davies, 1972).

Other cases of divergence due to environmental constraints have been found while screening populations of *B. tectorum* (Novak *et al.*, 1991; Rice and Mack, 1991a; Novak *et al.*, 1993) and *L. perenne* (Wedderburn *et al.*, 1990). In both cases it was concluded that the material had a close relationship with the original environment.

The hill country of New Zealand presents a heterogeneous environment where the topography is a relevant limiting factor because, as the slope increases, fertility and moisture status decrease (Gillingham, 1973; Gillingham and During, 1973). There is a strong animal effect on the fertility due to nutrient transference by grazing animals from steep zones to flat zones (Gillingham and During, 1973; Sagar *et al.*, 1990). All of these environmental differences generate environmental heterogeneity that can result in different selection pressures over the pasture. This has been reported to occur in the case of *L. perenne*, with a wide phenotypic variation in a resident population (Wedderburn and Pengelly, 1991).

Wedderburn *et al.* (1989) collected and characterised *L. perenne* from hill country pastures of New Zealand. Plants showed site significant physiological differences in P, K, Mg and Ca content, exhibiting a wide range of *L. perenne* types (Wedderburn *et al.*, 1989). The material also showed morphological differences in tiller number and tiller width (Wedderburn *et al.,* 1989). Further morphological variability has been found in a wider range of material (Wedderburn and Pengelly, 1991).

Another example of a local adaptation was found in *L. perenne* due to moisture stress (Wedderburn *et al.*, 1989), where plants that came from northern aspects had greater seed production than plants removed from other aspects. This behaviour was believed to be related to a survival strategy developed by moisture-stressed plants, with reduced vegetative growth and increased seed production, similar to that in the annual species.

Wedderburn *et al.* (1990) reported that *L. perenne* showed a significant nitrogen x aspect x slope interaction. For example, plants that came from steep slopes produced less dry matter when they were grown under zero and applied nitrogen than plants that came from flatter slopes. Therefore, plants removed from N-stressed environments, such as steep slopes, had low growth rate, and hence low production, and were unresponsive to nitrogen, compared to plants that came from less stressed environments. Moreover, they reported that plants that came from drier sites had lower productivity, even when they were fully watered, than plants that came from wetter sites. This supports the work of Grime and Hunt (1975) who recognised that nutrient poor soils tend to contain a higher proportion of low relative growth rate species than do fertile soils.

Finally, Wedderburn *et al.* (1990) recognised three types of plants of *L. perenne* collected from the hill country of New Zealand:

a) Plants removed from stressed environments that had high dry matter production under low nitrogen and/or a survival mechanism under moisture stress. However, those plants did not produce as much dry matter as plants that came from low stress environments when they were relieved from the stress.
b) Plants that were within the top 10% of dry weight producers under non-stress conditions, but were low producers under stress conditions.
c) Plants that were within the top 10% dry weight producers both under stressed and non-stress conditions.

Species composition has a close relationship to type of site and soil condition. Previous analyses have been conducted from the plant point of view, following the argument that plants can become genetically adapted as a response to changes in the environmental constraints. However, in the short term, it would seem more valid for this analysis to be conducted from the perspective of the environmental constraints. The presence of a certain degree of genetic diversity within a species may allow the species to survive and succeed following changes in environmental constraints. This may occur through the presence of ecotypes (individual plants within a species) that differ genetically and are compatible with changes to the environmental constraints. Further research is required to validate this hypothesis.

Plasticity: An Alternative Plant Response to Environmental Constraints

Genetic information and environmental conditions may co-determine phenotype, where fitness would be the result of the phenotype-environment interaction. Phenotypic plasticity is an individual plant characteristic through which an individual plant can maintain fitness (ability to survive and reproduce) in a heterogeneous and fluctuating environment (Sultan, 1987).

Plasticity has been defined as "the variation in phenotypic expression of a genotype that occurs in response to particular environmental conditions and which enhances the capacity of the individual to survive and reproduce under those conditions" (Sultan, 1987).

Phenotype is the result of the interaction between a particular genotype and a particular environment. Phenotypic plasticity is the variation in the phenotypic expression of a determined genotype through physiological, phenological and/or morphological changes, when this genotype is under different environmental conditions (Sultan, 1987), with a single genotype having the capability of displaying a range of phenotypes induced by the local environmental constraints and according to them (Turkington, 1989). This is why it is important to include in the plant response a description of the environment when analysing plant variation (Bazzaz and Sultan, 1987).

Therefore, plasticity is a fundamental characteristic of plant growth, through which an individual plant is able to respond to environmental constraints through variation of its morphology or physiology (Robinson and Rorison, 1988). Plasticity is a mechanism of individual adaptation to the unpredictable heterogeneous environment, that generates population adjustment and that buffers the effects of spatial and temporal environmental changes that would lead to natural selection (Grime *et al.*, 1986; Sultan, 1987). This would prevent the elimination of individuals and their genes from the ecosystem, maintaining genetic diversity in the population passively, thus plasticity has evolutionary consequences (Sultan, 1987).

Robinson and Rorison (1988) studied plasticity in *Poa annua*, *H. lanatus*, *Deschampsia flexuosa* and some cultivars of *L. perenne* in relation to environmental nitrogen availability and reported that the plants had different degrees of plasticity for different characteristics in the same plant. Plasticity occurs simultaneously in various characteristics of a growing plant, rather than one specific feature keeping other characteristics constant (Robinson and Rorison, 1988). It is usually not necessary for all of the plastic characters to respond to the same environmental constraints (Jefferies, 1984).

Plasticity of characters is based on genetic control (Bradshaw, 1965; Bradshaw, 1972; Petit *et al.*, 1996), where certain plant structures and processes are only able to change slightly (such as pinnate leaf shape and floral characters), while others are more flexible (such as hairiness and number of shoots) (Clausen *et al.*, 1940; Clausen *et al.*, 1948). Bradshaw (1965) and Sultan (1987) reported that phenotypic plasticity can be expressed through either morphological or physiological characteristics.

Plants growing in heterogeneous environments may show morphological and/or physiological plasticity as a response to the available resources in the environment (De Kroon and Hutchings, 1995; Hutchings and Wijesinghe, 1997). Plants that spread by stolons may have plastic responses to local environmental variation (Waite, 1994; Hutchings and Wijesinghe, 1997). In fertile areas stolons will produce more frequent branching and short internodes, which allow more intense foraging of resources. In areas with low fertility, stolons will increase the internode distance and will decrease the branching, which enables the stolons to cross rapidly through less favourable sites (Sutherland and Stillman, 1988; Waite, 1994; De Kroon and Hutchings, 1995). For example, *Ranunculus repens* has been reported to have a plastic response according to the fertility level of areas in the environment, foraging intensively in molehills where the fertility was higher and the competition low and showing an increased internode length between molehills, where the resources were low and the competition more intense (Waite, 1994). Dong and De Kroon (1994) reported that in *Cynodon dactylon*, 90% of the axillary buds were activated when the plants received the stimulus of light and nitrogen, but in an environment with low light and nitrogen, 70% of the buds remained dormant, increasing the distance between growing points. Stolons, organs that forage for light and nutrients, were highly plastic especially under the light stimulus but rhizomes, which are storage organs, showed little plasticity. In *T. repens* plasticity is an evident individual characteristic that may determine success (Turkington, 1989).

Physiological integration has also been measured within plants that produce stolons. Stolons allow the plant to transport resources obtained from sites with high availability to parts of the plant where that resource is scarce. Resources obtained in rich local environments can be utilised to allow the plant to span a wider area, such that the plant can locate more nutrient-rich patches (Hutchings and Wijesinghe, 1997). The size of the environmental patches is related to the final success of the plant. Plants grown in a environment where the size of the patches were small compared to the distance between ramets, have been shown to be unable to adjust their morphology to the high variation of the available resources. These plants grew less than those grown in patches with greater resources, suggesting that the plants in the small resource patches could not efficiently exploit the available resources (Hutchings and Wijesinghe, 1997; Wijesinghe and Hutchings, 1999).

Plants may have plastic responses influenced by their close neighbours. Different plastic growth responses have been induced by different species of grass to *T. repens* (Turkington, 1983a; Turkington, 1983b). In the same way, the behaviour of *A. odoratum* determining lifetime, reproductive output and growth, has been reported to be plastic depending on the neighbours (Platenkamp and Foin, 1990).

Therefore, plasticity may be a plant strategy that allows individual plants within plant species to colonise contrasting environments and/or to succeed when the levels of constraint of the environmental variables change.

SUMMARY AND CONCLUSIONS

The availability of soil resources, including water, light and germination sites, and defoliation are environmental constraints that affect the dynamics of the botanical composition and production of grassland ecosystems. Field condition analyses the state of the pastoral ecosystem based on successional development using botanical composition and pasture production, at a particular moment and through time. Field condition can change over time through ecological succession of plant species or plant functional groups in the field, due to interactions between the species and plant functional groups with environmental variables. The arrangement of plant species or plant functional groups and their presence in the field is determined by their capacity to compete for the available resources and the level of tolerance to the different environmental stresses and disturbances. A particularly important environmental constraint is selective grazing by animals such as sheep. However, despite the importance of selective grazing on the botanical composition of the sward, sheep grazing behaviour and in particular selective grazing in a highly heterogeneous sward, as is the case of the hill country sward of New Zealand, and how this changes throughout the year, has not been studied.

Genetic plasticity and the presence of ecotypes may allow plant species to persist under a variety of environmental constraints, such that plant species can colonise contrasting environments. Plasticity of plant species and ecotypes may also allow pastoral ecosystems to maintain their diversity of species when changes occur in the level of constraint of the environmental variables. However, no research have been conducted to test the importance of plasticity and ecotype presence as mechanisms that allow plants to survive under changes of environmental constraints.

Plant species diversity is, therefore, important to maintain the stability of grassland ecosystems, but diversity within plant species would appear to be important to maintain the stability of ecosystems under changing and heterogeneous environmental conditions.

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CHAPTER 3

Ecology of pastoral communities in a heterogeneous environment.

I. Abiotic environment

Plant production and development are constantly affected by environmental variables, which can constrain growth. Species competition and colonisation are affected by local variations in environmental constraints, which may produce genetic divergence within plant populations. In the hill country, slope can result in major differences in soil features. Further changes in soil properties can also occur as a result of intensification or extensification of the pastoral systems. The effect of these changes in relation to the soil attributes of the microrelief and soil-pasture relationship, such as pasture production, botanical composition and segregation of ecotypes, has not been investigated in the hill country. The objectives of the study described in the present Chapter were to evaluate the effects of long-term fertiliser-stocking rate and hill country microrelief on soil physical and fertility attributes and the pasture production of the hill country.

ABSTRACT

The long-term effects of fertiliser and livestock on soil physical and fertility characteristics and pasture production of micro-topographical units of the hill country of New Zealand were examined. Field treatments of high fertility-high stocking rate (HH) and low fertility-low stocking rate (LN) dating back to 1975 were used to reach the objectives, and were part of an overall study exploring the interrelationships between soil properties and the associated plant community. Soil samples were taken from three slope categories (0-12° low slope, LS; 13-25° medium slope, MS; >25° high slope, HS) from the HH and LN treatments and a range of soil fertility and physical features were assessed. Pasture growth (green matter) and dead matter accumulation were measured over 12 months on each microsite. The greatest differences between microsites were due to slope category rather than fertiliser and stocking rate history. Increasing slope decreased pasture production, total soil nitrogen (Total-N), Olsen-P, water holding capacity (WHC) and soil compressibility (SC), but increased unsaturated hydraulic conductivity (K_{unsat}), bulk density (BD) and soil rebound after compression (SR). Slope, WHC, K_{unsat}, SC, BD and Total-N were the variables of the soil that had the largest influence on the differentiation between microsites. Olsen-P and SR had less importance. Pasture production was strongly influenced primarily by slope, soil WHC and K_{unsat}, and secondly by soil Total-N and Olsen-P. Improvement in soil productive features was, however, associated with a loss in soil water conductivity and soil stability of the aggregates, suggesting that these soils would be more vulnerable to damage by treading traffic.

INTRODUCTION

Predictive ecological theory has been considered to be dependent on major environmental constraints, tradeoffs that organisms have to face when they are interacting with these constraints, and of the inclusion of these constraints and tradeoffs as mechanisms of intraspecific and interspecific interaction (Tilman, 1990). Environmental constraints that have an important impact on plant production and development are temperature (Huston and Smith, 1987); the availability of natural resources (Huston and Smith, 1987; Tilman, 1988; Tilman, 1990); and germination site and herbivory intensity (Tilman, 1988; Tilman, 1990). Local variations in environmental constraints affect the processes of species competition and colonisation (Huston, 1999). This may produce genetic divergence within plant populations. One example demonstrating this divergence is *Anthoxanthum odoratum* colonising close sites with two different categories of drainage (Platenkamp, 1990; Platenkamp, 1991; Platenkamp and Shaw, 1992).

New Zealand hill country is characterised by high local variation in microrelief, characterised by large differences in the slope angle over short distances (Gillingham, 1973; Lambert and Roberts, 1978; Lambert *et al.*, 1983; Lambert *et al.*, 1986). Three broad categories of slope, 0-12°, 13-25°, >25°; termed low slope (LS), medium slope (MS) and high slope (HS), respectively, have been developed to describe this microrelief. Slope influences soil depth, degree of soil development, nutrient status, moisture retention and the behaviour of the grazing animal, with respect to the return of nutrients in dung and urine. This in turn influences pasture composition and production (Gillingham, 1973; Lambert *et al.*, 1983). Thus slope can result in major differences in soil organic matter, nutrient pools, pH, physical properties and biological activities, measured by biomass and the presence of earthworms (Mackay *et al.*, 1999; Lambert *et al.*, 2000).

Mackay *et al.* (1999) and Lambert *et al.* (2000) have shown that in addition to the influence of slope on soil properties, further changes can also occur as a function of intensification or extensification of the pastoral systems. The impact of these changes in relation to the constituents of the soil in each slope category, and how these changes may affect the relationship between the soil and plant constituents of each microsite, such as pasture production, botanical composition and segregation of ecotypes, has not been investigated.

The objectives of the work were:

- To examine the long-term effect of fertiliser and livestock on the physical and fertility features of the soil and pasture production of the microrelief units that constitute a hill country slope.
- To examine the relationship between the soil and pasture components.
- To discriminate the soil features that have a dominant influence on plant growth.

MATERIALS AND METHODS

Site

The long-term fertiliser-grazing experiment at AgResearch's Ballantrae Hill Country Research Station, near Palmerston North, New Zealand, has been in progress since 1975. Between 1975 and 1980, phosphorus (P) as single-superphosphate (approximately 9% P, 11% S; Lambert *et al.*, 2000) has been applied at two rates: low (11 kg P/ha/year) and high (57 kg P/ha/year) to two, 7 to 9 ha farmlets. The HH paddock received 20 kg N/ha in 1975 and ground limestone in 1975 (1250 kg/ha) and in 1979 (2500 kg/ha) (Lambert *et al.*, 1990; Lambert *et al.*, 2000). From 1980 the input of fertiliser into the Low treatment ceased (LN), while the High treatment continued to receive P (HH) each year (34 kg P/ha/year) (Lambert *et al.*, 1986; Lambert *et al.*, 1990). Stocking rate also has been differentiated between farmlets, with the average from 1975 to 1993 for the LN paddock being 8.3 ewes/ha and that for the HH being 14.8 ewes/ha (Lambert *et al.*, 1996).

The soils on all farmlets corresponded to yellow-brown earths and related steepland soils; Ngamoko silt loam from silty drift material, and Mangamahu steepland soil from silty sandstone (Lambert *et al.*, 1990).

Measurements

Within paddocks of the LN and HH farmlets soil samples to a depth of 75 mm were taken from 3 slope categories (LS, MS and HS) in July 1997. For assessing soil fertility level within each slope class eight cores were taken. There were four microsites sampled in each slope class in each farmlet. A microsite was defined as the result of the interaction between field treatment (fertiliser and stocking rate) and slope category (LS, MS and HS). In October 1998, two intact soil cores (100 mm diameter x 75 mm deep) were taken from each microsite to characterise the physical properties of the soil. These were treated as subsamples. Again there were four microsites sampled within each slope class on the LN and HH farmlets.

Soil fertility variables measured included soil nitrate-nitrogen (NO_3-N), ammonium-nitrogen (NH_4-N), and total soil nitrogen (Total-N), pH (water, pH_w; and $CaCl_2$, pH_{CaCl2}), soil organic matter (SOM), Olsen-P, exchangeable potassium (K), sodium (Na), calcium (Ca), magnesium (Mg) and aluminium (Al), aluminium saturation (Al_{sat}) and soil sulphate (SO_4-S). Mineral N content, soil NH_4-N content and Total-N were analysed using the methodology described by Franzluebbers *et al.* (1996). Methodologies used to analyse the other fertility variables are described by Page (1982), Van Reeuwijk (1986) and Sadzawka (1990).

Fertility variables were analysed at the Soil Laboratory of the Institute of Soil and Agricultural Engineering, Agronomy Faculty, Universidad Austral de Chile, Valdivia, Chile, with the exception of soil NO_3-N and NH_4-N contents and Total-N content. These were analysed at AgResearch Grasslands, Palmerston North, New Zealand.

Soil physical characteristics measured included unsaturated hydraulic conductivity (K_{unsat}) at 4 tensions (K_5, K_{20}, K_{40}, K_{100}), bulk density (BD), volumetric soil moisture (VSM) at 10, 20, 50 and 100 cm of tension (VSM_{10}, VSM_{20}, VSM_{50}, VSM_{100}), total soil porosity (SP), field volumetric soil moisture (FVSM), soil compression (SC), soil rebound (SR) after compression and air permeability (AP). The methodologies used to evaluate the physical features of the soil are described in Lambert *et al.* (1996), Nie *et al.* (1997), and Betterridge *et al.* (1999). Physical features of the soil were analysed at the Soil Physical Laboratory of AgResearch Grasslands, New Zealand.

Pasture growth was measured using the pre-trimmed exclusion cages (0.5 x 1.0 m) technique (Radcliffe *et al.*, 1968) from July 1997 to July 1998. Cages were placed on four microsites within each slope class on each farmlet. The pasture was trimmed to approximately 10 mm height, after which the cages were moved to a different position. Before placing the cage the pasture was cut to a height of 10 mm. A rotation of three positions in analogous microsites was used for each cage during the year. During the evaluation period, seven cuts were taken. The trimmed material was collected and a sub-sample manually separated discriminating between green and dead matter. All collected pasture was dried in an oven at 60° for 48 hours. Pasture production and the amount of dead matter were calculated per hectare per year. Only green matter was used to calculate pasture production. The green:dead matter ratio was also calculated.

Statistical Analysis

All the statistical analyses were performed using the SAS program version 6.12 (1997). Univariate statistics were applied through an ANOVA to detect statistical differences between field treatments (LN and HH), slope categories (LS, MS and HS) and microsites (field treatments-slope categories interaction), and when appropriate PDIFF was used to separate means.

The statistical model used for analysis of the data from the soil was:

Y=Mean + field treat. + slope + soil sample + field treat.*soil sample + field treat.*slope + error (1)

The statistical model used for analysis of the pasture data was:

Y = Mean + field treatment + slope + cage + field treat.*cage + field treat.*slope + error (2)

As the LN and HH farmlets are not replicated, to test for differences between HH and LN the field treatment was tested against the field treatment-replication interaction (soil sample or cage) (Error type A).

Slope, soil NH_4-N, SOM, pH_w, pH_{CaCl2}, Al , VSM, SP, BD, FVSM, AP, SC, SR and rebound-compression ratio (SR:SC) had normal distributions. Pasture production, dead matter, Olsen-P, NO_3-N, Total-N, Al_{sat}, K_{unsat}, K, Na, Ca, Mg and soil total bases (STB) were transformed using natural logarithm before statistical analysis to obtain normal distributions of the data. Soil SO_4-S content reached a normal distribution after being transformed using square roots.

Multivariate statistic analyses were applied to further analyse the data. The analysed variables were slope, SOM, pH_{CaCl2}, Al, VSM (30 µm), BD, SC, SR, Olsen-P, total-N, K_{unsat} (<750 µm), STB and pasture production that were previously transformed using natural logarithm. Soil SO_4-S was transformed using square roots. Canonical Variate Analysis and Canonical Correlation Analysis were performed on the data. Soil rebound: compression ratio was also included in the canonical correlation analysis.

RESULTS

Soil Properties

Fertiliser and stocking rate

Water holding capacity (WHC) was always higher ($P<0.05$) in soil collected from HH than LN (Table 1). Differences in K_{unsat} were found between the LN and HH treatment with higher flow rates in the LN than HH (Table 2).

Total porosity, BD, VSM, AP and SC did not show significant differences between LN and HH treatments, but the soil rebound following compression did show significant ($P<0.05$) differences, being higher in the LN treatment (Table 3). When recovery of soil following compression was expressed as a function of compression, no differences were found between farmlets (Table 3).

The LN treatment had lower Olsen-P and Total-N (Table 4), and higher Mg (Table 5) than the HH treatment. For the other soil indicators NO_3-N, NH_4-N, SOM, SO_4-S (Table 4), pH_w, pH_{CaCl2}, Al, Al_{sat}, K, Na, Ca and STB (Table 5) no differences were found between the two systems.

Average slope sampled in the LN paddock was significant ($P<0.05$) higher (23.8°) than in the HH paddock (21.7°). However, these values of slope are included in the same slope category (Table 4). Total dry matter was significantly ($P<0.001$) higher in HH than LN (Table 4).

Table 1 Effect of fertility - stocking rate history and slope on water holding capacity.

	Volumetric Moisture Content (V/V %)			
	10 (cm)	20 (cm)	50 (cm)	100 (cm)
	Pore size			
	<300μm	<150μm	<60μm	<30μm
FT[3]				
LN	0.53 b[1]	0.50 b	0.45 b	0.43 b
HH	0.56 a	0.55 a	0.51 a	0.49 a
Significance[2]	*	*	*	*
s.e.m.	0.008	0.009	0.009	0.009
Slope[4]				
LS	0.60 a	0.58 a	0.55 a	0.54 a
MS	0.56 b	0.53 b	0.48 b	0.46 b
HS	0.50 c	0.46 c	0.41 c	0.40 c
Significance[2]	***	***	***	***
s.e.m.	0.010	0.011	0.011	0.011
Interaction				
LN-LS	0.59 a	0.58 a	0.54 a	0.53 a
LN-MS	0.54 a	0.50 a	0.44 b	0.43 a
LN-HS	0.48 a	0.42 a	0.36 c	0.36 a
HH-LS	0.61 a	0.59 a	0.55 a	0.54 a
HH-MS	0.59 a	0.56 a	0.52 a	0.49 a
HH-HS	0.54 a	0.51 a	0.46 b	0.44 a
Significance[2]	n.s.	n.s.	*	n.s.
s.e.m.	0.014	0.016	0.016	0.015

[1] Different letters in each section of each column indicate statistical differences amongst factors.

[2] * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s. Not significant ($P>0.05$).

[3] FT Field Treatment; LN Low-No paddock; HH High-High.

[4] LS Low Slope; MS Medium Slope; HS High Slope.

Slope

Water holding capacity was significantly ($P<0.001$) different between slope categories, decreasing with increasing slope (Table 1). Low slope held a greater quantity of water than MS or HS at all tensions. With one exception, where K_{100} on the MS was similar to HS, K_{unsat} increased with increasing slope (Table 2). Total porosity decreased with increasing slope (Table 3).

Table 2 Effect of fertility - stocking rate history and slope on unsaturated hydraulic conductivity.

	K-Unsaturated hydraulic conductivity							
	5 (mm)		20 (mm)		40 (mm)		100 (mm)	
	Pore size							
	<6000µm		<1500µm		<750µm		<300µm	
	ln (K_5)	K_5	ln(K_{20})	K_{20}	ln(K_{40})	K_5	ln(K_{100})	K_5
FT[3]								
LN	6.11 a[1]	(449.4)	5.74 a	(311.7)	5.29 a	(198.1)	4.66 a	(105.4)
HH	5.43 a	(228.0)	5.10 b	(164.5)	4.79 b	(120.3)	4.27 a	(71.5)
Significance[2]	n.s.		*		*		n.s.	
s.e.m.	0.074		0.092		0.072		0.123	
Slope[4]								
LS	5.19 c	(179.1)	4.74 c	(118.4)	4.35 c	(77.7)	3.93 b	(51.1)
MS	5.77 b	(320.8)	5.42 b	(226.9)	5.00 b	(147.7)	4.58 a	(97.7)
HS	6.35 a	(571.0)	6.11 a	(448.5)	5.77 a	(320.7)	4.88 a	(131.1)
Significance[2]	***		***		***		**	
s.e.m.	0.091		0.113		0.089		0.151	
Interaction								
LN-LS	5.16 d	(174.0)	4.73 c	(112.8)	4.34 c	(76.6)	3.97 a	(53.0)
LN-MS	6.22 b	(505.0)	5.88 b	(358.9)	5.34 b	(207.7)	4.89 a	(132.9)
LN-HS	6.94 a	(1032.8)	6.62 a	(748.1)	6.19 a	(489.3)	5.11 a	(166.4)
HH-LS	5.22 d	(184.3)	4.75 c	(115.4)	4.37 c	(78.8)	3.90 a	(49.2)
HH-MS	5.32 d	(203.8)	4.97 c	(143.4)	4.66 c	(105.1)	4.27 a	(71.8)
HH-HS	5.75 c	(315.7)	5.59 b	(268.8)	5.35 b	(210.2)	4.64 a	(103.3)
Significance[2]	***		*		*		n.s.	
s.e.m.	0.128		0.160		0.126		0.213	

[1] Different letters in each section of each column indicate statistical differences amongst factors.

[2] * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s. Not significant ($P>0.05$).

[3] FT Field Treatment; LN Low-No paddock; HH High-High.

[4] LS Low Slope; MS Medium Slope; HS High Slope.

Table 3 Effect of fertility - stocking rate history and slope on total soil porosity, bulk density, field volumetric soil moisture, soil compressibility, soil rebound, soil rebound:compression ratio and air permeability.

	Total Soil Porosity	Bulk density (g/cm3)	Field VSM (V/V%)	Compression (cm)	Rebound (cm)	Rebound: Compress. Ratio	Air permeability Tension 50 cm (m/s)
FT[3]							
LN	67.6 a[1]	0.86 a	0.37 a	4.5 a	4.7 a	1.1 a	1.9 E-11 a
HH	68.3 a	0.84 a	0.45 a	5.7 a	3.4 b	0.7 a	1.4 E-11 a
Significance[2]	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.
s.e.m.	0.42	0.01	0.02	0.30	0.16	0.08	1.6 E-12
Slope[4]							
LS	70.7 a	0.78 c	0.52 a	7.0 a	3.9 a	0.6 b	1.5 E-11 b
MS	68.3 b	0.84 b	0.38 b	4.8 b	4.4 a	1.0 a	1.3 E-11 b
HS	65.0 c	0.93 a	0.32 b	3.9 b	3.9 a	1.1 a	2.2 E-11 a
Significance[2]	***	***	***	***	n.s.	**	*
s.e.m.	0.52	0.01	0.02	0.37	0.20	0.10	2.0 E-12

[1] Different letters in each section of each column indicate statistical differences amongst factors.

[2] * P<0.05; ** P<0.01; *** P<0.001; n.s. Not significant (P>0.05).

[3] FT Field Treatment; LN Low-No paddock; HH High-High.

[4] LS Low Slope; MS Medium Slope; HS High Slope.

Bulk density differed (P<0.001) between slope categories, increasing with increasing slope (Table 3). Air permeability was significantly (P< 0.05) greater in the HS than MS and LS (Table 3).

Soil from LS was easier to compress (P<0.001) than soil from MS and HS. Soil rebound and recovery, expressed as a function of compression and rebound, was greater on MS and HS, than LS (Table 3).

Olsen-P was higher on LS than MS or HS (P<0.001). This was also true for SO_4-S (P<0.05; Table 4), K (P<0.001), Ca (P<0.001), Mg (P<0.001), and STB (P<0.001; Table 5), and NO_3-N, Total-N and SOM (P<0.001; Table 4). The exception was Na (Table 5).

Table 4 Slope of the studied sites and effect of fertility - stocking rate history and slope on soil mineralised nitrogen, ammonium, total nitrogen, organic matter, Olsen-P and sulphate contents.

	Slope	NO_3-N		NH_4-N	Total-N		SOM	Olsen-P		SO_4-S	
	(°)	ln(ppm)	(ppm)	(ppm)	ln(ppm)	(ppm)	(%)	ln(ppm)	(ppm)	ln(ppm)	(ppm)
FT [3]											
LN	24 a [1]	3.33 a	(27.9)	52.1 a	4.47 b	(87.2)	11.8 a	2.56 b	(13.1)	2.45 a	(6.0)
HH	22 b	4.09 a	(59.7)	67.3 a	5.00 a	(148.2)	10.3 a	3.76 a	(43.0)	3.48 a	(12.1)
Significance [2]	*	n.s.		n.s.	*		n.s.	*		n.s.	
s.e.m.	1.0	0.212		7.031	0.115		0.42	0.082		0.213	
Slope [4]											
LS	8 c	5.24 a	(189.0)	75.2 a	5.62 a	(275.5)	13.1 a	3.96 a	(52.7)	3.68 a	(13.5)
MS	24 b	3.68 b	(39.8)	64.8 a	4.67 b	(106.3)	11.0 b	2.87 b	(17.7)	2.47 b	(6.1)
HS	40 a	2.20 c	(9.0)	34.0 b	3.92 c	(50.2)	9.0 c	2.67 b	(14.4)	2.75 b	(7.6)
Significance [2]	***	***		*	***		***	***		*	
s.e.m.	1.2	0.260		8.611	0.140		0.52	0.100		0.261	

[1] Different letters in each section of each column indicate statistical differences amongst factors.

[2] * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s. Not significant ($P>0.05$).

[3] FT Field Treatment; LN Low-No paddock; HH High-High.

[4] LS Low Slope; MS Medium Slope; HS High Slope.

Table 5 Effect of fertility - stocking rate history and slope on pH (water and $CaCl_2$), soil exchangeable potassium, sodium, calcium, magnesium and aluminium, aluminium saturation and exchangeable total bases.

	pH water	pH $CaCl_2$	Exchangeable K		Exchangeable Na		Exchangeable Ca		Exchangeable Mg		Exchangeable Aluminium	Aluminium Saturation		Soil Total Exchangeable Bases	
			ln(ppm)	(ppm)	ln(meq/100gds)	(meq/100gds)	ln(meq/100gds)	(meq/100gds)	ln(meq/100gds)	(meq/100gds)	(meq/100gds)	ln(%)	(%)	ln(meq/100gds)	(meq/100gds)
FT[3]															
LN	5.0 a[1]	4.5 a	5.62 a	(274.7)	-1.79 a	(0.17)	1.65 a	(5.2)	0.57 a	(1.8)	0.49 a	1.37 a	(4.0)	2.08 a	(8.0)
HH	5.1 a	4.6 a	5.46 a	(235.1)	-1.80 a	(0.17)	1.70 a	(5.5)	0.26 b	(1.3)	0.45 a	1.48 a	(4.4)	2.04 a	(7.7)
Significance[2]	n.s.	**	n.s.		n.s.		n.s.		*		n.s.	n.s.		n.s.	
s.e.m.	0.04	0.03	0.130		0.048		0.056		0.048		0.064	0.208		0.051	
Slope[4]															
LS	5.1 a	4.7 a	6.20 a	(494.6)	-1.81 a	(0.16)	1.96 a	(7.1)	0.73 a	(2.1)	0.28 b	0.44 b	(1.6)	2.38 a	(10.8)
MS	5.0 a	4.5 b	5.32 b	(203.4)	-1.86 a	(0.16)	1.56 b	(4.8)	0.14 b	(1.2)	0.58 a	2.00 a	(7.4)	1.91 b	(6.8)
HS	5.1 a	4.6 b	5.09 b	(163.1)	-1.70a	(0.18)	1.49 b	(4.5)	0.34 b	(1.4)	0.55 a	1.83 a	(6.2)	1.88 b	(6.6)
Significance[2]	n.s.	**	***		n.s.		***		***		*	**		***	
s.e.m.	0.05	0.04	0.159		0.054		0.067		0.059		0.078	0.255		0.062	

[1] Different letters in each section of each column indicate statistical differences amongst factors.

[2] * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s. Not significant ($P>0.05$).

[3] FT Field Treatment; LN Low-No paddock; HH High-High.

[4] LS Low Slope; MS Medium Slope; HS High Slope.

Al_{sat} ($P<0.01$), pH_{CaCl2} ($P<0.01$) and Al ($P<0.05$) were greater in HS and MS than LS. There were no differences in pH_w between slope categories (Table 5).

Soil NH_4-N values were similar in the LS and MS, and both were greater ($P<0.05$) than HS (Table 4).

Fertiliser and stocking rate-slope interaction

While WHC was higher on HH than LN and decreased with increasing slope, there were also several interactions (Table 1). At 50 cm tension, VSM for soil collected from LS from the HH and LN sites and the MS from the HH site had similar WHC. Soil from HS of the HH site had an equivalent WHC to the MS of the LN site, both of which where higher than the LN-HS microsite.

For water flow through pores <300 µm (K_{100}) there were no significant interactions between slope and management history. At lower tensions interactions were present. For medium (<750 µm) and large pores sizes (< 1500 µm) soil from the HS microsite from the LN farmlet had the highest flow rates. The lowest flow rates for the same pore sizes (<750 µm and < 1500 µm) were measured in LN-LS, HH-LS and HH-MS. An intermediate situation was detected for the LN-MS and HH-HS. A similar order was found at K_5 (pores <6000 µm), with the exception that flow rates in soil from LN-MS were significantly higher than HH-HS (Table 2).

The other soil variables, BD, SP, FVSM, SC, SR, AP, NO_3-N, NH_4-N, Total-N, pH_w, pH_{CaCl2}, SOM, Olsen-P, K, Na, Ca, Mg, Al Al_{Sat} and SO_4-S, showed no interactions between field treatment and slope.

Pasture Production

Fertiliser and stocking rate

The HH treatment produced significantly ($P<0.01$) more total dry matter per hectare than the LN treatment (Table 6). There were no differences in the dead material accumulated between treatments, although on the HH the ratio between green and dead matter was higher ($P<0.001$).

Table 6 Effect of fertility - stocking rate history and slope on pasture production (green material), dead material and green:dead material ratio.

	Pasture Production		Dead Material		Green:Dead Material Ratio	
	ln(kgDM/ha)	(kgDM/ha)	ln(kgDM/ha)	(kgDM/ha)	ln(ratio)	(ratio)
FT[3]						
LN	8.36 b[1]	(4280)	6.71 a	(820)	1.57 b	(4.8)
HH	9.24 a	(10285)	6.32 a	(557)	2.80 a	(16.4)
Significance[2]	**		n.s.		**	
s.e.m.	0.078		0.106		0.148	
Slope[4]						
LS	9.44 a	(12568)	6.66 a	(777)	2.72 a	(15.2)
MS	8.67 b	(5806)	6.23 a	(508)	2.29 ab	(9.9)
HS	8.30 c	(4003)	6.66 a	(784)	1.54 b	(4.7)
Significance[2]	***		n.s.		**	
s.e.m.	0.096		0.130		0.181	
Interaction						
LN-LS	9.12 b	(9170)	6.41 bc	(610)	2.58 a	(13.3)
LN-MS	8.00 d	(2976)	6.32 c	(554)	1.57 b	(5.7)
LN-HS	7.96 d	(2872)	7.40 a	(1634)	0.56 c	(1.8)
HH-LS	9.75 a	(17226)	6.90 ab	(990)	2.86 a	(19.0)
HH-MS	9.33 b	(11324)	6.14 c	(466)	3.01 a	(21.3)
HH-HS	8.63 c	(5578)	5.93 c	(376)	2.52 a	(15.0)
Significance[2]	*		***		*	
s.e.m.	0.136		0.184		0.256	

[1] Different letters in each section of each column indicate statistical differences amongst factors.

[2] * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s. Not significant ($P>0.05$).

[3] FT Field Treatment; LN Low-No paddock; HH High-High.

[4] LS Low Slope; MS Medium Slope; HS High Slope.

Slope effect

Low slope produced significantly ($P<0.001$) more dry matter than the other two slope categories. The MS produced an intermediate pasture production and the HS the lowest yield. There were no differences in the amount of dead material between the three slope categories, however the green:dead material ratio was significantly greater in the LS than in the HS (Table 6).

Fertiliser and stocking rate-slope interaction

The significant interaction ($P<0.05$) between field treatments and slope category showed that the HH-LS produced the highest yield and LN-MS and LN-HS produced the lowest. Intermediate dry matter production was measured on the LN-LS and HH-MS, which yielded significantly more than HH-HS. Higher quantities of dead matter were present in the LN-HS and HH-LS, with LN-HS having the lowest green:dead material ratio (Table 6).

Relationship between Soil Physical, Fertility and Plant Constituents

The canonical variate analysis, also called canonical discriminant analysis, found that of the soil variables, K_{40}, BD, VSM, SC, SR, Total-N, slope and Olsen-P best described variation between microsites (Figure 1). The first canonical variate explained 88.5% of the total variation between microsites, while the second canonical variate explained 8.2% (Figure 2). Variables that were highly correlated to canonical variate 1, in one direction were K_{40}, slope and BD, while in the other direction VSM, Total-N and SC were highly correlated with canonical variate 1. Canonical variate 2 in one direction was highly correlated to SR, while in the other direction it was highly correlated to Olsen-P (Figure 1 and Figure 2).

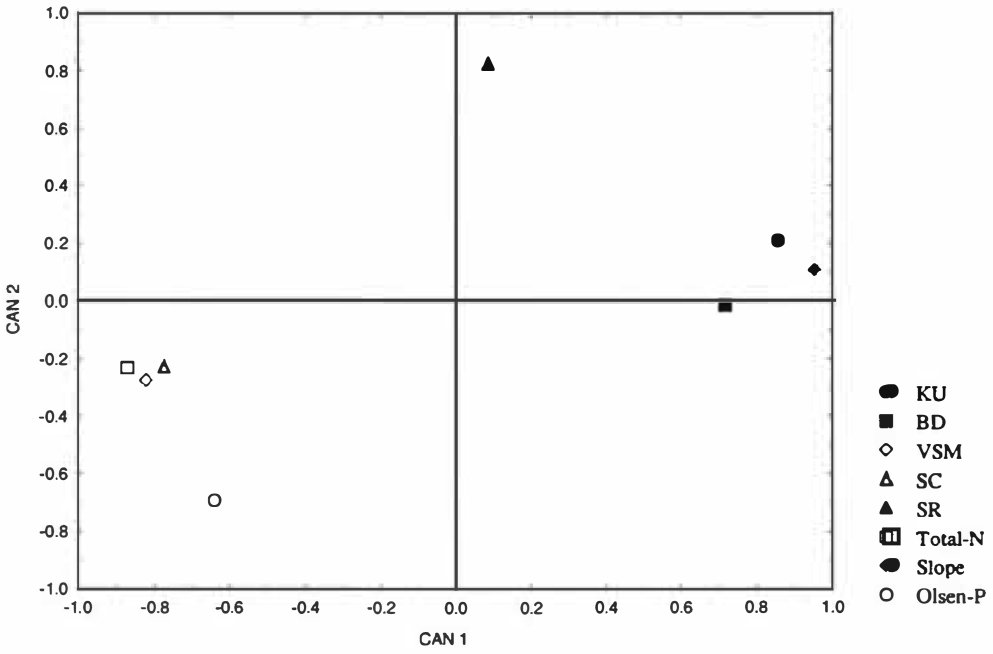

Figure 1 Canonical variates for soil variables.

KU Unsaturated hydraulic conductivity; BD Bulk density; VSM Volumetric soil moisture; SC Soil compressibility; SR Soil rebound; Total-N Soil total nitrogen content; Olsen-P Soil phosphorus content.

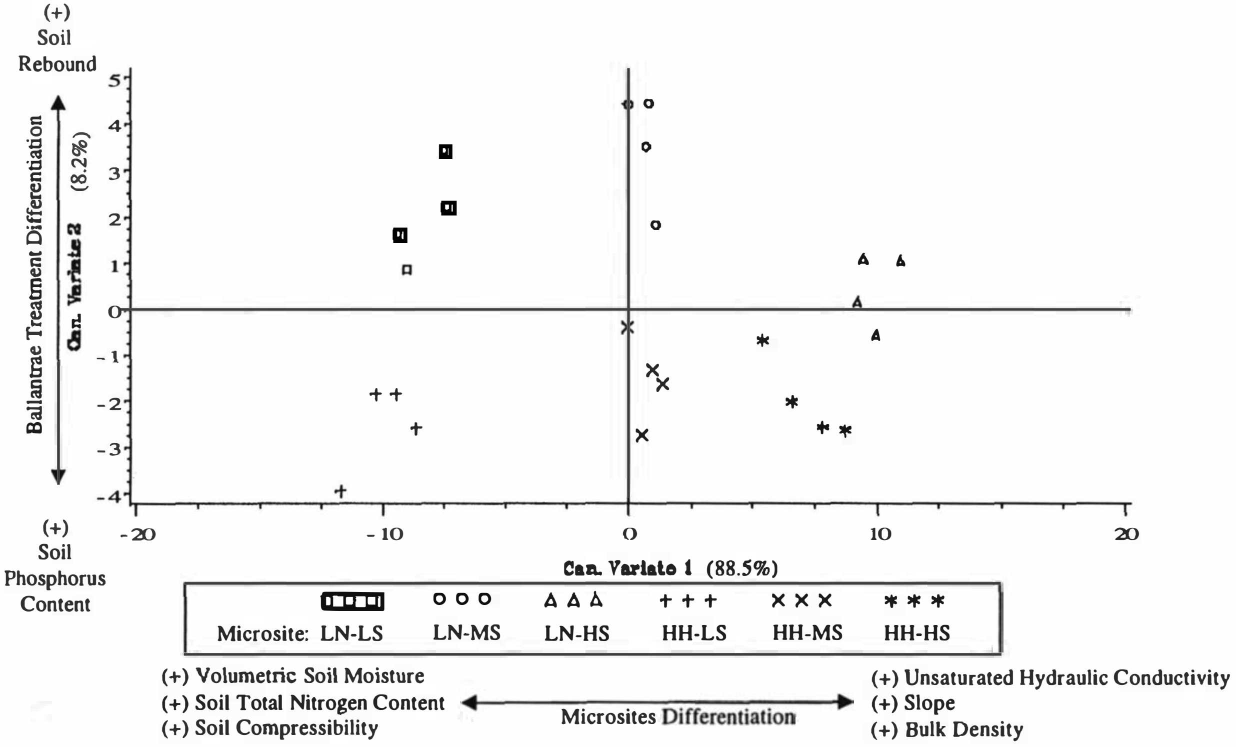

Figure 2 Canonical scores from soil features of the microsites.

LN-LS	Low-No, Low Slope microsite.	HH-LS	High-High, Low Slope microsite.
LN-MS	Low-No, Medium Slope microsite.	HH-MS	High-High, Medium Slope microsite.
LN-HS	Low-No, High Slope microsite.	HH-HS	High-High, High Slope microsite.

The canonical correlation analysis showed that there were strong positive correlations between dry matter production and WHC, Total-N, Olsen-P and SC and a high negative correlation between total dry matter production and slope, K_{40}, BD and SR:SC ratio (Table 7).

DISCUSSION

The objective of the present work was to examine the effect of fertiliser and stocking rate history on the soils and plant constituents of the microrelief that characterises much of the hill country of New Zealand, and to examine how the soil and plant communities are linked. Overall, the history of high P fertiliser inputs and the associated high stocking rate compared with the low stocking rate system had resulted in higher Olsen-P (Table 4), improved WHC (Table 1), higher Total-N (Table 4) and high pasture production (Table 6), but a decline in water conductivity (Table 2), and a number of other physical attributes. While the soil of the LN was characterised by low fertility, as indicated by the low Olsen-P and nitrogen status (Table 4) and pasture production (Table 6), the physical attributes of the soil, with respect to pore size and function, as indicated by water movement and resilience to compression, were better. A large number of attributes remain unchanged between the two systems, including TP, BD, AP, SC (Table 3), NO_3-N, NH_4-N, SOM (Table 4), K, Na, Ca, STB, pH_w, pH_{CaCl2}, Al and Al_{sat} (Table 5).

Soil Physical Features

Soils of the HH treatment held more water in pores sizes 300 μm, 150 μm, 60 μm and 30 μm than soil from the LN treatment (Table 1). There was a tendency for the difference in WHC between the treatments to increase with increasing slope. The higher WHC of the HH treatment is specifically relevant for plant growth; the water that is held in pores smaller than 60 μm, is where field capacity is located and constitutes the water available for plants. These data support the observations that have been made that high fertility blocks hold on to water a little longer in a drought (Lambert *et al.*, 1983). The data also demonstrate that with application of fertiliser, it is possible to extend the grazing season into Summer.

Table 7 Correlation amongst the relevant soil variables of the microsites and total dry matter.

	Soil variables of microsites and total dry matter														
	SLP	K_{unsat}	BD	SR	SC	RCratio	VSM	Total-N	OM	P	SB	Ex. Al.	SO_4-S	pH_{CaCl2}	DM
SLP	**1.000**	0.799	0.507	0.214	-0.657	0.533	-0.770	-0.787	-0.341	-0.634	-0.504	0.397	-0.309	-0.253	-0.703
K_{unsat}		**1.000**	0.648	0.342	-0.836	0.766	-0.923	-0.877	-0.428	-0.650	-0.497	0.369	-0.373	-0.369	-0.828
BD			**1.000**	-0.141	-0.730	0.404	-0.664	-0.735	-0.806	-0.619	-0.656	0.517	-0.606	-0.362	-0.645
SR				**1.000**	-0.380	0.737	-0.408	-0.273	0.344	-0.453	-0.031	0.143	-0.215	-0.431	-0.487
SC					**1.000**	-0.865	0.914	0.820	0.392	0.612	0.544	-0.517	0.459	0.521	0.789
RCratio						**1.000**	-0.844	-0.710	-0.097	-0.610	-0.365	0.368	-0.435	-0.491	-0.764
VSM							**1.000**	0.887	0.339	0.676	0.464	-0.362	0.427	0.365	0.851
Total-N								**1.000**	0.552	0.760	0.708	-0.569	0.569	0.481	0.869
OM									**1.000**	0.450	0.745	-0.568	0.552	0.342	0.368
P										**1.000**	0.562	-0.503	0.818	0.505	0.868
SB											**1.000**	-0.910	0.573	0.698	0.529
Ex. Al.												**1.000**	-0.466	-0.851	-0.497
SO_4-S													**1.000**	0.385	0.598
pH_{CaCl2}														**1.000**	0.557
DM															**1.000**

SLP	Slope	SC	Soil Compressibility	Total-N	Soil Total Nitrogen Content	Ex.Al.	Soil Exchangeable Aluminium
K_{-40}	Unsaturated Hydraulic Conductivity of <300 µm pore size			OM	Soil Organic Matter Content	SO_4-S	Soil Sulphate Content
BD	Bulk Density	RCratio	Rebound-Compression Ratio	P	Soil Phosphorus Content (Olsen-P)	pH_{CaCl2}	Soil Acidity Measured as pH $CaCl_2$
SR	Soil Rebound	VSM	Volumetric Soil Moisture of 30 µm pore size	SB	Soil Total Exchangeable Bases	DM	Total Dry Matter Production

In contrast to the improvement in WHC, which indicates a greater fraction of pore size in the range 30 to 300 μm in the HH treatment, results from the test of K_{unsat} indicate that water moves more slowly through the soil in the HH paddock for pore size <1500 μm and <750 μm (Table 2). In contrast to the greater pore volume (>60 μm) in the HH soils, as indicated by the major WHC, pore continuity, as evident by the lower infiltration rates at K_{20} and K_{40}, was inferior to the LN soil. Mackay *et al.* (1999) found a reduction in pore continuity under intensive agriculture and attribute the decline in pore function to the higher stocking rate, increased earthworm activity, reduction in root biomass and decline in soil organic matter.

Water infiltration and movement through the intact cores in the present study decreased in the order of LN-HS > LN-MS > HH-LS > LN-LS = HH-MS = HH-LS. This sequence reflects a number of processes occurring simultaneously with increasing slope and decreasing stock treading traffic. Based on the amount of pasture grown on each slope class in each of the two field treatments, assuming similar levels of utilisation, the amount of grazing time and treading traffic in each area is likely to increase in the order of LN-HS>= LN-MS> HH-HS> HH-MS>= LN-LS>= HH-LS. This hypothesis requires further investigation.

The reduction in the recovery of soil following compression in the HH compared with LN, indicates that the soils of the HH paddocks were more vulnerable and less resilient than soils from the LN. Compared with the soil from the LN, the HH soil was more developed, as reflected by the higher WHC. The soil collected from the HH also had a greater degree of micro-aggregate development and biological activity (Mackay *et al.*, 1999), and higher quality organic matter, as reflected in the higher Total-N content. The higher stocking rate combined with the higher WHC of the HH soil both would have contributed to a greater potential vulnerability to damage of this soil. These factors compromise pore continuity, which influences water movement. It is clear from BD and SP that the LN-MS and LN-HS are less well developed than the LN-LS or even HH-MS and HH-HS. Overall the statistical analysis did not show differences between treatments for AP, SP or SC (Table 3). This suggests that even though pore continuity was compromised in the HH treatment the reduction was not sufficient to cause deterioration in other physical attributes of the soil.

The HH and LN sites were sampled in October, the period in which the soil is wettest. At that time no significant differences were found in FVSM between paddocks (Table 3). Soil from LS, however, had a higher VSM than soil collected from MS and HS. Comparing FVSM (Table 3) with VSM at 50 cm tension (Table 1), provides an indication of field capacity. Only soil from the HH-LS microsites were close to field capacity at that time. These results suggest that either the MS and HS microsites were still wetting up or they had a constant water deficit throughout the year. This appeared to be more pronounced in the LN treatment. Possible factors that might contribute to water deficit include water being repelled and therefore not entering the soil profile or water flowing preferentially through large pores to the subsoil, limiting the contact time with small pore sizes and soil aggregates. Repellence would provoke surface runoff, while the process of greater macroflows could provoke greater subsurface flow and because of the reduced contact time in the topsoil limit the period for rewetting. Combined with the lower WHC on the LN treatment, the LN system would appear to be less able to utilise annual rainfall.

Slope and water repellence are factors that could prevent water from entering the soil. McGhie (1980) reported that the water repellency and runoff of neighbouring sites increased with increasing slope. In water repellent soils water needs a higher pressure to enter into the soil, due to the alteration of flow features such as finger velocity and water-entry (Bauters *et al.*, 1998). Water repellence disrupts aggregates on rapid wetting and accentuates flow of water between the aggregates increasing runoff (Wallis and Home, 1992). Organic matter particles are a source of severe water repellence (Chan, 1992; Hallet and Young, 1999), as organic matter is a carrier and reservoir of hydrophobic waxes that are released to the exterior (Franco *et al.*, 1995) coating soil particles (McGhie and Posner, 1980; Franco *et al.*, 1995). Organic matter particles with larger sizes induce a higher degree of hydrophobicity (Franco *et al.*, 1995), with the effect intensified by large molecules such as lignins, which have hydrophobic characteristics (Posner, 1966). Water repellence has been related to the original or current vegetation growing on a site (McGhie and Posner, 1980; McGhie and Posner, 1981). Therefore, the amount of litter and its quality are important factors in water repellency. The LN-HS and HH-LS generated the largest amount of dead matter (Table 6). Litter quality may, however, be different in both microsites, generating different degrees of soil water repellency. The LN-HS may have the poorest quality litter, due to many plants flowering annually, while in the HH-LS, non-grazed leaves would be the main constituent of the litter pool (Chapman *et al.*, 1984). This hypothesis needs further investigation.

Other sources of water repellency are fungal hyphae growing on the surface of the soil (McGhie and Posner, 1980; Chan, 1992), micro-organism activity increasing water-repellent materials (Hallet and Young, 1999) or clogged pores through the formation of gas bubbles (Vandevivere and Baveye, 1992; Seki *et al.*, 1998). The predominant decomposers in the LN are fungal, whereas in the HH bacteria are the predominant decomposers (Springett, 1999, pers. comm.).

Runoff has been reported in the hill country by Gillinham and During (1973), Lambert *et al.* (1985) and Lambert *et al.* (1996). Lambert *et al.* (1996) indicated that the amount of runoff in both treatments was similar. However, from the difference between the results of FVSM and VSM at a pore size of 30 µm, it is possible that there were differences in the contribution from each slope category to the amounts of runoff.

Soil Fertility Features

Olsen-P on the LN and HH has been diverging since the early 1970's. In 1972, soil from both treatments had an Olsen-P of 8 mg/kg dry soil (Lambert *et al.*, 1998). By 1993, after 17 years of differentiated fertiliser input, Olsen-P of the HH had increased to 33 mg/kg dry soil, while the LN had decreased to 6 mg/kg dry soil (Lambert *et al.*, 1996). Olsen-P levels in the present study were higher for both the HH (43 mg/kg dry soil) and LN treatments (13 mg/kg dry soil). However, there was a highly significant ($P<0.001$) effect of slope on the distribution of P within each treatment (Table 4), such that the P levels were higher on LS than MS or HS. Sampling in the current study was restricted to only a few microsites within the farmlets, so may not fully reflect the farmlets. This must be taken into consideration in the interpretation of the results.

As with Olsen-P a similar case was found for Total-N (Table 4), demonstrating the accumulation of P and N in the LS from the MS and HS, through the grazing and camping behaviour of the grazing animal. The grazing animal has been reported to be the major source of redistribution of the P and N within the paddock and amongst microsites (Saggar *et al.*, 1990). There is also some redistribution due to water runoff moving sediments (Lambert *et al.*, 1985). Lambert *et al.* (1996) reported that the amount of runoff was similar in both paddocks. Soil sulphur content (Table 4), K, Ca, Mg and STB (Table 5) also accumulated on the LS, with the grazing animals again the major factor causing the redistribution of these nutrients amongst microsites (Gillingham and During, 1973).

Lambert *et al.* (2000) reported that from 1975 to 1987 the pH_w has slowly increased from 4.8 to 5.1 for the LN and to 5.2 for the HH treatment. Eighteen years after the last application of ground limestone to the HH paddock, the pH has decreased slowly (Lambert *et al.*, 2000), such that in the current study LN and HH paddocks had a similar pH. These reported values for pH_w are very similar to those obtained for pH_w in the present evaluation (Table 5), indicating that the acidity of the soil has remained practically constant in both treatments over the last 10 years. Fixation of nitrogen by legumes, leaching of NO_3-N, soil N transformations, and increases in organic matter content all favour soil acidification (Bolan *et al.*, 1991). Lambert *et al.* (2000) reported that in the HH treatment only small amounts of NO_3-N and associated cations are lost by leaching, and annual N fixation rate during 1996/97 reached 147 kg/ha, greater than the average total of N fixed per year (34 kg/ha) reported by Grant and Lambert (1979). On the other hand, soil organic matter has been slowly decreasing in both the LN and HH treatment, limiting the supply of H^+ ion (Lambert *et al.*, 2000).

Pasture Production and Dead Matter

In both treatments pasture production decreased with increasing slope, however, dead matter did not show the same pattern. Similar amounts of dead matter were measured in HH-LS and LN-HS microsites (Table 6). The proportion of pasture plants that flowered on the HS was greater than on LS, possibly due to a greater defoliation pressure on the LS. Along with the differences in traffic, and physical disturbance on the soil, the amount of seed head returned to the soil as a proportion of total litter would have been greater on the HS.

In addition to the effect of litter quality on soil water repellency, previous studies have also related litter quality to the turnover rate of the SOM, uptake rate of resources from the soil for plants and to the plants' growth rates (Chapin, 1991; Hobbie, 1992). The microsites studied in the present study had two contrasting situations; HH-LS that had high fertility, high pasture production and presumably would have better quality litter and high turnover rate of the SOM, and the LN-HS that had low fertility, low pasture production and would have low quality litter with a slow turn over of the SOM. Species from high-nutrient environments have been shown to grow quickly, take up and lose nutrients rapidly, produce high-quality litter and sustain high rates of herbivory, all factors that result in rapid rates of nutrient cycling (Chapin, 1991; Hobbie, 1992). This would be the case of the HH-LS microsite. Wedin and Tilman (1990) reported that species characteristics may determine nutrient availability when grass species differ in litter quality and phenology. Because of this, the same soil can diverge in rates and timing of annual net nitrogen mineralisation according to the botanical composition. For example, in the USA, *Andropogon gerardi* and *Schizachrium scoparium* have been shown to be superior competitors in low nitrogen sites creating low rates of nitrogen mineralisation, while *Poa pratensis* and *Agropyron repens* were reported to be superior competitors on high nitrogen soils creating high rates of nitrogen mineralisation (Wedin and Tilman, 1990).

Relationship between Soil Attributes and Production

The canonical variate analysis indicated that amongst all the soil variables studied, slope, K_{40}, VSM, Total-N, BD, SC, Olsen-P and SR explained 97% of the total variation measured across sites. The first canonical variate differentiated across microsites, such that differences in slope amongst microsites were larger than differences in management regimens between treatment (Figure 2). This indicated that with increasing slope, there was an increase in the K_{40} and BD, and a decrease in WHC, Total-N, SC and Olsen-P (Figure 1).

The second canonical variate discriminated from the point of view of the previous management of the paddocks studied, differentiated the HH from LN treatment (Figure 2). Soil rebound and Olsen-P were variables that led to the differentiation between the two treatments (Figure 1).

With increasing slope, soil water conductivity increased (Table 2), WHC decreased (Table 1), BD increased (Table 3), SOM decreased (Table 4) and fertility levels especially with respect to Olsen-P (Table 4) and Total-N (Table 4) decreased. Results of SC and SR (Table 3), however, suggest that the soil from the LS microsites are more vulnerable to animal tramping than soil from HS. High activity of earthworms (Mackay *et al.* 1999) and less root mass (Barker D. J. pers. comm., unpublished data) both appear to contribute in combination with the greater animal treading traffic to the low stability of the soils from LS.

Slope category was the most important factor to explain differences in the soil condition, and previous management was of secondary importance. In spite of this, total dry matter production was sensitive to the management history of the paddocks, such that the interaction between management and slope category influenced the amount of pasture produced.

The variables that predicted differentiation amongst microsites were primarily VSM, Total-N, SC, K_{40}, slope and BD and secondarily were Olsen-P and SR. However, slope category was the variable that led to differentiation of the microsites. Therefore, slope, water availability, which is influenced by variables such as VSM and K_{40} and Total-N firstly and Olsen-P secondly were the factors that had the largest influence differentiating pasture production.

Soils and pastures were shown to diverge through time as a consequence of differentiated management. Slope was the driving factor influencing pasture production and soil development. In the low slopes, improvements in pasture production were found in response to increasing soil fertility, mainly increases in Total-N and Olsen-P, and physical soil attributes through WHC and SC, which reflect improvement in soil development. Associated with this development, however was a decline in pore continuity and function, reflecting the increased vulnerability of the soil to disturbances associated with the increasing number of treading events when the soil was wet and the greater biological activity. Low pasture production on high slope soils was associated with high K_{40}, BD and SR:SC ratio, which indicate a less well developed soil. The apparent high structural stability of the HS soil as indicated by the high K_{unsat} values compared with the LS soil reflected the limited degree of disturbance, due to low productivity and biological activity. The findings of the study highlight the interaction that occurs between slope position and stage of soil development, as it influences soil properties and subsequently pasture production. It also highlights that increased levels of disturbance and vulnerability to damage are associated with soil development and increased productivity. This is reflected in a reduction in pore continuity and function, particularly on the LS soils.

Aspects that may be important for the dynamics of the hill country pasture and soil that still remain to be assessed include the organic matter cycle and quality and its relationship to botanical composition, soil physical features and soil water repellence and runoff.

CONCLUSIONS AND IMPLICATIONS

Long-term differentiated management based on fertiliser application and stocking rate has induced changes in a number of soil and pasture attributes. However, greater differences in soil and pasture features were measured across slope categories than between treatments (fertiliser and stocking rate). Soil variables that had the largest influence on the differentiation between microsites were slope, WHC, K_{unsat}, SC, BD and Total-N. Olsen-P and SR were of secondary importance. Slope was the variable that led to differentiation of the microsites.

Soil variables that had the strongest influence on pasture production were primarily slope, WHC and K_{unsat}, and secondly Total-N and Olsen-P.

Microsites that showed the largest differentiation between them were HH-LS and LN-HS, such that HH-LS had higher fertility levels, greater water holding capacity and greater pasture production. The HH-LS was, however, less able to move water and more susceptible to loss of structure features. Therefore, improvement of soil fertility and productive characteristics and associated stocking rate and grazing pressure affected structural characteristics of the soil, such that soils under these conditions would be more susceptible to damage by animal treading.

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CHAPTER 4

Ecology of pastoral communities in a heterogeneous environment.

II. Botanical composition and the soil-pasture relationship.

In the study described in the previous Chapter, the variation of hill country soil attributes was shown to be highly associated with the slope category. Low slope soils were well developed and had high fertility levels, but showed a low aggregates stability. High slope soils were poorly developed with low fertility, but higher stability of the soil structure. Slope, water holding capacity, unsaturated hydraulic conductivity, bulk density, soil compressibility, soil rebound after compression, total soil nitrogen content and soil phosphorus content were the soil variables that explained most of the soil variation between slope categories. Pasture production increased with decreasing slope, and showed a high variation between both extremes of the soil attribute range. The significance of these soil variables on botanical composition has been not well described for the hill country pasture, as well as the relationship between the variables and species functional groups and field condition. In the study reported in the present Chapter the presence of plant functional groups, species segregation and soil variables-plant relationship were studied. The relationship between field condition and plant functional groups was also analysed.

ABSTRACT

The presence of plant functional groups, species segregation and the soil variables-plant species relationship were studied in paddocks with long-term differentiated management in the hill country. The relationship between plant functional groups and field condition was also analysed. The microrelief of the hills contains three slope categories (low, medium and high) with contrasting soil features. Soil attributes, botanical composition and annual total yield were measured. ANOVA, cluster analysis, canonical correlation analysis and canonical variate analysis were performed on the data. Seven functional groups were determined. High fertility grasses and *Lolium perenne* were strongly affected by changes in the levels of the environmental variables. Low fertility species were segregated indirectly by environmental variables, as they were bad competitors when availability of resources in the soil was high. Groups of species were present that were indifferent to changes in the levels of environmental variables, such as *Agrostis capillaris.* Species and functional groups were segregated according to the level of the environmental constraints and the inter-relationship between the environment and species. Species were shown to have the capability to respond positively to environmental constraints adjusting their growth according to the varying circumstances. Results suggested that field condition and plant functional groups are complementary concepts in grassland dynamic analyses.

INTRODUCTION

Botanical composition of a plant community in a naturalised sward is a function of past parent material and the impact of abiotic and biotic selection pressures. Environmental variables such as climate, topography, soil texture, depth and fertility, and historical management of the land, are variables that exert selection pressure on plant species, such that botanical composition is an indicator of the results of these environment-pasture interactions (Gastó *et al.*, 1993; Archer, 1994). At the paddock level, soil variables are continuously affecting the botanical composition, with plant species being permanently involved in processes of colonisation and competition for survival (Noble, 1973; Gastó *et al.*, 1993). Theories have been developed that group plants so as to explain the colonisation-competition relationship representing changes in the botanical composition of the pasture through ecological succession of the species in the field (Noble, 1973; Gastó *et al.*, 1993; Smith *et al.*, 1997; Wilson, 1999).

One method of grouping species has been through functional groups or functional types. In principle, species that use similar resources or respond in a similar manner to disturbances, might behave similarly under a range of circumstances and perturbations and can, therefore, be grouped together (Gitay and Noble, 1997). Two general types of behaviour of species or groups of species colonising diverse environments have been described; species that are able to colonise sites with specific characteristics (Lambert *et al.*, 1986a; Lambert *et al.*, 1986b; López *et al.*, 1997) and species that colonise a range of contrasting sites (Snaydon and Davies, 1982; Rapson and Wilson, 1988; López *et al.*, 1997). However, in order to combine species into groups that have an ecological meaning and are an accurate representation of occurrences in the field, it is necessary to use objective methodologies (Wilson, 1999) such as multivariate statistical techniques (Eagles and Othman, 1988; Grayston *et al.*, 1998), instead of using *a priori* grouping (Hadar *et al.*, 1999) that may not allow differences between species to be determined.

To better understand the dynamics of the ecosystem, it is also necessary to study its components and the interactions amongst them. Only a holistic analysis of the variables of the ecosystem would provide an accurate reflection of the interaction between environmental constraints and botanical composition, as individual species or groups of species. This information would allow a more complete explanation of the variation and interaction amongst the components of the ecosystem.

The hill country of New Zealand presents, in the faces of the hills, a microrelief where it is possible to distinguish three classes of slope: 1-12°, 13-25°, >25° from the horizontal, termed low slope (LS), medium slope (MS) and high slope (HS), respectively (Lambert *et al.*, 1983). Soil features (Saggar *et al.*, 1990) and pasture characteristics (Lambert *et al.*, 1983; Lambert *et al.*, 1986a; Lambert *et al.*, 1986b) differ amongst microsites. In the study reported in Chapter 3, several soil attributes were analysed using multivariate analysis and it was reported that, among the measured variables those that explained most of the soil differentiation amongst microsites were slope, WHC, unsaturated hydraulic conductivity, bulk density, soil rebound after compression, total soil nitrogen content and soil phosphorus content. However, the significance of these soil variables on botanical composition are not well described. Therefore, the hypothesis of the current work was that the microrelief of the hill country generates differences in the soil features of neighbouring microsites that are sufficiently contrasting to segregate species or functional groups of species. This segregation of the species would result in changes, gradual or abrupt, in the production of species along the range of the soil variables.

Therefore, the objectives of the present work were to analyse whether:

a) there are plant functional groups present in the hill country pasture.
b) species segregation has occurred in the hill country pastures and whether soil variables have had a role in segregating species or groups of species.

MATERIALS AND METHODS

Site

The present work was carried out at AgResearch's Ballantrae Research Station, near Palmerston North, New Zealand, in two paddocks that have had a long-term differentiated management history since 1975. One of the paddocks received a low level of phosphorus fertilisation between 1975 and 1980 (11 kg P/ha/year). Since 1980 this paddock has not received fertiliser, thus being called "Low-No" (LN). The second paddock received high phosphorus fertilisation since 1975 (period 1975-1980: 57 kg P/ha/year; after 1980: 34 kg P/ha/year) and has been called "High-High" (HH) (Lambert *et al.*, 1986b; Lambert *et al.*, 1996). Historically, both paddocks were set-stocked with Romney breeding ewes, at a stocking rate that related to herbage production (Lambert *et al.*, 1990). Average stocking rate for the LN treatment has been 8.3 ewes/ha and that for the HH paddock was 14.8 ewes/ha (Lambert *et al.*, 1996). The methodology of this long term experiment has been fully explained by Lambert *et al.* (1986a), Lambert *et al.* (1990) and Lambert *et al.* (1996).

In the present work, soil and pasture from the LN and HH treatments and from the three categories of slope (LS, MS and HS) were analysed. The result of the interaction between both categories of factors are called microsites (LN-LS, LN-MS, LN-HS, HH-LS, HH-MS and HH-HS).

Measurements

The pasture was sampled between 14 July 1998 and 14 July 1999. To evaluate the pasture yield at each microsite, cages of 0.5 m^2 (0.5 x 1 m) were placed on each type of microsite. Pasture was harvested after seven regrowth periods during the year of evaluation. Prior to each period the pasture at the measurement site was trimmed to about 10 mm height, and at the end of the period it was harvested to the same height. After each harvest, the cages were resited to one of three different locations in a similar category of microsite. Thus, within the year, each cage rotated around 3 different positions. For each category of microsite, four similar microsites (replications) were evaluated at the same time.

From each sample of pasture at each trimming date, a sub-sample was taken and the full botanical composition was determined by hand dissection, drying and weighing. All pasture samples were dried in an oven at 60°C for 48 hr or until the samples reached constant weight. The samples were then weighed using electronic scales. The weights were used to determine pasture yield in kg of dry matter per hectare per year.

To determine the relationship amongst the soil features of the microsites with species or groups of species, soil samples were taken from the same microsites that were analysed for pasture production and botanical composition. All the methodologies used to obtain the soil samples from the field and the laboratory methodologies used to analyse them have been reported in Chapter 3. Soil physical variables analysed were unsaturated hydraulic conductivity at 4 tensions (K_5, K_{20}, K_{40}, K_{100}), bulk density (BD), volumetric soil moisture at 10, 20, 50 and 100 cm (VSM_{10}, VSM_{20}, VSM_{50}, VSM_{100}), total soil porosity, field volumetric soil moisture, soil compression (SC), soil rebound after compression (SR) and air permeability. Soil fertility variables analysed were nitrate-Nitrogen, ammonium-Nitrogen, Total-Nitrogen (Total-N), pH (water and $CaCl_2$), soil organic matter, Olsen-P, exchangeable potassium, sodium, calcium, magnesium and aluminium, aluminium saturation and sulphate-sulphur. Slope and soil total bases were also included. After canonical variate analysis was applied slope, VSM_{100} (<30 μm), K_{40} (<750 μm), BD, SC, SR, Olsen-P and Total-N were the variables that explained the greater soil differentiation between microsites (Chapter 3).

Statistical Analysis

All statistical analyses were performed using SAS program version 6.12, with the exception of cluster analysis that was performed with Statistica program version 5.0. Pasture yield data was normalised using a natural log transformation (Davies, 1971; John and Draper, 1980; Seber, 1984):

$$Y = \ln (X + 1) \qquad (1)$$

Where, Y was the normalised data from pasture yield and X was the pasture yield (kg DM/ha/year).

The yield/species over the year were analysed by Cluster Analysis using the Weighted Pair-Group Average method, to determine the presence of functional groups or types (Jobson, 1992). Total pasture production and the yield of the determined functional groups were then analysed using ANOVA. The model fitted to the normalised data was:

$$Y = \text{Mean} + \text{field treatment} + \text{replication} + \text{slope} + \text{field treat.*rep.} + \text{field treat.*slope} + \text{error} \qquad (2)$$

As the field treatments (fertility and stocking rate) were not replicated, this effect (HH and LN), was tested against the field treatment-replication (cage) interaction (Error type A).

To determine the relationship between soil variables and functional groups and whether functional groups were segregated along an environmental gradient, multivariate analyses were conducted on both soil and species functional groups, using Canonical Correlation Analysis and Canonical Variate Analysis (Jobson, 1992; Weihs, 1995). The soil variables used in this analysis were slope, VSM_{100} (<30 µm), K_{40} (<750 µm), BD, SC, SR, Olsen-P and Total-N. Before applying multivariate analysis, soil variables were transformed using natural logarithm so that the data followed a normal distribution.

Canonical variate analysis, also called canonical discriminant analysis or Fisher's discriminant analysis, is a multivariate technique that allows, for different groups of individuals, low-dimensional representations to be determined that highlight, as accurately as possible, the true differences existing between the groups (Jobson, 1992; Weihs, 1995). Therefore this multivariate analysis explains the variation between the analysed variables through identifying differences among groups of individuals. Canonical variate analysis also shows the relationship amongst the measured variables within those groups. Canonical variate analysis was used in the present experiment to analyse the variation and the relationship amongst the soil variables and the groups of species obtained from the cluster analysis.

Linear or quadratic equations were fitted to the percentage contribution of each functional group to the total dry matter production/ha for each field treatment, and to the canonical scores of the canonical variate 1 from the canonical variate analysis of the soil variables. Coefficients of determination (r^2) were obtained for each equation fitted to the variables. To compare the behaviour of each functional group between paddocks, an ANOVA was performed to compare the fitted curves.

RESULTS

Plant Functional Groups Presence

Forty-one species were found in the hill country pasture. Cluster analysis grouped these species into 7 groups (Table 1), taking into account the total amount of dry matter production/species and dry matter production/species/microsite (Figure 1).

These results were supported by the results from the analysis of variance performed on the individual species data (Table 2, Table 3 and Table 4).

Table 1 Groups and sub-groups of species of the naturalised pasture of the hill country of New Zealand according to their functional type determined by cluster analysis.

Low Fertility (Group I)	Medium Fertility (Group II)	High Fertility Grasses (Group III)	Generalist Type A (Group IV)	Generalist Type B (Group V)	High Fertility dicotyledon (Group VI)
Rhytidosperma sp.	*Anthoxanthum odoratum*	*Holcus lanatus*	*Agrostis capillaris*	*Lolium perenne*	*Cerastium glomeratum*
Festuca rubra	*Cynosorus cristatus*	*Poa annua*			*Cirsium arvense*
Hypochaeris radicata	*Trifolium repens*	*Poa trivialis*			*Plantago lanceolata*
Leontodon taraxacoides					
Muscii sp.					
Trifolium dubium					

Group: Species with low presence (Group VII)			
Achillea millefolium	*Dactylis glomerata*	*Luzula sp.*	*Sagina procumbens*
Bellis perennis	*Galium arvense*	*Montia verna*	*Silene gallica*
Carex sp.	*Gnaphalium sp.*	*Nertera setulosa*	*Stellaria media*
Centella uniflora	*Hydrocotyle* sp.	*Poa pratensis*	*Taraxacum officinale*
Crepis capillaris	*Linum bienne*	*Polycarpon tetraphylum*	*Trifolium subterraneum*
Cymbalaria muralis	*Lotus pedunculatus*	*Rumex acetosella*	*Veronica persica*

Cluster analysis (Figure 1) firstly separated the species in to two large groups according to the total yield; high and low yielding species. Within the high yielding group, three groups were discriminated according to their yield amongst the slope categories: Group IV (*Agrostis capillaris*), group V (*Lolium perenne*) and group II (*Anthoxanthum odoratum*, *Cynosorus cristatus* and *Trifolium repens*).

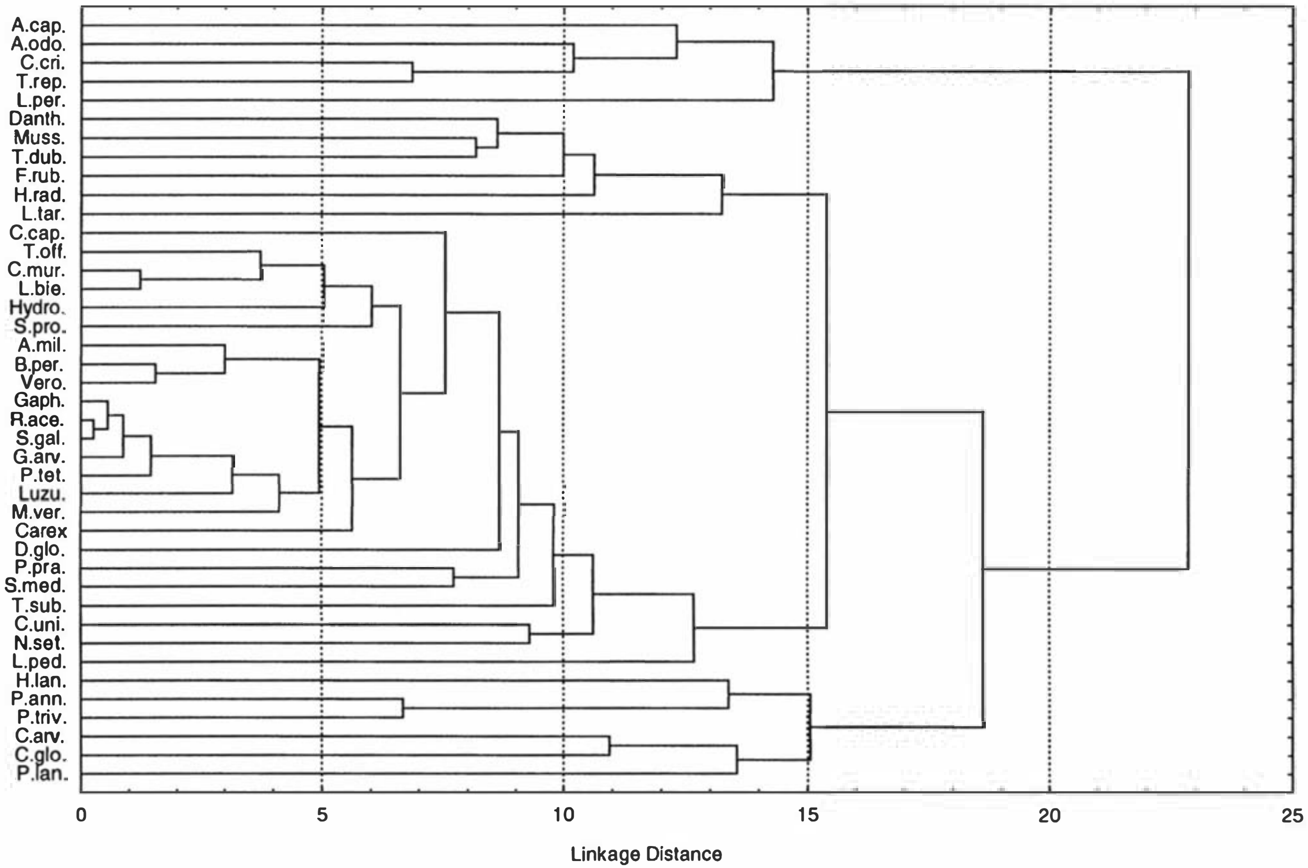

Figure 1 Functional types from cluster analysis for the naturalised pasture of the hill country of New Zealand. Ac *A. capillaris*; Lp *L. perenne*; Ao *A. odoratum*; Cc *C. cristatus*; Tr *T. repens*; Dant *Rhytidosperma* sp.; Fr *F. rubra*; Moss *Muscii* sp.; Lped *L. pedunculatus*; Hr *H. radicata*; Leont *L. taraxacoides*; Td *T. dubium*; Hl *H. lanatus*; Pa *P. annua*; Pt *P. trivialis*; Cirs *C. arvense*; Cglom *C. glomeratum*; Planc *P. lanceolata*; Crepis *C. capillaris*; Tarax *T. officinale*; Cymb *C. muralis*; Linum *L. bienne*; Hydro *Hydrocotyle* sp.; Sagina *S. procumbens*; Gaphal *Gnaphalium* sp.; Rumex *R. acetosella*; Silene *S. gallica*; Gall *G. arvense*; Poly *P. tetraphyllum*; Luz *Luzula* sp.; Mont *M. verna*; Ts *T. subterraneum*; Dg *D. glomerata*; Ach *A. millefolium*; Bellis *B. perennis*; Vero *V. persica*; Pp *P. pratensis*; Carex *Carex* sp.; Stell *S. media*; Cent *C. uniflora*; and Nert *N. setulosa*.

Cluster analysis within the low yielding group discriminated four groups according yield and distribution of species across microsites (Figure 1): Group I, composed of *Rhytidosperma* sp., *Festuca rubra*, *Muscii* sp., *Hypochaeris radicata*, *Leontodon taraxacoides* and *Trifolium dubium*; group III, composed of *Holcus lanatus*, *Poa annua* and *Poa trivialis*; group VI composed of *Cirsium arvense*, *Cerastium glomeratum* and *Plantago lanceolata*; and group VII composed of species such as *Cymbalaria muralis*, *Centella uniflora* and *Sagina procumbens* amongst others (Table 1).

Table 2 Total dry matter production and distribution of the yield for specific functional types (groups I, II and III) in the naturalised pasture in the hill country of New Zealand.

	Low Fertility (Group I)		Medium Fertility (Group II)		High Fertility (Group III)		Total Dry Matter Producction	
FT [3]	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)
LN	6.74 a [1]	(844)	6.34 b	(564)	4.08 b	(58)	8.36 b	(4280)
HH	4.17 b	(64)	7.24 a	(1396)	6.23 a	(505)	9.24 a	(10285)
Significance [2]	**		**		†		**	
s.e.m.	0.29		0.11		0.37		0.078	
Slope [4]	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)
LS	3.64 b	(37)	6.98 a	(1075)	7.60 a	(1990)	9.44 a	(12568)
MS	5.91 a	(367)	6.70 a	(809)	4.82 b	(123)	8.67 b	(5806)
HS	6.82 a	(913)	6.69 a	(805)	3.05 c	(20)	8.30 c	(4003)
Significance [2]	***		n.s.		***		***	
s.e.m.	0.36		0.14		0.46		0.096	
Interaction	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)
LN-LS	6.43 a	(622)	7.03 ab	(1129)	6.80 a	(900)	9.12 b	(9170)
LN-MS	6.99 a	(1083)	5.82 c	(337)	3.06 a	(20)	8.00 d	(2976)
LN-HS	6.79 a	(892)	6.16 c	(471)	2.39 a	(10)	7.96 d	(2872)
HH-LS	0.86 c	(1)	6.93 b	(1024)	8.39 a	(4401)	9.75 a	(17226)
HH-MS	4.83 b	(124)	7.57 a	(1938)	6.57 a	(716)	9.33 b	(11324)
HH-HS	6.84 a	(935)	7.23 ab	(1373)	3.72 a	(40)	8.63 c	(5578)
Significance [2]	***		**		n.s.		*	
s.e.m.	0.50		0.19		0.65		0.136	

[1] Different letters in each section of each column indicate statistical differences amongst factors.

[2] † P<0.1; * P<0.05; ** P<0.01; *** P< 0.001; n.s. Not significant (P>0.1).

[3] FT Field treatment; LN Low-No; HH High-High.

[4] LS Low slope; MS Medium slope; HS High slope.

Pasture Production

Field treatments (fertilisation level and stocking rate) and slope had a significant effect on total dry matter production. Microsites differed in pasture production according to the interaction between field treatment and slope category. The HH-LS microsite produced the highest yield, and the lowest yield was measured for the LN-HS microsite (Table 2). Overall the HH treatment produced significantly (P<0.01) greater dry matter than LN, and the low slopes produced a greater (P<0.001) amount of pasture than the steeper slopes (Table 2).

Table 3 Production and distribution of the yield for specific functional types (groups IV, V, VI and VII) in the naturalised pasture in the hill country of New Zealand.

	A. capillaris (Group IV)		*L. perenne* (Group V)		High Fertility Invaders (Group VI)		Low Presence Species (Group VII)	
FT[3]	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)
LN	7.27 b[1]	(1434)	4.29 b	(72)	4.34 a	(76)	4.36 a	(77)
HH	7.72 a	(2248)	7.86 a	(2589)	4.35 a	(77)	3.87 a	(47)
Significance[2]	†		**		n.s.		n.s.	
s.e.m.	0.13		0.40		0.34		0.37	
Slope[4]	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)
LS	7.58 a	(1958)	8.37 a	(4300)	5.11 a	(165)	3.87 a	(48)
MS	7.55 a	(1901)	5.50 b	(245)	3.98 a	(53)	4.15 a	(63)
HS	7.35 a	(1555)	4.35 b	(77)	3.95 a	(51)	4.31 a	(74)
Significance[2]	n.s.		***		n.s.		n.s.	
s.e.m.	0.16		0.50		0.42		0.45	
Interaction	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)	ln	(Kg DM/ha)
LN-LS	7.63 a	(2051)	7.74 ab	(2294)	4.32 ab	(74)	5.18 a	(176)
LN-MS	7.12 a	(1231)	2.65 c	(13)	4.12 ab	(61)	4.24 ab	(68)
LN-HS	7.06 a	(1167)	2.48 c	(11)	4.57 ab	(96)	3.66 ab	(38)
HH-LS	7.53 a	(1869)	8.99 a	(8058)	5.90 a	(364)	2.59 b	(12)
HH-MS	7.99 a	(2936)	8.36 ab	(4272)	3.84 b	(46)	4.07 ab	(58)
HH-HS	7.64 a	(2071)	6.22 b	(503)	3.32 b	(27)	4.96 a	(142)
Significance[2]	n.s.		*		†		*	
s.e.m.	0.23		0.70		0.60		0.64	

[1] Different letters in each section of each column indicate statistical differences amongst factors.

[2] † P<0.1; * P<0.05; ** P<0.01; *** P< 0.001; n.s. Not significant (P>0.1).

[3] FT Field treatment; LN Low-No; HH High-High.

[4] LS Low slope; MS Medium slope; HS High slope.

Table 4 Correlation amongst found functional types determined by canonical correlation analysis of the naturalised pasture of the hill country of New Zealand.

Groups	I	II	III	IV	V	VI	VII
I	**1.000**	-0.203	-0.699	-0.041	-0.603	-0.482	0.463
II		**1.000**	0.552	0.670	0.709	-0.094	0.291
III			**1.000**	0.344	0.864	0.356	0.024
IV				**1.000**	0.498	-0.153	0.169
V					**1.000**	0.238	-0.072
VI						**1.000**	-0.226
VII							**1.000**

I Group I; II Group II; III Group III; IV Group IV; V Group V; VI Group VI; VII Group VII.

Distribution of the Plant Functional Groups in the Field

Analysis of variance performed on the different cluster groups, showed that the amount of *A. capillaris* was not affected by field treatment and slope (Table 3). The HH treatment, however, tended to have the largest dry matter production of *A. capillaris* (P<0.1). The HH paddock had a significantly greater dry matter production than the LN paddock for the species of group V (P<0.01), composed of *L. perenne* (Table 3), and group II (P<0.05), that included *T. repens*, *A. odoratum* and *C. cristatus* (Table 2). The species of group III, such as *P. trivialis*, *P. annua* and *H. lanatus*, showed the same trend (P<0.1) of producing a higher yield in the HH paddock (Table 2). There were no statistically significant differences in the amount of species of the groups VI and VII between the two paddocks (Table 4).

Group I, formed by *T. dubium*, *L. taraxacoides*, *H. radicata*, *Muscii* sp., *F. rubra* and *Rhytidosperma* sp. was the only group that had a statistically significant higher yield (P<0.05) in the low fertility paddock (LN) than the high fertility paddock (HH) (Table 2 and Table 4).

Category of slope affected the yield of the species in the field, with the exception of the species of group IV and group VI (Table 3). A significant interaction between field treatment-slope category was measured for group I, group II (Table 2), group V, group VII (Table 3) and total dry matter production, but not for group III (Table 2).

Relationship between Plant Functional Groups

Canonical correlation analysis provided information about correlations between the groups of species (Table 4) and the relationship of the groups of species to the soil variables that were measured (Table 5). Groups of species that were positively highly correlated were II with IV (0.670) and V (0.709); and III with V (0.864). Groups of species with high negative correlations were I with III (-0.699) and V (-0.603) (Table 4).

Relationship between Soil Features and Plant Functional Groups

Canonical correlation analysis amongst soil features and groups of species gave positive high correlations (Table 5) between group I with slope (0.661); group III with VSM (0.882), SC (0.782), Total-N (0.818) and Olsen-P (0.763); between group V with VSM (0.786), SC (0.698), Total-N (0.757) and Olsen-P (0.804). High negative correlation was detected between group I with Total-N (-0.625) and Olsen-P (-0.774); group II with SR (-0.661); group III with K_{40} (-0.863), BD (-0.621) and slope (-0.777); group V with K_{40} (-0.772) and BD (-0.648).

Table 5 Correlation amongst soil variables and functional types determined by canonical correlation analysis of the naturalised pasture of the hill country of New Zealand.

Groups	KU	BD	VSM	SC	SR	Total-N	SLP	Olsen-P
I	0.543	0.350	-0.543	-0.453	0.471	-0.625	0.661	-0.774
II	-0.531	-0.215	0.567	0.553	-0.661	0.411	-0.231	0.455
III	-0.863	-0.621	0.882	0.782	-0.375	0.818	-0.777	0.763
IV	-0.313	-0.136	0.431	0.361	-0.427	0.279	-0.270	0.249
V	-0.772	-0.648	0.786	0.698	-0.385	0.757	-0.589	0.804
VI	-0.246	-0.281	0.180	0.208	-0.061	0.318	-0.301	0.391
VII	-0.086	0.164	0.171	0.150	-0.099	-0.097	0.112	-0.296

KU Unsaturated hydraulic conductivity; BD Bulk density; VSM Volumetric soil moisture; SC Soil compressibility; SR Soil rebound; Total-N Soil total nitrogen content; SLP Slope; I Group I; II Group II; III Group III; IV Group IV; V Group V; VI Group VI; VII Group VII.

Three canonical variates were significant in explaining the variation of the analysed variables. Canonical variate 1 (CAN 1) explained 80.5% of the total variation (P<0.001), canonical variate 2 (CAN 2) explained 13.8% (P<0.001), with canonical variate 3 (CAN 3) explaining 3.6% of the variation ($P<0.05$). Therefore the first two canonical variates explained 94.3% of the total variation, and were the canonical variates with more weight. Variables that were relevant to explain CAN 1 were in one direction: VSM, soil compressibility, Olsen-P, Total-N, species group III and species group V. In the inverse direction these were: slope, K_{40}, BD and species group I (Figure 2 and Figure 3).

Canonical variate 2 was composed in one direction of Olsen-P, and species groups II and V, while in the other direction SR and species group I were significant (Figure 2 and Figure 3).

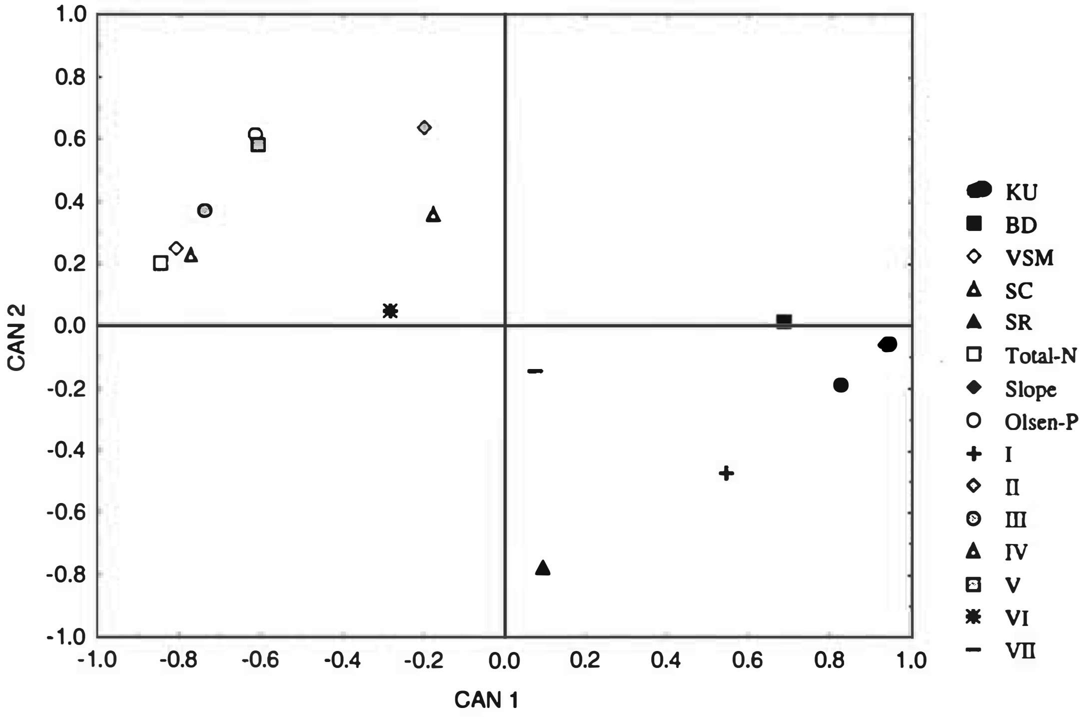

Figure 2 Canonical variates for soil and functional types relationship.

KU Unsaturated hydraulic conductivity; BD Bulk density; VSM Volumetric soil moisture; SC Soil compressibility; SR Soil rebound; Total-N Soil total nitrogen content; I Group I; II Group II; III Group III; IV Group IV; V Group V; VI Group VI; VII Group VII.

A plot of the microsite replicates (Figure 3) indicated that low slopes of either field treatments were similar on CAN 1 but distinguished by CAN 2. Medium slope microsites were mostly distinguished by CAN 2, while steep slopes were distinguished on both axes.

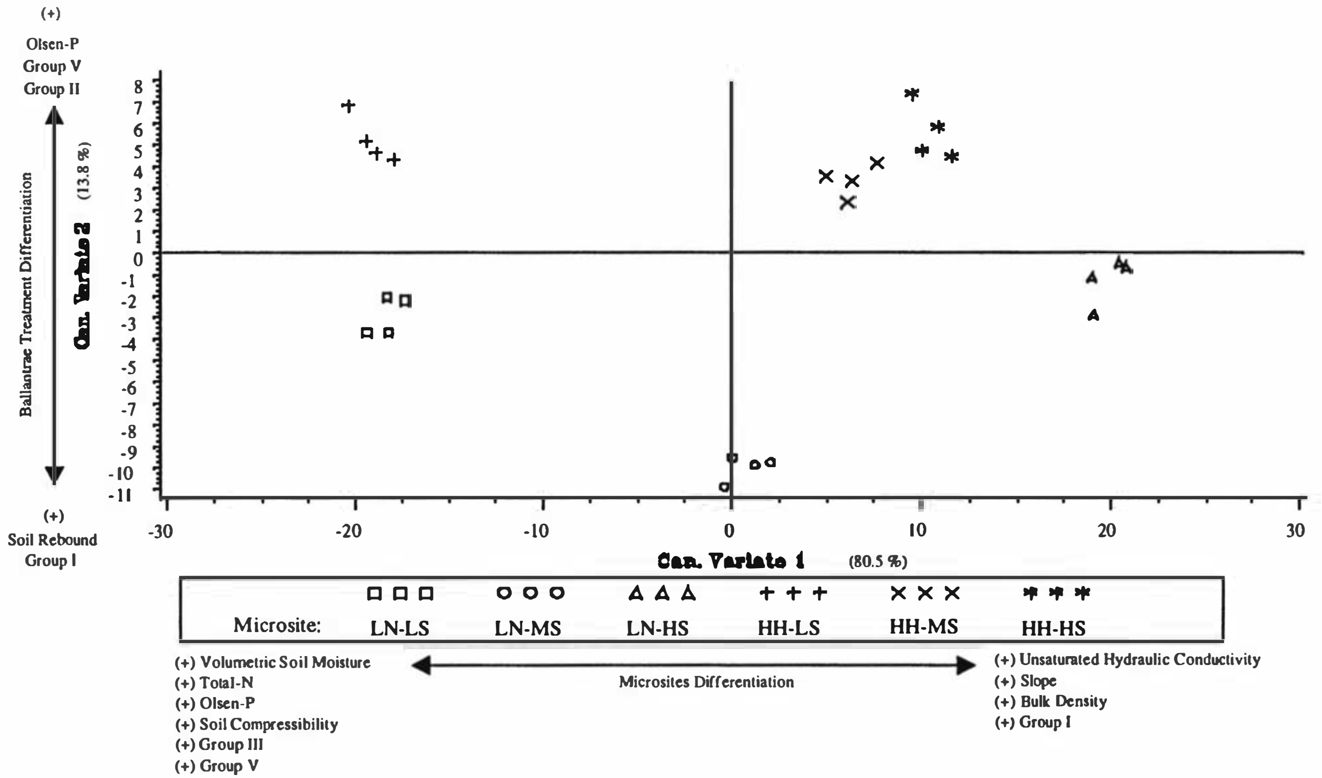

Figure 3 Canonical scores from soil features and functional types of the replicated microsites.

LN Low-No paddock; HH High-High paddock.

LS Low slope; MS Medium slope; HS High slope.

The equations that were fitted for the contribution of functional groups to the total dry matter production, and canonical scores of the CAN 1 of the soil variables are presented in Figure 4. Comparison of the equations between paddocks for similar functional groups indicated that the equations that were fitted were highly statistically different for group I ($P<0.0001$), group III ($P<0.01$), group V ($P<0.001$), group VI ($P<0.05$) and group VII ($P<0.05$).

DISCUSSION

Hill Country Heterogeneity and Pasture Production

A distinctive feature of the hill country field of New Zealand is that there is a high variability in environmental conditions over short distances (micro-scale) (Lambert and Roberts, 1978). Within metres, soil variables change from those containing a high availability of resources for plant growth, such as Total-N and Olsen-P, to those constraining plant development because of their low availability. Soil physical features, such as water holding capacity (WHC) and water conductivity, also significantly change. Thus, amongst the soil variables analysed, slope was the variable that led to soil heterogeneity in the hill country (Chapter 3). Environmental heterogeneity had a strong effect on pasture production, which decreased with increasing slope category (Table 2). These results agree with early studies in the hill country reported by Lambert *et al.* (1983) and Lambert *et al.* (1996).

Functional Groups

Multivariate statistics allowed the integration of the measured variables, both soil variables and species data, which cannot be achieved using univariate statistical analysis. The results from the univariate analysis supported the results obtained from the multivariate analysis. This method of analysing the data has been recommended by Wilson (1999) to obtain functional types and has been used previously for a similar objective by Thompson (1974), Eagles and Othman (1988), Chapin *et al.* (1996), Smith *et al.* (1997), Díaz and Cabido (1997) and Grayston *et al.* (1998).

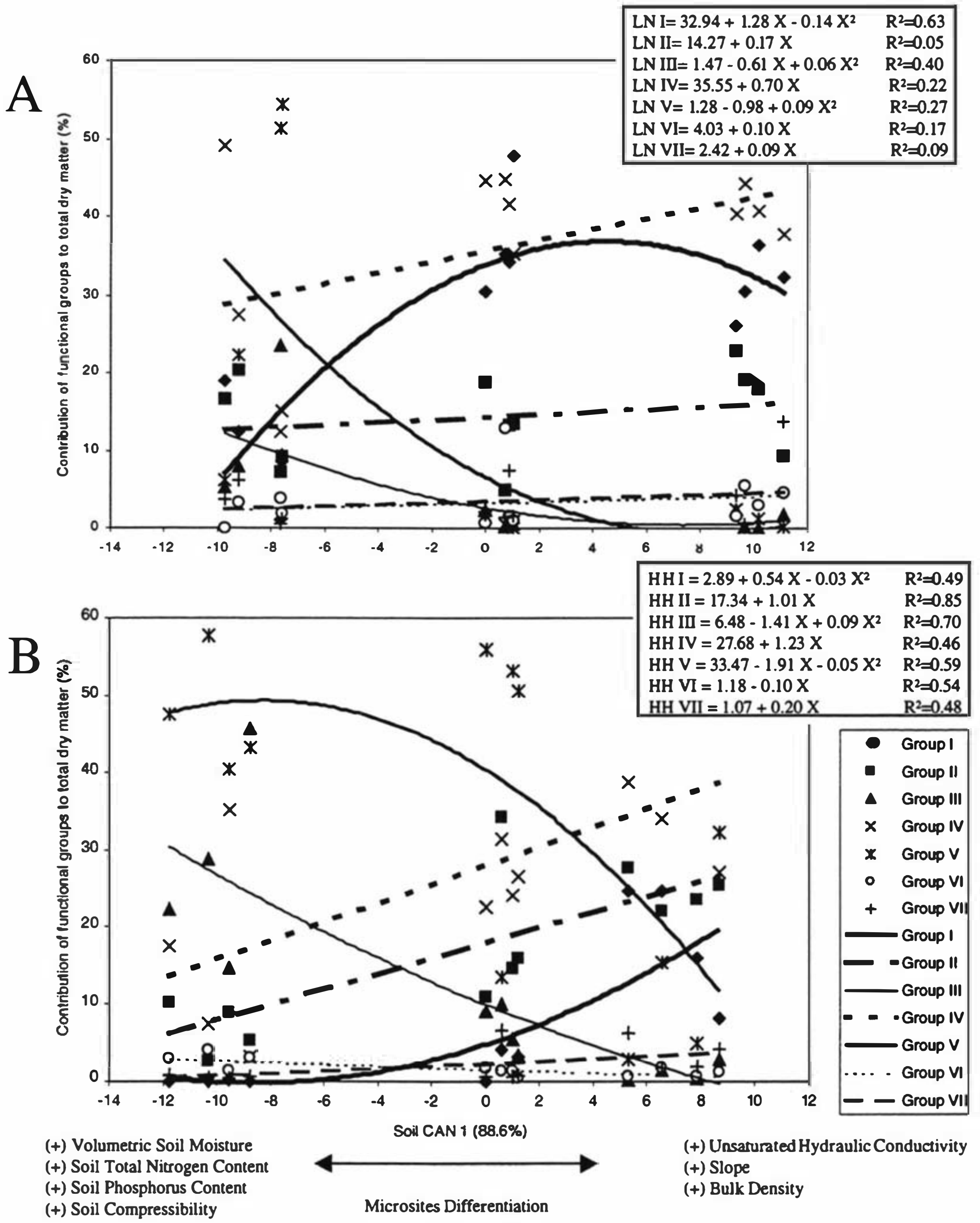

Figure 4 Succession of functional groups according to changes in soil condition.

A: Non-fertilised paddock (LN); B: Fertilised paddock (HH).

Cluster analysis grouped the species according to their yield across microsites and their total yield (Figure 1). *Agrostis capillaris* (group IV) was present in all the measured microsites. Even when there were large differences in the soil condition, as was the case comparing the HH-LS microsite with the LN-HS microsite (Chapter 3), *A. capillaris* contribution to the total dry matter production ranged from 10.8% in the HH-LS to 40.6% in the LN-HS (Table 3).

Lolium perenne (Table 1) was another species that had high yields. However, in contrast to *A. capillaris*, *L. perenne* tended to disappear when the availability of soil resources decreased (Table 3), dropping the yield from 8058 kg DM/ha/year in the HH-LS to 11 kg DM/ha/year in the LN-HS. *L. perenne* in the HH-LS accounted for 46.8% of the total production of the microsite, while in the LN-HS 0.4% of the total production of the microsite was *L. perenne*.

The species of group II were present in all of the microsites but were not as productive as *A. capillaris* and *L. perenne* (Table 2). Group II species had higher productivity when the condition of the soil was medium (LN-LS, HH-MS and HH-HS), decreasing toward the extremes, especially toward the microsites where the constraints of the soil variables were enhanced (LN-HS).

Group I increased its percentage in the field with increasing slope and decreasing availability of soil resources, from almost 0% in the HH-LS to 31.1% in the LN-HS, thus being a group of low fertility species (Table 2). Groups III (Table 2) and VI (Table 3) increased their production in the field with the increasing availability of soil resources. Cluster analysis differentiated between group III and VI according to their yield, such that group III reached much higher yields than group VI. All of the species grouped into group III were grasses, while all the species of group VI were dicotyledons. Group VII was present in low amounts across the whole range of environmental variables (Table 3). Its lowest yield was in the HH-LS microsite. Group III increased its percentage of the total dry matter production from 0.3% in the LN-HS to 25.5% in the HH-LS.

In previous studies (Lambert *et al.*, 1986b) hill country species have been grouped into 5 categories: a) *L. perenne*; b) high fertility responsive grasses (*H. lanatus*, *P. trivialis*, *P. annua* and *Dactylis glomerata*); c) low fertility tolerant grasses (*A. capillaris*, *A. odoratum*, *C. cristatus*, *F. rubra* and *Rytidosperma* sp.); d) legumes (*T. repens*, *Trifolium pratense*, *T. dubium* and *Lotus pedunculatus*); and e) other species including *H. radicata*, *L. taraxacoides*, *P. lanceolata*, *Muscii* sp., *C. glomeratum* and

Nertera setulosa. The grouping resulting from the cluster analysis in the present study differed from that reported by Lambert *et al.* (1986b) because the criteria used to group the species was different. In the present work, the multivariate statistical methodology used gave an accurate reflection of occurrences in the field.

Functional Groups-Soil Variables Relationship

Canonical correlation analysis showed that groups I, II, III and V had a close relationship with some of the soil variables that were measured (Table 5). An increased percentage of group I species was associated with increased slope and a diminishment of Total-N and Olsen-P (Table 5 and Figure 4). These results are supported by the univariate analysis, which showed that group I increased its production with increasing slope category (Table 2). From this evidence it is possible to infer that group I would be a poor competitor for resources when resources are not limited, especially when competing with faster growing species such as *L. perenne*. Group I would be able to tolerate a high level of stress from the environment and colonise sites where aggressive species are not productive due to a lack of availability of resources. Therefore, group I would be a group that would grow under poor soil conditions and the level of colonisation of this group to a specific site would give an indication of the soil resource availability.

Group II was negatively correlated with soils with a low rebound following compression (Table 5 and Figure 2). Soil rebound was defined as the capacity of a soil to recover its original functionality and structure following a disturbance (Seybold *et al.*, 1999). Group II also tended to be positively related to soil with high phosphorus content (Table 5 and Figure 2). The species in group II tended to colonise soils where species of group V were productive, as was shown by the CAN 2 (Figure 2). This tendency was also apparent from the results of the analysis of variance for group II (Table 2). The production of the species in group II increased in the microsites with medium fertility levels, but declined in the soils with high levels of resource availability. This suggests that the species of group II would be less aggressive competitors for resources than species of groups III and V, which were the groups that dominated in those conditions. However, the species in group II would be more tolerant to environmental constraints than those in groups III and V.

Group III was strongly associated with variations in soil characteristics. A high percentage of group III species in the field was related to soil that was easily compressible, with high WHC, high Total-N, high Olsen-P, low slope and low K_{40} (Table 5 and Figure 2). Therefore, the species of group III colonise well-developed soils and have a low capacity to tolerate increasing levels of constraint among the soil variables.

Species in functional group V were more productive in flat areas with high soil compressibility, low BD, high levels of Olsen-P, WHC and a high Total-N (Table 5 and Figure 2). Functional group V was more tolerant to changes in soil variables than functional group III (Table 2 and Table 3), such that the production of plants in group III diminished faster in the field than those in group V with the diminishment of the availability of resources in the soil (Figure 4).

The species in groups IV, VI and VII did not have strong correlations with the environmental variables that were analysed in this study (Table 5), suggesting that there were different variables than those analysed in the present study affecting their production, such as adequate capture of resources and ability to match competitors. The percentage of the total yield of the species of group IV was most likely related to the interaction between availability of soil resources and competition. The low slope category had a plentiful availability of soil resources, which may have enhanced competition for light due to the presence of larger tiller populations (Lambert *et al.*, 1986a). Therefore, this microsite was dominated by species that grew faster under grazing, that is, species that after grazing were able to fill the gap left by the grazed material more rapidly due to a high grazing tolerance (Briske, 1996). This was the case of functional group V (Figure 4). Chapman *et al.* (1983) reported that *L. perenne* has a faster tiller appearance rate than *A. capillaris*. In the high slope category, the level of the available resources in the soil was restricted, so competition for resources would have been an important issue for the development of species and tolerance to the stress of low resource availability. In these conditions group IV was the most successful functional group. These findings are in agreement with the Nutrient:Light ratio hypothesis (Tilman, 1994). Additionally the present study showed that faster growing species have the advantage in grazing conditions when competition for light is critical.

Plants in groups VI and VII maintained a very low profile along the range of environmental variables (Figure 4). The reasons for this behaviour would have been different for the two extremes of the environmental range. In circumstances with high availability of resources, these groups would grow slower in relation to other groups of species present, such that these plants would be poor competitors for light. On the other hand, low tolerance to environmental stress and low capacity to compete for the available resources would explain the low percentage of these groups when available resources were scarce.

Dynamic of the Functional Groups in Relation to Soil Variables

Canonical variate analysis showed that despite the long term field treatments, the largest differences in the field were between microsites, explained by the variables of CAN 1 (Figure 3). The effects of field treatments were shown by CAN 2. Soil WHC, Total-N, Olsen-P, SC, slope, K_{40} and BD were the soil variables that varied the most between microenvironments in the hill country (Figure 2 and Figure 3). In a previous study in the hill country productivity had a strong relationship to available soil nitrogen and available phosphate levels (Lambert and Roberts, 1978). The present work has introduced additional variables that are related to the levels of Total-N and Olsen-P and could influence productivity. It should be noted that there are strong interrelationships amongst the measured slope/soil variables, but correlations do not necessarily indicate a causal relationship.

Canonical variate 1 differentiated between high and low resource availability and between levels of soil physical features (Figure 2 and Figure 3). High proportions of the species of groups III and V in the pasture were associated with higher WHC, Total-N, SC, and Olsen-P (Figure 2). These features reveal that groups III and V were highly sensitive to changes in the level of these soil variables. It would be expected, therefore, that species of groups III and V would be present in a high proportion in the field under specific soil conditions, those of high availability of soil resources; both water and fertility (Table 5). However, measurements of SC and SR indicate that these soils are susceptible to lose their structural functionality because of treading traffic, and this hypothesis is supported by the loss of water conductivity measured in these soils (Chapter 3).

On the other extreme, species of group I showed a strong tolerance to environmental constraints (Table 5 and Figure 2), as shown by the increasing population with increasing environmental constraints (Figure 4 and Table 5). However, this behaviour would indicate that group I would be a poor competitor when soil resources are plenty. Canonical variate 2 showed that group I was associated with soils with high SR (Figure 2). This group appeared to be increasing its percentage in less developed soils with low fertility.

The species in groups II, IV, VI and VII appeared to be non-responsive under the changes of the environmental variables that composed CAN 1. However, CAN 2 showed that species in group II tended to have a closer relationship with soils with high Olsen-P and low SR (Figure 2). In the hill country, soils with a large rebound have been shown to have low fertility levels and low WHC with steep slopes, as was the case of LN-HS microsite, but they are more structurally stable (Chapter 3). Soil variables such as WHC, Total-N, SC, BD, slope and K_{40} would have a limited effect on group II. Therefore this group would have a wider tolerance to these soil variables than the species in groups III and V. However, the distribution of the population in group II would suggest that these species would be sensitive to competition for soil resources against aggressive species such as the species of groups III and V.

There were also groups of species that were totally indifferent to changes in the levels of the environmental variables, such as group IV, VI and VII.

Agrostis capillaris was present in significant amounts in all of the different environmental conditions studied, showing a great capability to adapt its growing to the variation in availability of soil resources (Table 2). This suggests that *A. capillaris* has a genetic pool that confers the capability to adjust to very extreme environmental conditions, which is evidence of high plasticity. This finding agrees with that reported by Rapson and Wilson (1988). This is important, because the environmental variables that, according to the canonical variate analysis, explained a significant amount of the environmental variability have direct consequences on the field botanical composition.

Segregation of Species and Functional Groups

There were 3 types of behaviour detected in the groups of species (Figure 4). The first was by species that were segregated directly by the environmental constraints. These species were strongly affected by changes in the levels of the environmental constraints, as was the case of species in groups III and V.

The second was characterised by species that were segregated indirectly by environmental constraints, through competition, as was the case of those in group I. When resources in the environment increase in availability, the percentage of plants that are in group I diminished in the field as more aggressive species were able to grow, such as those that composed groups III and V.

The third type of behaviour occurred in the groups composed of species that were indifferent to the changes in the levels of the environmental constraints that were measured. *Agrostis capillaris* was able to compete successfully with *L. perenne* in conditions of high availability of resources, even though the percentage of this species in relation to other species diminished with a high availability of resources (Figure 4), as happened in the HH-LS microsite. *Agrostis capillaris* was also productive in conditions of low resource availability, thus showing a large tolerance to environmental stress. This large capability of *A. capillaris* to survive, colonise and also dominate in contrasting environments has also been reported by Rapson and Wilson (1988), Grime *et al.* (1989), Rapson and Wilson (1992) and López *et al.* (1997).

Species with individuals that survive in highly contrasting environments could have two strategies to persist under those conditions, through genetic plasticity or ecotypes. These hypotheses are supported by Rapson and Wilson (1988) in relation to *A. capillaris* and Snaydon and Davies (1982) in relation to *A. odoratum*, respectively. Rapson and Wilson (1988) proposed that *A. capillaris* is able to respond in a plastic fashion to a wide range of environments, while Snaydon and Davies (1982) reported that *A. odoratum* showed population divergence as a response to environmental changes.

The presence of ecotypes in the hill country pasture would add another dimension to the diversity-stability hypothesis (Pimm, 1984; Lawton and Brown, 1994; Tilman and Downing, 1994), which predicts a positive relationship between the species diversity and ecosystem stability. The presence of ecotypes would be related to diversity within species, and would be another plant strategy that would allow individual plants to persist in contrasting environments and enhance ecosystem stability.

Field Condition and Functional Groups

Gastó *et al.* (1993) defined field condition as a measure that allows the state of an ecosystem to be given a value at a specific moment, in relation to the ideal state according to the use and management of the ecosystem. Based on field condition (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973; Archer and Smeins, 1991; Gastó *et al.*, 1993; Pieper, 1994) the presence and abundance of species in the field are the reflection of external factors, such that their presence and abundance increases or decreases in the field according to the results of the relationship between species and environmental variables. Therefore, botanical composition is an indicator of field condition.

The concept of field condition also proposes that species may be grouped according to their behaviour in the field, increasing or decreasing their percentage of the total plants, when field condition varies (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973). According to this, general patterns of behaviour have been established that have generated 4 possible groups of species: decreasers, increasers (Type I and Type II), invaders (Type I and Type II) and indifferents (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973; Gastó *et al.*, 1993).

On the other hand, functional types have been defined as groups of species that are able to use the same resources or perform similarly to a specific constraint (Gitay and Noble, 1997). A broader definition of functional types was given by Wilson (1999) as: "a group of species that are similar in some way that is ecologically relevant, or might be". Therefore, field condition and functional types are complementary concepts, since plant species of a "condition group" would have similar requirements for resources and would respond similarly to environmental changes as plants species grouped by functional groups.

Applying these concepts to the results of the present research, it is possible to distinguish 4 types of behaviour. Groups III and V had a high production when the soil has a high availability of resources, but when resources began to be scarce, the proportion of these species in the field fell quickly (Figure 4, Table 2 and Table 3). Groups VI and VII remained stable along the environmental variation and constituted the second behaviour, as groups that are indifferent to the environmental changes that were studied in the present experiment (Figure 4, Table 2 and Table 3). Group II increased its production when the soil fertility was medium, but diminished when soil fertility was high or low (Table 2). Finally, groups I and IV increased their proportion of the total yield with the deterioration of the field condition (Figure 4, Table 2 and Table 3). Therefore, groups III and V would correspond to the behaviour of decreasers, group II would be an increaser type I, and groups I and IV would correspond to increaser type II. Groups VI and VII would conform to the group called indifferent.

CONCLUSIONS AND IMPLICATIONS

The hill country of New Zealand has, at a micro-scale, contrasting environments that segregate species according to the level of the environmental variables and the inter-relationship between the environment and species. It was also shown that there are species that have the capability to respond positively to environmental constraints adjusting their growth according to the varying circumstances. However, even where the environment segregated species, there were individual plants within species that survived despite environmental constraints. This raises the question of whether the genetic material of those plants would correspond to the same as the segregated plants or whether those plants have a different genetic pool as an ecotype. For cases where the species were not segregated by the environmental variables, it is necessary to go further in the environment-species relationship study to determine whether these species have a large plasticity or whether there are different ecotypes present that are able to survive under contrasting environments.

The study reported here is the first time that pasture species in the hill country have been divided into functional groups based on properties such as yield, and the relationship between functional groups and a range of soil conditions was studied. Results appeared to be complementary between field condition and plant functional groups in the grassland dynamic analyses. The presence of plants from specific groups as determined in this study in a hill country pasture allows an easy determination of the successional stage of the field.

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CHAPTER 5

Ecology of pastoral communities in a heterogeneous environment. III. Selective defoliation of *Agrostis capillaris*, *Anthoxanthum odoratum* and *Lolium perenne* by grazing sheep

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In hill country pastures, segregation of plant species and plant functional groups have been associated with changes in soil features related to the microrelief as reported in Chapter 4. Previously, grazing sheep have been reported to be an important factor redistributing fertility through the slope categories. Sheep have been recognised to be selective grazers. Therefore, sheep may be another source of selection pressure on hill country plant species. The objectives of the study reported in this Chapter were to analyse sheep selective grazing behaviour in hill country pastures in relation to landscape microrelief, species distribution and seasonal contrasts.

ABSTRACT

Selective grazing behaviour of sheep was evaluated in hill country pastures in relation to landscape microrelief, species distribution and seasonal contrasts. Paddocks with long-term differentiated fertilisation and stocking rate (high fertility-high stocking rate: HH; low fertility-low stocking rate: LN) were studied. Pasture production and selective grazing were evaluated in three slope categories (low slope, LS; medium slope, MS; high slope, HS). Selective grazing was determined by using transects with marked tillers of *Agrostis capillaris* (Ac) and *Lolium perenne* (Lp) in the LS; Ac, *Anthoxanthum odoratum* (Ao) and Lp in the MS; and Ac and Ao in the HS. Length of leaves was measured during Summer, Autumn, Winter and Spring. The highest pasture growth rates were measured during Spring and low pasture growth rates were present in Summer and Winter. Between the slope categories, LS showed the highest pasture growth rates and HS the lowest. The marked tillers were more frequently grazed in the HH treatment than in LN, except for Autumn. During Summer, Autumn and Spring grazing frequency was in the order LS>MS>HS. During Winter sheep did not discriminate between slope category. Sheep selectively grazed *L. perenne*, which had the longest leaves, rather than *A. capillaris*, with *A. odoratum* having a leaf length between those of the former two species. Selective grazing changed through the year according to available pasture. Sheep discriminated according to accessibility of the grazing area when available pasture was high, grazing mainly LS. They did not discriminate between slope categories when available pasture was low, and enlarged the grazing areas towards the less accessible, steep slopes. However, sheep selectivity grazed *L. perenne* instead of *A. capillaris* when little pasture was available.

INTRODUCTION

Grazing animals can affect grassland attributes such as botanical composition and dry matter production (Milton, 1994; Pieper, 1994) and through grazing intensity the proportion of each plant species can be modified (Noble, 1973). Grazing animals may also alter nutrient distribution in the field, such that alteration in soil features is reflected in changes in botanical composition and generates patchiness (Pieper, 1994).

Environments rich in resources favour the development of plant species with fast growth, while slow growing plants are favoured when resources are limited (Coley *et al.*, 1985). In grazing systems, this relationship can be altered by selective grazing, such that the frequency of less defoliated species is increased relative to species subject to more severe defoliation (Mitchley, 1988; Brown and Stuth, 1993). Slow growing species are less selected by herbivores than faster growing species because slow growing species normally have antiherbivore features such as a high content of lignins, a low leaf protein content and high amounts of defence metabolites (Coley *et al.*, 1985). In naturalised grasslands, where there are many botanical species interacting with each other, intense grazing can promote successional changes in the field. In this way, features of the grassland, such as productivity, density and growth rate are affected (Milton *et al.*, 1994). Selective grazing implies that the grassland is not homogeneously grazed (Brown and Stuth, 1993), so grazing pressure on the different species is not uniform (Noy-Meir *et al.*, 1989), with variables such as height and frequency of defoliation having a direct effect on the survival of the grazed plants (Fulkerson and Slack, 1995).

The species balance of naturalised pasture of the hill country of New Zealand is influenced, amongst other things, by the slope of the microrelief (Lambert *et al.*, 1986a), which can be defined in terms of three types of slope: low (LS), medium (MS) and high (HS) (Lambert *et al.*, 1983). Soil characteristics, botanical composition and pasture production change significantly according to the slope category (Chapter 3 and Chapter 4). In this way, LS has been shown to differ notably from HS in soil characteristics such as water holding capacity, water conductivity, bulk density, soil compressibility, contents of total nitrogen and phosphorus of the soil (Chapter 3) and total dry matter production (Lambert *et al.*, 1983; Chapter 4). LS is colonised by *Lolium perenne*, *Holcus lanatus*, *Poa annua* and *Poa trivialis*, and HS by species such as *Hypochaeris radicata*, *Festuca rubra* and *Danthonia* sp. (Chapter 4). Density of the pasture, tillering of species like *L. perenne* and density of *T. repens* diminish significantly with increasing slope (Lambert *et al.*, 1986a; Lambert *et al.*, 1986b).

Grazing animals are another variable that contributes to the contrast between the slope categories. Non uniform distribution of faeces and urine re-arranges the fertility between the slope categories (Gillingham and During, 1973; Saggar *et al.*, 1990; Lambert *et al.*, 2000), such that LS areas gain fertility while medium and HS areas lose fertility (Saggar *et al.*, 1990). Thus grazing animals affect botanical composition through moving fertility between the slope categories. Because soil characteristics of the microsites are largely different between slope categories, in Chapter 4 it was suggested that differences between environmental variables may be important in segregating species in the neighbouring microsites.

Sheep have been recognised to be selective grazers, at least for *L. perenne* and *T. repens* (Briseño de la Hoz and Wilman, 1981; Laidlaw, 1983; Parsons *et al.*, 1994; Newman *et al.*, 1994), and between *L. perenne*, *A. capillaris* and *T. repens* (Clark *et al.*, 1984). Therefore in the hill country pasture, sheep could discriminate between landscape microrelief and/or between species. Furthermore, if sheep exert selective grazing on species, they could constrain the growth of selected plant species and segregate species between slope categories.

The hypothesis of the present work was that sheep selectively graze hill country pasture, discriminating between slope category and species. To test this hypothesis, the objective of the present work was to evaluate selective grazing behaviour of sheep in the hill country pastures in relation to landscape microrelief, species distribution and seasonal contrasts.

MATERIALS AND METHODS

The trial was carried out in AgResearch's Ballantrae Research Station, near Palmerston North, New Zealand, in two paddocks with long-term differentiated fertiliser and stocking rate history. One of the paddocks received a low amount of phosphorus fertilisation as superphosphate (11 kg P/ha/year) between 1975 and 1980, and was termed "Low fertility" (LF). During the same period the other paddock received a high phosphorus fertilisation as superphosphate (57 kg P/ha/year), and was called "High fertility" (HF) (Lambert *et al.*, 1986a). From 1980 no phosphorus fertilisation was applied to the LF paddock, thus being called "Low-No" (LN), while the other paddock continued to receive a high level of phosphorus fertilisation as superphosphate (60 kg P/ha/year), thus being termed "High-High" (HH) (Lambert *et al.*, 1996). Both paddocks have been under continuous sheep grazing with Romney breeding ewes since 1975. The stocking rate has been adjusted annually according to the pasture production response to the fertiliser treatments (Lambert *et al.*, 1990). During the experimental period the HH paddock had a stocking rate of 15.8 sheep/ha and the LN paddock 6.2 sheep/ha. Historically, the average stocking rate for the LN paddock has been 8.3 ewes/ha, while that for the HH paddock has been 14.8 ewes/ha (Lambert *et al.*, 1996).

The result of the combination between the field treatments (LN and HH) and slope categories (1 – 12 ° from the horizontal, LS; 13 – 25 °, MS; > 25 °, HS) constituted the microsites that were studied.

Dry matter production was measured in each type of microsite using cages of 0.5 m^2 (0.5 x 1 m) through the year. The pasture was measured using the pre-trimmed exclusion cages technique (Radcliffe *et al.*, 1968) and was trimmed to a height of approximately 10 mm at the beginning and end of each exclusion period. Cuts were made during the year with an average frequency of 52 days. Dry matter production and botanical composition were determined from the pasture collected from each cage. All the collected pasture was dried in an oven at 60°C for 48 hr or until the samples reached constant weight. Botanical composition was reported in Chapter 4. Between cutting dates, cages were placed on different microsites of the same category, such that each cage had a rotation of 3 positions in the year. Four microsites of each category were used in each paddock as replications to measure pasture production and botanical composition. Curves of growth rate of the pasture were calculated from this data.

In the study reported in Chapter 4, it was shown that across the range of microsites the more frequent species were *Agrostis capillaris*, *Anthoxanthum odoratum* and *Lolium perenne*. *Agrostis capillaris* was common to all the microsites, while *A. odoratum* was frequent in MS and HS and *L. perenne* in LS and MS. Therefore, the grazing of *Agrostis capillaris* (Ac) was evaluated in all the microsites, *Anthoxanthum odoratum* (Ao) in MS and HS and *Lolium perenne* (Lp) in LS and MS.

To measure selective grazing, six microsites additional to those used to measure pasture production, were used as replications for each type of microsite per field treatment. A transect was placed on each microsite and individual tillers were marked every 5 cm, alternating species until 5 vegetative tillers/species/transect were marked. Each tiller was marked by placing a coloured paper clip around the tiller and attaching the paper clip to the ground with a nail. To recognise whether the marked tillers were grazed or not, the lengths of live leaves (laminas) of each marked tiller were measured weekly for 4 consecutive weeks with digital callipers and the information recorded. The comparison of the information of the lengths of the leaves of each individual tiller between two consecutive weeks allowed a determination of whether the tillers were grazed. All grazed tillers were replaced each week, so that the total number of marked tillers per transect was the same for each recording session. None of the marked tillers became reproductive during the measurement periods, which were carried out once each season during February, April, July and October of 1999.

For each season, statistical analyses were performed to determine the total probability of the marked tillers being grazed over 3 weeks. The defoliation probability data were analysed using a model for a factorial design, with main effects for paddock, slope and species, and paddock by slope and slope by species interactions. Each month's data were analysed separately using a generalised linear model with a binomial distribution fitted using SAS Proc GENMOD (SAS version 6.12, 1997), through which significant differences between the experimental treatments within each season were determined (McCullagh and Nelder, 1989; Dobson, 1990). Slope and species factors were unbalanced because not every species was present on every degree of slope, so a Type 3 analysis was performed, which means that each effect was tested, allowing for differences in other factors. Repeated measures ANOVA on logits of proportions was used to analyse data across seasons using SAS Proc GLM. This analysis was carried out comparing consecutive seasons. ANOVA was also performed to determine whether the length of the leaves influenced which tillers were grazed, by comparing leaf length on grazed and ungrazed tillers.

RESULTS

Pasture Growth Rate

There were three types of curves of sward growth (Figure 1 and Figure 2). HH-LS showed high growth during Spring and maintained high to medium pasture growth rates during Summer and Autumn. The swards of the LN-MS and LN-HS microsites had their highest growth rates in Spring, but subsequently the sward growth rate constantly diminished until it reached the minimum during Winter. LN-LS, HH-MS and HH-HS showed high pasture growth rates during Spring, low growth in Summer, substantial re-growth in Autumn and low growth in Winter.

The HH paddock produced 10,285 kg DM/ha/year (ln(DM)= 9.24; s.e.m.= 0.078), which was significantly more ($P<0.01$) than the 4,280 kg DM/ha/year produced by the LN paddock (ln(DM)=8.36; s.e.m.= 0.078) as reported in Chapter 4.

Defoliation Probability within Seasons

No significant interactions between field treatments and slope category and between slope category and species were found.

Treatment effects (phosphorus fertilisation and stocking rate, FT) were significantly different in Summer, Winter and Spring and overall (Table 1).

Sheep discriminated amongst slope categories (SLP) during Summer, Autumn and Spring (Table 1). During Summer, sheep defoliated the marked tillers of LS and MS significantly more frequently than tillers of HS. During Autumn, the probability that marked tillers of LS and MS would be grazed was statistically similar, but greater than the probability that the marked tillers of HS would be grazed. In Winter, the probability that marked tillers would be grazed was similar for each category of microsite. During Spring, the probability of being grazed was statistically greater for the marked tillers of LS than those of the other slope categories. The overall analysis for the year showed that the defoliation frequency of the marked tillers was: LS> MS> HS (Table 1).

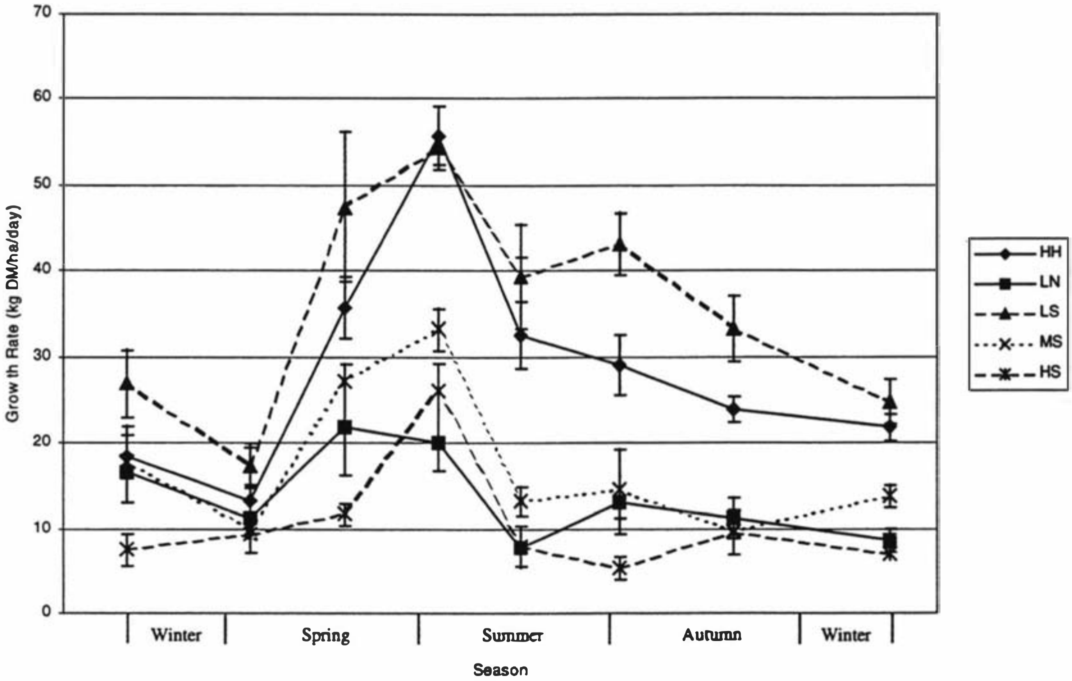

Figure 1 Seasonality of the growth rate of a fertile (HH) and infertile (LN) paddocks and of the three categories of slopes (LS Low slope, MS Medium slope, HS High slope) in a hill country pasture.

Sheep showed a tendency to discriminate amongst species (SPP) during Winter (P<0.07), such that *L. perenne* was grazed more than *A. capillaris*, but similar to *A. odoratum* (Table 1). Overall the probability of being grazed was statistically greater for *L. perenne* than for *A. capillaris* and *A. odoratum*.

Change in the Defoliation Probability between Consecutive Seasons

Statistical differences in changes of the probability of the marked tillers being grazed between consecutive seasons are shown in Table 2. The field treatment - slope category interaction showed a statistically significant increase in the grazing probability in the LN-LS and LN-MS microsites from Summer to Autumn. From Autumn to Winter the probability of being grazed decreased significantly in the LN-MS and showed a tendency of increasing in the LN-HS and in the HH-MS microsites (P<0.1). From Winter to Spring the probability of the marked tillers being grazed diminished significantly in the LN-HS, increased in the HH-LS, and showed a tendency (P<0.1) to increase in the LN-MS microsite (Table 2).

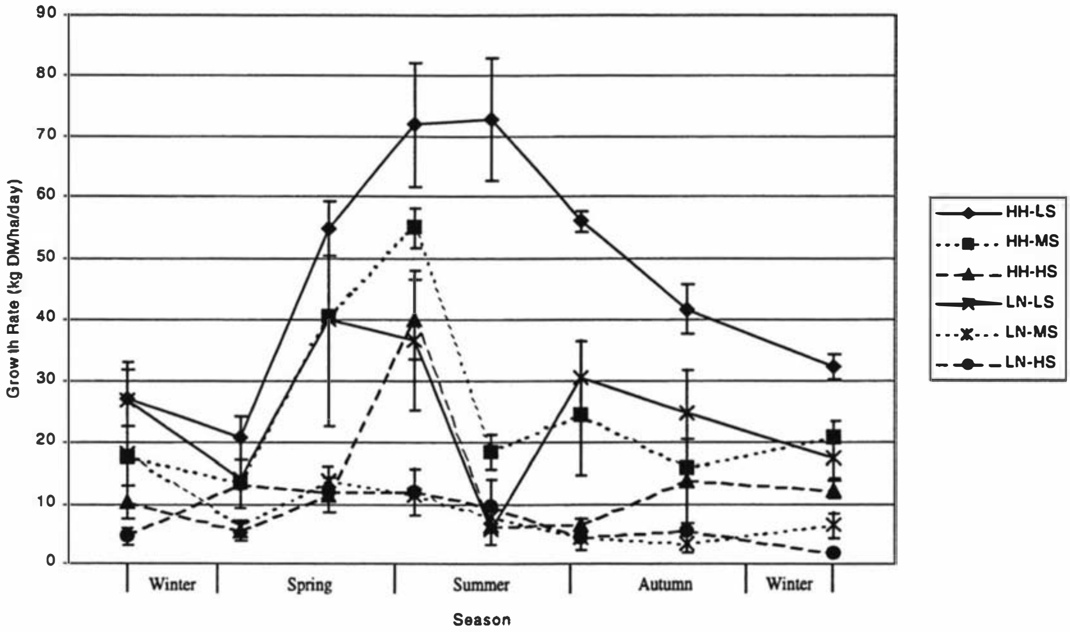

Figure 2 Growth rate of the pasture in three slope categories (LS Low slope, MS Medium slope, HS High slope) of fertile (HH) and infertile (LN) paddocks in the hill country.

Slope category-species interaction

The interaction between slope and species showed that grazing selection for *A. odoratum* significantly diminished in MS from Autumn to Winter. From Winter to Spring grazing selection varied for *A. capillaris* in the LS and *A. odoratum* in the MS, such that the probability of being grazed for both species significantly increased. The probability of being grazed tended (P<0.1) to increase for *A. capillaris* in the HS from Summer to Autumn and for *L. perenne* (P<0.1) in the MS from Autumn to Winter (Table 2).

Table 1 Probability of marked tillers being grazed within season and overall.

	Summer		Autumn		Winter		Spring		Year	
FT[3]		s.e.m.		s.e.m.		s.e.m.		s.e.m.		s.e.m.
LN	0.103 a[1]	0.026	0.253 a	0.038	0.236 a	0.037	0.267 a	0.038	0.234 a	0.037
HH	0.383 b	0.042	0.296 a	0.040	0.367 b	0.042	0.530 b	0.043	0.409 b	0.043
Significance[2]	***		n.s.		***		***		***	
Slope[4]		s.e.m.		s.e.m.		s.e.m.		s.e.m.		s.e.m.
LS	0.383 a	0.056	0.379 a	0.056	0.370 a	0.055	0.572 a	0.057	0.441 a	0.057
MS	0.242 a	0.040	0.283 ab	0.042	0.306 a	0.043	0.403 b	0.046	0.332 b	0.044
HS	0.100 b	0.034	0.166 b	0.043	0.244 a	0.049	0.233 c	0.049	0.197 c	0.046
Significance[2]	***		**		n.s.		***		***	
SPP[5]		s.e.m.		s.e.m.		s.e.m.		s.e.m.		s.e.m.
Ac	0.194 a	0.037	0.248 a	0.041	0.239 a	0.040	0.371 a	0.045	0.279 a	0.042
Ao	0.133 a	0.039	0.228 a	0.048	0.254 ab	0.050	0.315 a	0.053	0.263 a	0.051
Lp	0.444 a	0.057	0.355 a	0.055	0.427 b	0.057	0.488 a	0.057	0.413 b	0.057
Significance[2]	n.s.		n.s.		‡		n.s.		*	

[1] Different letters in each section of each column indicate statistical differences amongst factors

[2] ‡ $P<0.07$; * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s. Not significant ($P>0.1$).

[3] FT Field treatment (phosphorus fertilisation and stocking rate); LN Low-No; HH High-High.

[4] LS Low slope; MS Medium slope; HS High slope.

[5] SPP Plant species; Ac *Agrostis capillaris*; Ao *Anthoxanthum odoratum*; Lp *Lolium perenne*.

Main effects

The results of the analysis of the probability of marked tillers being grazed between consecutive seasons at field treatment level showed that from Summer to Autumn the probability of the marked tillers being grazed significantly increased in the LN paddock. In the HH paddock there was only a significant increase in the probability of being grazed from Winter to Spring (Table 2).

At the slopes category level, the defoliation probability on LS and MS increased from Winter to Spring and the probability of the marked tillers being grazed on the HS increased from Summer to Autumn. From Autumn to Winter the probability of the HS being grazed showed a tendency to increase ($P<0.1$) (Table 2).

Table 2 Change in the probability of the marked tillers being grazed from one season to the next.

	Summer-Autumn	Autumn-Winter	Winter-Spring
FT[2]			
LN	0.150 (*) [1]	-0.017 (n.s.)	0.031 (n.s.)
HH	-0.087 (n.s.)	0.071 (n.s.)	0.163 (*)
SLP[3]			
LS	0.004 (n.s.)	0.009 (n.s.)	0.202 (*)
MS	0.041 (n.s.)	-0.023 (n.s.)	0.071 (*)
HS	0.066 (*)	0.078 (†)	-0.036 (n.s.)
SPP[4]			
Ac	0.054 (*)	-0.009 (n.s.)	0.132 (†)
Ao	0.095 (†)	-0.026 (n.s.)	0.061 (n.s.)
Lp	-0.089 (n.s.)	0.072 (†)	0.061 (n.s.)
FT*SLP			
LN-LS	0.155 (*)	0.016 (n.s.)	0.081 (n.s.)
LN-MS	0.155 (*)	-0.097 (*)	0.050 (†)
LN-HS	0.092 (n.s.)	0.049 (†)	-0.074 (*)
HH-LS	-0.163 (n.s.)	-0.035 (n.s.)	0.325 (*)
HH-MS	-0.111 (n.s.)	0.121 (†)	0.137 (n.s.)
HH-HS	0.041 (n.s.)	0.107 (n.s.)	0.052 (n.s.)
SLP*SPP			
LS-Ac	0.047 (n.s.)	-0.060 (n.s.)	0.298 (*)
LS-Lp	-0.055 (n.s.)	0.042 (n.s.)	0.107 (n.s.)
MS-Ac	0.027 (n.s.)	-0.046 (n.s.)	0.137 (n.s.)
MS-Ao	0.125 (n.s.)	-0.025 (*)	0.107 (*)
MS-Lp	-0.108 (n.s.)	0.122 (†)	0.018 (n.s.)
HS-Ac	0.087 (†)	0.078 (n.s.)	-0.038 (n.s.)
HS-Ao	0.046 (n.s.)	0.077 (n.s.)	0.017 (n.s.)

[1] † Represent significant differences at $P<0.1$; * $P<0.05$; n.s. Not significant ($P>0.1$).

[2] FT Field treatment (phosphorus fertilisation and stocking rate); LN Low-No; HH High-High.

[3] SLP Slope; LS Low slope; MS Medium slope; HS High slope.

[4] SPP Plant species; Ac *Agrostis capillaris*; Ao *Anthoxanthum odoratum*; Lp *Lolium perenne*.

The probability of *A. capillaris* being grazed increased significantly from Summer to Autumn. A tendency in increasing (P<0.1) the grazing selection of *A. capillaris* was present from Winter to Spring, for *A. odoratum* from Summer to Autumn and for *L. perenne* from Autumn to Winter (Table 2).

Leaf length-defoliated tillers relationship

Agrostis capillaris and *A. odoratum* had similar leaf lengths but were significantly shorter than *L. perenne* during Summer (P<0.001), Winter (P<0.001) and Autumn (P<0.001). During Autumn leaf lengths were similar for *L. perenne* and *A. odoratum*, which were significantly longer (P<0.0001) than those of *A. capillaris* (Table 3).

Table 3 Leaf length (mm) of the marked tillers of *A. capillaris*, *A. odoratum* and *L. perenne* within season.

	Summer		Autumn		Winter		Spring	
FT[3]		s.e.m.		s.e.m.		s.e.m.		s.e.m.
LN	21.8 a[1]	1.35	14.0 a	0.93	19.2 a	0.82	23.2 a	0.79
HH	22.3 a	0.98	14.6 a	0.86	17.5 a	0.73	22.0 a	0.66
Significance[2]	n.s.		n.s.		n.s.		n.s.	
Slope[4]		s.e.m.		s.e.m.		s.e.m.		s.e.m.
LS	18.2 a	1.52	14.9 a	1.18	17.9 a	1.04	21.9 a	0.95
MS	19.4 a	1.38	14.4 a	0.96	18.0 a	0.93	23.8 a	0.76
HS	28.5 b	1.80	13.5 a	1.31	19.1 a	1.08	22.1 a	1.08
Significance[2]	***		n.s.		n.s.		n.s.	
SPP[5]		s.e.m.		s.e.m.		s.e.m.		s.e.m.
Ac	20.3 a	1.31	11.0 a	0.92	15.6 a	0.82	19.4 a	0.76
Ao	18.1 a	2.15	14.8 b	1.24	17.4 a	1.13	19.2 a	1.00
Lp	27.8 b	1.77	17.1 b	1.33	22.0 b	1.06	29.2 b	0.98
Significance[2]	***		**		***		***	

[1] Different letters in each section of each column indicate statistical differences amongst factors.

[2] ** P<0.01; *** P<0.001; n.s. Not significant (P>0.1).

[3] FT Field treatment (phosphorus fertilisation and stocking rate); LN Low-No; HH High-High.

[4] LS Low slope; MS Medium slope; HS High slope.

[5] SPP Plant species; Ac *Agrostis capillaris*; Ao *Anthoxanthum odoratum*; Lp *Lolium perenne*.

Table 4 Leaf length (mm) of the marked tillers of *A. capillaris*, *A. odoratum* and *L. perenne* grazed and ungrazed within season.

	Summer		Autumn		Winter		Spring	
Leaf Length[3]		s.e.m.		s.e.m.		s.e.m.		s.e.m.
No Gr.	21.4 a[1]	0.84	15.1 a	0.82	16.0 a	0.72	22.5 a	0.67
Gr.	22.7 a	1.35	13.4 a	0.99	20.7 b	0.84	22.6 a	0.79
Significance[2]	n.s.		n.s.		***		n.s.	
SLP[5]*LL		s.e.m.		s.e.m.		s.e.m.		s.e.m.
LS- No Gr.	18.7 a	1.60	16.1 a	1.59	14.9 a	1.40	22.2 ab	1.30
LS- Gr.	17.6 a	2.57	13.8 a	1.75	20.8 a	1.53	21.6 b	1.40
MS-No Gr.	20.1 a	1.38	15.1 a	1.20	15.6 a	1.06	22.0 b	0.97
MS- Gr.	19.0 a	2.39	13.7 a	1.49	20.5 a	1.52	25.7 a	1.17
HS- No Gr.	25.5 a	1.61	14.2 a	1.62	17.5 a	1.42	23.5 ab	1.32
HS- Gr.	31.4 a	3.25	12.8 a	2.07	20.7 a	1.62	20.6 b	1.71
Significance[2]	n.s.		n.s.		n.s.		*	
SPP[6]*LL		s.e.m.		s.e.m.		s.e.m.		s.e.m.
Ac-No Gr.	17.9 a	1.11	11.1 a	1.18	13.7 a	1.04	19.9 a	0.97
Ac- Gr.	22.6 a	2.37	10.9 a	1.40	17.4 a	1.27	18.8 a	1.19
Ao- No Gr.	18.5 a	1.97	16.3 a	1.62	14.5 a	1.42	19.5 a	1.32
Ao- Gr.	17.7 a	3.80	13.2 a	1.87	20.3 a	1.76	19.0 a	1.49
Lp- No Gr.	27.9 a	1.92	18.1 a	1.62	19.8 a	1.43	28.3 a	1.30
Lp- Gr.	27.7 a	2.98	16.1 a	2.11	24.3 a	1.55	30.1 a	1.46
Significance[2]	n.s.		n.s.		n.s.		n.s.	
FT[4]*SLP*LL		s.e.m.		s.e.m.		s.e.m.		s.e.m.
LN-LS-No Gr.	17.9 a	2.10	14.2 a	2.15	12.8 d	1.89	23.1 a	1.76
LN-LS- Gr.	17.4 a	3.47	12.5 a	2.28	18.7 abc	2.03	21.0 a	1.96
LN-MS- No Gr.	22.3 a	2.09	13.0 a	1.73	14.5 cd	1.52	22.1 a	1.37
LN-MS- Gr.	20.7 a	5.33	13.4 a	2.17	24.6 a	2.62	25.7 a	1.91
LN-HS- No Gr.	27.0 a	2.17	15.9 a	2.24	20.0 ab	1.97	26.8 a	1.83
LN-HS- Gr.	25.4 a	5.09	15.0 a	3.08	24.6 a	2.27	20.4 a	2.75
HH-LS- No Gr.	19.5 a	2.10	18.0 a	2.15	17.0 bcd	1.89	21.4 a	1.76
HH-LS- Gr.	17.8 a	2.69	15.1 a	2.40	22.9 a	2.03	22.2 a	1.78
HH-MS- No Gr.	18.0 a	2.10	17.2 a	1.67	16.7 bcd	1.47	21.9 a	1.37
HH- MS- Gr.	17.2 a	2.71	13.9 a	2.00	16.4 bcd	1.52	25.6 a	1.37
HH-HS- No Gr.	24.0 a	2.09	12.5 a	2.15	15.0 bcd	1.89	20.2 a	1.76
HH-HS- Gr.	37.4 a	3.50	10.6 a	2.59	16.9 bcd	2.09	20.8 a	1.85
Significance[2]	n.s.		n.s.		*		n.s.	

[1] Different letters in each section of column indicate statistical differences amongst factors.

[2] * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s. Not significant ($P>0.1$).

[3] LL Leaf length; No Gr. Leaf length (mm) of ungrazed tiller. Gr. Leaf length (mm) of grazed tiller.

[4] FT Field treatment (phosphorus fertilisation and stocking rate); LN Low-No; HH High-High.

[5] SLP Slope; LS Low slope; MS Medium slope; HS High slope.

[6] SPP Plant species; Ac *Agrostis capillaris*; Ao *Anthoxanthum odoratum*; Lp *Lolium perenne*.

Tillers with greater leaf length were selectively grazed over tillers with shorter leaves only during Winter and Spring (Table 4). During Winter sheep significantly ($P<0.05$) selected tillers with longer leaves only in LN-LS, LN-MS and HH-LS. During Spring sheep grazed tillers with longer leaves rather than tillers with shorter leaves only in MS ($P<0.05$).

DISCUSSION

Technique used to Evaluate Grazing

The methodology used in the present study to evaluate selective grazing by sheep using marked tillers in a pasture have been used previously by Hodgson (1966), Hodgson and Ollerenshaw (1969), Clark *et al.* (1984), Chapman *et al.* (1984) and Betteridge *et al.* (1994). However, it has been recognised that this technique has disadvantages, for example tiller identification and recording is very time-consuming and there is the risk of losing the markers or being unable to find the marked tillers (Hodgson, 1966; Hodgson and Ollerenshaw, 1969). These problems did occur in the present study but there were very few lost markers.

Pasture Production

The microrelief of the faces of the hill generated contrasts in soil characteristics over short distances (Chapter 3). These contrasting features of the soil had a strong influence on total pasture production (Chapter 4) and pasture growth through the year (Figure 1 and Figure 2). Overall, as the angle of the slope increased, soil fertility, soil moisture retention and pasture production decreased (Chapter 3), as well as field condition (Chapter 4) and pasture growth rate (Figure 2). Condition is the actual state of an ecosystem in relation to the ideal state according to the use and management of the ecosystem (Dyksterhuis, 1949; Noble, 1973; Archer and Smeins, 1991; Gastó *et al.*, 1993). Soil features, botanical composition and yield vary according to changes in condition (Archer and Smeins, 1991; Milton *et al.*, 1994; Chapter 4). The results of the present study when considered with information on pasture and soil reported in Chapters 3 and 4 suggest that growth of pasture during Summer and Autumn has a close relationship to field condition. In this way, a better field condition did sustain a pasture with a high percentage of species such as *H. lanatus*, *L. perenne* and *P. trivialis*, which grew for longer into the Summer, had a better re-growth in Autumn and a better Spring growth (Figure 2). The pasture growing in the LS microsites showed these characteristics.

Grazing Analysis at Paddock Level

Differences at paddock level in the probability of the marked tillers being grazed were most likely due to both differences in stocking rate between the HH (15.8 sheep/ha) and the LN paddocks (6.2 sheep/ha) and pasture growth rate. These differences in stocking rate reflected the differences in pasture production of the two paddocks, with the HH paddock producing 10,285 kg DM/ha/year, while the LN produced 4,280 kg DM/ha/year (Chapter 4). Differences in dry matter production within paddocks were strongly influenced by differences in soil fertility and moisture of the microsites, features that have been analysed in Chapter 3. Furthermore, the pasture of the HH paddock showed higher growth rates (Figure 1), which would allow a faster recovery after being grazed and thus the pasture on the HH paddock could be grazed more frequently. An earlier study using the same paddocks (Clark *et al.*, 1984) measured defoliation frequency of *L. perenne* and *A. capillaris* and reported similar results for Winter and Spring. Moreover, Chapman *et al.* (1983) reported that *L. perenne* and *A. capillaris* growing in the HH paddock tended to have higher leaf extension rates than those in the LN, such that tillers grown in the HH paddock would reach a height suitable for grazing sooner than those in the LN paddock (Clark *et al.*, 1984).

Microrelief and Species Selection through the Year

Results from the present study suggest that sheep grazing behaviour had a strong relationship with pasture mass through the year. Because of this, sheep showed a contrasting grazing behaviour during Winter relative to that in Spring. However, to better understand this contrasting behaviour, it is necessary to analyse the behaviour of sheep through the year.

During Summer grazing sheep discriminated according to slope categories. The more accessible slope categories (LS and MS), that also were the slopes that presented the highest pasture growth, were the slopes that sheep grazed more frequently during this season (Table 1). During Summer the sheep grazing area also included the LS and

MS, which may have been related to the lower pasture production in Summer in relation to Spring.

The grazing behaviour of sheep during Autumn was slightly different to that registered during Summer; even when grazing frequency increased in the HS, sheep showed selectivity for the low and medium slopes. These results suggest that pasture mass in the accessible areas (LS and MS) diminished during Autumn. Therefore, sheep increased the grazing area to less accessible slopes. The significant increase in *A. capillaris* defoliation and the tendency towards an increase in the defoliation of *A. odoratum* were also indications that the sheep were under a greater pressure for pasture during Autumn than in Summer.

During Winter sheep enlarged the grazing area, due to the low pasture mass, especially increasing the grazing pressure on HS (Table 1 and Table 2). In the LN paddock sheep modified their grazing behaviour from Autumn to Winter. The diminution in the grazing frequency in LN-MS was an indicator of the low pasture mass in that category of slope. In the LN paddock during the Autumn, pasture grew mainly in LS but very little in MS and HS (Figure 2). Also the grazing pressure on LS and MS increased during the Autumn (Table 2). Therefore, these results also would explain why the pasture mass in LN-MS decreased in Winter, and consequently the change in the grazing behaviour of sheep.

During Winter sheep enlarged their grazing area, but at the same time selective grazing for species increased (Table 1). *Lolium perenne* was grazed significantly more than *A. capillaris* but at similar level to *A. odoratum*. Therefore, because of the low pasture mass during Winter, sheep responded by increasing their grazing areas, including the less accessible steep slopes, such that grazing selection at slope level disappeared. However, grazing selection at species level increased, suggesting that there were differences between species, possibly related to leaf length. Sheep selected tillers that had longer leaves mainly in Winter, but not in Summer or Autumn (Table 4). Selection between species may also have been related to quality and this hypothesis needs further investigation. Stuth (1991) reported that sheep selected the best quality material from that available during periods when pasture mass was restricted. Stuth (1991) indicated that in these periods the competition between grazing animals increases, total grazing time increases and the herd fragments into smaller feeding groups which graze on a larger area, such that the unexploited feeding areas diminish, as happened with the pasture of the HS category.

Grazing behaviour of sheep changed during Spring in relation to behaviour in Winter. Selection increased for LS and MS, mainly due to the increase in grazing frequency on HH-LS ($P<0.05$) and LN-MS ($P<0.1$) microsites. Also during this period, grazing pressure significantly decreased in LN-HS. All of these changes in sheep grazing behaviour indicate that grazing pressure declined on the steep slopes, significantly increasing the pressure on the LS category (Table 1).

The highest pasture growth rates of the year were measured during Spring (Figure 2). Also during this period, species of the naturalised pasture may have had a good nutritional quality, measured as digestibility and protein content (Balocchi and López, 1996), though no nutrient analyses are conducted for the current study. Clark and Brougham (1979) reported that hill country pastures composed mainly of 'low fertility tolerant' species, under high grazing pressure can reach similar values of digestibility of the dry matter to lowland pastures.

The high fertility levels measured in the soil of the LS microsites (Chapter 3) may also have had an effect on pasture quality especially during Spring. The movement of nutrients across microsites by sheep through faeces and urine (Gillingham and During, 1973; Saggar *et al.*, 1990; Lambert *et al.*, 2000) will generate a high soil total nitrogen content as occurred in the LS microsites (Chapter 3). This would be expected to improve the quality of the species in LS in relation to the MS and HS microsites, especially the protein content. This hypothesis warrants further investigation.

The LS microsites, due to their slope, were easy to graze and in Spring had a high pasture mass and good quality pasture as was reported in the study by Clark *et al.* (1982). This would explain the selection by sheep for these types of microsites during Spring and also the reason that sheep did not discriminate between longer and shorter leaves of the grazed tillers in LS. However, in MS leaf length was relevant in the selection of the grazed tillers by sheep.

All selective grazing at species level disappeared during Spring due to an increase in the selection for *A. capillaris*, especially in LS, and *A. odoratum*, in MS, relative to *L. perenne* (Table 2), such that the three species showed similar probabilities of being grazed during this period. Both *A. capillaris* and *A. odoratum* may present good quality features during Spring (Ballochi and López, 1996).

Factors Influencing Site and Species Selection

The high heterogeneity of these grasslands implies that sheep are constantly selecting, that is, accessibility of the components of the sward affect grazing decisions (Hodgson *et al.*, 1994). The pattern of behaviour shown by sheep in the present study is in agreement with that reported by Stuth (1991) who recognised five hierarchical levels regarding the process of animal diet selection by grazing animals: landscape, plant community, patch, feeding station and plant (Stuth, 1991).

Sheep used the angle of the slope as a first filter of selection. Pasture that grew on steeper slopes was less frequently grazed by sheep, while with diminishing slope, sheep increased the grazing frequency, such that LS microsites were more frequently grazed than the MS, and HS was grazed the least (Table 1). However, available pasture also affected grazing decisions, such that sheep grazed preferentially the LS microsites when pasture availability was high, otherwise sheep enlarged the grazing area towards the MS and HS microsites. Therefore, the behaviour pattern would most likely have been the result of the combination between accessibility for grazing and position with respect to slope angle and available pasture. According to the interaction between occupancy time:area ratio and utilisation:herbage mass area ratio (Stuth, 1991), the slope categories can be classified as preferred (LS), low impact (MS), and avoided (HS).

The results suggest that LS microsites were most intensely grazed over the whole year, receiving a higher grazing pressure than the other categories of slope, especially in comparison with HS. As a consequence of this, the structure of the sward in LS microsites should be different from the sward that grew in HS microsites. The LS microsites would be expected to present a sward that grows closer to the ground, and have been shown to have a higher tiller density than HS

(Lambert *et al.*, 1986b), which lends support to this hypothesis. On the other hand, the sward that grew on the HS microsites would be expected to grow more upright with a lower tiller density. These suggestions are supported by the results of Chapman *et al.* (1983), who reported that the sward that grew in LS had a higher tiller density than the sward on HS, while MS swards had a tiller density intermediate to the other two slope categories. Chapman *et al.* (1983) also reported that the tillers in the LS sward had higher growth rates than the tillers in the other slope categories. This was also the case for pasture that grew in the LS in the present study.

The overall analysis for the whole year at species level showed that sheep grazed *L. perenne* in preference to *A. capillaris* and *A. odoratum*. Stuth (1991) indicated that higher successional species receive more selective pressure and are selected by grazing animals regardless of the abundance and the presence of other species, such that these species have the greater probability of being grazed, as was the case of *L. perenne* in the present experiment.

Earlier studies have reported that sheep select their diets at species level (Edwards *et al.*, 1993; Laca and Demment, 1996), and also that animals may select at individual plant and plant-part levels (Tainton *et al.*, 1996). In this way, Clark *et al.* (1984) reported for hill country pasture that *L. perenne* had a higher defoliation rate by sheep than *A. capillaris*. In another experiment, Grant *et al.* (1984) reported that sheep discriminated in favour of *L. perenne* instead of *Poa annua* and other grasses. De Leeuw and Bakker (1986) reported that sheep grazing in a naturalised pasture discriminated between different communities of species such as *A. capillaris*, *Holcus lanatus* and *Juncus effusus* amongst others. Laidlaw (1983) and Ridout and Robson (1991) indicated that sheep grazing mixed pastures preferred legumes to grasses. All this evidence supports the hypothesis that sheep can distinguish between species to graze and maintain a mixed diet between legumes and grasses (Parsons *et al.*, 1994). Furthermore, sheep adjust their sward strata grazing according to the changing distribution of the species in the sward between seasons (L'Huillier *et al.*, 1986). For example, in a mixed sward of *T. repens* with *L. perenne*, sheep were able to select species and different parts of individual plants from the different grazed strata (Milne *et al.*, 1982). In the present study sheep did not consistently discriminate between tillers according to leaf length through the year. This tiller selection for grazing appeared to be affected by other variables, such as tiller length, available pasture and tiller quality. Tiller length is defined as the distance from ground to the tip of the longest lamina (Clark *et al.*, 1984). Clark *et al.* (1984) measured different tiller attributes, such as leaf length and tiller length, and found that tiller length had the main influence on total leaf length removed by grazing sheep. Whether tiller length and quality have an influence on the selection by sheep needs further investigation.

Selective grazing by sheep has consequences for the sward, such as increases in tiller density, and the dominant species can change according to the grazing pressure applied (Briseño de la Hoz and Wilman, 1981). In naturalised pastures, where there are several species competing for resources and light (Tilman, 1994), selective grazing can become an important factor influencing species dominance in the field, such that the presence of highly defoliated species diminishes, while species that have low selectivity increase (Briske, 1991; Brown and Stuth, 1993; Briske and Richards, 1994). This was also reported to occur in a study of sheep grazing described by Silvertown *et al.* (1994), where firstly the sheep selected *L. perenne*, then *Poa pratensis* and finally *Festuca rubra.* The consequence of this was that the proportion of *L. perenne* in the pasture diminished, while *F. rubra* increased. Wilman *et al.* (1995) also demonstrated that set stocked sheep provoked changes in species presence in a naturalised pasture. However, in this experiment *Poa trivialis* and *A. odoratum* increased, while *L. perenne*, *A. capillaris* and *H. lanatus* maintained their presence, and *C. cristatus* and *T. repens* decreased. Therefore, sheep can provoke changes in species dominance in the field through grazing selection. These changes would be related to changes in the comparative advantages between species in factors such as uptake of available resources (Thornton and Millard, 1996), replacement of photosynthetic grazed areas (Briske, 1991), availability of active meristems after defoliation and levels of carbohydrate reserves (Briske and Richards, 1994). Further investigation is required to determine whether this pattern of selection exacerbates the contrast between microsites in terms of vegetation over time, acting to emphasise the effect of soil attribute differences.

CONCLUSIONS AND IMPLICATIONS

Sheep selectively grazed hill country pastures, discriminating between slope categories and species. Selective grazing varied through the year according to the available pasture. Sheep discriminated according to accessibility of the grazing area when available pasture was high, grazing mainly the microsites easy to graze and to access (LS). When available pasture was low, sheep enlarged the grazing areas towards the less accessible microsites, such as HS, with no discrimination according to slope category; however, sheep showed selectivity at the species level.

It appears that grazing preference of sheep for slope and species can produce different structured pastures in the extremes of the slope category with different plant dynamics and survival strategies. Furthermore, sheep appear to be able to affect species dominance in the sward through selective grazing. It would be possible, therefore, that sheep, through the same mechanisms (selective grazing), would segregate ecotypes, especially within a contrasting environment such as in the hill country of New Zealand. This hypothesis requires testing.

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CHAPTER 6

Ecology of pastoral communities in a heterogeneous environment.

IV. Plasticity and ecotype segregation of grass species.

Soil attributes and grazing sheep have been shown to be important environmental variables affecting hill country pasture in studies reported in Chapters 3, 4 and 5. Plant species and groups of plant species were shown to be segregated along the range of environments generated by soil attributes associated with the hill country microrelief. Slope, water holding capacity, water conductivity, bulk density, soil compressibility, soil rebound after compression, soil total nitrogen and Olsen-P were soil features that strongly influenced the variation in hill country pasture. However, some species were present across the whole range of soil conditions. Moreover sheep were shown to selectively graze the different slope categories and species according to the accessibility of the grazing area, available pasture and plant species. The objective of the study reported in this Chapter was to evaluate, in five species of grass, whether ecotype segregation had occurred in response to environmental pressures or whether plants had tolerated environmental changes through plasticity.

ABSTRACT

To evaluate whether ecotype segregation had occurred in response to environmental constraints or whether plants had tolerated environmental changes through plasticity, physiological and morphological attributes of genotypes from contrasting microsites were analysed. *Agrostis capillaris* (Ac), *Anthoxanthum odoratum* (Ao), *Cynosorus cristatus* (Cc), *Holcus lanatus* (Hl) and *Lolium perenne* (Lp) were collected from hill country fertile and infertile paddocks that had received long-term differentiated management. *Lolium perenne* cv. Super Nui (SN) and *L. perenne* Hill Country Selection (HCS) were used as controls. The material that was collected was grown in a glasshouse in pots under five levels of soil phosphorus and three of soil nitrogen. Total dry matter production, height, plant architecture, plant horizontal expansion and leaf growth were measured. Ac did not show differences between genotypes. Genotypes of Lp showed physiological and morphological differences. Genotypes of Ao and Cc showed physiological differences. Genotypes of Hl did not show consistent differences. It was concluded that hill country environmental constraints have segregated Lp, Ao and Cc ecotypes. Differences shown by Hl genotypes did not clearly show ecotype differentiation. Genotypes of Ac showed a high plasticity with no ecotype differentiation.

INTRODUCTION

The diversity-stability hypothesis states that species have different ecological characteristics and that ecosystems that have larger species diversities have a higher probability of containing species that could successfully survive under a given environmental perturbation (Tilman and Downing, 1994). Furthermore, there is a strong positive relationship between ecosystem diversity, resistance and resilience, such that a more diverse ecosystem will be more resistant to variation when it is under an environmental perturbation and will recover faster (resilience) after the disturbance cessation than will a less diverse ecosystem (Tilman and Downing, 1994). However, ecosystem stability is at the expense of species stability with populations of individual species fluctuating widely under environmental perturbations (Tilman *et al.*, 1996).

Noble (1973), Gastó *et al.* (1993) and Pieper (1994) have used the dynamics of the pasture species when the pastoral ecosystem is affected by environmental constraints to measure field condition. Species or groups of species (functional groups or functional types) increase or decrease in frequency and production under a given intensity of environmental constraint (Díaz and Cabido, 1997; Díaz Barradas *et al.*, 1999; Hadar *et al.*, 1999; Chapter 4). The presence and phenotypic expression of species that are colonising a given site change when the site is under different environmental constraints (Archer and Smeins, 1991; Wedderburn and Pengelly, 1991; Chapter 4). The resistance to this change is related not solely to the species' diversity, but also to the diversity within species (ecotypes and phenotypic plasticity), such that specific individual plants are able to tolerate the environmental constraint, survive and re-colonise the site. Therefore, ecosystem stability and species diversity could be analysed at a within species level and this analysis could demonstrate an important mechanism of survival and colonisation for species (Snaydon, 1970; Snaydon and Davies, 1976; Snaydon and Davies, 1982; Meharg *et al.*, 1994).

An ecotype has been defined as a subset of individual plants within a species, which have genetic differences resulting in differences in characteristics such as growth patterns and environmental tolerances between populations. Thus the genetic differences are reflected in survival under specific environmental conditions (Begon *et al.*, 1996). Plant plasticity has been defined as the capability of an individual genotype to express phenotypic variation as a response to particular environmental conditions, such that the plant is able to survive and reproduce (Sultan, 1987).

The presence of ecotypes (Snaydon and Davies, 1982; McCain and Davies, 1983; Karlsen, 1988; Meharg *et al.*, 1994) or genotypes with high plasticity (Rapson and Wilson, 1988) would allow specific compatible individuals to persist when changes occur to environmental conditions in a specific ecosystem. High diversity within species would increase the probability of having genetically compatible plants in relation to the new environmental conditions and would be as important as high species diversity for the stability of the ecosystem.

The success of a particular plant genotype in an ecosystem depends on the result of the relationship between the plant and its environment. Thus, the survival, performance and persistency of one genotype will depend on the degree of compatibility between the specific plant and its particular environment (Tilman, 1990). This selection pressure leads to genetic changes that occur over generations (Snaydon, 1970; Snaydon and Davies, 1972; Snaydon and Davies, 1976; Snaydon and Davies, 1982). In this manner, plant material may become more adapted to a particular environment, expressing this adaptation through plasticity (Rapson and Wilson, 1988) or ecotypes (Snaydon and Davies, 1982).

Therefore, the hypotheses of the present work were:
A- Environmental factors would exert a selection pressure on field species causing segregation of ecotypes within each species.
B- Plants species would prosper under different selection pressures if they have adequate plasticity, with no ecotype segregation.

The objectives were to determine the presence of ecotype differentiation and phenotypic plasticity in plant species colonising analogous sites but with contrasting field condition. This was done through physiological and morphological analysis of plant features.

MATERIALS AND METHODS

Site

AgResearch's Ballantrae Research Station is located close to Palmerston North, New Zealand, and presents the typical Hill Country micro-topographical relief (Rumball and Esler, 1968). The microrelief can be classified into three categories of slopes: 1-12° (low slope, LS), 13-25° (medium slope, MS) and >25° (high slope, HS) from the horizontal (Lambert *et al.*, 1983).

Phosphorus Fertilisation

A fertilisation-grazing experiment has been carried out on Ballantrae Station for 21 years, where one paddock, termed "High-High" (HH), received an average of 625 kg of superphosphate/ha/yr from 1975 to 1980 and since 1980 this paddock has received 375 kg superphosphate/ha/yr. Another paddock has received 125 kg of superphosphate/ha/yr between 1975 and 1980, following which it received no further applications of superphosphate. This latter area is termed "Low-No" (LN) (Lambert *et al.*, 1983, Lambert *et al.*, 1996). Notable differences in the available phosphorus content of the soil have been measured between both paddocks (HH=33.2 mg/kg Olsen P; LN=6.3 mg/kg Olsen P; Lambert *et al.*, 1996). The interaction between fertility treatment-stocking rate treatment with slope category has been termed microsite (Chapter 4).

Grazing Management

Continuous sheep grazing has been applied to both paddocks with Romney breeding ewes since 1975. Stocking rate has been adjusted annually, to maintain similar grazing pressure in both paddocks, according to changes in pasture production due to the fertiliser treatments (Lambert *et al.*, 2000). The historical average stocking rate for the LN paddock has been 8.3 ewes/ha, and for the HH paddock has been 14.8 ewes/ha (Lambert *et al.*, 1996).

Pasture Production

Pasture production differed in the HH and LN paddock due to fertiliser treatment. Higher amounts of digestible organic matter produced has been measured in the HH paddock than in the LN (HH=9.2 t DOM/ha/yr; LN=4.4 t DOM/ha/yr; Lambert *et al.*, 1996).

Lambert *et al.* (1983) reported that there is an effect of the slope category on total dry matter production. The low slope produces 1.5 times more dry matter than on the medium slope and 2.0 times more than that on the high slope.

Collection of Parent Material

Based on the information reported by Lambert *et al.* (1983) and Lambert *et al.* (1996) the two extremes of fertility in the range of microsites were identified as the low slope from the High-High paddock and the high slope from the Low-No paddock. The material collected for the present experiment came from these microsites: High High- low slope (HH-LS, fertile microsite) and Low No- high slope (LN-HS, infertile microsite).

In September 1996, swards of three analogous microsites from the fertile paddock and from the infertile paddock were sampled. Table 1 shows soil features of the microsites from which the plants used in this study originated. The methodologies applied to obtain and analyse the soil samples have been described in Chapter 3.

Table 1 Soil characteristics of the microsites where the vegetative material utilised in the genotypes evaluation grew before being placed in glasshouse conditions.

Soil features	Microsites	
	HH-LS	LN-HS
Slope (°)	4	43
Bulk density (g/cm^3)	0.79	0.95
Volumetric soil moisture (100 cm)	0.54	0.36
Total Nitrogen (ppm)	275	75
Phosphorus-Olsen (ppm)	106	11

Five cores were taken from randomised areas from each of the three microsites in each area. The cores were grown in trays in a glasshouse of the Plant Growth Unit of Massey University, Palmerston North, New Zealand. The frequency of the different species was determined, and the most frequent species were found to be *Agrostis capillaris*, *Anthoxanthum odoratum*, *Cynosorus cristatus*, *Holcus lanatus* and *Lolium perenne*. Therefore, the remaining work concentrated on these species.

Management of the Parent Material and Controls

When the plants grown from the original cores reached 10 cm height, the individual species to be studied were isolated, and placed in individual pots with maintenance levels of fertility. During this phase, whenever the average height of the plant material reached 15 cm, all plants were cut to a height of 2 cm. In order to obtain sufficient plant material to establish the experiment, tillers were separated from the plants and grown to produce clones of the original material. The plant material was maintained under these conditions for six months, deemed sufficient time to remove environmental memory.

Seeds of *Lolium perenne* cv. Super Nui and *Lolium perenne* Hill Country Selection were sown in pots and grown under identical conditions as the plants taken from the field, to act as controls. The clones from the plants taken from the field and the controls constituted the parent material for the study.

Individual tillers with roots were removed from the parent material and placed in groups of three in pots. Each pot contained one tiller from the three selected plants per field fertility treatment (HH-LS or LN-HS), such that each tiller within a pot came from a different plant collected from the field replications of each microsite. In total tillers were planted into 45 pots per species per field fertility treatment. A further 45 pots were planted with the control species. Each pot of the controls contained three tillers, where each tiller came from a different plant. Therefore, three plants per control generated the tillers used to establish the control group. The 45 pots for each species per field fertility were divided into three groups of 15 pots with a total of 540 pots overall.

The soil used in the pots was obtained in June 1997, and came from the top 10 cm of an unfertilised site at Ballantrae, that received Roundup (Gliphosate a.i., 6 l/ha) to eliminate the pasture cover one month before collection of the soil. Every pot contained 1.4 kg of dry soil. The soil was analysed by the AgResearch Soil Fertility Service, and had a pH of 5.3 and Olsen P of 5.0 ppm.

Fertilisation Treatments and Management of the Experimental Material

Phosphorus was applied as calcium monophosphate (40% P) at the levels of 0, 50, 100, 150 and 300 mg/kg of dry soil. Nitrogen was applied as calcium nitrate (15.5% N) at the levels of 20, 150 and 300 mg/kg of dry soil. The rest of the macro and micronutrients were applied as used by the Plant Nutrition Group at AgResearch's Ruakura Research Station, New Zealand (Currie, 1996, pers. comm.). All the nutrients were applied as a nutrient solution.

After planting the tillers, 40 mg N/kg of dry soil was applied as a nutrient solution to help establish the tillers. Once all the tillers were established and growing, they were trimmed to a height of 2 cm, after which the phosphorus and nitrogen nutrient solutions were applied in the levels described above and the experiment commenced.

The pots were arranged in three blocks within the glasshouse. Each block contained all of the species and treatments and the pots in each block were randomly distributed. To eliminate the variation produced by the glasshouse's effects within the blocks, the pots were randomly re-arranged within the blocks weekly. The plants were classified according to origins (LN-HS, HH-LS and control group) and genotypes within origins. The experiment was carried out between September and December 1997.

A total of three cuts were made when tillers of the controls reached the fourth leaf stage. The plants were cut to a height of 2 cm and the cut material was retained. After each cut, nitrogen was applied according to the amount of material produced by each pot, in order to maintain the level of nitrogen in each treatment. The nitrogen level applied after cutting was calculated as follows:

$$N\ (g) = (YD * (CPC/100)) / CF$$

Where: N, YD, CPC and CF corresponded to nitrogen to be applied per pot (g), yield (g of dry matter per pot), crude protein content (18%) and a correction factor, respectively. The correction factor of 6.25 was used in this equation, to convert nitrogen to crude protein.

The crude protein content of the material was taken from the average of naturalised grasses actively growing in spring (October - November) (Balocchi and López, 1996) in a wet temperate climate (Gastó *et al.*, 1993).

Measurements

The following variables were measured:

a) Total dry matter production - the harvested material obtained from the three cuts. The material was oven dried at 60°C for 48 hr before measurement.

b) Height to first random contact. Before the third cut, the height of the plants was measured with 6 measurements taken per pot.

c) Plant architecture was considered in the present study as the vertical arrangement of the plant. The angle of the tillers was measured at the end of the experiment to give an indication of the growth habit of the plants. This variable was quantified using a 1-5 scale as used by Wedderburn *et al.* (1989): 1 = <15°; 2 = 15°-35°; 3 = 35°-55°; 4 = 55°-75°; 5 = >75° from the horizontal, where 1 was prostrate and 5 was erect.

d) The expansion of leaves horizontally from the pot was determined at the end of the experiment to evaluate the plants' horizontal structure, with a value given according to the distance from the leaf tip to the pot. A value of 1 corresponded to the tip of the outer most leaves remaining within the pot (the pot had a radius of 6 cm) and 2, 3, 4, 5 and 6 represented distances of 3, 6, 9, 12 and 15 cm, respectively from the pot. This variable was measured in the four quarters of the pots and the average value used in the statistical analysis.

e) Leaf growth was measured by the rate of increasing leaf length. Immediately following the first cut, a new growing tiller was marked in each pot. The growth of the leaves of the marked tillers was recorded every 3 days over 19 days, which was the period of time between the first and second harvest.

The minimum and maximum temperatures in the glasshouse were recorded in two positions daily throughout the study. Growing degree days (GDD) were calculated according to Buxton and Marten (1989) and Onstad and Fick (1983), with a base temperature of 5°C. The length of the leaves was related to the accumulated growing degree days of the period. Only the second leaf was statistically analysed because this was the only leaf which grew to its full length, with its growth unaffected by the preceding cut as may have occurred with the first leaf, and at the end of the period of measurement the second was fully developed in all cases.

Statistical Analysis

All the data was analysed using the SAS program version 6.12. An ANOVA was used to detect statistical significant differences, and when required PDIFF was used as a method to separate means. To obtain a normal distribution the natural logarithms of the data were statistically analysed (Davies, 1971; John and Draper, 1980).

The model fitted to the normally distributed data was:

$$Y = \mu + \alpha_i + \beta_j + \delta(\beta_j)_k + \lambda_l + \phi_m + \lambda\phi_{lm} + \beta\lambda_{jl} + \beta\phi_{jm} + \lambda\delta(\beta_j)_{lk} + \phi\delta(\beta_j)_{mk} + \lambda\phi\delta(\beta_j)_{lmk} + \varepsilon_{ijklm} \qquad (1)$$

Where: α_i = Block; β_j = Origin; $\delta(\beta_j)_k$ = Genotype (Origin); λ_l = Phosphorus; ϕ_m = Nitrogen; $\lambda\phi_{lm}$ = Phosphorus-nitrogen interaction; $\beta\lambda_{jl}$ = Origin-phosphorus interaction; $\beta\phi_{jm}$ = Origin-nitrogen interaction; $\lambda\delta(\beta_j)_{lk}$ = Phosphorus- genotype (origin) interaction; $\phi\delta(\beta_j)_{mk}$ = Nitrogen- genotype (origin) interaction; $\lambda\phi\delta(\beta_j)_{lmk}$ = Phosphorus-nitrogen-genotype (origin) interaction; ε_{ijklm} = Experimental error.

Curves were fitted to the data generated from the length of the leaves using the negative exponential function (Mitscherlich):

$$Y = a\,(1 - be^{(-cx)}) \qquad (2)$$

Where, Y = natural logarithm of leaf length (mm); a, b and c = coefficients; X = growing degree days. At the highest point of the function: Y = a , corresponding to the maximum leaf extension, which happened at the end of the period of evaluation; and the area under the curve for the studied period was calculated by integrating the Mitscherlich function.

RESULTS

Overall Analysis

The plant species differed significantly ($P<0.001$) for all measured variables depending on their origin; fertile microsite, infertile microsite and controls, and according to genotype ($P<0.001$). The different levels of phosphorus and nitrogen applied had a significant ($P<0.001$) effect on the analysed variables with the exception of the effect of phosphorus on leaf length and the effect of nitrogen on architecture which were not statistically significant. There was a significant interaction between phosphorus and nitrogen for yield ($P<0.001$) and the leaf length ($P<0.001$). Origin and phosphorus had a significant interaction for architecture ($P<0.01$), while origin and nitrogen had a significant interaction for horizontal structure ($P<0.05$).

There was a significant interaction between genotype and phosphorus for yield ($P<0.05$) and height ($P<0.01$). Genotype and nitrogen had a significant interaction for yield ($P<0.001$), height ($P<0.001$), horizontal structure ($P<0.001$) and the leaf length ($P<0.05$). The three way interaction between genotype, phosphorus and nitrogen was not significant for all the measured variables.

All of the measured variables showed significant differences ($P<0.001$) between the fertile microsite and infertile microsite except for horizontal structure. In general, plants that came from the fertile microsite had a larger dry matter production than plants from the infertile microsite, but were similar to the controls ($P<0.001$). The plants from the fertile microsite were shorter, producing shorter leaves, but covered a similar area to the material from the infertile microsite. The height ($P<0.001$), horizontal structure ($P<0.001$), architecture ($P<0.001$) and leaf length ($P<0.001$) were significantly greater in controls than the studied genotypes.

Plants that obtained the highest yield were *H. lanatus*, from both types of microsites, and *A. odoratum* from the fertile microsite; while the lowest yields were obtained by *L. perenne* and *C. cristatus* from the infertile microsite (Table 2). The controls had an intermediate dry matter production. *Lolium perenne* cv. Super Nui and *L. perenne* from the infertile microsite were tallest, while *H. lanatus* plants were shortest independent of their origin. *Holcus lanatus* from the infertile microsite, the genotypes of *L. perenne* from the fertile microsite, Hill Country Selection and cv. Super Nui had the largest horizontal structures, while *C. cristatus* had the smallest. From the architecture point of view *C. cristatus*, from both microsites, and *L. perenne* from the infertile microsite were the most erect material, tending to be semi-erect, while *H. lanatus* was at the other extreme, being prostrate. *Lolium perenne* from the infertile microsite and cv. Super Nui were the plants that presented the largest leaf length, while *A. odoratum* and *A. capillaris* from the fertile microsite and *H. lanatus*, independent of origin, presented the shorter leaf length (Table 2).

Table 2 Total yield (ln g DM/pot), height (ln cm), horizontal structure (ln score), architecture (ln score) and leaf length (ln mm) of genotypes from two contrasting environments and its controls tested under glasshouse conditions.

Origin [3]	Genotype [4]	Total Yield	Height	Horizontal Structure	Architecture	Leaf Length
LN	Ac	1.67 de [1]	1.83 ef	1.17 de	1.15 e	4.11 def
LN	Ao	1.81 bc	1.78 ef	1.21 cd	1.27 cd	4.29 c
LN	Cc	1.53 f	1.93 cd	1.00 g	1.60 a	4.23 cd
LN	Hl	1.89 ab	1.40 g	1.33 ab	0.89 f	4.08 ef
LN	Lp	1.50 f	2.13 ab	1.09 ef	1.60 a	4.67 a
HH	Ac	1.75 cd	1.82 ef	1.15 de	1.15 e	4.15 de
HH	Ao	1.90 a	1.75 f	1.14 def	1.22 d	4.00 f
HH	Cc	1.68 de	1.98 c	1.04 fg	1.59 a	4.34 c
HH	Hl	1.93 a	1.38 g	1.28 bc	0.88 f	4.08 ef
HH	Lp	1.74 cd	1.85 de	1.30 ab	1.29 c	4.52 b
Ctr	HCS	1.62 e	2.07 b	1.32 ab	1.47 b	4.49 b
Ctr	SN	1.80 c	2.18 a	1.37 a	1.51 b	4.69 a
Significance [2]		***	***	***	***	***
s.e.m.		0.029	0.031	0.032	0.023	0.048

[1] Different letters in each column indicate statistical differences amongst genotypes.

[2] *** $P<0.001$

[3] LN Low-No	HH High-High	Ctr Control
[4] Ac *A. capillaris*	Ao *A. odoratum*	Cc *C. cristatus*
Hl *H. lanatus*	Lp *L. perenne*	SN *L.perenne* cv. Super Nui
HCS *L. perenne* Hill Country Selection		

Comparing the material with different origin but within species, *A. odoratum*, *C. cristatus* and *L. perenne* showed significant differences for total yield (HH>LN), but not *A. capillaris* and *H. lanatus* (Table 2). Only *L. perenne* showed significant differences for height, with the material from the infertile microsite being taller than the material that grew in the fertile microsite. Analysis of the horizontal structure gave the same results with only *L. perenne* plants showing significant differences, with the material from the fertile microsite covering a larger surface. Architecture was significantly different only for *L. perenne*, where plants from the infertile microsite were semi-erect and plants from the fertile microsite were semi-prostrate. Leaf length showed significant differences for *A. odoratum* and *L. perenne*, where the plants from the infertile microsite produced larger leaves than the plants from the fertile microsite.

Effect of Phosphorus and Nitrogen on Yield

All the species had an increased yield with increasing phosphorus level in the soil (Table 3). *Agrostis capillaris* material from the infertile microsite reached the maximum yield with 100 ppm of phosphorus ($P<0.05$), while the genotype from the fertile microsite had a maximum yield at the level of 150 ppm ($P<0.05$). However, both genotypes always had statistically similar yields ($P<0.05$). The genotypes of *A. odoratum* from both microsites reached the maximum yield with 50 ppm of phosphorus ($P<0.05$) and under all the phosphorus levels showed a statistically similar yield ($P<0.05$). *Cynosorus cristatus* from the infertile microsite reached the maximum yield at 100 ppm of phosphorus ($P<0.05$), while the genotype from the fertile microsite reached a maximum yield at 50 ppm of phosphorus ($P<0.05$). *Cynosorus cristatus* genotypes showed statistically different yields at 0 and 50 ppm of phosphorus ($P<0.05$). The *H. lanatus* genotype from the infertile microsite reached the maximum yield at 50 ppm of phosphorus level ($P<0.05$), while the genotype from the fertile microsite reached a maximum yield at 100 ppm ($P<0.05$). Genotypes of *H. lanatus* had statistically different yields at 0 ppm of phosphorus ($P<0.05$). Genotypes of *L. perenne* reached the maximum yield at the level of 100 ppm of phosphorus ($P<0.05$), but had statistically different yields at 50 , 100 and 150 ppm of phosphorus ($P<0.05$) (Table 3).

Table 3 Effect of five levels of phosphorus on the dry matter production (ln g DM/pot) of genotypes from two contrasting environments and controls grown under glasshouse conditions.

Origin [3]	Genotype [4]	Phosphorus Level (ppm)					s.e.m.
		0	50	100	150	300	
LN	Ac	0.84 bcd [1]	1.79 d	1.85 d	1.88 cd	2.01 bcd	0.078
LN	Ao	0.98 ab	1.92 abcd	2.05 abc	2.04 abc	2.09 abcd	0.037
LN	Cc	0.67 de	1.61 e	1.75 d	1.79 d	1.81 e	0.066
LN	Hl	0.84 bcd	2.09 a	2.18 a	2.12 a	2.24 a	0.050
LN	Lp	0.56 e	1.35 f	1.82 d	1.84 d	1.95 cde	0.091
HH	Ac	0.92 abc	1.87 cd	1.86 cd	1.99 abc	2.09 abcd	0.048
HH	Ao	0.97 abc	2.05 ab	2.16 ab	2.14 a	2.18 ab	0.035
HH	Cc	0.90 bc	1.86 cd	1.78 d	1.91 bcd	1.94 cde	0.061
HH	Hl	1.10 a	2.03 abc	2.14 ab	2.16 a	2.23 a	0.054
HH	Lp	0.70 cde	1.89 bcd	1.98 bc	2.01 abc	2.10 abcd	0.051
Ctr	HCS	0.59 e	1.81 d	1.87 d	1.91 bcd	1.93 de	0.061
Ctr	SN	0.87 bc	1.92 abcd	2.03 abc	2.09 ab	2.11 abc	0.036
Significance [2]		*	*	*	*	*	
s.e.m.		0.078	0.085	0.077	0.090	0.066	

[1] Different letters in each column indicate statistical differences amongst genotypes per phosphorus level.

[2] * P<0.05

[3] LN Low-No HH High-High Ctr Control

[4] Ac *A. capillaris* Ao *A. odoratum* Cc *C. cristatus*
Hl *H. lanatus* Lp *L. perenne* SN *L.perenne* cv. Super Nui
HCS *L. perenne* Hill Country Selection

Agrostis capillaris genotypes had a maximum yield at the maximum level of soil nitrogen (P<0.001) (Table 4), while genotypes of *A. odoratum*, *H. lanatus* and *C. cristatus* reached a maximum yield at 150 ppm of nitrogen in the soil (P<0.001). *Lolium perenne* from the fertile microsite reached a plateau of dry matter production under the 150 ppm level (P<0.001), while the material that came from the infertile microsite had increased yields at each increased soil nitrogen content (P<0.001). Only *C. cristatus* and *L. perenne* had significantly different yields between genotypes at the different nitrogen levels in the soil (Table 4): *Cynosorus cristatus* at 150 and 300 ppm of nitrogen (P<0.001) and *L. perenne* at 20, 150 and 300 ppm of nitrogen (P<0.001).

Table 4 Effect of three levels of nitrogen on dry matter production (ln g DM/pot) of genotypes from contrasting environments and controls grown under glasshouse conditions.

Origin [3]	Genotype [4]	Nitrogen Level (ppm)			s.e.m.
		20	150	300	
LN	Ac	1.10 h [1]	1.88 cd	2.03 b	0.061
LN	Ao	1.35 cde	1.99 abc	2.10 b	0.029
LN	Cc	1.27 defg	1.71 ef	1.60 f	0.051
LN	Hl	1.50 ab	2.05 ab	2.13 ab	0.038
LN	Lp	1.21 fgh	1.58 f	1.73 e	0.071
HH	Ac	1.23 efgh	1.92 bcd	2.09 b	0.037
HH	Ao	1.47 abc	2.09 a	2.14 ab	0.027
HH	Cc	1.34 cdef	1.92 bcd	1.78 de	0.048
HH	Hl	1.52 a	2.07 a	2.20 a	0.042
HH	Lp	1.39 abcd	1.88 cd	1.94 bc	0.039
Ctr	HCS	1.17 gh	1.81 de	1.88 cd	0.047
Ctr	SN	1.36 bcde	1.97 abc	2.08 b	0.028
Significance [2]		***	***	***	
s.e.m.		0.055	0.045	0.046	

[1] Different letters in each column indicate statistical differences amongst genotypes per nitrogen level.

[2] *** P<0.001

[3] LN Low-No HH High-High Ctr Control

[4] Ac *A. capillaris* Ao *A. odoratum* Cc *C. cristatus*
Hl *H. lanatus* Lp *L. perenne* SN *L.perenne* cv. Super Nui
HCS *L. perenne* Hill Country Selection

Effect of Phosphorus and Nitrogen on Height

Lolium perenne was the only species with significant differences in height between genotypes under the different levels of phosphorus (Table 5). These differences were under 0, 50 and 100 ppm of phosphorus, where the plants that came from the infertile microsite were always taller (P<0.01).

Only *L. perenne* showed significant differences in height with nitrogen level ($P<0.01$) for the genotypes that came from both microsites. *Lolium perenne* plants from the infertile microsite were also taller than the plants from the fertile microsite under 150 and 300 ppm of nitrogen in the soil (Table 6).

Table 5 Effect of five levels of phosphorus on the height (ln cm) of genotypes from two contrasting environments and its controls grown under glasshouse conditions.

Origin [3]	Genotype [4]	Phosphorus Level (ppm)					s.e.m.
		0	50	100	150	300	
LN	Ac	1.74 ab [1]	1.82 de	1.92 bc	1.83 d	1.80 d	0.062
LN	Ao	1.55 cd	1.92 cde	1.77 c	1.88 d	1.78 d	0.057
LN	Cc	1.56 bcd	1.99 cd	1.95 bc	2.09 bc	2.03 bc	0.060
LN	Hl	1.14 fg	1.43 f	1.44 d	1.44 e	1.51 e	0.069
LN	Lp	1.71 abc	2.23 a	2.28 a	2.23 ab	2.16 ab	0.066
HH	Ac	1.66 bcd	1.90 cde	1.79 c	1.87 d	1.85 cd	0.081
HH	Ao	1.49 de	1.81 de	1.86 bc	1.83 d	1.76 d	0.073
HH	Cc	1.73 abc	2.01 bc	2.01 b	2.01 cd	2.12 ab	0.076
HH	Hl	1.07 g	1.42 f	1.41 d	1.49 e	1.48 e	0.047
HH	Lp	1.31 ef	1.78 e	1.93 bc	2.14 abc	2.06 b	0.071
Ctr	HCS	1.71 abc	2.04 bc	2.30 a	2.17 abc	2.11 ab	0.088
Ctr	SN	1.87 a	2.19 ab	2.26 a	2.30 a	2.27 a	0.057
Significance [2]		**	**	**	**	**	
s.e.m.		0.070	0.069	0.071	0.073	0.065	

[1] Different letters in each column indicate statistical differences amongst genotypes per phosphorus level.

[2] ** $P<0.01$

[3] LN Low-No HH High-High Ctr Control

[4] Ac *A. capillaris* Ao *A. odoratum* Cc *C. cristatus*
Hl *H. lanatus* Lp *L. perenne* SN *L.perenne* cv. Super Nui
HCS *L. perenne* Hill Country Selection

Effect of Phosphorus and Nitrogen on Horizontal Structure

From the point of view of the horizontal structure, only the *L. perenne* material showed significant differences ($P<0.001$) and that was only with changing nitrogen level. *Lolium perenne* from the fertile microsite always tended to cover a greater surface area than the material that came from the infertile microsite, with significant differences under the 150 and 300 ppm nitrogen level. (Table 7).

Table 6 Effect of three levels of nitrogen on the height (ln cm) of genotypes from contrasting environments and on controls grown under glasshouse conditions.

Origin[3]	Genotype[4]	Nitrogen Level (ppm)			s.e.m.
		20	150	300	
LN	Ac	1.71 de[1]	1.79 c	1.96 cd	0.048
LN	Ao	1.65 e	1.90 bc	1.79 e	0.044
LN	Cc	1.88 bc	1.99 ab	1.91 cde	0.046
LN	Hl	1.43 f	1.34 d	1.40 f	0.054
LN	Lp	2.02 bc	2.14 a	2.21 a	0.051
HH	Ac	1.60 e	1.92 bc	1.93 cde	0.063
HH	Ao	1.62 e	1.79 c	1.84 cde	0.056
HH	Cc	1.87 c	2.09 a	1.98 bc	0.059
HH	Hl	1.39 f	1.38 d	1.35 f	0.036
HH	Lp	1.85 cd	1.85 bc	1.82 de	0.055
Ctr	HCS	1.98 bc	2.09 a	2.12 ab	0.069
Ctr	SN	2.22 a	2.11 a	2.20 a	0.044
Significance[2]		**	**	**	
s.e.m.		0.054	0.049	0.054	

[1] Different letters in each column indicate statistical differences amongst genotypes per nitrogen level.

[2] ** P<0.01

[3] LN Low-No HH High-High Ctr Control

[4] Ac *A. capillaris* Ao *A. odoratum* Cc *C. cristatus*
Hl *H. lanatus* Lp *L. perenne* SN *L.perenne* cv. Super Nui
HCS *L. perenne* Hill Country Selection

Effect of Phosphorus and Nitrogen on Leaf Length

A. odoratum showed statistical differences for length of the leaf (P<0.001) with changing nitrogen level, with the plants that came from the infertile microsite having longer leaves than the plants from the fertile microsite (Table 8). *Anthoxanthum odoratum* showed differences under 20 and 300 ppm.

The equations generated from fitting the Mitscherlich function to leaf growth are shown in Table 9 and Figure 1 and the results of the statistical analysis for the parameters of each curve are showed in Table 10. The resultant curves were similar in shape and only the curve for *A. odoratum* has been presented (Fig. 1).

Table 7 Effect of three levels of nitrogen on horizontal structure (ln score) of genotypes from two contrasting environments and controls grown under glasshouse conditions.

Origin [3]	Genotype [4]	Nitrogen Level (ppm)			s.e.m.
		20	150	300	
LN	Ac	2.21 g [1]	3.51 abcd	4.28 a	0.073
LN	Ao	2.66 def	3.64 abc	3.91 ab	0.043
LN	Cc	2.39 fg	3.00 e	2.71 c	0.083
LN	Hl	3.22 abc	4.01 a	4.24 ab	0.054
LN	Lp	2.97 bcd	3.03 de	2.92 c	0.070
HH	Ac	2.15 g	3.58 abc	4.07 ab	0.046
HH	Ao	2.44 efg	3.42 bcde	3.65 b	0.040
HH	Cc	2.37 fg	3.29 cde	2.91 c	0.061
HH	Hl	2.84 cde	3.97 ab	4.08 ab	0.045
HH	Lp	3.45 ab	3.72 abc	3.88 ab	0.043
Ctr	HCS	3.38 ab	3.83 abc	4.09 ab	0.047
Ctr	SN	3.62 a	3.89 ab	4.31 a	0.035
Significance [2]		***	***	***	
s.e.m.		0.053	0.051	0.057	

[1] Different letters in each column indicate statistical differences amongst genotypes per nitrogen level.

[2] *** $P<0.001$

[3] LN Low-No HH High-High Ctr Control

[4] Ac *A. capillaris* Ao *A. odoratum* Cc *C. cristatus*
Hl *H. lanatus* Lp *L. perenne* SN *L.perenne* cv. Super Nui
HCS *L. perenne* Hill Country Selection

The total area under the curve determined by integrating the Mitscherlich function gives a value for the total growth of the second leaf, and allows a comparison between genotypes of the whole growth process. Although *A. odoratum*, *C. cristatus* and *L. perenne* from the infertile microsite and *C. cristatus* from the fertile microsite and *L. perenne* cv. Super Nui had the largest areas under the curves, there were no significant differences between ecotypes for this variable (Table 10).

Table 8 Effect of three levels of nitrogen on leaf length (ln mm) of genotypes from contrasting environments and controls grown under glasshouse conditions.

Origin [3]	Genotype [4]	Nitrogen Level (ppm)			s.e.m.
		20	150	300	
LN	Ac	3.895 cde [1]	4.166 e	4.263 def	0.080
LN	Ao	4.049 bcd	4.367 de	4.465 cd	0.057
LN	Cc	4.086 abc	4.356 de	4.256 def	0.066
LN	Hl	3.782 ef	4.286 e	4.173 ef	0.053
LN	Lp	4.202 ab	4.903 ab	4.912 a	0.115
HH	Ac	3.930 cde	4.240 e	4.284 def	0.050
HH	Ao	3.625 f	4.238 e	4.123 f	0.085
HH	Cc	4.259 ab	4.365 de	4.395 cde	0.052
HH	Hl	3.845 def	4.215 e	4.170 ef	0.080
HH	Lp	4.166 ab	4.680 bc	4.707 ab	0.083
Ctr	HCS	4.272 ab	4.586 cd	4.618 bc	0.082
Ctr	SN	4.291 a	4.931 a	4.834 ab	0.114
Significance [2]		***	***	***	
s.e.m.		0.103	0.070	0.074	

[1] Different letters in each column indicate statistical differences amongst genotypes per nitrogen level.

[2] *** P<0.001

[3] LN Low-No HH High-High Ctr Control

[4] Ac *A. capillaris* Ao *A. odoratum* Cc *C. cristatus*
Hl *H. lanatus* Lp *L. perenne* SN *L.perenne* cv. Super Nui
HCS *L. perenne* Hill Country Selection

The calculated final leaf length showed that *L. perenne* was the species that produced the longest leaves, and within it, *L. perenne* from both microsites and cultivar Super Nui had the longest leaf length (Table 10). Only *A. odoratum* presented genotype differentiation for this characteristic.

Lolium perenne Genotypes

Comparison of the controls and the genotypes of *L. perenne* showed that *L. perenne* cv. Super Nui did not have a significantly different yield and horizontal spread in relation to the genotype from the fertile microsite, but was different from the genotype from the infertile microsite. However, the height of the plant and the length of the leaves were statistically similar to the genotype from the infertile microsite, and statistically different than the fertile microsite *L. perenne* genotype (Table 2).

Table 9 Adjusted equations for the leaf length (ln mm) development of a full leaf of genotypes from two contrasting environments and controls grown under glasshouse conditions.

Origin	Genotype	Equation	R^2
LN	*A. capillaris*	$LL = 4.2916 (1 - 1.0798 * e^{(-0.0149 GDD)})$	0.917
LN	*A. odoratum*	$LL = 4.4348 (1 - 0.9324 * e^{(-0.0152 GDD)})$	0.935
LN	*C. cristatus*	$LL = 4.3281 (1 - 0.3086 * e^{(-0.0147 GDD)})$	0.977
LN	*H. lanatus*	$LL = 4.2377 (1 - 1.0131 * e^{(-0.0145 GDD)})$	0.813
LN	*L. perenne*	$LL = 5.0566 (1 - 1.0195 * e^{(-0.0109 GDD)})$	0.909
HH	*A. capillaris*	$LL = 4.2526 (1 - 1.0834 * e^{(-0.0188 GDD)})$	0.916
HH	*A. odoratum*	$LL = 4.1668 (1 - 0.9782 * e^{(-0.01494 GDD)})$	0.901
HH	*C. cristatus*	$LL = 4.4345 (1 - 0.3813 * e^{(-0.0136 GDD)})$	0.889
HH	*H. lanatus*	$LL = 4.1944 (1 - 1.0499 * e^{(-0.0168 GDD)})$	0.899
HH	*L. perenne*	$LL = 4.8276 (1 - 1.0960 * e^{(-0.0116 GDD)})$	0.982
Ctr	*L. perenne* HCS	$LL = 4.6341 (1 - 1.1052 * e^{(-0.0146 GDD)})$	0.933
Ctr	*L. perenne* cv. Super Nui	$LL = 4.9097 (1 - 1.1019 * e^{(-0.0135 GDD)})$	0.939

LN Low-No; HH High-High; Ctr Control; HCS Hill Country Selection; LL Leaf Length (ln mm); GDD Growing Degree Days.

The results for yield and architecture of *L. perenne* Hill Country Selection were between the values of the fertile site and infertile microsite *L. perenne* genotypes, and were statistically different in relation to them (Table 2). Height did not statistically differ for the genotypes from the infertile microsite, but were different to those from the fertile microsite *L. perenne* genotype, but leaf length was statistically similar only to *L. perenne* from the fertile microsite (Table 2). Horizontal structure (Table 2) and calculated final leaf length of *L. perenne* Hill Country selection (Table 10) were statistically similar to those from the fertile microsite, but different to those from the infertile microsite.

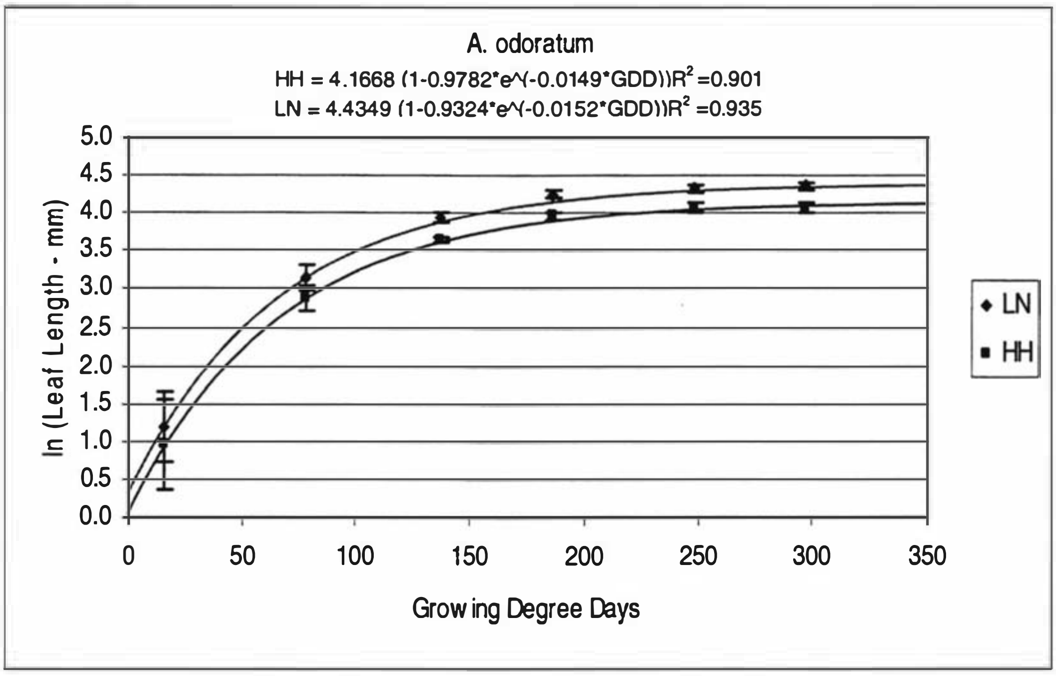

Figure 1 Leaf length (mm) development of a full leaf of two genotypes of *A. odoratum* from two contrasting environments grown under glasshouse conditions.

DISCUSSION

Experimental gardens and glasshouse experiments have been developed to determine whether plants from the same species that have grown in diverse climates or physical environments are genetically different, becoming genotypes, or whether the plant material has high plasticity that allows it to survive in these different environments (Sultan, 1987). This methodology for screening vegetative material is called the reciprocal transplant technique and has been previously used with *Potentilla glandulosa* (Clausen and Hiesey, 1958), *A. odoratum* (Antonovics and Bradshaw, 1970; Snaydon, 1970; Davies and Snaydon, 1973a; Davies and Snaydon 1973b; Davies and Snaydon, 1974; Snaydon and Davies, 1976; Snaydon and Davies, 1982), *L. perenne* (Aarssen and Turkington, 1985; Wedderburn *et al.*, 1989; Wedderburn *et al.*, 1990), *H. lanatus* and *T. repens* (Aarsen and Turkington, 1985), and *A. capillaris*

(Rapson and Wilson, 1992a; Rapson and Wilson, 1992b; Wilson and Rapson, 1995). The present study was designed, using the reciprocal transplant technique, to screen for ecotypes or genotypes with plasticity from plant material collected from two contrasting environments on the hill country of New Zealand: high fertility - low slope (1°-12°) and low fertility - high slope (>25°) microsites. Clones from the collected plants were tested under two of the main constraints for the hill country sward; namely phosphorus and nitrogen.

Table 10 Area under the adjusted curve for the leaf length development and final leaf length (ln mm) estimated by the adjusted equations for the leaf length development of a full leaf of genotypes from two contrasting environments and controls grown under glasshouse conditions.

Origin [3]	Genotypes	Area under the curve	Final Leaf Length
LN	*A. capillaris*	968 c [1]	4.37 de
LN	*A. odoratum*	1127 abc	4.43 d
LN	*C. cristatus*	1148 a	4.33 de
LN	*H. lanatus*	962 c	4.24 de
LN	*L. perenne*	1045 abc	5.06 a
HH	*A. capillaris*	1017 c	4.27 de
HH	*A. odoratum*	961 c	4.17 e
HH	*C. cristatus*	1150 a	4.44 cd
HH	*H. lanatus*	982 c	4.19 e
HH	*L. perenne*	997 c	4.83 ab
Ctr	*L. perenne* HCS [4]	1032 bc	4.65 bc
Ctr	*L. perenne* cv. Super Nui	1066 abc	4.92 a
Significance [2]		***	***
s.e.m.		36	0.082

[1] Different letters in each column indicate statistical differences amongst genotypes.

[2] *** P<0.001

[3] LN Low-No HH High-High Ctr Control

[4] HCS Hill Country Selection

Differentiation between Populations from Contrasting Conditions

A general trend of the results of this experiment is obtained from analysing the measured variables in relation to the origin of the plant material. The material from the fertile microsite produced higher levels of dry matter than the material from the infertile microsite. Plants from the infertile microsite were, however, taller, and tended to be more erect with longer leaves than the plants from the fertile microsite. From a global point of view, it is possible that plants from the groups adopt different strategies for growth. Plants from the fertile microsite were faster growing, while plants from the infertile microsite were slower growing and tended to have a more erect structure suggesting that the grazing pressure may not be as high in the low fertility microsite. Tolerance is a plant resistance mechanism that increases plant growth after defoliation (Briske, 1991; Briske, 1996). In Chapter 5, it was reported that sheep grazed low slopes more intensively than high slopes during the year, except during winter, when both slopes were similarly grazed. Grime and Hunt (1975) reported that soils with low levels of fertility tended to be colonised by species with lower relative growth rates than fertile soils, and given the fertility levels of the microsites reported in Chapter 3 and for the soil features of the studied areas in the present work (Table 1), this hypothesis appears reasonable.

Agrostis capillaris

Agrostis capillaris was the only species that showed high uniformity between the material collected from both types of microsite for all the measured characteristics. This means that *A. capillaris* can survive and colonise the entire range of environments found in the hill country due to its high plasticity. This finding is supported by McCain and Davies (1983) who studied populations of *A. capillaris* and found that plants that spontaneously grew in acid soils with low phosphorus content and under those conditions had a slow growth rate, were capable of producing a high yield when phosphorus was supplied. In New Zealand ten populations of *A. capillaris* from contrasting environments have been previously tested and no ecotypes were detected, with the material showing high plasticity (Rapson and Wilson, 1988).

In contrast, however, the presence of ecotypes of *A. capillaris* has been reported by Karlsen (1988), who tested 12 different populations of *A. capillaris* from Northern Norway and found ecotypes that showed significant differences for total yield, nitrogen uptake, and protein content. Similarly, McCain and Davies (1983) screened six populations of *A. capillaris* from contrasting environments in the U.K. and found the presence of ecotypes which differed in the accumulation of phosphorus in the shoots, a variable that was not evaluated in the present study. Wilson and Rapson (1995) suggested that the lack of formation of ecotypes of *A. capillaris* in New Zealand may be due to its limited gene pool present in the country, and that there may not have been sufficient time for *A. capillaris* to produce ecotypes since its introduction into New Zealand.

Holcus lanatus

Holcus lanatus plants originating from both microsites behaved in a similar manner for all of the variables that were measured, except for dry matter production under the different levels of phosphorus. Plants of *H. lanatus* from the fertile microsite had a significantly higher dry matter production under the lowest level of phosphorus in the soil than plants from the infertile microsite (Table 3). These results suggest that the differences in yield are due to tillering, where *H. lanatus* from the fertile microsite produced more tillers, when phosphorus was the limiting factor, than plants from the infertile microsite. Meharg *et al.* (1994) studied two ecotypes of *H. lanatus* and reported that ecotypes performed differently solely when the supply of phosphorus was limited. In this work, the biomass of the shoots and roots was measured when *H. lanatus* was grown under different levels of phosphorus applied in nutrient solutions. Plants that produced greater amounts of shoots and had a greater total biomass production allocated less biomass to the roots, and this effect disappeared when phosphorus was not limited (Meharg *et al.*, 1994). Therefore, plants from the fertile microsite in the present study could have had different strategies for growth, biomass allocation and resource acquisition than plants from the infertile microsite, which would only be detectable when the availability of phosphorus is limiting.

Anthoxanthum odoratum

The genotypes of *A. odoratum* presented differences in total yield, with the genotype from the fertile microsite reaching a higher total yield (Table 2). However, the genotype from the infertile microsite presented a higher leaf length (Table 2), final leaf length (Table 10) and leaf length under extremes levels of nitrogen in the soil (Table 8) than the genotype from the high fertility microsites. However, *A. odoratum* maintained its plant structure with regard to height, horizontal structure and architecture in spite of those differences. Therefore, these results suggest the presence of ecotypes, where the ecotype from the fertile microsite would produce a larger amount of dry matter through emphasising the growth of new tillers, instead of the growth of individual leaves as in the infertile microsite ecotype. Davies and Snaydon (1974) reported that plants of *A. odoratum* collected from fields that had received long term phosphorus fertilisation produce a larger amount of dry matter in response to phosphorus application than plants collected from non-phosphorus fertilised fields. Moreover, they reported that these differences in dry matter production were due to greater tillering rather than due to an increment in tiller weight.

Snaydon and Davies (1982) analysed two populations of *A. odoratum* and found differences in dry matter production, but not in vegetative height. However, they reported that the populations had differences in plant diameter, which did not occur in the present study.

Cynosorus cristatus

The significant differences that *C. cristatus* presented for the total yield (Table 2) are due to the significant differences in response to increasing phosphorus level (Table 3) and nitrogen level (Table 4). In both cases the genotypes that came from the fertile microsite reached a higher dry matter production than the genotypes from the infertile microsite. The behaviour for both genotypes of *C. cristatus* under the phosphorus levels was similar to that showed by *H. lanatus*, but the differences in yield were more prolonged for *C. cristatus*. *Cynosorus cristatus* also showed differences in dry matter production under medium and high nitrogen levels (Table 4). These results indicate a difference in the growth strategy of the two genotypes. Plants from the fertile microsite will survive and colonise soils containing a high availability of resources. In this situation, competition for light will be more important than competition for nutrients (Tilman, 1994) and faster growth is required to succeed under these conditions (Grime and Hunt, 1975; Coley *et al.*, 1985; Grime *et al.*, 1989). Resource-rich environments have favoured plant species with a potentially rapid growth (Coley *et al.*, 1985). In the present study this high growth rate was evident even when plant material from the fertile microsite was grown under limiting resources. Other characteristics of fast-growing species are high maximum growth rates and short leaf lifetimes (Coley *et al.*, 1985). These latter variables were not measured in the present study.

Plants that colonise low fertility environments have high nutrient allocation to the roots (Tilman, 1990; Meharg *et al.*, 1994), greater root longevity (Tilman, 1990), low nitrogen content in the tissue (Coley *et al.*, 1985; Tilman, 1990), low capacity to absorb nutrients, long leaf lifetimes (Coley *et al.*, 1985), low relative growth rates (Grime and Hunt, 1975) and low maximum growth rates (Coley *et al.*, 1985; Tilman, 1990). Furthermore, because availability of resources is limited in infertile soils, competition for resources between plants is enhanced (Tilman, 1994).

Therefore, differences in growth between genotypes of *H. lanatus* and *C. cristatus* from the fertile and infertile paddocks, fast-growing and slow-growing material respectively, could be explained by differences in physiological features such as resource absorption and resource allocation within the plant.

Lolium perenne

Lolium perenne was the species that presented most morphological and physiological differences between the studied genotypes. Plants from the fertile microsite tended to be semi-prostrate, covering a large surface of ground and producing a higher yield with shorter leaves than the genotype from the infertile microsite (Table 2). In contrast, plants from the infertile microsite were semi-erect with longer leaves (Table 2) and taller (Table 2 and Table 6). *Lolium perenne* from the fertile microsite was more responsive to phosphorus application than *L. perenne* from the infertile (Table 3). Similarly, the genotype from the fertile microsite also grew faster than those from the infertile microsite when the level of nitrogen was increased (Table 4). Wedderburn *et al.* (1990) studied a wide collection of *L. perenne* from several sites from the Hill Country of New Zealand and reported that the material from steep slopes (>30°) produced less dry matter than plants from the easy slopes (10-25°). Furthermore, Wedderburn *et al.* (1990) indicated that *L. perenne* genotypes that grew in environments with stress due to lack of nitrogen were, under all circumstances, low producers. Even when there was a plentiful availability of nitrogen in the media, they were unable to equal the production of plants that came from a high nitrogen environment.

Genotypes from the infertile microsite had increased dry mater production with increasing phosphorus and nitrogen soil contents through emphasising vertical growth (Table 5 and Table 6) and leaf length (Table 2), but not horizontal growth (Table 7).

Lolium perenne from the fertile microsite tended to maintain its height (Table 6), horizontal structure (Table 7) and architecture with increasing soil phosphorus and nitrogen availability. Therefore, these results suggest that this genotype had an increased dry matter production, with increasing nitrogen and phosphorus soil contents, based on an increase in tillering. Widdup and Ryan (1992) found that *L. perenne* had a close relationship between short leaf length and high tiller density.

Wedderburn *et al.* (1989) characterised the *L. perenne* from the hill country environment as prostrate with many short and narrow tillers. This description of architecture would apply only to the genotype from the fertile microsite in the present work.

These results suggest that *L. perenne* presented two ecotypes that differed morphologically and physiologically with different growth strategies. The ecotype that came from the infertile microsite was slow growing with an erect structure, emphasising the vertical growth. The ecotype from the fertile microsite was fast growing and presented a structure with tillers that tended to grow at sharp angles and that would prioritise tillering. These findings are in agreement with that of Charles (1970) and Brock and Fletcher (1993) who reported that *L. perenne* types that survive under intensive grazing pressure had been selected for prostrateness and high tillering, as vegetative propagation had an important role in the persistency of individual plants. On the other hand, Charles (1970) argued that *L. perenne* from the infertile microsite had been under a low grazing pressure suggested that plant structure would be controlled by factors that operate at genetic level.

Effects of Environmental Heterogeneity on Plant Species

The paddocks that were studied in the present work, LN and HH, differed in stocking rate, soil fertility and physical features and these affected pasture production (Saggar *et al.*, 1990; Lambert *et al.*, 1996; Chapter 3; Chapter 4; Chapter 5). Differences due to the microrelief given by the slope also have an effect on pasture production (Lambert *et al.*, 1983; Chapter 3). From the results reported by Lambert *et al.* (1983), Lambert *et al.* (1986a), Lambert *et al.* (1986b), Lambert *et al.* (1996) and in Chapters 4 and 5, the characteristics of micro-relief of the soil, soil fertility, soil physical features, that include moisture content and selective grazing, together confer sufficient differentiation between the LN-HS and HH-LS microsites to produce a selection pressure high enough to segregate ecotypes within species. In this way Snaydon (1970), Snaydon and Davies (1982) and Wedderburn *et al.* (1990) found a close relationship between plant response and site of origin. Environmental heterogeneity would be an important factor in the degree of morphological and physiological differentiation of plant material (Snaydon, 1970; Snaydon and Davies, 1982).

CONCLUSIONS AND IMPLICATIONS

The present study showed two extreme cases, *L. perenne* and *A. capillaris*, where these species had different strategies to persist in contrasting environments. *Lolium perenne* had two morphologically and physiologically different ecotypes in contrasting environments.

In contrast *A. capillaris* showed a high capability for adaptation from one condition to the other. This high plasticity would confer on *A. capillaris* the ecological capacity to colonise many different environments without the necessity of specialising.

The other three species, *A. odoratum*, *C. cristatus* and *H. lanatus*, showed differences between the genotypes, but to different degrees. *A. odoratum* and *C. cristatus* showed physiological differences that would indicate ecotype differentiation. The differences showed by *H. lanatus* genotypes at the lowest level of phosphorus would suggest that there may be ecotype formation, but more research is required to confirm this.

It is relevant to point out that in order to identify ecotypes from different species it is necessary to test the characteristic that the ecotypes have been naturally selected for. For example, *H. lanatus* in the U.K. that have shown a wide range of ecotypes with a high polymorphism for arsenate tolerance (Meharg and Macnair, 1990; Meharg and Macnair, 1991; Meharg and Macnair, 1992; Meharg *et al.*, 1993). The species that were studied in the present work were tested to evaluate their behaviour only under phosphorus and nitrogen. It is possible, however, that this species would show the presence of ecotypes for other characteristics such as drought tolerance and variables other than those measured in the present study, such as protein content of the plants.

Finally, this study supports the importance of diversity within species in their survival strategy to environmental constraints. This may be an important element within the diversity-stability debate. Species, and genotypes within species, will be segregated according to their survival under different environmental constraints. Therefore the genetic information for the compatibility of individual plants under environmental constraints would regulate the presence and expression of the different species and genotypes within species in the field. Species that have high genetic diversity would have a higher probability of survival. Thus the presence of ecotypes and genetic plasticity are different but important survival strategies of plants. Through these mechanisms, plants can persist under a range of environmental changes.

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CHAPTER 7

General Discussion

THE GRASSLAND ECOSYSTEM

Topography, soil physical and fertility attributes, plant species and grazing animals are grassland ecosystem variables that are interrelated (Archer and Smeins, 1991; Briske and Heitschmidt, 1991; Stuth, 1991; Gastó *et al.*, 1993; Chapter 3; Chapter 4). Thus, botanical composition at a determined moment is the result of complex dynamics between the grassland ecosystem constituents (Archer, 1994; Pieper, 1994; Chapter 3; Chapter 4). A grassland is composed of abiotic elements that are dynamic and can produce changes in the botanical composition and productivity of the sward, for example, through changes in water availability and soil fertility levels (Gastó *et al.*, 1993; Chapter 3). Grazing animals can also provoke changes in grassland botanical composition and productivity (Miller *et al.*, 1994; Milton *et al.*, 1994) through selective grazing (Silvertown *et al.*, 1994), redistributing fertility (Saggar *et al.*, 1990) or changing physical attributes of the soil through treading (Archer and Smeins, 1991; Thurow, 1991). Selection pressure of sheep on plant species in the hill country were analysed in Chapter 5 and sheep were shown to be selective at both the species and site scale. However, selective grazing can have two consequences that still require further investigation. Firstly, the extent that selective grazing changes the botanical composition of the sward needs to be investigated. Secondly, it is important to determine whether sheep, through selective grazing at slope class level (Chapter 5), are affecting soil physical characteristics (Chapter 3). These potential consequences could have further implications (directly and indirectly) on botanical composition and pasture production (Chapter 4).

ECOLOGICAL DYNAMIC OF HILL COUNTRY GRASSLANDS

The hill country field studied has a high environmental heterogeneity within a small scale (Chapter 3), which results in a highly variable sward (Chapter 4). The presence of species or groups of plant species fluctuate, increasing or decreasing according to their tolerance to stress, such as water availability (Chapter 4), disturbance, such as selective grazing (Chapter 5), and competition, such as for light (Tilman, 1994). Changes in botanical composition (Chapter 4) are associated with changes in environmental pressures. However, results from Chapter 6 show that plant species use different strategies to survive under high environmental heterogeneity. The presence of ecotypes and plant species with plasticity (Chapter 6) gave a new element in the analysis of the grassland dynamic.

Ecotypes and Phenotypic Plasticity

The scale of analysis of the species dynamics in the field is important for an understanding of the plant species-environment relationship. The study reported in Chapter 4 showed that the relative presence of plant species changed according to variances in environmental pressures, such as soil physical and fertility features (Chapter 3) or grazing frequency (Chapter 5). This scale of analysis only allowed a determination of changes in populations at species level, but gave no indication of the genotypic features of the plant population that were colonising the site.

The value of species diversity in a ecosystem (McNaughton, 1994; Elmore and Kauffman, 1994; Milton *et al.*, 1994; Tilman, 1999) and the effects of losing plant species on the ecosystem sustainability and productivity (Archer and Smeins, 1991; Milton *et al.*, 1994; Pieper, 1994) have been widely recognised. However, the value of genotypic diversity within species on ecosystem stability needs to be more thoroughly assessed.

An ecotype has been defined as a group of individual plants within species that have genetically determined differences in growth features, with these differences in performance reflected in the plant's survival in particular environments (Begon *et al.*, 1996). Phenotypic plasticity is an individual plant feature that allows an individual plant to maintain the ability to survive and reproduce in a heterogeneous and changing environment (Sultan, 1987). Ecotype generation and phenotypic plasticity are survival strategies and through these strategies plants can colonise contrasting environments. For example *L. perenne* (Chapter 6) showed the presence of two types of plants growing in contrasting neighbouring environments (Chapter 3), while *A. capillaris* colonised those environments through phenotypic plasticity (Chapter 6).

Snaydon and Davies (1976) indicated that differences between ecotypes are related to the steepness of the change of environmental features, which means that larger differences between environmental features of neighbouring sites would result in larger differences between plant populations. Sharp differences were measured in hill country soils between microenvironments, especially in relation to characteristics such as water holding capacity, water conductivity, soil Total-N and Olsen-P (Chapter 3). The study reported in Chapter 6 showed that plants species were able to colonise contrasting microenvironments through ecotypes and phenotypic plasticity.

The presence of ecotypes or plants with phenotypic plasticity allows a plant species to survive changes in the levels of environmental variables (Snaydon and Davies, 1972; Snaydon and Davies, 1982; Sultan, 1987). In this way ecotypes and plants with phenotypic plasticity would be able to buffer the effects of changes in environmental variables on grassland ecosystems, such as they would be able to survive with decreasing fertility levels due to redistribution of the nutrients by grazing animals (Saggar *et al.*, 1990). In this way ecotypes and phenotypic plasticity would have an important role in maintaining stability in grasslands ecosystems.

The diversity-stability hypothesis argues that species have different characteristics, and as the diversity of an ecosystem increases, so too does the probability that it will contain species that can grow during an environmental perturbation (Tilman and Downing, 1994). After changes in the levels of environmental variables that affect a sward, the plant community can reach a new hypothetical internal balance or equilibrium between its components through ecological successions (Archer and Smeins, 1991; Gastó *et al.*, 1994; McNaughton, 1994; Pieper, 1994; Tilman and Downing, 1994). Resistance, resilience and stability of a grassland community have been related to plant species diversity (Tilman and Downing, 1994).

Ecotypes and phenotypic plasticity are individual plant characteristics that increase diversity within species and increase plant diversity in grassland ecosystems. Therefore ecotypes and phenotypic plasticity (Chapter 6) would increase the probability of plant species remaining in an ecosystem after perturbation and would also allow a species to colonise a wider range of environments (Chapter 4). For example, *A. capillaris* is a plant species that has not shown the presence of ecotypes in New Zealand, however, through plasticity it has been very successful at colonising a wide range of environments (Rapson and Wilson, 1988; Rapson and Wilson, 1992; Chapter 4; Chapter 6). *L. perenne* is another plant species that has been widely spread throughout New Zealand, however, several studies have shown the presence of diverse ecotypes

(Wedderburn *et al.*, 1989; Wedderburn *et al.*, 1990; Widdup and Ryan, 1992; Chapter 6).

Genotypic diversity within plant species provides a new perspective to the diversity-stability hypothesis, such that ecotypes and plants with phenotypic plasticity would have important buffering effects on grassland ecosystems after changes in the levels of constraints of environmental variables. Plant species with a high diversity of genotypes would have a higher probability of surviving after environmental changes. In the same manner, plant species can also survive environmental changes through phenotypic plasticity. Thus, persistency of plant species could be related to the presence of ecotype and plants with phenotypic plasticity. Through these strategies plant species could reach the same objective; survival in the new environmental conditions. Further investigation is needed to test this new hypothesis.

Ecotypes and Phenotypic Plasticity in Relation to Field Condition and Plant Functional Groups

Field condition proposes that the relative presence of plant species in the field is related to the level of constraint that environmental variables exert on plant species (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973; Archer and Smeins, 1991; Gastó *et al.*, 1993). Decreasers, increasers, invaders and indifferents are the main groups of plant species that would be present in different proportions in the sward according to a particular field condition (Dyksterhuis, 1949; Dyksterhuis, 1958; Noble, 1973; Gastó *et al.*, 1993). Plant species within each of these groups respond in a similar way to environmental pressures.

The concept of functional groups or types aggregates together plant species that use similar resources or plant species that have similar responses to disturbances (Gitay and Noble, 1997).

In Chapter 4 the variation of the relative presence of each functional group with changes in the level of environmental variables was discussed. Functional groups behaved in a similar manner as the groups proposed by field condition. This lends support to the hypothesis that functional groups and field condition are complementary concepts. However, the integration of ecotypes and plants with phenotypic plasticity to the dynamic of the pasture would provide a different approach to those concepts.

According to the definition of functional types, plant species that are in the same functional groups would use similar resources or would behave in a similar manner under disturbances (Gitay and Noble, 1997). However, ecotypes from the same plant species do not necessarily use similar resources or have similar responses to disturbances; this is the ecological advantage of ecotypes. The results reported in Chapter 4, Chapter 5 and Chapter 6 support this hypothesis. For example, the ecotype of *L. perenne* that colonises the LS had characteristics that allowed it to tolerate a high frequency of grazing and high competition for light. *Lolium perenne* from the LS was fast-growing and had a semi-prostrate architecture. *Lolium perenne* that colonised the HS had to survive under different environmental pressures than plants of LS, for example the HS had a low availability of soil resources such as water, nitrogen and phosphorus. *Lolium perenne* from the HS was also slow-growing and semi-erect. Therefore, ecotypes from the same species may not belong to the same plant functional group, however more investigation is required to test this assertion.

Further investigation is also required in relation to defining plant functional groups when there are different types of plants with variable phenotypic plasticity. Phenotypic plasticity allows individual plants to regulate their morphology and physiology according to changes on the levels of environmental variables (Hutchings and Bradbury, 1986; Sultan, 1987; Platenkamp, 1990; Dong and De Kroon, 1994; Waite, 1994). This ecological advantage allows these plants to persist under different environmental perturbations (Sultan, 1987; Chapter 4; Chapter 5; Chapter 6).

The presence of ecotype may also affect the determination of field condition. Ecotypes of the same plant species may have different requirements, thus may survive under different soil conditions, for example high and low availability of soil nitrogen (Chapter 4; Chapter 6). Therefore, these ecotypes may belong to different groups and colonise the sward under different field conditions. In the same way, phenotypic plasticity may produce distortions in the determination of field condition. Individual plants, through phenotypic plasticity, can adjust their morphology and physiology under a range of environmental constraints and succeed (Chapter 4; Chapter 5; Chapter 6). However, these hypotheses require further investigation.

Ecotype Segregation

A mechanism that plant species may use, that allows adaptation to new conditions after environmental changes have occurred, is genotypic variability. Under certain circumstances the selection pressure can form distinct populations or ecotypes (Snaydon and Davies, 1972; Snaydon and Davies, 1976; Snaydon and Davies, 1982). Ecotypes are also a mechanism that allows individual plants of a species to survive and colonise contrasting environments (Rice and Mack, 1991; Chapter 6). Adaptation implies that individuals can survive and colonise an environment after genetic changes occur in the plants through time (Wu *et al.*, 1975; Snaydon and Davies, 1976; Snaydon and Davies, 1982).

Ecotypes are part of a pool of genotypes present in a particular moment in the field, that constitute diversity within plant species. After environmental changes occur to the whole field or part of it, only the genotypes that can tolerate the new environmental conditions will be able to survive. Therefore, it would be possible to find different types of plants of the same species, that at some point were segregated by environmental constraints, surviving in neighbouring contrasting environments. This hypothesis is not contradictory to the adaptation hypothesis. The findings of the present work support the segregation hypothesis.

CONCLUSIONS

The present work has shown that the hill country of New Zealand has contrasting environmental conditions over short distances, such that soil physical and fertility attributes varied largely between microsites. Slope, however, was the variable that led to soil differences between the hill country microenvironments. Sheep also constituted an important source of selection pressure on plant species through selective grazing.

There were plant species in the hill country that responded in a similar way to environmental constraints, such that they can be grouped into functional groups. The results suggested that field condition and plant functional groups are complementary concepts in grassland dynamic analyses. Different groups of plant species responded in different manners to environmental variables, such that plant species were segregated between the different microenvironments. However, even though diversity within plant species buffered the effect of environmental variables on the plant community, environmental selection pressures have produced ecotype segregation to the different microenvironments. Plant species with high plasticity were able to survive and colonise the different hill country microenvironments. Therefore, ecotypes and plant species with phenotypic plasticity constitute diversity within plant species and provide a new approach to the diversity-stability hypothesis and ecosystem function.

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