THE RESPONSE AND RECOVERY OF TEN HILL COUNTRY PASTURE SPECIES SUBJECTED TO WATER DEFICIT STRESS

A thesis presented in fulfilment of the requirements for the degree of Masters in Agricultural Science

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January 1995

ABSTRACT

The objectives of this study were to: screen the response of several pasture species when subjected to water deficit stress, use these responses to test some predictions of plant strategy theory (Grime *et al.* 1988) in relation to stress, and examine some plant functional characteristics related to stress and interpret the responses in relation to plant community structure in hill country pastures. The rationale here is that by testing a range of species responses to controlled stress in artificial conditions significant patterns of ecological specialisation in plant traits may be detected.

Ten hill country pasture species were exposed to a controlled water deficit stress in a glasshouse experiment. The response of the plants to a progressively severe water stress followed by the resumption of water and nutrient supply for a three-week recovery period was assessed, using measurements of leaf extension, dry mass, senescence and tissue nutrient contents.

The ranking of species for resistance to water stress (defined as the ability of the plant to continue functioning during the stress) based on the measurements of leaf/petiole extension rate, was (lowest to highest): *Lolium perenne* < *Dactylis glomerata* < *Holcus lanatus* < *Agrostis capillaris* < *Plantago lanceolata* < *Agrostis castellana* < *Trifolium repens* < *Rytidosperma clavatum* < *Lotus corniculatus* < *Hieracium pilosella*. *Lolium perenne*, *Dactylis glomerata* and *Rytidosperma clavatum*, followed by *Trifolium repens* showed the highest resilience (defined as the rate of recovery after the stress is removed) again measured by leaf/petiole extension rate.

The difference in total dry mass between control and stress treatments was used to assess the effect of the stress on biomass accumulation. Those species classified with C attributes according to plant strategy theory survived the water stress through rapid plastic adjustments in leaf extension and senescence and developed a large difference in dry mass between the stress and control treatments. The stress tolerant type species had the least response in terms of difference in biomass accumulation and senescence.

The broad differences between plants with S-type and C-type attributes are consistent with plant strategy theory. However within the CR-CSR classification several different types of response to water deficit stress were evident. In particular, the CR-CSR strategists *Lolium perenne* and *Dactylis glomerata* showed a well developed capacity to cease leaf elongation early and senescence leaf material so as to preserve meristems in a viable state to allow recovery when water supply resumed. Other CR-CSR strategists did not have this capacity and several species died as a result of water stress.

This suggests that secondary functional types may be recognised within the primary types of CSR theory.

The results are discussed in relation to the coexistence of hill country pasture species. It is suggested that the persistence of *Lolium perenne* and *Dactylis glomerata* in hill country pastures may be partly related to a capacity for rapid plastic adjustments in leaf extension and leaf area so preserving dormant vegetative meristems during water stress, allowing rapid recovery in the cooler period of the year with adequate water.

ACKNOWLEDGMENTS

I would like to acknowledge and thank the following people for their assistance in various stages of this work. Their help is deeply appreciated

Peter Kemp
Bruce Campbell
Ian Valentine
Technicians at the Plant Growth Unit. Massey University.
Plant Science Department. Massey University.
Massey University Agricultural Research Foundation
Hugh and Angela Davis
Jill Lawler
Glen Houghton
Ian (Piggy) Millward
Shelly Wrigly
Anne-Marie O'Neill
John Lockhart
Ashby Howitt
Jeannie Rossiter
Janet McAllister

> *'. . . omnes observationes nostrae propter instrumentorum sensuumque imperfectionem non sint nisi approximationes ad veritatem . . .'*
>
> Gauss 1890

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1 INTRODUCTION

The supply of moisture to plants has been reported as the primary environmental factor limiting the attainment of production potentials in New Zealand pastures (Lancashire 1984). Work by Levy, (1970) broadly described the influence of climate on grassland farming, and work on individual species (eg. Stevens *et al.* 1993; Thomas 1986; Turner 1991) gives us an understanding of the response of pasture species to water deficit stress and drought, however, presently the ability to predict hill country vegetation responses to drought and other environmental and management disturbances is limited. Furthermore the investigation of the response to water deficit stress by plants in relation to plant strategy theory (Grime 1979, Grime *et al.*) is not as well documented as it is in the study of changes in nutrient supply (Campbell and Grime 1989, Olff 1992). In particular, there are few experiments testing CSR theory predictions on stress, in which the plants are so severely stressed that they die during the course of the experiment.

In this introduction some of the main physiological effects of water deficit stress will be discussed, this will include an examination of the response of plants water stress in terms of their plasticity and their adaptations to better survive water deficit stress. Plant strategy theory is discussed as an example of a model capable of predicting plant behaviour and response to environmental conditions. A description and comparison of the species is made in terms of their expected response to water stress and their positioning within the C-S-R model.

1.1 Responses to water deficit stress in plants

1.1.1 Physiological and morphological responses

The literature indicates that almost any parameter or process of the plant can be altered by a water stress that is severe and long enough (Hsiao and Acevedo 1974). Rather than look at all the metabolic and physiological changes observed under stress this section will focus on a comparative analysis of plant responses to water stress and will attempt to differentiate the various plant processes in terms of their sensitivity and determine the sequence of events set in motion by the onset of moisture stress. As plants are highly integrated systems it is assumed that when stress disturbs some process in the system, a variety of control mechanisms are bought into play so as to adjust other processes for maintaining balance and coping with the stress (Hsiao and Acevedo 1974). Under natural conditions water stress does not occur suddenly, usually it increases gradually. Therefore the process that is the most sensitive to stress is normally altered first and this in turn may lead to many secondary and tertiary changes (Hsiao and Acevedo 1974).

The photosynthetic uptake of CO_2 by the moist apoplast of the leaf mesophyll is inevitably associated with water loss to the atmosphere, and potentially loss of turgor. Therefore the leaves of plants are exposed to some degree of water stress throughout their lives during the daily periods of illumination (Rook 1973, Fitter and Hay 1987). Coping with water deficit stress is clearly a routine aspect of the physiology of most plant species. Under conditions of a more severe water stress there is a rapid loss of turgor, declining at a rate per unit of water potential. A severe water stress normally involves the complete loss of turgor, and leaf wilting occurs (Fitter and Hay 1987). As the volume of the cell content decreases there is a tendency for the plasmalemma to shrink away from the cell wall (plasmolysis) (Fitter and Hay 1987). However plasmolysis of leaf cells is rare in nature since it is difficult for water or air to move inward to fill the space vacated between the plasmalemma and cell wall (Meindner and

Sheriff 1976). The stomata of many mesophytic species close at leaf water potentials below -0.5 MPa thereby cutting off the CO_2 supply to the mesophyll (Fitter and Hay 1987). The stomata occupy a key position in the pathway for gaseous exchange between the plant and the atmosphere, and thereby regulate both photosynthesis and water loss. However, Johns (1978) reported in a study on four pasture species that stomatal closure reduced water use per unit foliage cover by only 20-30%. Both water use and gross photosynthesis were reduced more as a result of mechanistically reduced leaf area available for gaseous exchange than by the influence of stomatal action. It is now generally recognised that the stomata do not respond to changes in leaf water potential (Ψ_{Leaf}) or relative water content (RWC) until a critical threshold level of these parameters is reached, and then stomatal closure occurs over a narrow range of Ψ_{Leaf} or RWC (Turner and Begg 1978). Values of Ψ_{Leaf} for a 50% decrease in leaf conductance are given for a number of grasses in Table 1.

Table 1 Values of leaf water potential required to halve stomatal conductance in a range of grasses.

Observations taken either in the field (F) or under controlled environmental conditions (C). (Taken from Turner and Begg 1978)

Species	Ψ_{Leaf} MPa	Conditions
Panicum maximum		
var. *trichoglume*	-0.6	C
Lolium perenne	-1.0	C
Lolium perenne	-1.4	F
Pennisetum typhoides	-1.6	F
Astrebla lappacea	-2.4	C
Dactylis glomerata	-1.4	F
Wheat	-1.3	C
- at tillering		
- at heading	-1.7	C
- at flowering	-2.4	C
- grain filling	-3.1	C
Wheat		
- at flowering and grain filling	-1.9	F
Barley	-3.0	F
Maize	-1.2	C
Maize	-0.8	C
Maize	-1.1	C
Maize	-1.7	F
Sorghum	-1.0	C
Sorghum	-1.5	C
Sorghum	-0.8	C
Sorghum	-2.0	F
Sorghum	-1.6 to -2.2	F

There is no unique value of Ψ_{Leaf} for stomatal closure. The Ψ_{Leaf} for stomatal closure depends on the age of the plants, whether the plants were grown in the field or controlled environment, the position of the leaf in the canopy and the stress history of the plant (Turner and Begg 1978).

Cell expansion and therefore leaf extension are the processes most sensitive to water stress because of their dependence on turgor. Cell growth is defined as the irreversible enlargement or expansion of cells (Hsiao and Acevedo 1974). Although seemingly purely physical, this definition incorporates implicitly all metabolic aspects of growth. Cell enlargement cannot be sustained without accompanying synthesis of membranes, organelles, proteins, and cell wall material, and it is almost always occurring with differentiation at the subcellular level (Hsiao and Acevedo 1974). The possible effects and feedback on leaf area development, CO_2 assimilation and root growth is shown in Figure 1 where the dashed lines indicate negative feed back effects. The water deficit represented is assumed to be short and mild and not affect stomata and photosynthesis directly.

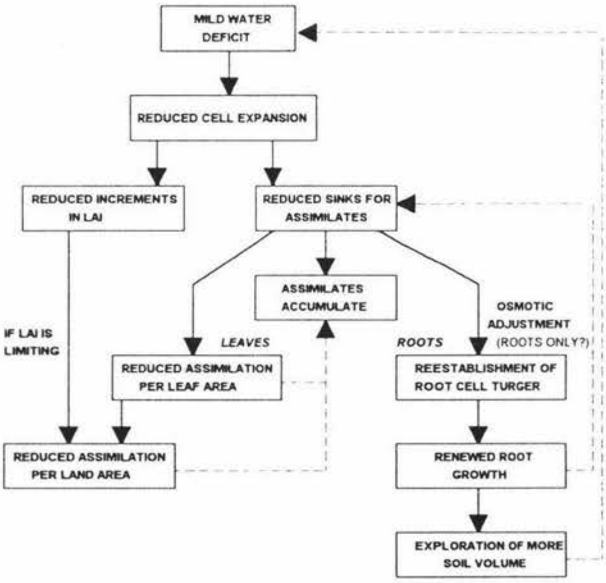


Figure 1 Possible effects of mild water deficits

(Taken from Hsiao and Acevedo 1974)

In short term exposure to water stress, expansion of leaves and other tissues can take place at night when stomatal closure permits the rehydration of above ground tissue, and also because CO_2 assimilation and respiration are less sensitive to leaf water potential than is cell expansion. As water stress increases cell biochemistry is increasingly disturbed, protein and chlorophyll synthesis is reduced. In severe water stress, nitrate reductase and the levels of growth substances begin to be affected and there is severe disruption of metabolism as indicated by increases in respiration and the accumulation of proline and sugars. Table 2 shows levels of sensitivity of plant processes to water stress.

Table 2 Generalised sensitivity to water stress of plant processes [After Hsiao and Acevedo (1974) and Fitter & Hay (1987)]

Process affected where (-) signifies decrease (+) an increase	Reduction in tissue Ψ required to affect process † (0 – 0.1 – 0.2 MPa)
Cell growth (-)	——— – – –*
Cell wall synthesis (-)[a]	———
Protein synthesis (-)[a]	———
Protochloropyll formation (-)[b]	———
NO_3 reductase level (-)	———
ABA accumulation (+)	– – – ———
Stomatal opening (-)	– – – – ——————— – – – –
CO_2 assimilation (-)	– – – – ——————— – – – –
Respiration (+)	– – – ———
Xylem conductance (-)[c]	– – – ———
Proline accumulation (+)	– – – ———
Sugar accumulation (+)	———

[a] Rapidly growing tissue; [b] etiolated leaves; [c] should depend on xylem dimensions

* Length of lines represent range of stress within which a process first becomes affected. Dashed lines signify more tenuous data.

† With Ψ of well watered plants under mild evaporative demand as reference point.

Sensitivity to water deficit is dependent largely on growing conditions which influence both the osmotic potential of the tissue and the gradients in potential between mature and expanding leaf tissue. This means that little confidence can be placed on actual comparisons between species for the relationship between leaf extension and osmotic water potential. It is evident that extension growth is more sensitive to water deficits than stomatal closure or photosynthesis (Turner and Begg 1978). Severe water stress involves mechanical stress as well as dehydration hence the interpretation of the effects of different degrees of water stress on plant function can be complicated by the fact that responses can be seen at both the tissue and cell level. Cell division is therefore regarded as being less sensitive to water deficits than cell enlargement, which is almost entirely due to the uptake of water. The high turgor associated with rapid growth is required because of the structural characteristics of the wall that do not permit wall extension when the turgor falls below the threshold value (Hsiao and Acevedo 1974). This means that the range of turgor that permits growth can be very narrow making it highly sensitive to fluctuations in the evaporative demand of the environment (Boyer 1973). The observation that plants exposed to water stress frequently have cell numbers of the same general order as controls but cells of smaller size and exhibit more rapid growth on recovery from stress provide evidence for this point of view (Turner and Begg 1978). Since water stress has less effect on the duration (than the rate) of leaf expansion, long term depression of the rate of expansion under water stress results in smaller leaves and less extensive leaf canopies. (Fitter and Hay 1987). Generally water stress affects the growth of organs growing at the time of stress; it cannot affect the size of organs that have reached their final size, except by senescence and death. One of the most important consequences of the sensitivity of cell enlargement is the marked reduction in leaf area. Water stress can also affect leaf area by reducing tillering and hastening the death of leaves and tillers (Dougherty 1973). The shedding of plant parts spans both the physiological and morphological changes that occurs in water stressed plants. Although total plant growth is reduced during water stress, root growth is generally favoured relative to shoot growth, as indicated by the frequently reported increase in root:shoot ratio, and in some cases, water stress may enhance root growth not only relative to shoot growth, but absolutely (Turner and Begg 1978).

1.2 Physiological and morphological adaptations

A classification of plant strategies for dealing with water stress (drought) is discussed by Shantz (1927) following that proposed by Ten Eyck in 1910, which divided plants living in dry habitats into four groups; drought escaping, drought evading, drought enduring, and drought resistant (Parker 1968). The drought escaping plants are those with mechanisms to escape the drought. They may not necessarily have any other mechanisms other than drought resistant seed, but it is through such a trait that the particular genotype is able to survive. Drought evading plants include those that economise on water use. The third type, drought enduring plants include desert shrubs that do not conserve water but lose their leaves, drying to low levels yet surviving. The fourth group, "drought resistant" plants have characteristics such as water storage organs as in succulents, understood to make the plants truly resistant to drought. A more recent classification (Fitter and Hay 1987), the physiological and morphological characteristics and life cycles which have evolved in response to water deficits is divided into three main classes:

1. Adaptations leading to the acquisition of the maximum amount of available water (avoidance of water stress, and the correction of its effects);
2. Adaptations leading to the conservation and efficient use of the acquired water (correction and tolerance, but also avoidance in the case of those species which restrict their activities to periods of water availability);
3. Adaptations (mainly biochemical and ultra structural) which protect cells and tissue from injury and death during severe desiccation (tolerance).

This classification is very useful in terms of understanding the different mechanisms that are used by water stress resistant plants, and relates to the typical characteristics of the stress tolerators and competitors in plant strategy theory (Grime 1979). The mechanisms that have been adapted can be seen in the characteristics of different plant components.

1.2.1 Leaves

Leaves can possess several xenomorphic structures which work to cut down the loss of water through transpiration (Parker 1968).

The characteristics are:

1. Greater thickness of leaf vein per leaf surface
2. Greater number of stomatal openings
3. Smaller size of stomata
4. Smaller size of epidermal and mesophyll cells
5. Greater numbers of hairs per surface, but smaller hairs
6. Thicker outer walls of epidermis and cuticle

It is however noted by Parker (1968) that transpiration rate per leaf area is more a function of leaf area per root absorbing surface than of leaf characteristics. Leaf shedding is common in trees and other semidesert plants, with some Mediterranean plants having large leaves during the winter and replacing them with smaller leaves during the dry summer (Oppenheimer 1960). Leaf loss in grasses however seems to be more of a function of leaf damage than a purposeful shedding to reduce leaf area although the death of leaves does ultimately reduce the leaf surface area especially in relation to root area. Some grasses however do have the ability to fold or roll the leaves using specialised "bulbiform" cells that shrink causing the leaf to fold or roll. Tall fescue (*Festuca arundinacea*), for example, is reported to have this trait (Johns 1978).

1.2.2 Stems

Adaptations of the stem in relation to water stress resistance can be divided into three categories; adaptations for water storage, prevention of water loss, and lowered resistance to water conduction (Parker 1968). In grasses which do not possess a true stem the main adaptation is the prevention of water loss through the photosynthetic material of the pseudo stem. In legumes there is some evidence of differences in conductance between stressed and unstressed plants especially in the petiole which would control water movement to the leaves while leaving water to flow down a path of least resistance in the stolons enabling the stolon tip to survive (Turner 1990).

1.2.3 Roots

Root development and the capacity of plants to adsorb water are closely related, generally as width, depth, and branching of root systems increase, plant water stress decreases (Hurd 1976). The importance of the root depth is indicated by Garwood and Sinclair (1979) who note that in a comparison of rooting depths of perennial ryegrass, cocksfoot and tall fescue, that the increased rooting depth of tall fescue favoured this species in a time of natural water stress. Additional differences in root function can occur in the speed of moisture uptake. Garwood and Sinclair (1979) found that though there was no difference in rooting depth between perennial ryegrass and cocksfoot there was however an indication that cocksfoot drew water from the soil profile at a slower rate than ryegrass.

As noted above, the general CSR theory of plant functional types may have value in predicting adaptations and responses to water deficit stress. This is examined further in the next section.

1.3 Plant strategy theory

1.3.1 Background

The ideas leading to the C-S-R model first appeared in 1973 in *Nature*. A debate developed and the issue centred on the role of competition in the control of species diversity in herbaceous vegetation (Grime 1988). Newman (1973) maintained that on fertile soils, the low diversity of species in productive and relatively undisturbed vegetation was the result of competition for light and that on infertile soils the intense competition for limiting mineral resources was the dominant process, but this did not lead to competitive exclusion because fine scale heterogeneity in the rhizosphere permitted a degree of niche differentiation that far exceeded that possible in the aerial environment. In contesting this view Grime (1973^{ab}) used conclusions from the work of Donald (1958) to back up his assertion that competitive exclusion in undisturbed productive vegetation is the result of intense competition both above and below ground (light and mineral nutrients). On infertile soils there is a decline in the intensity of competition as a consequence of the low potential growth rates of the species found in this habitat. The debate lead to the evolution of the C-S-R model (Grime 1974) in which it is proposed that competition reached its maximum intensity in habitats of high productivity and low disturbance that allowed large, fast growing perennial plants to dominate.

1.3.2 Stress and disturbance

Stress and disturbance are of critical importance to plant strategy theory, and that stress and disturbance were capable of restricting competition. Stress is defined by Grime as *" the external constraints which limit the rate of dry matter production of all or part of the vegetation"*. Disturbance is said to consist of *" the mechanisms which limit the plant biomass by causing it partial or total destruction"* (Grime 1979). Stress exerts its effect by reducing the growth of potentially strong competitors whereas disturbance exerts its effect by preventing the development of robust phenotypes by repeated physical damage to the developing plants (Grime 1988). At severe intensities, both stress and disturbance are capable of exerting distinctive forms of natural selection. As an example, the low productivity associated with severe and continuous stress will be conducive to long-lived, slow-growing evergreens, and in productive but frequently disturbed habitats short lived annual types will be promoted. The model proposes that the vegetation that develops in a particular place at a particular time is the result of an equilibrium between the intensities of stress, disturbance and competition. Over a longer time period, control of the species and genotypic composition occurs through the selective effects of extinctions and immigration. The equilibria between stress, disturbance and competition occupy a triangular ordination and the characteristics of the plant expected to occupy any particular position within the triangle are predictable from the location at a particular intersection between the three coordinates of the triangle (Grime 1979).

1.3.3 Plant strategies

Despite the range of functional types that exist in nature and the thought that only a complex array can adequately describe the different responses that occur from the same selection pressure (Grubb 1985), CSR theory predicts that there are stereotypical basic characteristics of life history and physiology paths of ecological and evolutionary specialisation in response to stress, disturbance and competition (Grime 1988). This has lead to the suggestion that primary strategies exist (Grime 1977), each recognisable from a characteristic set of traits. A strategy is defined by Grime (1979) as *"groupings of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology"*. As with other organisms there arises an immediate complication with the need to consider the different phases of the life cycle of the same organism (ie juvenile-adult). Grime (1979) examines the strategies adopted in the two different parts of the life history; the established phase, and the regenerative phase. Within the regenerative phase there has been identified five major types of strategy which are based on features such as the parental investment, mobility and dormancy, that bestow different predictable sets of capacities and limitations upon the organism. In many plants, the same species may be capable of having more than one regenerative mechanism which leads to the idea proposed by Grime (1979), that ecological range is determined by genetic variability, phenotypic plasticity and in addition, by regenerative flexibility, or a function of the number of regenerative strategies (Grime 1988). Table 3 below lists the three extreme strategies (C, S, and R) and some of their characteristics, including regenerative and established strategies their response to stress. The functional characteristics in bold are important in the later discussion of the study.

Table 3 Some characteristics of competitor (C), stress-tolerant (S) and ruderal (R) plants (Taken from Grime *et al.* 1988)

Characteristic	Competitor	Stress-tolerant	Ruderal
(i) Morphology			
Life forms	Herbs, shrubs, and trees	Lichens, byrophytes, herbs, shrubs and trees	Herbs, byrophytes
Morphology of shoot	High dense canopy of leaves. Extensive lateral spread above and below ground	Extremely wide range of growth forms	Small stature, limited lateral spread
Leaf form	Robust often mesomorphic	Often small or leathery, or needle like	Various, often mesomorphic
Canopy structure	Rapidly elevating monolayer	Often multi layered. If monolayer not rapidly elevating	Various
(ii) Life history			
Longevity of established phase	Long or relatively short	Long-very long	Very short
Longevity of leaves and roots	Relatively short	Long	Short
Leaf phenology	Well defined peaks of leaf production coinciding with periods of maximum potential productivity	Evergreens, with various patterns of leaf production	Short phase of leaf production in period of high potential productivity
Phenology of reproduction	Occurring after (or, more rarely, before) periods of maximum potential productivity	Many different phenologies occur	Occurs early in life history
Frequency of reproduction	Established plants usually reproduce each year	Intermittent over a long life history	High
Proportion of annual production devoted to seeds or spores	Small	Small	Large
Perennation	Dormant buds and seeds	Stress-tolerant leaves and roots	Dormant seeds
Regenerative[1] strategies	V, S, W, B_S	V, B_i, W	S, W, B_S
(iii) Physiology			
Maximum potential relative growth rate	**High**	**Low**	**High**
Response to stress	**Rapid morphological responses maximising resource capture and vegetative growth**	**Morphological responses slow and small in magnitude**	**Rapid curtailment of vegetative growth; diversion of resources into flowering**
Photosynthesis and uptake of mineral nutrients	Strongly seasonal, coinciding with long continuous period of vegetative growth	Opportunistic, often uncoupled from vegetative growth	Opportunistic, coinciding with vegetative growth

Table 3 continued ...

Characteristic	Competitor	Stress-tolerant	Ruderal
Acclimation of photosynthesis, mineral nutrition and tissue hardiness to seasonal change in temperature, light, and moisture supply	**Weakly developed**	**Strongly developed**	**Weakly developed**
Storage of photosynthate and mineral nutrients	Most photosynthate and mineral nutrients are rapidly incorporated into vegetation structure but a proportion is stored and forms the capital for expansion of growth in the following growing season	Storage systems in leaves, stems and, or, roots	Confined to seeds
(iv) Miscellaneous			
Defence against herbivory	Relatively specialised and often ineffective	Constitutive and effective against a wide range of herbivores	Relatively specialised and often ineffective
Litter decay	Rapid	Slow	Rapid
Genome size	usually small	Various	Small-very small

[1] Key to regenerative strategies: V, vegetative expansion; S, seasonal regeneration in vegetation gaps; W, numerous small widely-dispersed seeds or spores; B_S, persistent seed or spore bank; B_j, persistent juveniles.

The model of primary plant strategy proposes three extremes of evolutionary specialisation, each characterised by a particular set of traits. There are, in addition to the three primary strategies, various secondary strategies in the established phase which have evolved in conditions of intermediate intensities of competition, stress and disturbance.

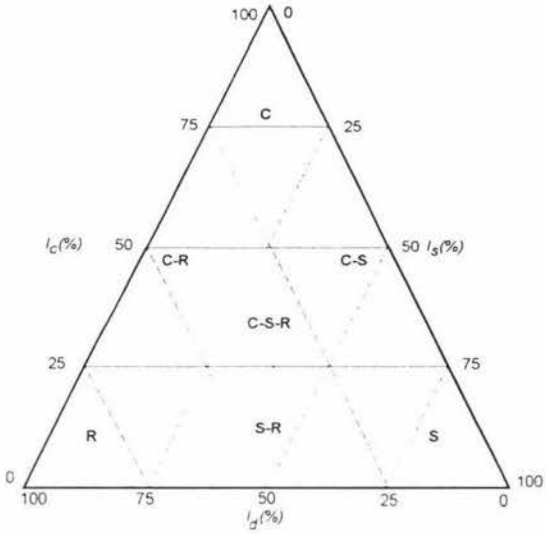


Figure 2 Triangular model describing the various equilibria between stress, disturbance and competition

C, competitor; S, stress tolerator; R, ruderal; C-R, competitor ruderal; S-R, stress tolerant ruderal; C-S, stress tolerant competitor; C-S-R, 'C-S-R' strategist. I_c, intensity of competition (——); I_s, intensity of stress (- · -); I_d, intensity of disturbance (- - -) (Taken from Grime, 1979).

The secondary strategies (Grime 1979) that exist are intermediate in the triangular ordination to the extreme or primary strategies

they are:

1. Competitor ruderals (C-R :- adapted to circumstances in which there is a low impact of stress and competition is restricted to a moderate intensity by disturbance;
2. Stress-tolerant ruderals (S-R):- adapted to lightly-disturbed, unproductive habitats;
3. Stress-tolerant competitors (C-S):- adapted to relatively undisturbed conditions experiencing moderate intensities of stress;
4. 'C-S-R strategists':- adapted to habitats in which the level of competition is restricted by moderate intensities of both stress and disturbance

1.3.4 Plasticity

An important characteristic of plants in CSR theory is the capacity for plasticity. Plasticity has come to be regarded primarily as a mechanism compensating for the lack of locomotion in plants and supplementing the role of genetic variation as a determinant of wide ecological amplitude and persistence in fluctuating conditions. As noted in (Grime *et al.* 1986). *"Plastic responses of plants to environmental factors may be placed in an ecological context by regarding them as components of sets of traits which are predictably related to habitat stability and productivity"*. Plants suffer a scarcity of resources because of interplant competition and local environmental variation. The strategy adopted by many plants to help mitigate these problems is phenotype plasticity. Phenotypic plasticity of morphology is a universal feature of plants (Bradshaw 1965). Most pasture species (grasses and legumes) can be considered to have a population structure of tillers and shoots (Harper 1977). The growth of the plant body is adjusted to best exploit the scarce resources and help achieve growth and reproductive goals. This requires heritable mechanisms that are concerned with the diversion of scarce growth resources to one facet of development rather than another (Trewas 1986). It is suggested that plasticity is of vital importance in resource acquisition by plants (Grime *et al.* 1986). Changes in plant number, size, form, and physiology of vegetative and reproductive structures arise not only because of constraints on development imposed directly by the environment but also, and more usually, from the operation of these complex, heritable mechanisms of response, activated by specific environmental cues (Grime *et al.* 1986). In the triangular model of primary plant strategy theory (Grime 1979) it is proposed that the three basic extremes of evolutionary plant specialisation (competitors, stress tolerators, and ruderals) are each characterised by a set of traits, within which distinctive forms of plasticity are of importance. Competition for nutrients and water generates spatial gradients in resources and selection is likely to favour those genotypes in which high morphological plasticity facilitates escape from depletion zones, sustains resource capture and maintains reproductive fitness (Grime 1988). The competitor strategy is represented by plants in stable productive habitats, in which success depend on an ability to sustain high levels of resource capture in conditions of intense competition and spatial patterns of resource depletion. Foraging is accomplished by morphological plasticity (Hutchings and De Kroon 1994) and in these conditions morphological plasticity in the development of roots and shoots brings about a continuous adjustment in the spatial distribution of absorbent surfaces, and is thus part of an 'active foraging' mechanism. There is however a high cost in terms of reinvestment of captured resources into the new tissue and an advantage is only gained if the active foraging increases access to large reserves of the resource. In plants of the ruderal strategy (which are plants characteristic of frequently disturbed habitats), the plastic response to environmental stress leads to the premature development of reproductive structures which in conjunction with the other features of the ruderal (rapid growth rate, short life history) apparently to increase the probability that some offspring will be produced. The third strategy, the stress tolerators, show only a small amount of morphological plasticity. As the plants of this strategy occupy habitats in which productivity is low and the supply of the limiting resource is brief and unpredictable their ability to survive depends upon the ability to capture and retain scarce resources. This leads to the prediction that the leaves and roots will be comparatively long lived structures. A feature of stress tolerators is low phenotypic plasticity due to differentiating tissue making up a small proportion of the plant biomass (Grime 1979). Any plasticity in these plants is expressed as reversible physiological changes which take advantage of temporary periods of resource availability. The success of the stress tolerator is not just in the physiological changes but also in conjunction with other traits that characterise the stress tolerator, such as a slow growth rate (Grime *et al.* 1986).

Some of these predictions are tested in the following study, using ten New Zealand hill country species. In the following section these species are classified using CSR theory and other criteria.

1.4 A comparative description of ten hill country species

The ten species of New Zealand hill country pastures were used in the following experiment are described in Table 4. The predicted response of the species to stress, based on their in established plant strategy classification is given in Table 5 in terms of the potential growth rate, morphological response to stress and their acclimation of photosynthesis, mineral nutrition and tissue hardiness to changes in temperature, light and moisture supply, based on Table 3. These characteristics will be related to measured parameters of the study in the discussion of the response of the species to stress.

Table 4 Comparative characteristics of the ten hill country species

Species	Description	Agronomic use	Established strategy type[1]	Seedling RGR week^{-1}[2]	Moisture requirements[3]	Fertility requirements[4]
Lolium perenne	Tufted, moderately densely tillered perennial grass, cool season growth with summer dip due to flowering and intolerance to hot dry conditions, moderate-high fertility	Arguably the most important pasture species in NZ, this species forms the basis of most lowland pastures and is an important component of hill country pastures	C-R to C-S-R	1.0 - 1.4	4-6	1-5
Agrostis capillaris	Rhizomatous, prostrate, densely tillered, perennial grass, warm-season active, low fertility sites	Common pasture species found in most pastures in NZ especially in lower fertility hill country pastures (Levy 1970)	C-S-R	1.0 - 1.4	4-6	4-6
A. castellana	Rhizomatous, prostrate, densely tillered, perennial grass, low fertility sites	Component of hill country pastures, important amenity species in sports turf and golf courses	C-S-R	Not known	5-7	5-7
Dactylis glomerata	Tufted perennial grass, moderate fertility sites, warm season active, tolerant of low soil moisture	Valuable component of mixed pasture and often sown as the main species in summer dry areas (Langer 1982)	C-S-R to C	1.0 - 1.4	4-7	2-5
Holcus lanatus	Tufted perennial especially humid and only moderately fertile conditions (Langer 1982)	Widely distributed and a major constituent of North Island hill country pastures and is also evident in low land dairy pastures (Langer 1982)	C-S-R	1.5 - 1.9	1-5	2-6
Rytidosperma clavatum	Tufted perennial grass, variable in size and habitat, common in dry hill country up to 1000m, New Zealand native species	Not considered important in New Zealand pastures despite the prevalence in hill country south of Auckland	S-R	Not known	5-7	5-7

Table 4 continued ...

Species	Description	Agronomic use	Established strategy type	Seedling RGR week^{-1}	Moisture requirements	Fertility Requirements
Lotus corniculatus	Most drought tolerant of the *Lotus* sp. Because of its deep much branched taproot (Smetham 1982)	Used as forage crop in small quantities in summer dry areas as replacement for lucerne in less fertile dryland soils (Charlton and Belgrave 1992)	S to C-S-R	1.0 - 1.4	5-7	5-7
Trifolium repens	Prostrate stoloniferous, adventitious-rooting, perennial legume, warm-season active, moist, high fertility sites	Used in New Zealand wherever climate allows as the most productive and persistent legume species under close continuos grazing. Not relied upon in areas where the annual rainfall is less than 630mm (Langer 1982)	C-S-R to C-R	1.0 - 1.4	4-6	1-5
Plantago lanceolata	Polycarpic perennial, rosette hemicryptophyte. Abundant in low fertility pastures but found in a wide range of habitats, thought to be drought tolerant due to a deep tap root	Common in hill country, palatable to sheep but usually not available to cattle due to a prostrate growth habit.	C-S-R	1.0 - 1.4	Not known	Not known
Hieracium pilosella	Polycarpic perennial, rosette hemicryptophyte with numerous prostrate leafy stolons. Stoloniferous herb of dry soils. Associated with relatively unproductive habitats, patch forming	A major weed of the inland grassland regions of the South Island of New Zealand because the plants exclude other species and the dense mats of rosettes limit sheep grazing (Scott *et al.* 1990)	S to C-S-R	1.0 - 1.4	Not known	Not known

[1] C, competitor; S, stress tolerator; R, ruderal; C-R, competitive-ruderal; S-R, stress-tolerant ruderal; C-S, stress-tolerant competitor; C-S-R, 'C-S-R strategist' (Grime *et al.* 1988)

[2] (Grime *et al.* 1988)

[3] 1=tidal salt mud flats; 2=swamp and flood areas; 3=very wet or water logged; 4=wet soils; 5=average soil moisture; 6=modearatly dry; 7=dry; (Levy 1970)

[4] 1=extremly high fertility; 2=high fertility; 3=moderatly high fertility; 4=average fertility; 5=Moderately low fertility; 6=low fertility; 7=very low fertility (Levy 1970)

Table 5 Predicted responses of the ten hill country species to water deficit stress, based on CSR theory

Species	C-S-R classification	Relative growth rate in non stress conditions	Response to stress	Acclimation of photosynthesis, mineral nutrition and tissue hardiness
Lolium perenne	C-R to C-S-R	High/moderately high	Rapid/moderate morphological responses	Weak/moderately developed
Agrostis capillaris	C-S-R	Moderately high	Moderate morphological responses	Moderately developed
A. castellana	C-S-R	Moderately high	Moderate morphological responses	Moderately developed
Dactylis glomerata	C-S-R to C	Moderate high/high	Moderate/rapid morphological responses	Moderate/weakly developed
Holcus lanatus	C-S-R	Moderately high	Moderate morphological responses	Moderately developed
Rytidosperma clavatum	S to S-R	Low/moderately low	Morphological responses slow and small/diversion of resources into flowering	Strong/moderately developed
Lotus corniculatus	S to C-S-R	Low/moderately high	Morphological responses slow and small/moderate morphological responses	strong /moderately developed
Trifolium repens	C-S-R to C-R	Moderately high/high	Rapid/moderate morphological responses/diversion of resources into flowering	Moderate/weakly developed
Plantago lanceolata	C-S-R	Moderately high	Rapid/moderate morphological responses	Moderately developed
Hieracium pilosella	S to C-S-R	Low /moderately high	Morphological responses slow and small/moderate morphological responses	Strong to moderately developed

2 MATERIALS AND METHODS

2.1 Principle

The objective of the experiment was to impose a controlled and synchronised onset of the water stress for all the individual plants, while still ensuring root support. In order to achieve this a free draining gravel was used. The majority of available water in the containers was supplied by regular (15-30 min.) irrigation events. The water supply was lost quickly from the container by drainage when the water supply was removed. Therefore the medium is primarily for support rather than water and nutrient supply.

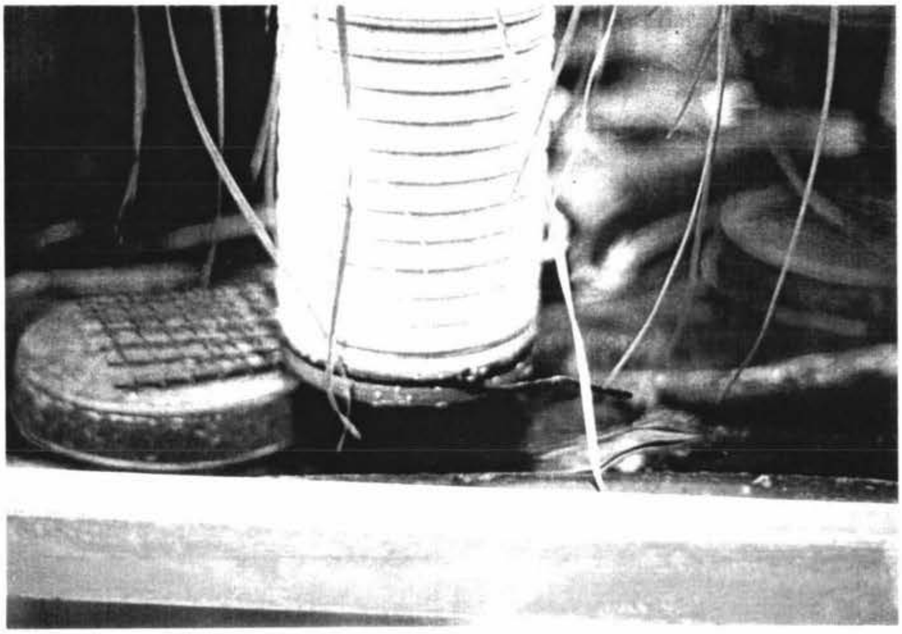
2.2 Pot design

The containers were made from 300 mm lengths of 'Corflo' 110 mm diameter PVC drainage tubing. Each length was closed off at one end with aluminium fly screen mesh held in place by a 600 mm 'bar-lok' cable tie. Grade 6 (Child Metal Ltd, Palmerston North) Greywacke, river stone chip of 5- 10 mm diameter was used as the medium for growth. Each pot had a removable individual whisker for water and nutrient delivery. To provide a water table, the cylinders stood in a flooded plastic dish 20 mm deep.

The plants were grown directly in the cylinders from seed sown into approximately 5 ml of agar as support for the germination (Plate 2). To ensure at least one plant established per pot, five seeds were placed on the agar surface. During the germination period each pot was covered with a polyethylene bag to reduce water loss through evaporation. Seeds were planted on 1 October 1993 with all species germinated by 9 October 1993. The plastic bags were removed 11 October 1993 and irrigation of the pots commenced with watering for 30 seconds every 30 minutes. After the first three weeks one seedling was selected for each pot, with an attempt to have the plants within each species a similar size, and the remaining seedling were removed by hand weeding.

Plate 1 Germination of seed directly into stone chip with agar

Plate 2 Cylinder elevated during stress to facilitate drainage of moisture from cylinder



2.3 Irrigation and Nutrient supply

Tap water was supplied to each pot via an individual whisker. The average flow rate of the slowest flowing whiskers was established and this flow rate was used to calculate the amount of water and nutrients delivered to each pot. Full basic Rorison solution (Booth *et al.* 1993) was fed into the irrigation system via a positive displacement pump set at a rate of 1.6%. Nutrient levels supplied by Rorison solution are summarised in Table 6. Adjustment of the nutrient solution to pH 6·2 using 9:1 dilution HCl was necessary to avoid precipitation in the solution.

Table 6 Rorison nutrient solution

Element	mg/l	Stock solution	g/l
Calcium/Nitrogen	80/56	$Ca(NO_3)_2 \cdot 4H_2O$	476.1
Magnesium	24	MgSO4 · 7H2O	248.0
Potassium/Phosphorus	78/31	$K_2HPO_4 \cdot 3H_2O$	230.7
Iron	3	Fe EDTA	25.0
Manganese	0.5	$MnSO_4 \cdot 4H_2O$	2.028
Boron	0.5	H_3BO_3	2.863
Molybdenum	0.1	$(NH_4)_6Mo_7O_{24} \cdot 4H_2O$	0.184
Zinc	0.1	$ZnSO_4 \cdot 7H_2O$	0.44
Copper	0.1	$CuSO_4 \cdot 5H_2O$	0.393

On 16 October 1993 the irrigation flow rate was adjusted due to slow plant growth to 45 seconds every 15 minutes. Legumes were inoculated 26 November and 23 December. The irrigation was further adjusted on 23 December 1993 to 60 seconds every 15 minutes to meet the demand of the plants. The water flow rates and nutrient supply are summarised in Table 7.

Table 7 Water and nutrient supply rates

Dates	Water regime	Water supplied /pot/24 hrs (litres)	mmol P supplied /pot/24 hrs
11-16 Oct.	30sec every 30min	2.7	43.3
16 Oct-23 Dec	45sec every 15min	8.1	129.8
23 Dec-24 Feb	60sec every 15min	10.8	172.8

During the experimental period the water delivery rate remained at 60 seconds every 15 minutes. During the stress period control plants received no nutrients. During the first 12 days during the periods of watering both the control and stress treatments received both water and nutrients.

2.4 Experimental design

The experiment was conducted in a temperature controlled glass house at the Plant Growth Unit (PGU), Massey University, Palmerston North. The experimental design was a randomised complete block design, with ten species, two water levels and two harvests in factorial combination with five replicates blocked for plant size at the beginning of the experimental period.

All procedures were carried out in the order of the block sequence from replicate one to five throughout the experimental period. The plants were sorted into their blocks by size two days before the water stress period was to begin and the four treatments were randomly allocated at this stage. The ten species are listed in Table 8.

Table 8 Plant species used in the experiment

Species	Common name
Lolium perenne L. cv. Grasslands SuperNui	perennial ryegrass
Agrostis capillaris L.	brown top
Agrostis castellana Boiss. & Reut.	dryland brown top
Dactylis glomerata L.	cocksfoot
Holcus lanatus L. cv. Massey Basyn	Yorkshire fog
Rytidosperma clavatum (Zotov.) Connor & Edgar	danthonia
Lotus corniculatus L. cv. Grasslands Goldie	birdsfoot trefoil
Trifolium repens L. cv. Grasslands Huia	white clover
Plantago lanceolata L.	narrow leaved plantain
Hieracium pilosella L.	mouse-ear hawkweed

The species were selected to represent a range of hill country pasture species that included perennial grasses, legumes and forbs. They reflect the variety of habitats and were expected to exhibit different responses due to preferred habitat, established plant strategy (Grime *et al.* 1988) and characteristic growth form. The plants selected were all perennial species and can be described as first season perennials. The species were at such an age at the beginning of the experiment that none had perenniating organs developed that could give any one species an advantage over the others in this regard. Specific details about each species is presented in Table 4.

2.4.1 Treatments

Two water levels (control and stress) and two harvests in factorial combination were replicated five times. The treatments are listed in Table 9. The water stress period began at 1200hrs, 10 January 1994. The stress plants were brought under water stress by simply removing the individual water/nutrient delivery whiskers from the pots and elevating the pots from the table to drain (Plate 2). A conditioning of the plants was achieved by starting the time without watering at two hours and increasing this by two hours each day until day 12 where the time without watering reached 24 hours. Water was then not applied to the stress plants for a further nine days, (total 216 hours without watering). The 100 harvest one plants were removed at the end of the water stress period. Water and nutrients were resumed for the stress and control plants to be harvested at the end of the recovery period at the same rate as before the stress treatment started. The duration of the recovery period was 21 days.

Table 9 Experiment Treatments

Name	Description
Control/Harvest 1	Continued water through stress period and harvested at the end of the stress period.
Stress/Harvest 1	Restricted water for three weeks then harvested at the end of the stress period.
Control/Harvest 2	Continued water through stress period, followed by resumption of nutrients and harvested at the end of the three week recovery period.
Stress/Harvest 2	Restricted water for three weeks then resumed water and nutrients for the three week recovery period and harvested at the end of the recovery period.

2.5 Moisture characteristics of pots

Graded metal was chosen as the medium for growth due to the free draining properties that it has, while being affordable and readily available. During the first 24 hour stress period and after 180 hours of water stress, five stress treatment plants from the low growing legume *Trifolium repens* and the erect leafy grass *Holcus lanatus* were randomly selected and the pots weighed to establish the rate of water loss from the columns, and to investigate any difference in water loss between two species with contrasting above ground biomass.

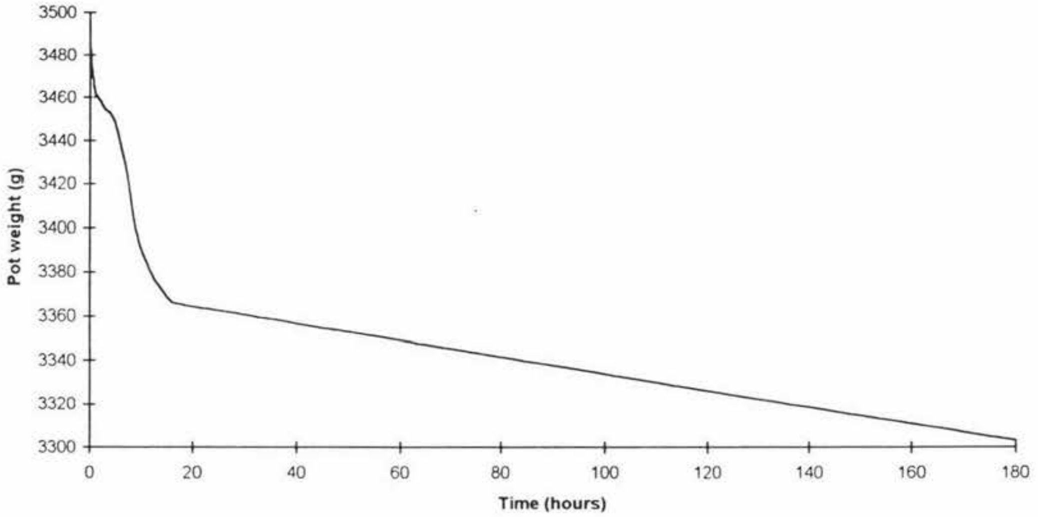


Figure 3 Weight loss of water stress pots over time

Figure 3 shows the mean weight of the ten water stress treatment pots selected. All showed most (≈ 65%) weight loss occurred over the first 16 hours with a relatively slow rate of weight loss over the last 172 hours. There was no significant difference ($P < 0.05$) between plant species.

2.6 Measurements

2.6.1 Leaf/petiole extension

During the period from the beginning of the water stress period until the end of the recovery period, measurements of leaf extension were made on selected leaves or petioles. Lamina length in the grasses was measured from the collar of the preceding leaf to the tip of the marked leaf. The marked leaf was the youngest on a randomly selected tiller. Petiole length in the legumes was measured from the branching point of the proceeding leaf to the base of the leaflets of the marked leaf and leaf length in the weeds species from the point of emergence at the crown to the tip of the marked leaf.

2.6.2 Fresh mass/dry mass

Harvested plants were placed in cold storage (9°C) while the grass and forb plant material were separated into root, leaf, dead and reproductive material, and the legumes had additional separation of stem and leaf. The material was dried at 60°C for 72 hours and the dry mass of these components was recorded. The whole plant was sub sampled for plant nutrient analysis of nitrogen and phosphorus.

2.6.3 Plant tissue nutrient content

Nitrogen contents of total plant tissue were analysed by Kjeldahl determination (McKenzie and Wallace 1954) and phosphorus contents measured by to give an indication of root function and activity by comparing control and water stressed plants. Only the six species that survived the water stress were analysed.

2.7 Data analysis

Data was analysed with the use of Microsoft Excel version 4 and 5 and Statistical Analysis Systems (SAS) packages.

Total, above-ground and root dry mass data was transformed by logarithm after it was established that the mean was positively correlated to the variance. Back-transformed means are presented and the differences between the means was tested using the LSD of the transformed data as the least significant ratio (LSR) on the back-transformed means (Steel and Torrie 1981).

For comparison between species for total, above-ground and root dry mass, the difference between the treatments of the logarithm data was used to obtain the ratio between control and stress treatments by:

$$e^{\text{differnce}} = \ln(\text{stress})\text{-}\ln(\text{control})$$

The confidence interval for a species treatment difference was given by:

$$\ln(\text{stress}) - \ln(\text{control}) \pm \text{SED} \times t$$

where SED × t is the same as the LSD. When back transformed becomes:

$$e^{\text{differnce}} \times e^{\text{LSD}} \text{ for the upper limit}$$

$$e^{\text{differnce}} \div e^{\text{LSD}} \text{ for the lower limit}$$

Dead material dry mass was likewise transformed but as logarithm of x+1 due to zero values in the data.

The root:shoot ratio was established by taking the ratio of root and shoot dry mass for each plant and then transforming the value using the natural log of that ratio for statistical tests. The least significant difference was established as in Steel and Torrie (1987) using the pooled variance of the ratio and then back transformed, using the antilog for both the LSD and the ratio.

The relative growth rate over the recovery period was found for control and stress treatments of the surviving species according to Hunt (1982).

$$_{1-2}\overline{\mathbf{R}} = \frac{\log_{e2} W - \log_{e1} W}{_2T - _1T}$$

$_1W$ & $_2W$ = The total dry mass of the plant at the end of the stress period ($_1W$) and at the end of the recovery period ($_2W$).

$_2T$-$_1T$ = The recovery period interval = 3 weeks.

The difference between control and stress treatments was tested using a one-tailed *t* test for each species.

Plots of total nutrient uptake against plant functional characteristics were tested for significance using the Spearman rank correlation coefficient r_S (Fowler and Cohen 1992) where appropriate. For weak to moderate correlations the values are not shown unless they are relevant to the discussion.

3 RESULTS

3.1 Leaf/petiole extension rate

The daily extension rate of leaves and petioles on every second day is presented for improved clarity. The stress period began on day 0 and finished on day 20. The recovery period began on day 20. Error bars in all figures indicate the standard error of the mean

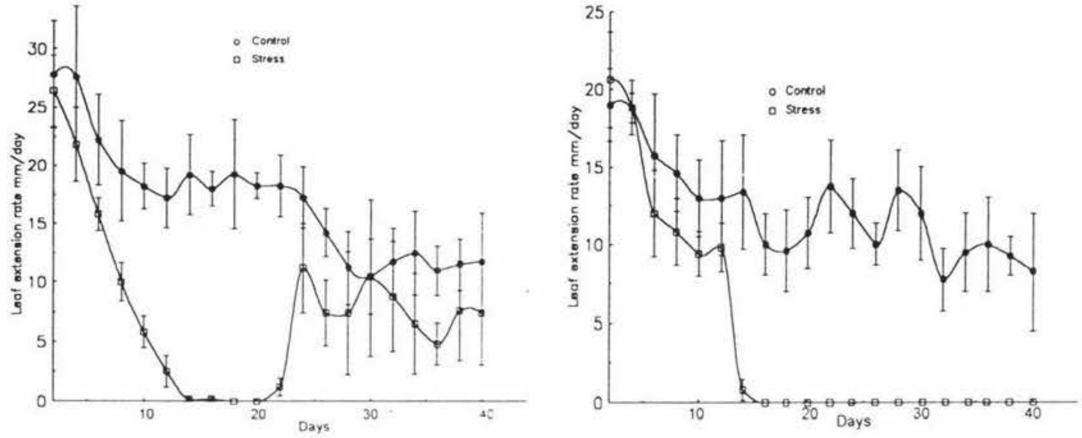
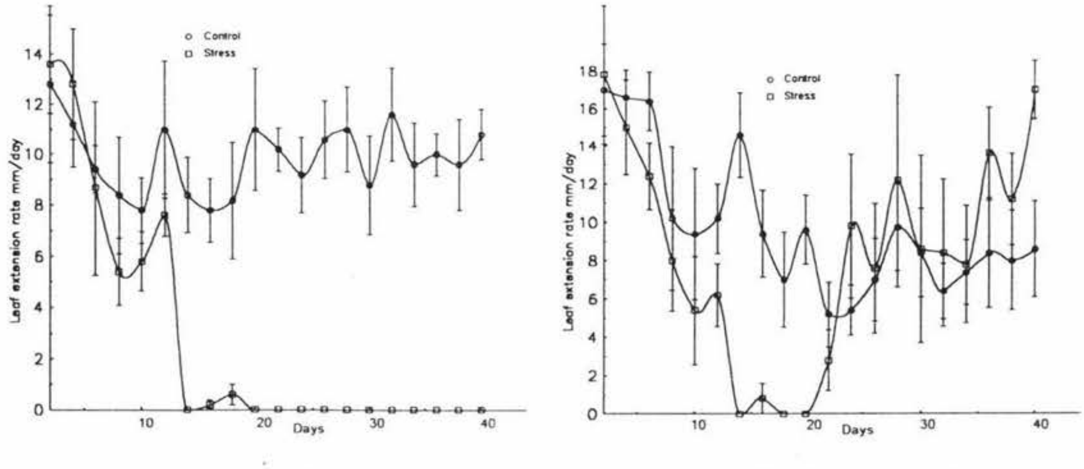


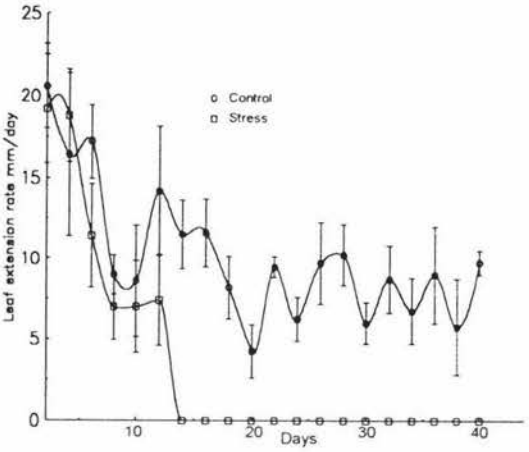
Figure 4 a. ***Lolium perenne*** **leaf extension rate**

b. ***Agrostis capillaris*** **leaf extension rate**

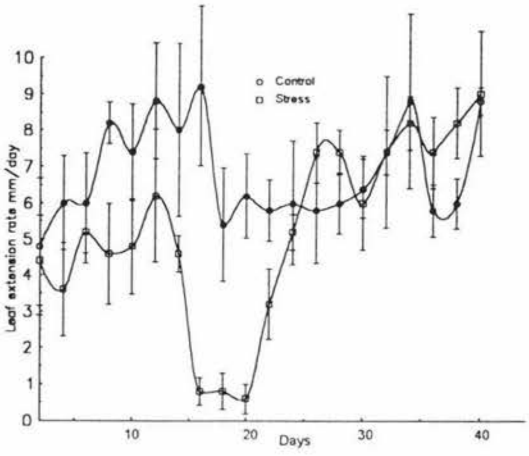


c. ***Agrostis castellana*** **leaf extension rate**

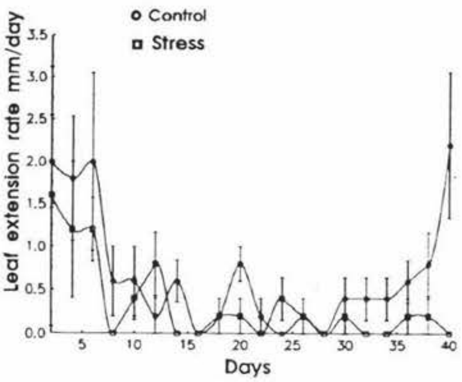
d. ***Dactylis glomerata*** **leaf extension rate**



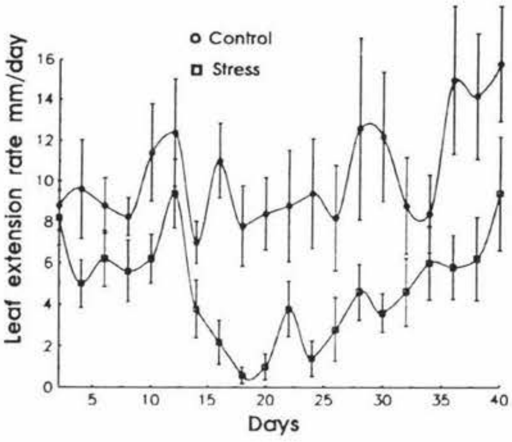
e. ***Holcus lanatus*** **leaf extension rate**



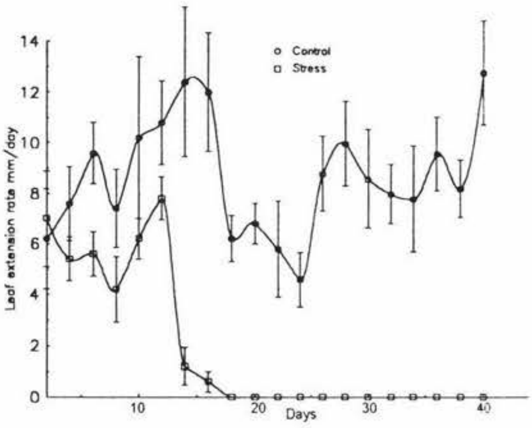
f. ***Rytidosperma clavatum*** **leaf extension rate**



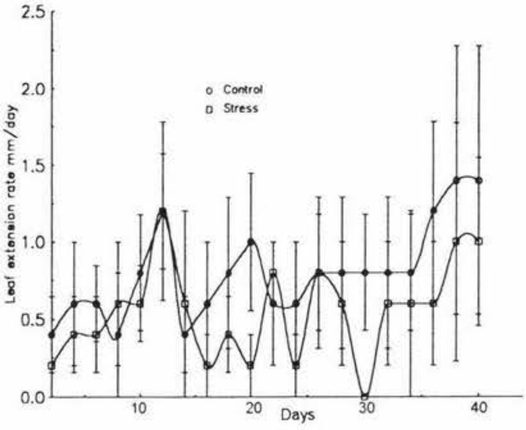
g. ***Lotus corniculatus*** **petiole extension rate**



h. ***Trifolium repens*** **petiole extension rate**



i. *Plantago lanceolata* leaf extension rate



j. *Hieracium pilosella* leaf extension rate

The leaf extension rate of *Lolium perenne* decreased rapidly and ceased 14 days after the stress treatment had began and recovered to be the same as that of the control treatment by day 24. The extension rate of *Agrostis capillaris* was not significantly reduced by the stress (relative to the control) until day 12, but the extension rate had reached zero by day 15. Only a single leaf of this species showed any recovery following rewatering and the plants were effectively killed by the water stress. The extension rate of *Agrostis castellana* in the stress treatment was not different from the control until day 12, but the extension rate had reached zero by day 14. Again there was no recovery seen in this species. The extension rate of *Dactylis glomerata* leaves reached zero by day 14 and recovered to the rate of the control by day 22, the second day after water was resumed. In this species, leaf extension rate was greater in the stress treatment than the control by day 40. The extension rate of the *Holcus lanatus* leaves in the stress treatment was not different from the control until day 12, but dropped to zero by day 14, and then remains at zero through to the end of the recovery period, no recovery was seen in this species. The extension rate of *Rytidosperma clavatum* was not reduced by stress relative to the control until day 12 and had reached its lowest rate by day 16. Extension rate then recovered to be no different from the control treatment by day 24.

The petiole extension rate of *Lotus corniculatus* stress treatment was not different from the control during the stress period. A reduction in the petiole extension rate of the control was seen after day six. It appears that a difference in leaf extension rate between the control and stress treatments was beginning to occur towards the end of the recovery period from around day 30 onwards, with a return of the control to a pre-stress level. The petiole extension rate of *Trifolium repens* dropped below the control on day 14 and reached its lowest rate by day 18. The petiole extension rate of the stressed plants increased during the recovery period but not to the rate of the control plants, though the increase in extension rate is immediate at the beginning of the recovery period. The extension rate of *Plantago lanceolata* leaves in the stress treatment dropped below the control treatment on day 12 and reached an extension rate of zero on day 18. There was no recovery of the stress treatment in this species. The extension rate of *Hieracium pilosella* leaves in the stress treatment was at no time significantly different from the control. There was no response by either the control or the stress treatments to the resumption of water and nutrients, except for a small increase in both treatments towards the end of the recovery period.

3.2 Total dry mass

The mean total dry mass for each species at the end of the stress and the end of the recovery for both the control and stress treatments is presented in Table 10.

Table 10 Mean total dry mass (g) of control and stress treatments for each species at the end of the recovery and the end of the stress period

Species	End of stress		End of recovery	
	Control	Stress	Control	Stress
L. perenne	25.9767	14.33207	77.0458	24.12383
A. capillaris	8.008472	4.043053	23.91964	4.727989
A. castellana	12.54974	8.025308	38.56712	10.00615
D. glomerata	31.4752	14.59969	76.27918	18.16688
H. lanatus	30.38959	22.03429	37.12535	17.05767
R. clavatum	0.613055	0.555604	1.581383	1.631663
L. corniculatus	0.179874	0.093247	0.60647	0.33588
T. repens	1.238127	0.762845	18.66593	2.320772
P. lanceolata	4.235494	2.410659	3.02981	0.801556
H. pilosella	0.036699	0.023546	0.048393	0.034222

LSR = 0.2238 for end of stress

LSR = 0.3445 for end of recovery

LSR = 0.2519 for stress plants across end of stress and end of recovery

LSR = 0.3325 for control plants across end of stress and end of recovery

The values in Table 10 are the back-transformed means of the logarithm-transformed total dry mass data. The equivalent of the LSD-test on logarithm-transformed data is performed when the ratio of two back-transformed means is compared with the least significant ratio (LSR) value (Steel and Torrie 1981). The same format also follows for the presentation of the means of above-ground dry mass (Table 11) and for the root dry mass (Table 12).

Dactylis glomerata showed the largest difference between stress and control of the species in total dry mass at the end of the stress period. *Dactylis glomerata* was followed in order of greatest to least difference by *Lotus corniculatus*, *Lolium perenne*, *Agrostis capillaris*, *Plantago lanceolata*, *Hieracium pilosella*, *Trifolium repens*, *Agrostis castellana*, *Holcus lanatus*, *Rytidosperma clavatum*. No significant difference ($P < 0.05$) was evident between control and stress treatments for all species at the end of the stress.

At the end of the recovery period a much greater difference was evident between the stress and control treatments. The greatest difference between control and stress at the end of the recovery period was seen in *Trifolium repens* followed in order of greatest to least by *Agrostis capillaris*, *Dactylis glomerata*, *Agrostis castellana*, *Plantago lanceolata*, *Lolium perenne*, *Holcus lanatus*, *Lotus corniculatus*, *Hieracium pilosella*, and *Rytidosperma clavatum*. Significant differences ($P < 0.05$) were found between the control and stress treatments in the species *Trifolium repens*, *Agrostis capillaris*, *Dactylis glomerata*, *Agrostis castellana*, *Plantago lanceolata*, and *Lolium perenne*, using the least significant ratios in the comparisons.

An analysis of variance was performed on logarithm transformed data. The interaction of harvest (end of stress and end of recovery) and species was not significantly different ($P > 0.05$) for stress plants. There was a significant difference between harvest ($P < 0.05$) and also between species ($P < 0.001$). For the control plants the interaction was not significant but there was a significant difference ($P < 0.001$) for both species and harvest separately.

3.2.1 Relative difference between control and stress treatments

The difference between the species is presented in Figure 5 as the ratio between stress and control of the logarithm transformed data (Section 2.7)

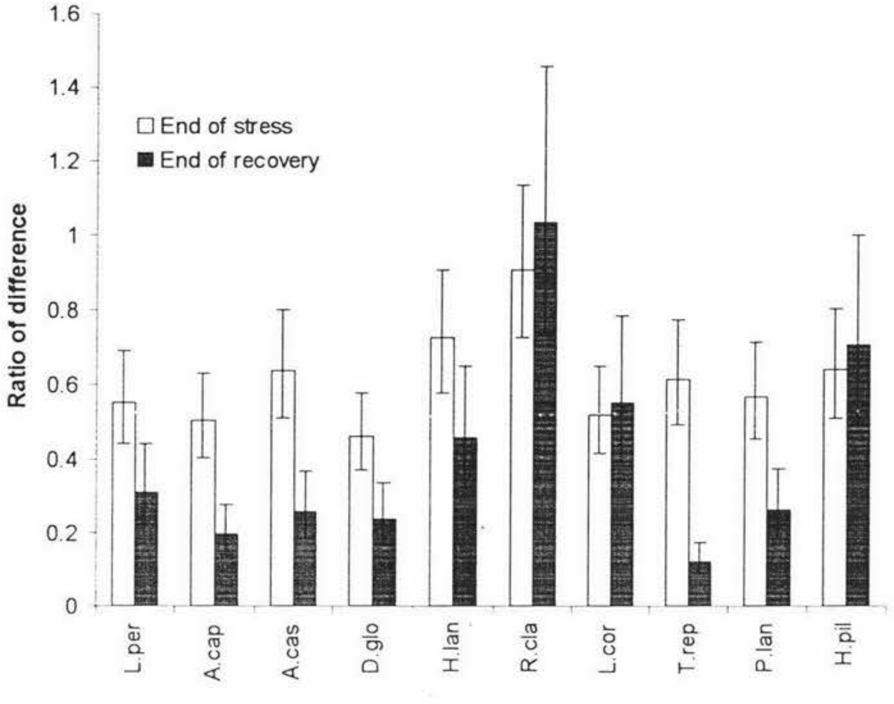


Figure 5 Ratio difference in total dry mass between control and stress

Vertical lines indicate the 95% confidence interval

Significant differences can be established for comparisons between species that exceed the 95% confidence limits.

3.3 Above-ground dry mass

The mean above-ground dry mass for each species at the end of the stress and the end of the recovery for both the control and stress treatments is presented in Table 11.

Table 11 Mean above-ground dry mass (g) of control and stress treatments for each species at the end of the recovery and the end of the stress period

Species	End of stress		End of recovery	
	Control	Stress	Control	Stress
L. perenne	9.900646	5.578947	8.126254	6.01406
A. capillaris	3.364906	1.780332	9.643653	2.814825
A. castellana	4.18539	4.255022	24.47862	4.93474
D. glomerata	11.70949	6.885378	9.969197	8.449439
H. lanatus	14.05109	9.071159	6.191021	6.205277
R. clavatum	0.289124	0.28176	1.137463	0.778645
L. corniculatus	0.069878	0.047744	0.512425	0.162805
T. repens	0.668178	0.324782	1.114382	0.419371
P. lanceolata	2.415002	1.303431	9.054845	1.4547
H. pilosella	0.012259	0.015078	0.041594	0.015305

LSR = 0.2163 for end of stress

LSR = 0.5284 for end of recovery

LSR = 0.2528 for stress plants across end of stress and end of recovery

LSR = 0.5190 for control plants across end of stress and end of recovery

Trifolium repens showed the largest difference between stress and control of the species in above-ground dry mass at the end of the stress period. *Trifolium repens* was followed in order of greatest to least difference by *Agrostis capillaris*, *Plantgo lanceolata*, *Lolium perenne*, *Dactylis glomerata*, *Holcus lanatus*, *Lotus corniculatus*, *Rytidosperma clavatum*, *Agrostis castellana*, *Hieracium pilosella*. No significant difference ($P < 0.05$) was evident between control and stress treatments for all species at the end of the stress.

At the end of the recovery period the greatest difference between control and stress was seen in *Plantago lanceolata*, followed in order of greatest to least by *Agrostis* *castellana*, *Agrostis capillaris*, *Lotus corniculatus*, *Hieracium pilosella*, *Trifolium repens*, *Rytidosperma clavatum*, *Lolium perenne*, *Dactylis glomerata* and *Holcus lanatus*. Significant differences ($P < 0.05$) were found between the control and stress treatments in the species *Plantago lanceolata*, *Agrostis capillaris*, *Agrostis castellana*, *Lotus corniculatus*, *Hieracium pilosella*, and *Trifolium repens*, using the least significant ratios in the comparisons.

An analysis of variance was performed on logarithm transformed above-ground data. The interaction of harvest (end of stress and end of recovery) and species was not significantly different ($P > 0.05$) for stress plants. There was not a significant difference between harvests but there was a significant difference ($P < 0.001$) between species. For the control plants the interaction was not significant. There was not a significant difference between harvests but there was a significant difference ($P < 0.001$) between species in the control plants.

3.3.1 Relative difference between control and stress treatments

The relative differences between the species in terms of the above ground components were investigated for any possibility of differences in the species growth allocation to the above ground parts that may have occurred during both the stress period and the recovery period. The back-transformed differences are shown as a ratio between treatments in Figure 6.

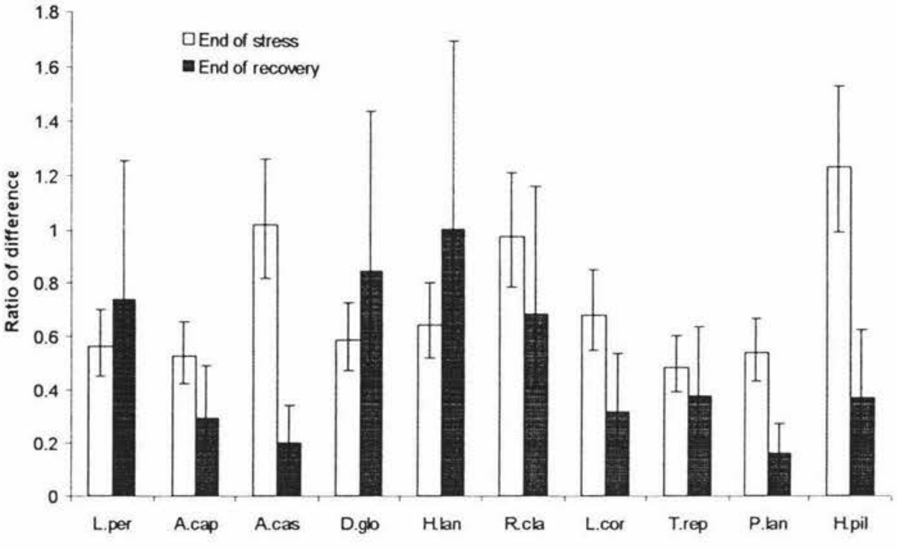


Figure 6 Ratio difference in above-ground dry mass between control and stress

Vertical lines indicate the 95% confidence interval

Significant differences in ratio of dry mass between treatments can be established for comparisons between species that exceed the 95% confidence limits.

3.4 Root dry mass

The mean root dry mass for each species at the end of the stress and the end of the recovery for both the control and stress treatments is presented in Table 12.

Table 12 Mean root dry mass (g) of control and stress treatments for each species at the end of the recovery and the end of the stress period

Species	End of stress		End of recovery	
	Control	Stress	Control	Stress
L. perenne	15.78721	8.70067	10.45207	13.64673
A. capillaris	3.685477	2.251508	9.823721	1.51801
A. castellana	6.505188	3.70284	21.21058	3.696181
D. glomerata	17.98791	7.672941	17.29643	11.81536
H. lanatus	16.19496	12.80838	7.874266	5.186194
R. clavatum	0.312735	0.26775	0.383775	0.467199
L. corniculatus	0.109044	0.042947	0.536494	0.170231
T. repens	0.563719	0.420715	0.801156	0.287999
P. lanceolata	1.806696	0.891277	14.90356	0.853082
H. pilosella	0.021537	0.002516	0.014854	0.017478

LSR = 0.2966 for end of stress

LSR = 0.5429 for end of recovery

LSR = 0.2977 for stress plants across end of stress and end of recovery

LSR = 0.560 for control plants across end of stress and end of recovery

Hieracium pilosella showed the largest difference between stress and control of the species in root dry mass at the end of the stress period. *Hieracium pilosella* was followed in order of greatest to least difference by *Dactylis glomerata*, *Lotus corniculatus*, *Plantgo lançeolata*, *Lolium perenne*, *Agrostis capillaris*, *Agrostis castellana*, *Holcus lanatus*, *Trifolium repens*, *Rytidosperma clavatum*. No significant difference ($P < 0.05$) was evident between control and stress treatments for all species except for *Hieracium pilosella* at the end of the stress.

At the end of the recovery period the greatest difference between control and stress was seen in *Plantago lanceolata*, followed in order of greatest to least by *Agrostis* *capillaris*, *Agrostis castellana*, *Lotus corniculatus*, *Trifolium repens*, *Holcus lanatus*, *Dactylis glomerata*, *Hieracium pilosella*, *Rytidosperma clavatum*, *Lolium perenne*. Significant differences ($P < 0.05$) were found between the control and stress treatments in the species *Plantago lanceolata*, *Agrostis castellana*, *Agrostis capillaris*, *Lotus corniculatus*, and *Trifolium repens* using the least significant ratios in the comparisons.

An analysis of variance was performed on logarithm transformed root data. The interaction of harvest (end of stress and end of recovery) and species was significantly different ($P > 0.05$) for stress plants. For the control plants the interaction was not significant. There was not a significant difference between harvests but there was a significant difference ($P < 0.001$) between species in the control plants.

3.4.1 Relative difference between control and stress treatments

The differences between the species in terms of the root components were investigated for differences in the species growth allocation that may occur during both the stress period and the recovery period. The back-transformed differences is presented as a ratio between treatments in Figure 7.

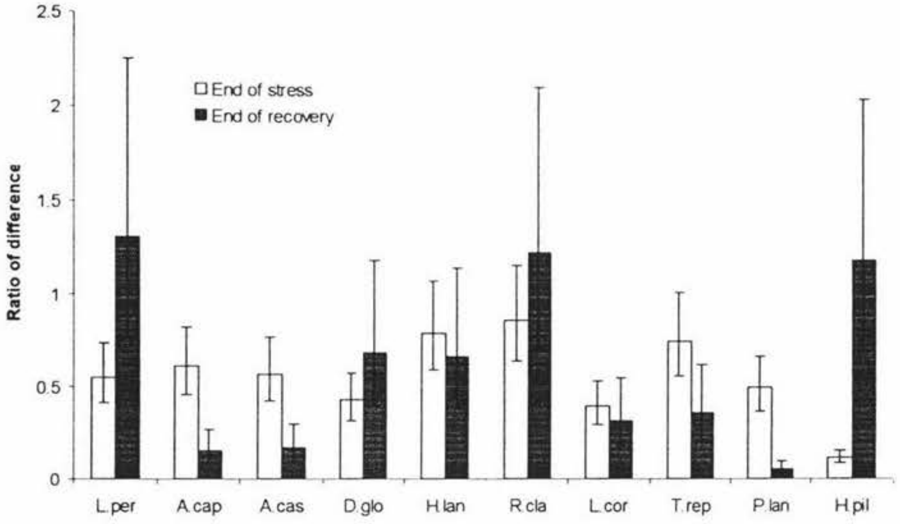


Figure 7 Ratio difference in root dry mass between control and stress

Vertical lines indicate the 95% confidence interval

Significant differences can be established for comparisons between species that exceed the 95% confidence limits.

3.5 Root:shoot ratio

The root:shoot ratio was investigated for stress effects on allocation in both the stress period and the recovery period.

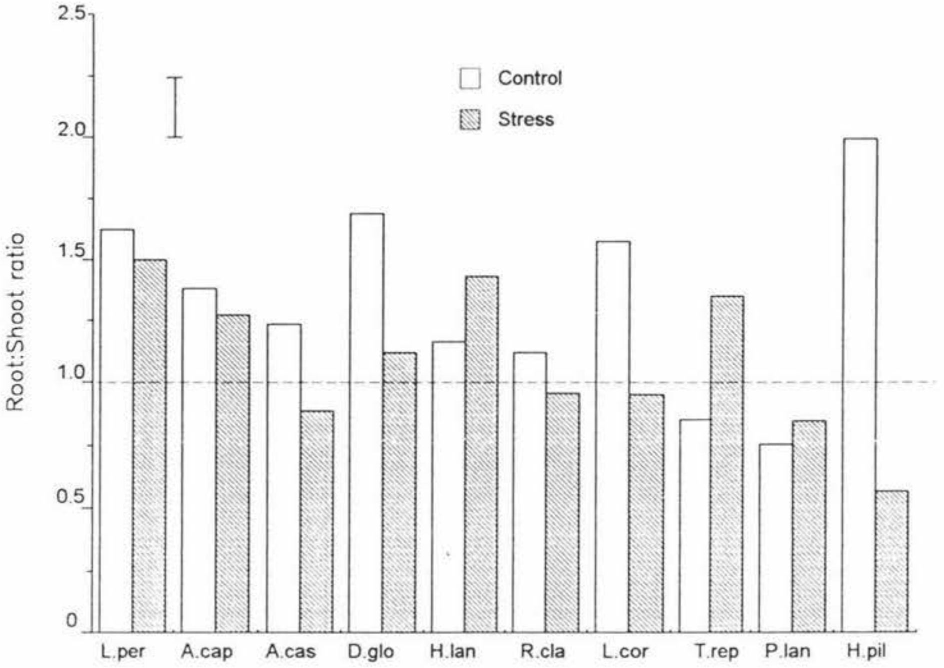


Figure 8 Root:shoot ratio at the end of stress period

Error bar indicates LSD ($P < 0.05$)

The root:shoot ratio of the control treatment at the end of the stress period was above one in all species except *Trifolium repens* and *Plantago lanceolata*, indicating that these two species had a greater shoot dry mass than root dry mass. Some of the plants in the stress treatment had reduced ratios, showing an increase in shoot dry mass relative to root. The species that showed this response were; *Agrostis castellana*, *Rytidosperma clavatum*, *Lotus corniculatus*, *A. capillaris*, and *Hieracium pilosella*. These were all not significant (LSD $P < 0.05$) between the control and stress except for the ratios of *Lotus corniculatus* and *Hieracium pilosella*. In contrast *Holcus lanatus*, *Trifolium repens* and *Plantago lanceolata* showed a higher root:shoot ratio in their stress treatments than in their control treatments but only *Trifolium repens* was significantly different (LSD $P < 0.05$). The largest differences between control and stress occurred with *Dactylis glomerata*, *Lotus corniculatus* and *Hieracium pilosella* with the difference occurring in the stress treatment having ratios closer to one or even more shoot than root in the case of *Lotus corniculatus* and *Hieracium pilosella*. *Agrostis castellana* showed a much larger difference in root:shoot ratio than *A. capillaris*.

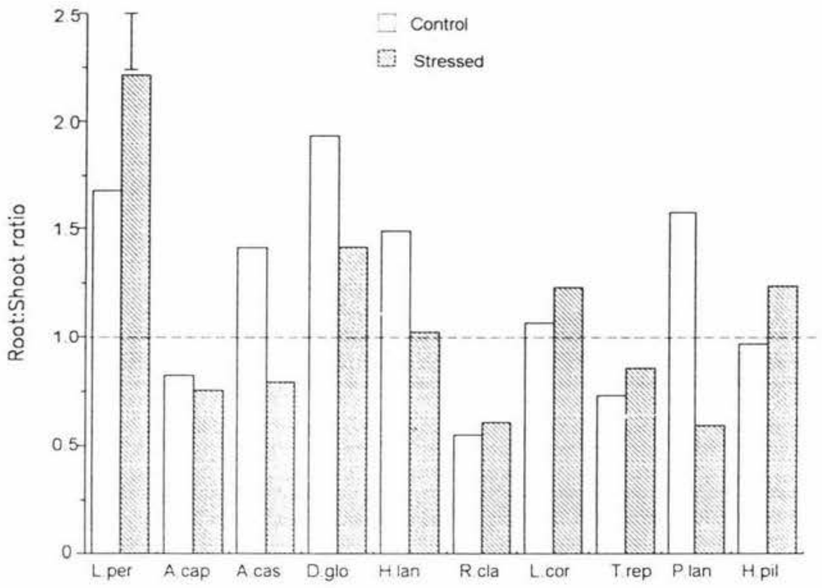


Figure 9 Root:shoot ratio at the end of recovery period

Error bar indicates LSD ($P < 0.05$)

At the end of the recovery period only three of the control treatment species had a root:shoot ratio below one, these were *Trifolium repens* (as it was at the end of the stress period), *Agrostis capillaris* and *Rytidosperma clavatum*. Of the stressed plants that were alive, only *Rytidosperma clavatum* and *Trifolium repens* had a ratio below one. *Lolium perenne* had a significantly higher root:shoot ratio in the stress treatment than the control. A greater root:shoot ratio was also seen in the stress treatment of *Rytidosperma clavatum*, *Lotus corniculatus* *Trifolium repens* and *Hieracium pilosella* but these were not significant at LSD $P < 0.05$.

3.6 Dead material content

The percent of dead material of above ground material was calculated to investigate any differences occurring between species in the amount of leaf death.

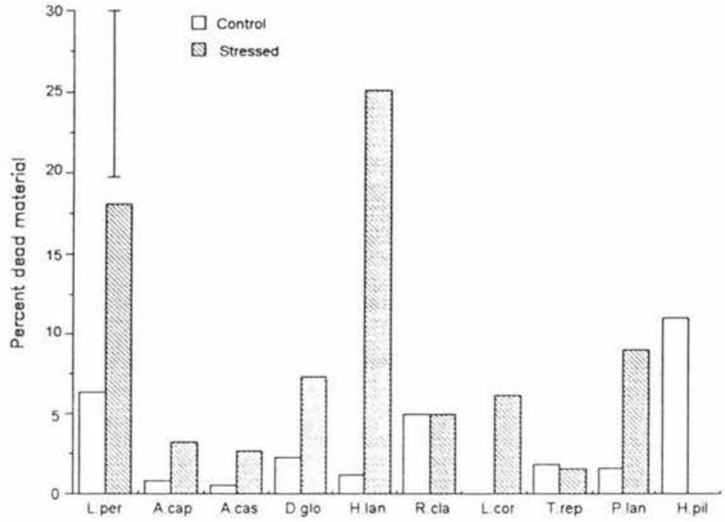


Figure 10 Percent of dead material in above-ground at the end of stress period

Error bar indicates LSD ($P < 0.05$)

At the end of the stress period, leaf death was apparent in some of the stressed species. The most significant (LSD $P < 0.05$) amount of leaf death occurred in the species *Holcus lanatus,* The other species that showed levels of leaf death was *Lolium perenne*.

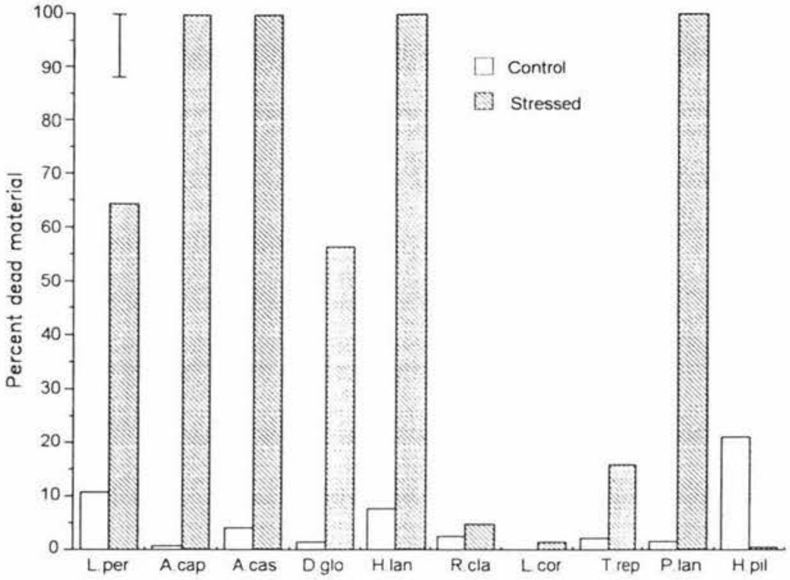


Figure 11 Percent of dead material in above-ground at the end of recovery period

Error bar indicates LSD ($P < 0.05$)

The non-surviving species (*Agrostis capillaris*, *Agrostis castellana*, *Holcus lanatus*, and *Plantago lanceolata*) had the highest percentages of dead material at the end of the recovery period. *Lolium perenne* and *Dactylis glomerata* both survived the stress and recovered but still showed a high proportion of dead material at the end of the recovery period. *Trifolium repens* also had an observed high leaf death rate but this is not reflected in the non significant difference between stress and control possibly because of rapid regrowth rates. A higher dead material concentration was also observed in unstressed *Hieracium pilosella*.

When the dead material was analysed in terms of the ratio difference between control and stress treatments the analysis of variance of the interaction of harvest and species was significantly different ($P > 0.001$).

3.7 Relative growth rate

Of the surviving species, the difference in the relative growth rate between control and stress treatments was highly significant ($P < 0.01$) for *Lolium perenne* alone. Numerically the greatest differences were for *Lolium perenne*, *Dactylis glomerata*, *Rytidosperma clavatum*, *Lotus corniculatus* and *Trifolium repens*. *Hieracium pilosella* had a higher relative growth rate in the stress than in the control, though this was not significant at $P < 0.05$. *Rytidosperma clavatum* experiencing water deficit in the stress period showed a similar growth rates to stressed *Lolium perenne* and *Dactyls glomerata* (approx 0.1 g g^{-1} $week^{-1}$).

Table 13 Relative growth rate over recovery period (g g^{-1} $week^{-1}$)

Species	Control	Stress	$P < t$
T. repens	0.374	0.014	ns.
L. perenne	0.426	0.110	**
D. glomerata	0.333	0.112	ns.
R. clavatum	0.190	0.123	ns.
L. corniculatus	0.113	0.084	ns.
H. pilosella	0.004	0.020	ns.

$P < t$. * = < 0.05, ** = < 0.01, *** = < 0.001

3.8 Plant tissue nutrient content

The analysis of phosphorus and nitrogen concentration in the surviving species in the total plant material at the end of the stress period and at the end of the recovery was taken to give an indication of tissue function and root activity.

Table 14 Plant tissue nitrogen concentration (mg g^{-1}) at end of stress period

Species	Control	Stress	*P < t*
L. perenne	14.310	12.399	ns.
D. glomerata	13.480	11.340	**
R. clavatum	13.115	17.224	***
L. corniculatus	18.838	17.538	ns.
T. repens	25.074	28.202	**
H. pilosella	23.33	21.212	ns.

P < t. * = <0.05, ** = <0.01, *** = <0.001

Plant tissue nitrogen concentration at the end of the stress was higher in the control treatment for four of the surviving species but with no significant difference in *Lotus corniculatus* and *Hieracium pilosella*. Two of the species, *Rytidosperma clavatum* and *Trifolium repens* had higher concentrations in the stress treatment ($P < 0.01$ and $P < 0.001$ respectively). *Trifolium repens* had the highest tissue concentration of the species in both control and stress treatment.

Table 15 Plant tissue nitrogen concentration (mg g^{-1}) at end of recovery period

Species	Control	Stress	*P < t*
L. perenne	14.4952	9.280	**
D. glomerata	15.130	9.301	**
R. clavatum	17.922	18.314	ns.
L. corniculatus	20.164	21.880	ns.
T repens	29.758	27.869	ns.
H. pilosella	18.155	19.531	ns.

P < t. * = <0.05, ** = <0.01, *** = <0.001

Nitrogen content at the end of the recovery period was significantly different ($P < 0.01$) between the control and stress treatments for *Lolium perenne* and *Dactylis glomerata* with the control having the largest concentrations. There were no significant differences for the other species.

Table 16 Plant tissue phosphorus concentration (mg g^{-1}) at end of stress period

Species	Control	Stress	$P < t$
L. perenne	2.487	2.205	ns.
D. glomerata	2.708	2.286	*
R. clavatum	1.285	1.507	*
L. corniculatus	1.180	1.824	ns.
T. repens	1.533	1.714	ns.
H. pilosella	2.000	1.818	ns.

$P < t$. * = <0.05, ** = <0.01, *** = <0.001

Plant tissue phosphorus concentration at the end of the stress period was higher in the control treatment of *Dactylis glomerata* ($P < 0.05$) *Rytidosperma clavatum* had a higher phosphorus concentration in the stress treatment than the control ($P < 0.05$). The greatest difference between control and stress was with *Dactylis glomerata*. The highest overall phosphorus concentration was in the *Dactylis glomerata* stress treatment.

Table 17 Plant tissue phosphorus concentration (mg g^{-1}) at end of recovery period

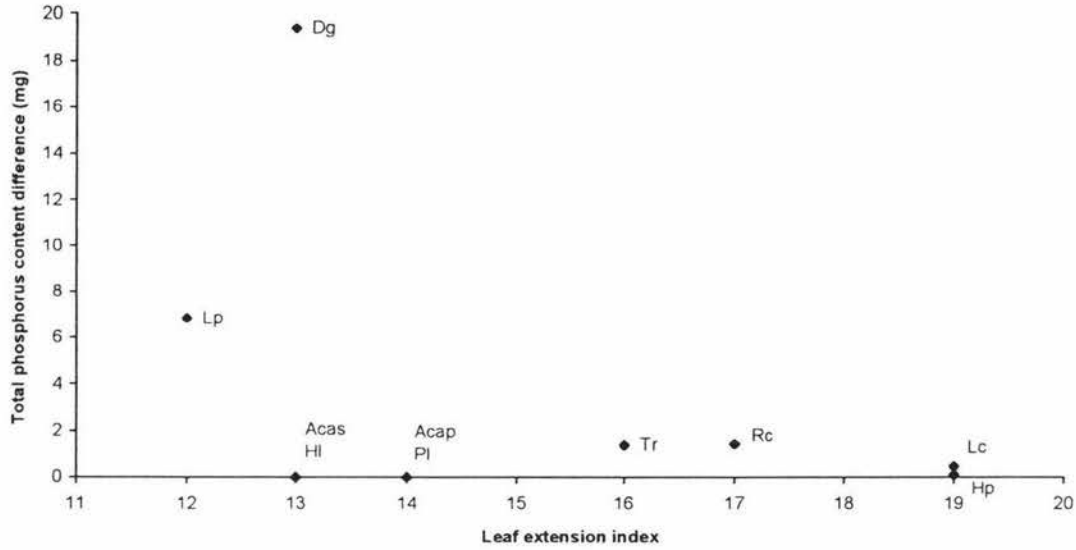
Species	Control	Stress	$P < t$
L. perenne	2.501	1.924	*
D. glomerata	3.283	2.580	ns.
R. clavatum	1.605	1.809	ns.
L. corniculatus	2.269	1.590	ns.
T. repens	2.997	2.986	ns.
H. pilosella	2.109	2.343	ns.

$P < t$. * = <0.05, ** = <0.01, *** = <0.001

Plant tissue phosphorus concentration of *Rytidosperma clavatum* at the end of the recovery was higher in the stress than the control but this difference was not significant. A significant difference was seen with the control having a higher concentration than the stress treatment in *Lolium perenne* ($P < 0.05$).

3.9 Total plant tissue uptake plotted against functional attributes

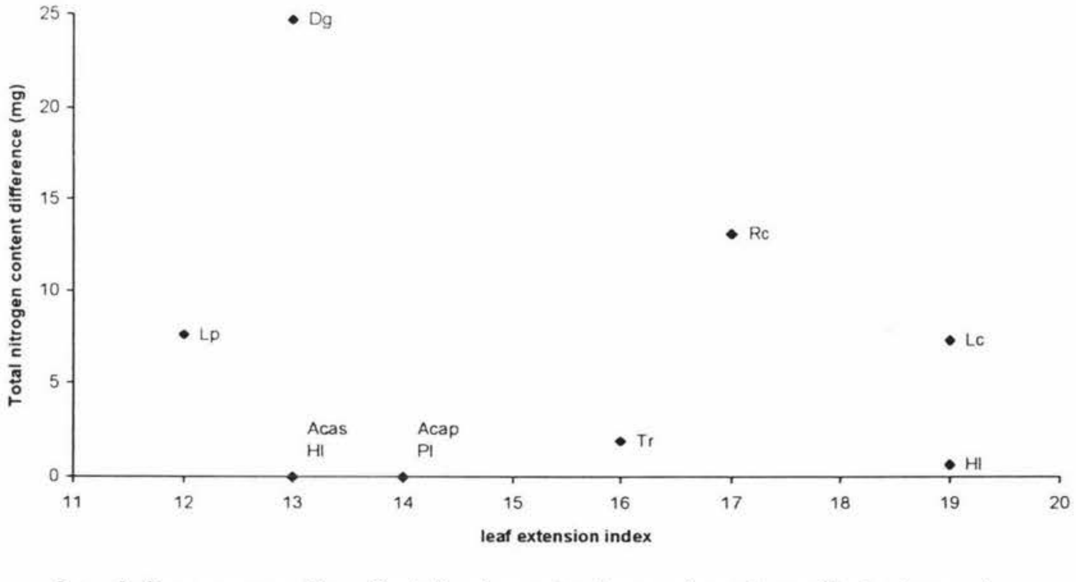
Trends between nutrient uptake during the recovery period and some plant functional characteristics were investigated by plotting the difference in total plant nutrient content between the end of the stress period and the end of the recovery period against an index of each of four different characteristics.



Lp - *Lolium perenne*, Dg - *Dactylis glomerata*, Acap - *Agrostis capillaris*, Acas - *A. castellana*, Lc - *Lotus corniculatus*, Tr - *Trifolium repens*, Rc - *Rytidosperma clavatum*, Hl - *Holcus lanatus*, Pl - *Plantago lanceolata*, Hp - *Hieracium pilosella*

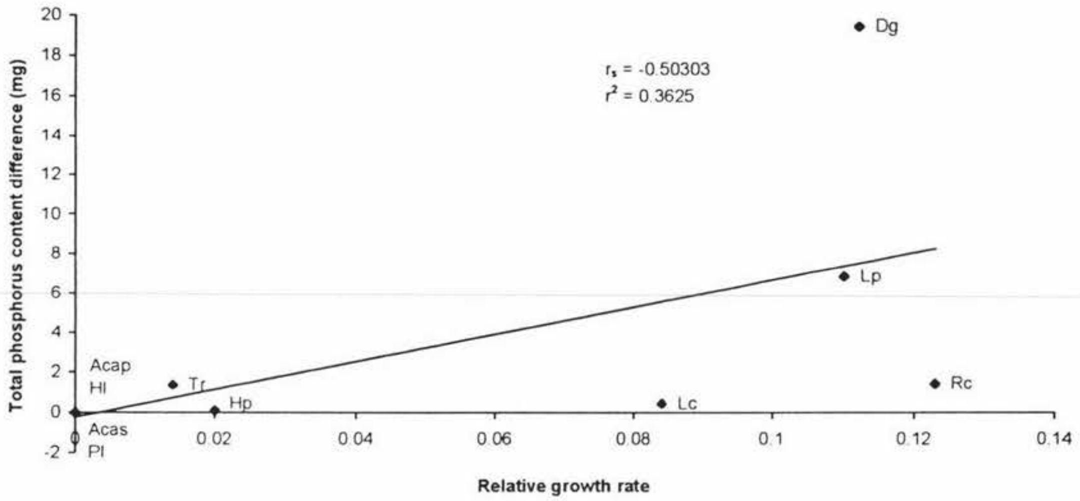
Figure 12 Change in phosphorus over the recovery period plotted against leaf extension index

Leaf extension index is the number of days into the stress that the leaf extension rate of the stress plants went below 15% that of the controls



Lp - *Lolium perenne*, Dg - *Dactylis glomerata*, Acap - *Agrostis capillaris*, Acas - *A. castellana*, Lc - *Lotus corniculatus*, Tr - *Trifolium repens*, Rc - *Rytidosperma clavatum*, Hl - *Holcus lanatus*, Pl - *Plantago lanceolata*, Hp - *Hieracium pilosella*

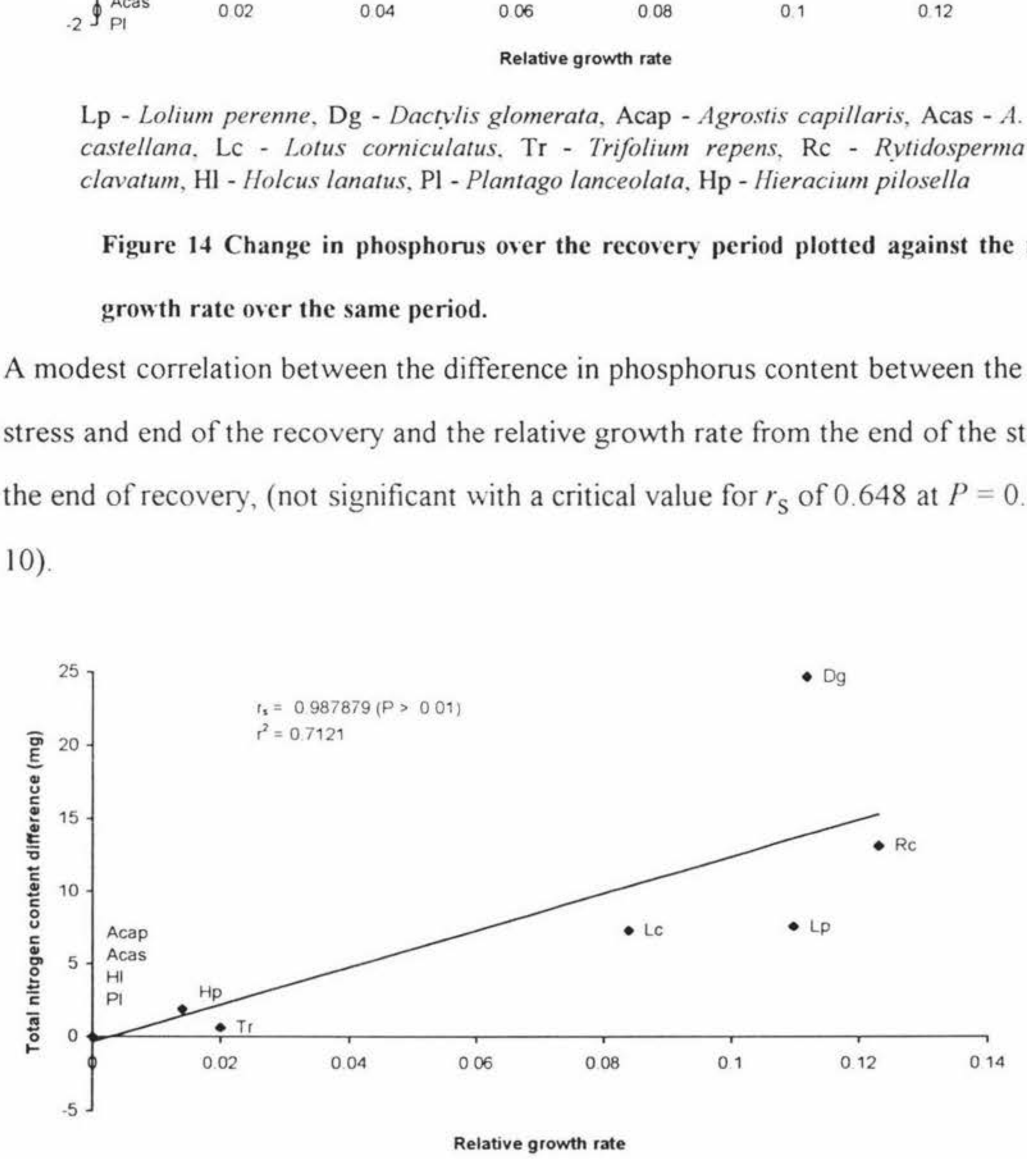
Figure 13 Change in nitrogen over the recovery period plotted against leaf extension index



Lp - *Lolium perenne*, Dg - *Dactylis glomerata*, Acap - *Agrostis capillaris*, Acas - *A. castellana*, Lc - *Lotus corniculatus*, Tr - *Trifolium repens*, Rc - *Rytidosperma clavatum*, Hl - *Holcus lanatus*, Pl - *Plantago lanceolata*, Hp - *Hieracium pilosella*

Figure 14 Change in phosphorus over the recovery period plotted against the relative growth rate over the same period.

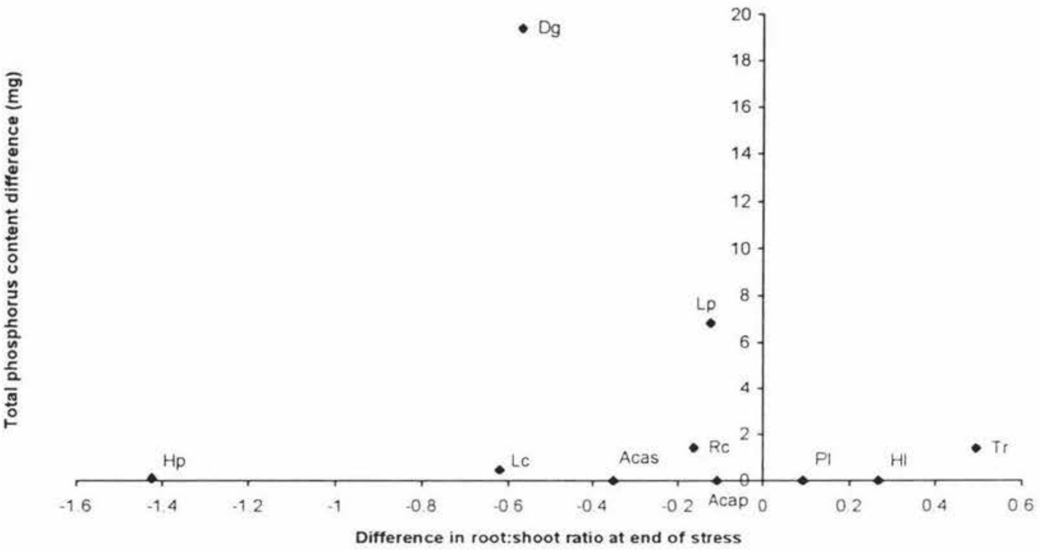
A modest correlation between the difference in phosphorus content between the end of stress and end of the recovery and the relative growth rate from the end of the stress to the end of recovery, (not significant with a critical value for r_S of 0.648 at $P = 0.05$ $n = 10$).



Lp - *Lolium perenne*, Dg - *Dactylis glomerata*, Acap - *Agrostis capillaris*, Acas - *A. castellana*, Lc - *Lotus corniculatus*, Tr - *Trifolium repens*, Rc - *Rytidosperma clavatum*, Hl - *Holcus lanatus*, Pl - *Plantago lanceolata*, Hp - *Hieracium pilosella*

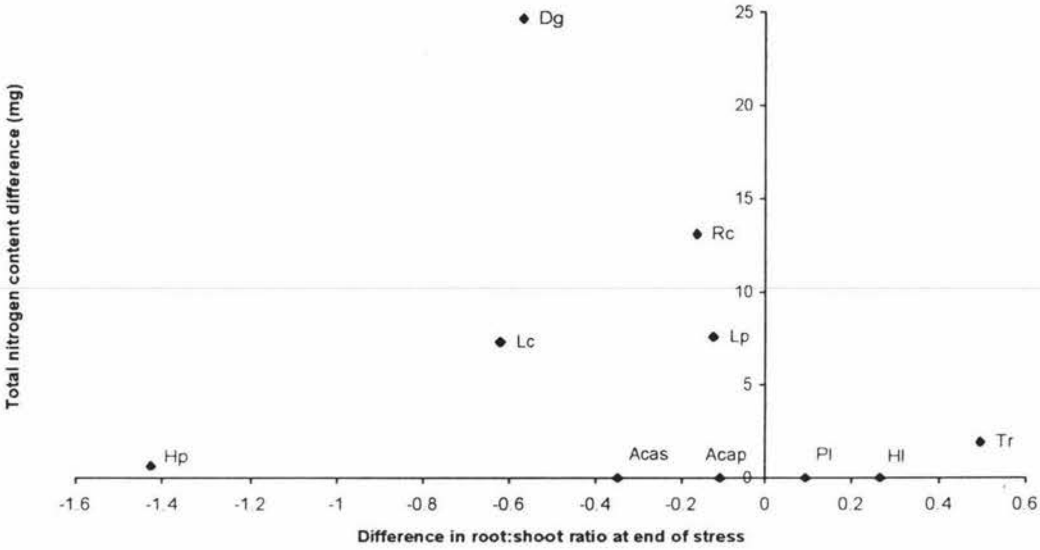
Figure 15 Change in nitrogen over the recovery period plotted against the relative growth rate over the same period.

A strong correlation between the difference in nitrogen content between the end of stress and end of the recovery and the relative growth rate from the end of the stress to the end of recovery, (significant with a critical value for r_S of 0.648 at $P = 0.05$ $n = 10$).



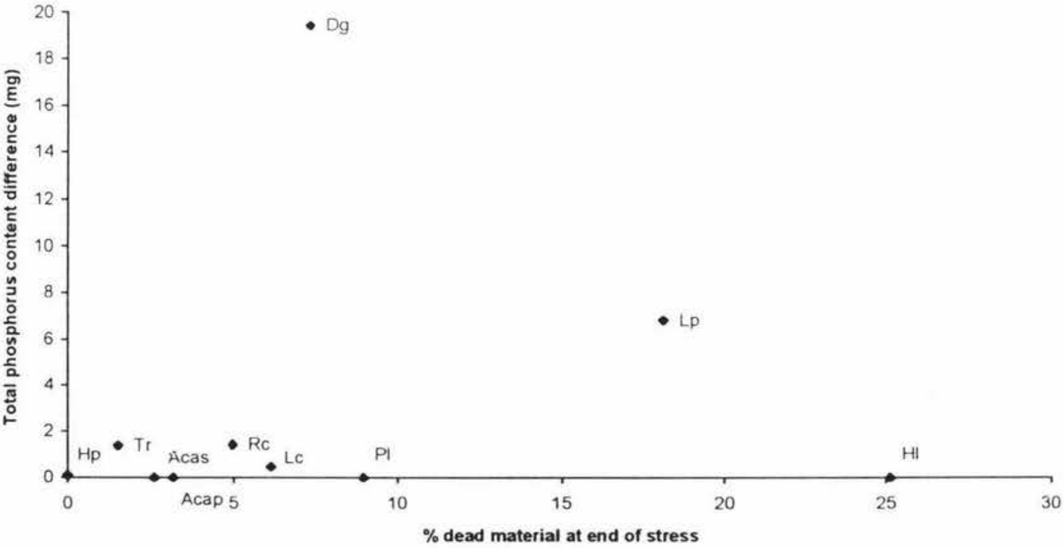
Lp - *Lolium perenne*, Dg - *Dactylis glomerata*, Acap - *Agrostis capillaris*, Acas - *A. castellana*, Lc - *Lotus corniculatus*, Tr - *Trifolium repens*, Rc - *Rytidosperma clavatum*, Hl - *Holcus lanatus*, Pl - *Plantago lanceolata*, Hp - *Hieracium pilosella*

Figure 16 Change in phosphorus over the recovery period plotted against the difference in control and stress treatments root:shoot ratio at the end of the stress period



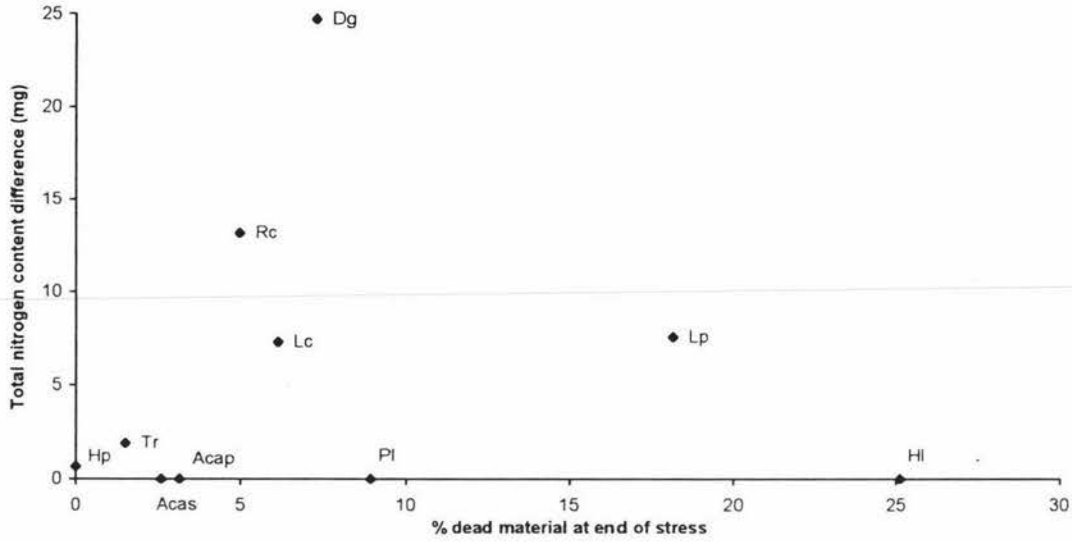
Lp - *Lolium perenne*, Dg - *Dactylis glomerata*, Acap - *Agrostis capillaris*, Acas - *A. castellana*, Lc - *Lotus corniculatus*, Tr - *Trifolium repens*, Rc - *Rytidosperma clavatum*, Hl - *Holcus lanatus*, Pl - *Plantago lanceolata*, Hp - *Hieracium pilosella*

Figure 17 Change in nitrogen over the recovery period potted against the difference in control and stress treatment root:shoot ratio at the end of the stress period



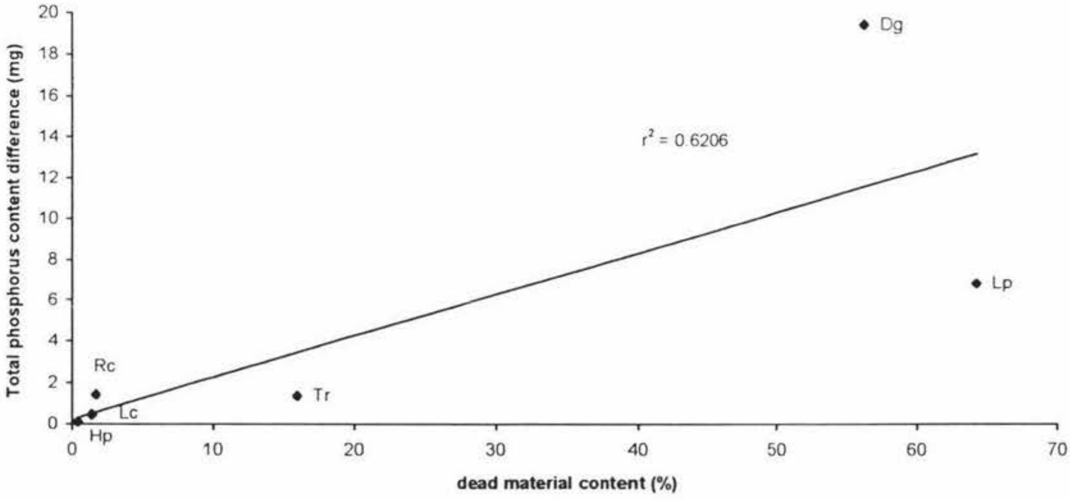
Lp - *Lolium perenne*, Dg - *Dactylis glomerata*, Acap - *Agrostis capillaris*, Acas - *A. castellana*, Lc - *Lotus corniculatus*, Tr - *Trifolium repens*, Rc - *Rytidosperma clavatum*, Hl - *Holcus lanatus*, Pl - *Plantago lanceolata*, Hp - *Hieracium pilosella*

Figure 18 Change in phosphorus over the recovery period plotted against percent dead material at the end of the stress period



Lp - *Lolium perenne*, Dg - *Dactylis glomerata*, Acap - *Agrostis capillaris*, Acas - *A. castellana*, Lc - *Lotus corniculatus*, Tr - *Trifolium repens*, Rc - *Rytidosperma clavatum*, Hl - *Holcus lanatus*, Pl - *Plantago lanceolata*, Hp - *Hieracium pilosella*

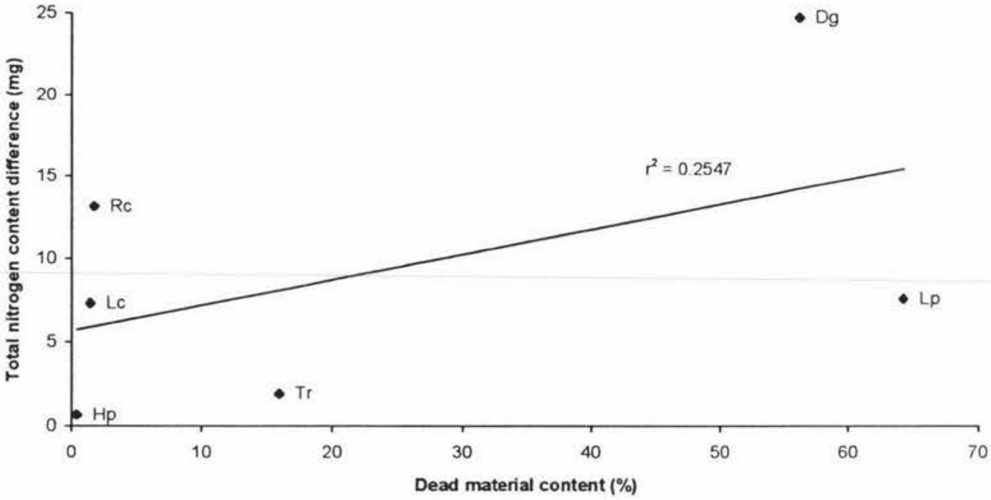
Figure 19 Change in nitrogen over the recovery period plotted against the dead material percentage at the end of the stress period



Lp - *Lolium perenne*, Dg - *Dactylis glomerata*, Lc - *Lotus corniculatus*, Tr - *Trifolium repens*, Rc - *Rytidosperma clavatum*, Hp - *Hieracium pilosella*

Figure 20 Change in phosphorus over the recovery period plotted against the dead material percentage at the end of the recovery period

A strong correlation between the difference in phosphorus content between the end of the stress and the end of the recovery and the percentage dead mater of the surviving species at the end of the recovery.



Lp - *Lolium perenne*, Dg - *Dactylis glomerata*, Lc - *Lotus corniculatus*, Tr - *Trifolium repens*, Rc - *Rytidosperma clavatum*, Hp - *Hieracium pilosella*

Figure 21 Change in nitrogen over the recovery period plotted against the dead material percentage at the end of the recovery period

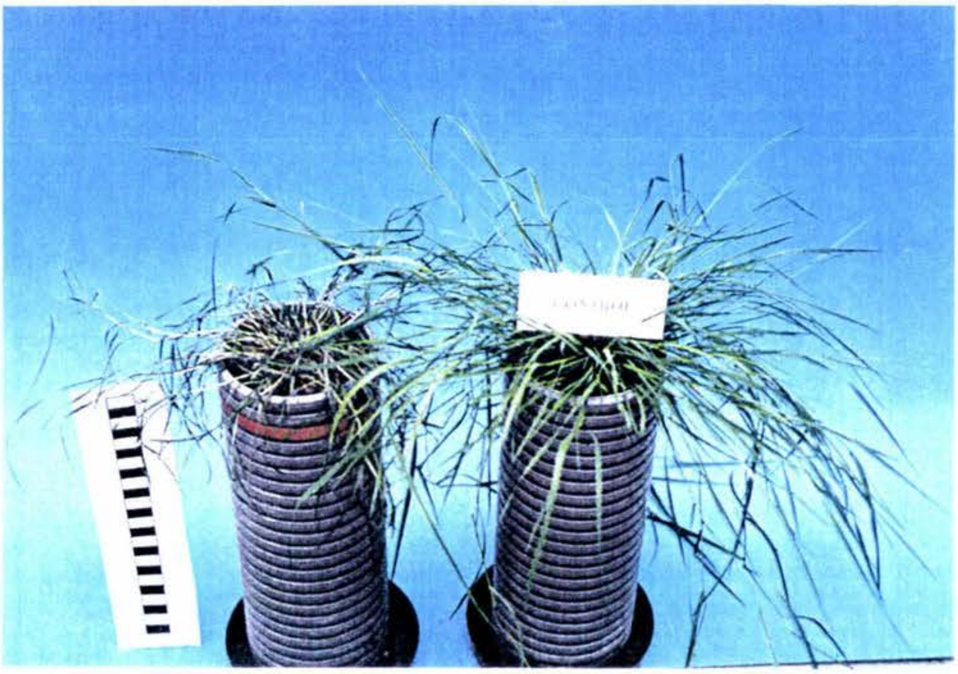
A modest correlation between the difference in phosphorus content between the end of the stress and the end of the recovery and the percentage dead material of the surviving species at the end of the recovery.

Plates 3 and 4 show the stress and control treatments of the plants at the end of the stress and the end of the recovery period

Plate 3 a-j Control and stress treatments at the end of the stress period

a) *Lolium perenne*

b) *Agrostis capillaris*



c) *Agrostis castellana*

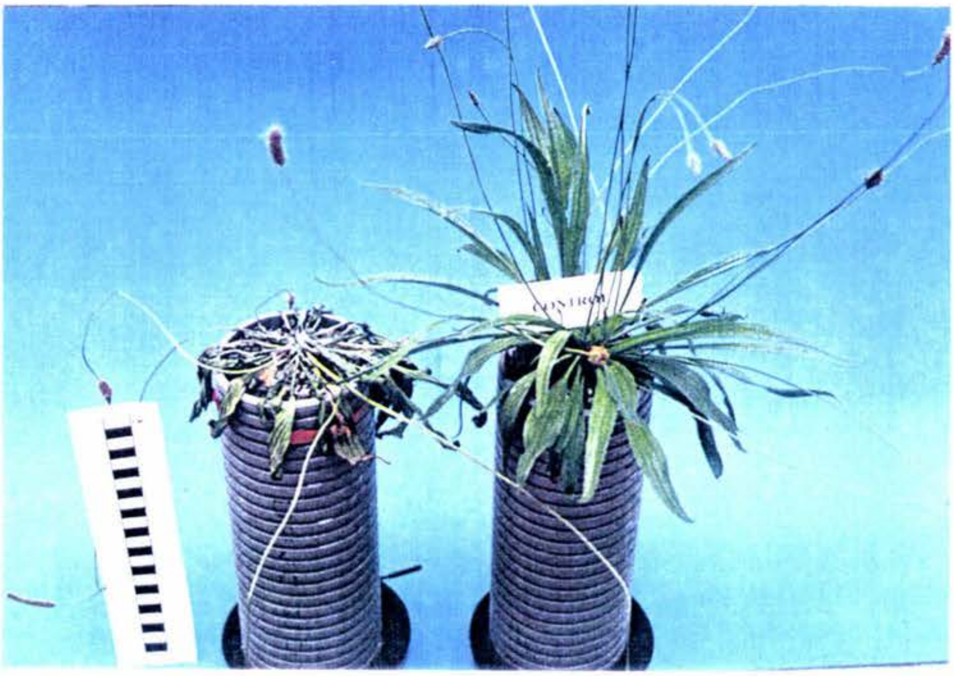
d) *Dactylis glomerata*

e) *Holcus lanatus*

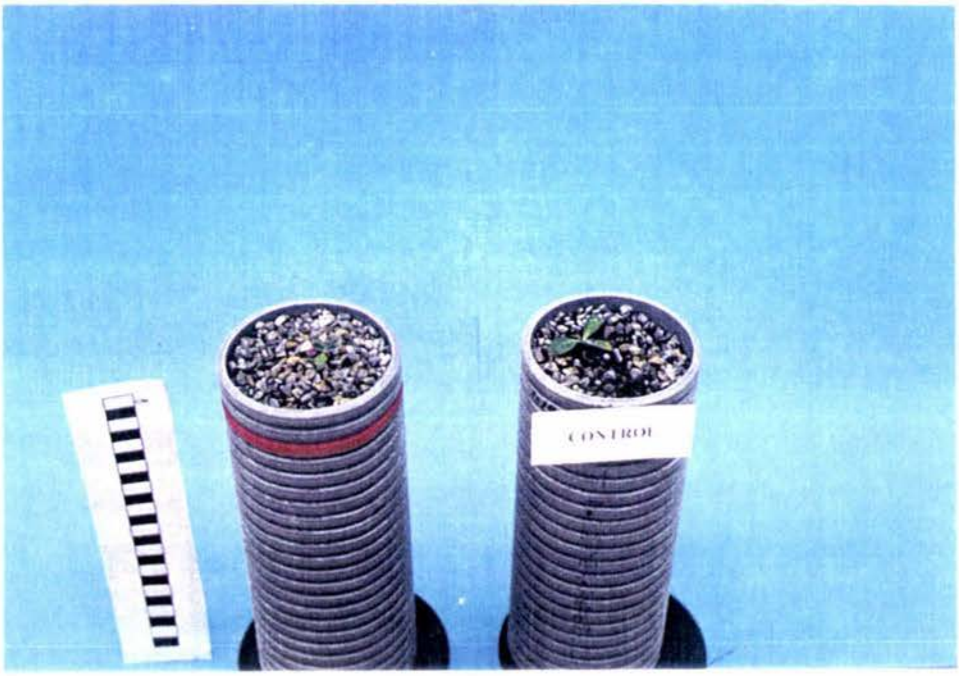
f) *Rytidosperma clavatum*

g) *Lotus corniculatus*

h) *Trifolium repens*



i) *Plantago lanceolata*



j) *Hieracium pilosella*

Plate 4 a-j Control and stress treatments at the end of the recovery period

a) *Lolium perenne*

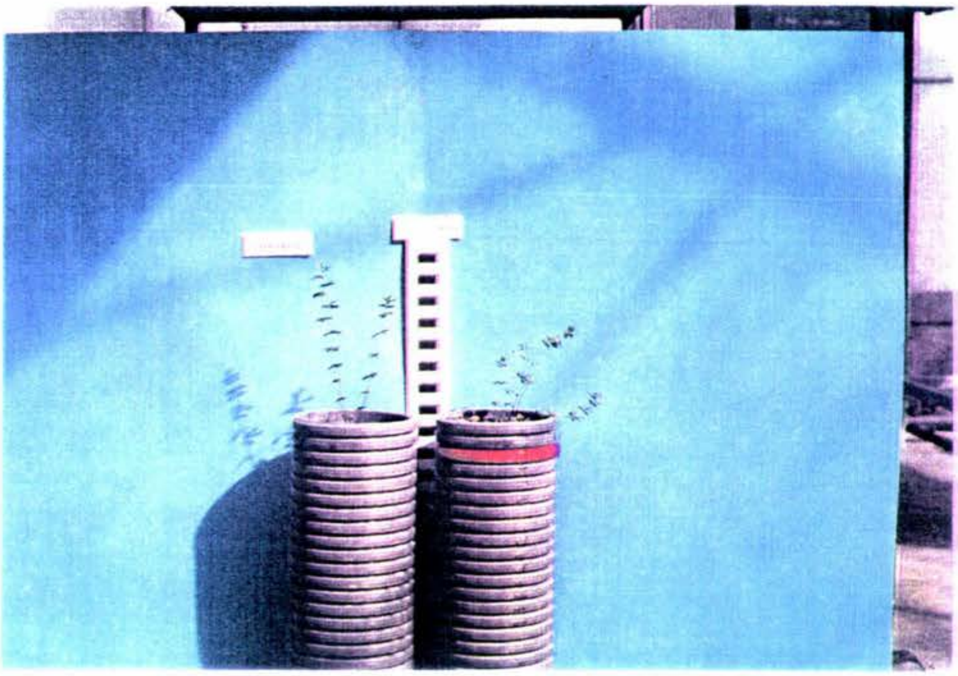
b) *Agrostis capillaris*

c) *Agrostis castellana*

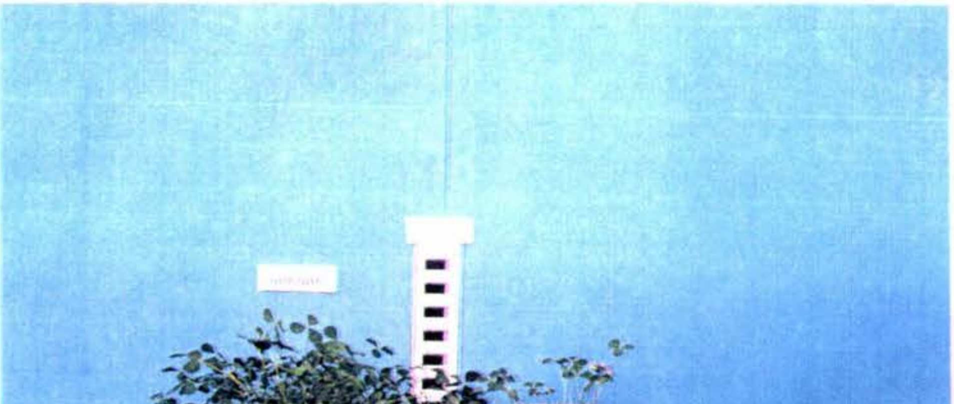
d) *Dactylis glomerata*

e) *Holcus lanatus*

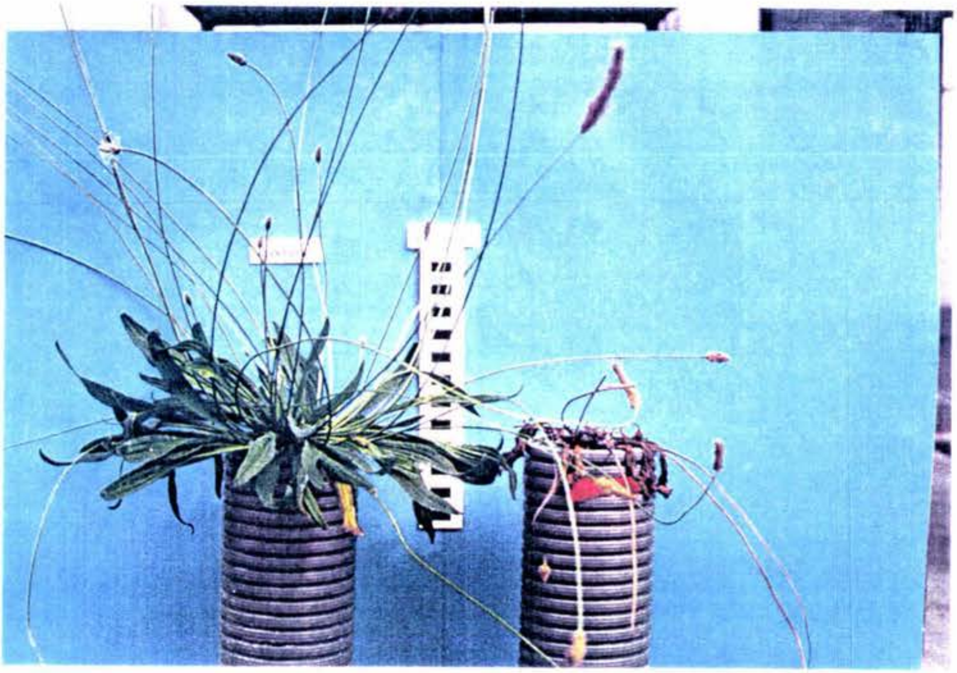
f) *Rytidosperma clavatum*



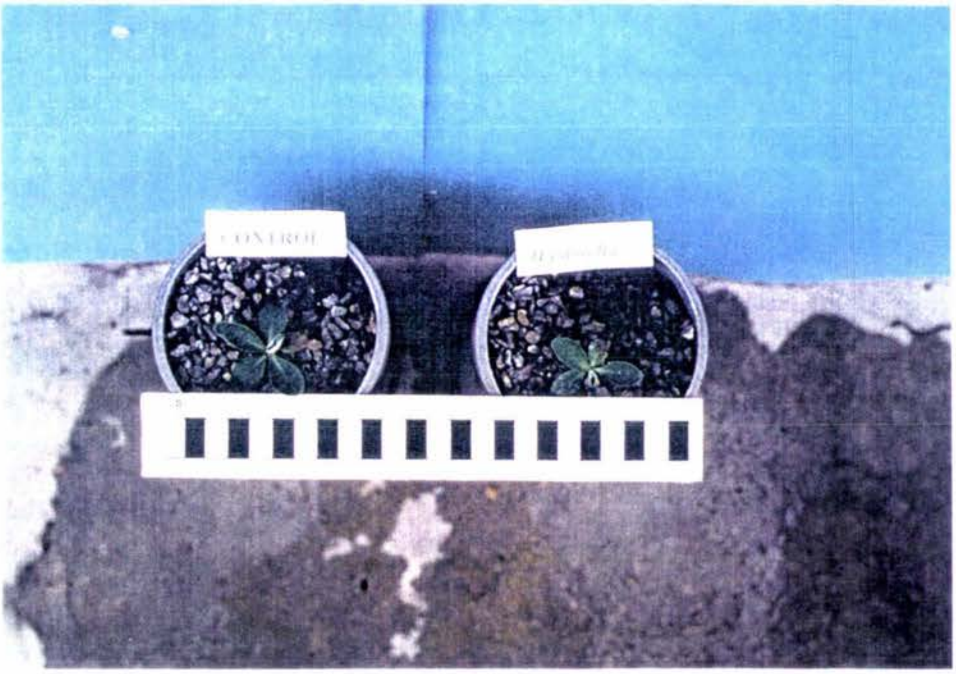
g) *Lotus corniculatus*



h) *Trifolium repens*



i) *Plantago lanceolata*



j) *Hieracium pilosella*

4 DISCUSSION

4.1 Introduction

There are a range of possible models that can be used to investigate the response of plants to stress. I have concentrated on the changes in plant functional attributes, their morphological plasticity and the concept of resistance and resilience in the species and have related these to plant strategy theory.

The advantages and limitations of the experimental technique, and a consideration of whether it was successful in meeting the objectives of the study and the possible changes that could be made to further improve the technique are discussed first. The discussion has examined the plant attributes that were measured and the differences in species response during the stress. Aspects of changes to leaf elongation rate and dry mass are discussed in the model of resistance and resilience and are related to plant strategy theory. As the morphological and physiological plasticity of plants is a key component in the predictions of plant strategy theory, the response of some functional attributes and the differences in plasticity in response to stress are discussed and related to the predictions in plant strategy theory. Finally the results are discussed in the context of coexistence in hill country pasture communities.

4.2 Experimental technique

The technique used in this experiment is a modification of that used by Raynal *et al.* (1985) in which herbaceous plants were subjected to drought involving daily transfers of root systems between nutrient solutions and air. The advantages of this type of system are that the timing and intensity of the drought is closely controlled. (Raynal *et al.* 1985). A possible problem foreseen in using this method is the difference in the amount of moisture retained by the range of different root structures of the species when they collapse together following the removal from a nutrient solution. To overcome this, my technique provided support to the roots during the drying periods. Stone chip was provided as a medium that would support the root structure during the dry periods but allow moisture to be lost in a rapid and uniform manner. In addition it was intended that the root would be easily removed from the container. The stone chip also had the advantage of being readily available at a low cost. Problems that occurred using the stone chip became evident at the harvest stage of the experiment, in particular during root extraction. Fine root structures were difficult to remove as the usual root washing procedures were ineffective. There was also a slight tendency for parts of the root system to grow down the side of the cylinder rather than through the stone chip.

The experimental technique was considered to be successful in enabling the objective to be met. Further treatments establishing the effect of not applying nutrients to the control would have been useful by having a true control treatment that continued to receive the same level of nutrient throughout the experiment period. The results on some aspects of plasticity became complicated due to a nutrient deficiency in the control treatments through the stress period. The changes in resource allocation especially to root material is known to be strongly related to nutrient availability (Bradshaw 1965, Campbell and Grime 1989).

4.3 Plant characteristics

Differences in specific attributes of the species and treatments were studied and species were ranked and grouped in terms of their response and recovery to water stress. The attributes measured were: leaf extension rate, total dry mass and relative growth rate, leaf growth, above-ground and root dry mass and root:shoot ratio, total tissue phosphorus and nitrogen concentration and change in total plant phosphorus and nitrogen content. The results taken during and at the end of the stress period are discussed first followed by those from during, and at the end of the recovery.

4.4 Leaf extension during stress

The leaf and petiole extension rates plotted against time were used to give an indication of the severity of the stress. Leaf expansion is more sensitive to water deficits than most other plant processes and the extent that water deficit will reduce growth by reducing leaf area depends on the relationship between leaf expansion rate and leaf water potential during the stress and recovery (Hsiao and Acevedo 1974, Ludlow and Ng 1977). Differences in response will be associated with morphological response (plasticity) and this is of crucial importance in distinguishing the physiology of competitors and stress tolerators (Grime 1979).

All species except *Lotus corniculatus* and *Hieracium pilosella* showed at some stage during the stress a difference between the control and stress treatment in leaf/petiole extension. The most dramatic effect was seen in the species *Lolium perenne*, which had the earliest and greatest difference between the control and stress treatments and in addition the leaf extension rate in *Lolium perenne* ceased before any of the other species. The species *Dactylis glomerata* which is generally considered to be amongst temperate pasture species most able to withstand drought and recover afterwards (Thomas 1986), also had a rapid response in terms of a lower leaf extension rate early in the stress period. Jackson (1974) reported that in *Dactylis glomerata*, the leaf water status is more sensitive to water deficit than in *Lolium perenne*, but this was not reflected in the leaf extension rate, it does explain however the rapid response to the stress. It is known that this species responds to drought stress by reducing transpiration rate, conserving the available soil moisture and therefore being apparently more resistant under field conditions (Jackson 1974). In this experiment any advantage a plant may have in terms of its ability to conserve soil moisture or to actively forage for water was removed. It was expected that like *Lolium perenne* the response in leaf extension rate in *Dactylis glomerata* would be seen as early in the stress period. The early response seen in these two species indicates that they have the potential for mechanistic changes in response to the stress which is characteristic of the competitor type species. Further functional traits of the competitor, such as short leaf longevity and rapid potential growth rate (Grime *et al.* 1986), are discussed later.

Between the two extremes of a small response to the stress and a marked response, are the species that had a somewhat delayed response during the stress period. Within this group are the species that showed no sign of recovery at the end of the recovery period; *Holcus lanatus*, *Plantago lanceolata*, *Agrostis capillaris* and *Agrostis castellana*. The species *Trifolium repens*, which did recover, is also included in this group as a species that showed an intermediate level of response to the water stress. The petiole extension rate for *Trifolium repens* did not cease entirely. This is possibly due to selective allocation of water resources from leaves to stem material as reported by Turner (1990). *Rytidosperma clavatum* had the latest and least response in leaf extension rate of the species that had a noticeable response to the stress period, but only towards the end of the stress period.

The two species that did not show any response to the water stress in terms of leaf extension rate; *Hieracium pilosella* and *Lotus corniculatus*, had initially a low leaf extension rate. Slow leaf growth and low leaf turnover are characteristic of the stress tolerant type species (Grime *et al.* 1986). The relationship between the leaf extension rates and plant strategy theory is discussed in section 4.13.

The control treatments of *Lolium perenne*, *Agrostis capillaris*, *Dactylis glomerata*, *Holcus lanatus* and *Lotus corniculatus* all showed depressed leaf extension rate during the stress period. This is presumably due to the lower level of nutrients received by the control plants during the stress period. The most extreme of these species was *Lotus corniculatus* which had a marked decrease in petiole extension rate in both the control and stress treatments so that no difference was seen between the treatments. This leads to the possible conclusion that the effect of reducing nutrients was the main factor in the response of petiole extension rate in this species during the stress period.

One of the factors effecting the change in leaf extension rate of all the stressed plants in the first twelve days of the stress period was the ability of the plants to continue leaf extension during the watering period which occurred at night. Jackson (1974) was surprised at the rapidity of recovery that both *Lolium perenne* and *Dactylis glomerata* achieved at sunset in simulated swards grown in soil with unlimited rooting depth where rainfall was excluded. It is reported that for most of the night, leaf water potentials would only be associated with low levels of water stress, and in view of the critical response of extension growth to leaf water potentials that is reported by Boyer (1970), leaf extension would have continued at night. However the effect of the progressive water deficit in the first twelve days of the stress would have still had an adverse effect on extension growth by reducing the duration and magnitude of high turgor levels. As suggested in Jackson (1974) the amount of compensation achieved during darkness for reduced daytime growth is open to speculation even if optimum conditions are regained during darkness, as lost photosynthesis cannot be regained. The situation regarding recovered cell extension is uncertain (Acevedo *et al.* 1971). The sensitivity of the plant to the low levels of water stress, duration and magnitude of high turgor explains the difference between the species in the reduction of leaf/petiole extension rate during the early part of the stress period.

4.5 Total dry mass at end of stress

Although none of the differences between stress and control treatments at the end of the stress were significant the order of rank that was produced in the response is still of interest. The greatest response was in the species that are C-CSR in their strategy classification (Table 3), with characteristics of weakly developed acclimation to change in moisture supply (Grime *et al.* 1988). The exception to this occurred in *Lotus corniculatus* a S-CSR strategist that ranked high in terms of the difference between control and stress. *Lolium perenne* exhibited a similar response to *Dactylis glomerata* to the water stress. *Rytidosperma clavatum* an S-R strategist exhibited the least difference between control and stress treatments at the end of the stress period than the other species. Plants of the CSR strategy such as *Holcus lanatus* and *Agrostis castellana*, appeared at the bottom of the ranking in terms of the difference between control and stress treatments. *Agrostis capillaris* had a greater difference between control and stress than *Agrostis castellana* despite the similarities in strategy and form. This highlights the differences that the role of habitat has in the development of plant functional attributes.

4.6 Division of dry mass between shoot and root at end of stress

The response of the plants to the water stress in terms of allocation of resources to either above ground growth or root tissue was investigated by the breakdown of the total dry mass into above ground and root dry mass. The changes in allocation between above ground and below ground indicates the levels of plasticity in the plants in terms of resource allocation and strongly relates to their established plant strategy.

The ranking of the differences between control and stress in the above ground dry mass at the end of the stress period placed the species that are S-CSR and S-R such as *Hieracium pilosella*, *Lotus corniculatus* and *Rytidosperma clavatum* with the least difference. These three species that are the species that are recognised as exhibiting the characteristics of the stress tolerator type plants (Grime 1988). *Lolium perenne* and *Dactylis glomerata* continued as in total dry mass to rank next to each other while the two *Agrostis* sp. ranked at little to no difference between control and stress dry mass for *A. castellana* and second to highest difference between control and stress for *A. capillaris*. The difference in above ground dry mass at the end of the stress period divided the species into two main groupings. These consisted of the species that the water stress affected by a reduction in biomass accumulation, and the second group of species that the water stress had little effect in terms of the difference in above ground biomass of the stress treatment compared to the control. The first group included all the species except for *Hieracium pilosella*, *Rytidosperma clavatum* and *Lotus corniculatus* and *Agrostis castellana*.

The difference between control and stress for root dry mass was least at the end of the stress period for *Rytidosperma clavatum*, *Holcus lanatus* and *Trifolium repens*. *Hieracium pilosella*, which had the least difference in above-ground dry mass between control and stress treatments at the end of the stress period, had the greatest difference in root dry mass. The species *Trifolium repens* and *Holcus lanatus* changed in their ranking from the above-ground dry mass to have less difference in comparison with the other species in the ratio difference between the stress and control treatments.

The root:shoot ratio at the end of the stress period for the stress treatment plants favoured above ground dry mass for the species; *Agrostis capillaris*, *Rytidosperma clavatum*, *Lotus corniculatus*, *Plantago lanceolata* and *Hieracium pilosella*. It is noted that this group includes the species that were deemed least affected by the water stress and also includes two of the species that did not recover. Of these species only *Plantago lanceolata* favoured above ground dry mass in the control treatment as well as the stress treatment. Of the other species that had a root:shoot ratio above one in the stress treatment at the end of the stress period only *Trifolium repens* and *Holcus lanatus* had a higher ratio than their control treatments. The greatest differences between control and stress treatments occurred in the species *Trifolium repens*, *Holcus lanatus*, with higher ratios in the stress treatment and *Dactylis glomerata*, *Lotus corniculatus*, *Hieracium pilosella*, *Agrostis capillaris* with higher ratios occurring in the control treatment. The response of the species in root:shoot ratio at the end of the stress period was not expected and contradicts the findings of most other previous work, where the response is that root growth is favoured relative to shoot growth (Turner and Begg 1978, Hsiao and Acevedo 1974). The only species that had a higher root:shoot ratio in the stress treatment at the end of the stress period were *Trifolium repens* and *Holcus lanatus*. The possible reason for this is that the control plants were also allocating growth to the root due to a nutrient deficiency effect (Bradshaw *et al.* 1960).

4.7 Dead material percentage at end of stress

The percentage of dead material in above-ground at the end of the stress treatment was higher in the stress treatment for all species except *Hieracium pilosella* and *Rytidosperma clavatum*. The most dead material was in *Holcus lanatus*. It would be expected that plants of the stress tolerator type would not readily lose leaves to tissue death as part of their characteristic of tissue efficiency, long leaf longevity and low tissue turnover (Grime *et al.* 1988). Plants that are attempting to avoid water stress will shed leaves in a process to reduce transpiring surface area to prevent dehydration to lethal levels (Kozlowski 1973). Whether this is the case in the level of tissue death in the species that had dead material at the end of the stress period is not able to be assessed, but it can be seen that tissue death occurred in the more competitor type species as a non-reversible plastic response. *Trifolium repens* is expected to have a rapid morphological response to stress as a C-S-R to C-R strategist, has poor stomatal control of leaf hydration and water loss, stomatal closure that is incomplete even when turgor is low (Hart 1987). It is suggested by Turner (1990) that this may explain the rapid wilting of leaves and petioles when water supply is restricted. The high hydraulic resistance in the petiole limits water flux to the leaves and limits water loss from the plant during water stress. Water flow to the stolon tip could continue down the path of least resistance and favours stolon tip survival. Johns (1978) also reports that white clover has an inability of stomatal response to control leaf hydration. This may explain the low percentage of dead material in this species at the end of the stress as stolon and petiole material remained alive.

4.8 Leaf extension rate during recovery

The species response in the recovery period in terms of leaf extension rate were more variable than during the stress period. This is also reported by Thomas and Norris (1981) where proportional differences between species were found to be greater after a drought than during.

The species that showed the highest response in recovery in leaf elongation rate were *Lolium perenne*, *Dactylis glomerata* and *Rytidosperma clavatum*. It would be expected that any advantage in recovery of *Dactylis glomerata* in comparison to *Lolium perenne* would not be apparent as the ability to conserve the soil moisture was removed, but although the two species show a similar pattern of recovery, *Dactylis glomerata* retained some advantage due to compensatory growth. *Dactylis glomerata* was the only species to exhibit any compensatory growth in leaf elongation rate, with a higher leaf extension rate in the stress treatment than in the control toward the end of the recovery period. This compensatory or 'stored growth' in leaf elongation is also reported in maize after mild water stress (Hsiao and Acevedo 1974), and indicates continued cell division during the water stress.

The leaf extension rate for the species; *Agrostis capillaris*, *Agrostis castellana*, *Holcus lanatus* and *Plantago lanceolata* remained at zero through to the end of the recovery period due to death. The species *Trifolium repens* continued to have a depressed petiole extension rate in the stress compared to the control, *Lotus corniculatus* and *Hieracium pilosella* had little difference between the control and stress treatments through the recovery period. There was however some indication of an increase in the difference of the petiole extension rate developing in *Lotus corniculatus* towards the end of the recovery period, as the control treatment returned to pre-stress leaf extension rate and the stress treatment remained at the stress period rate. This was possibly a response in the control to the renewed availability of nutrients.

4.9 Total dry mass at end of recovery

The non-response exhibited in the stress period by *Rytidosperma clavatum* and *Hieracium pilosella* continued in the recovery period, reflecting the continued small to non-effect that the stress had on these species. The species that had a significant difference between the dry mass of the control compared to the stress treatments did not include *Rytidosperma clavatum*, *Lotus corniculatus* and *Hieracium pilosella*. There was a general increase in dry mass of all the surviving species with a significant increase in the dry mass of the stress plants of *Lotus corniculatus* from the end of the stress period to the end of the recovery. Of the species that were dead at the end of the recovery period the *Agrostis* sp. were the only species to have an increase in dry mass over the recovery period, indicating that the species were not yet dead at the end of the stress. Their appearance of being dry but still a dull green also suggests this, and at dissection most plant material was not deemed to be dead material.

4.10 Relative growth rate

The relative growth rate of the species over the recovery period (Table 13) shows in the control treatment the potential growth rate under the prevailing conditions with the highest in the more competitor type species *Lolium perenne* and *Dactylis glomerata*. The relative growth rate of the stress treatments show the stress tolerant species close to or even exceeding their controls while *Lolium perenne*, *Dactylis glomerata* and *Trifolium repens* did not meet their potential. Potential growth rate has proved particularly useful in classifying plant strategies (Grime *et al.* 1988). An example of this is the observations of Makepeace (1985) on *Hieracium pilosella* which has a low dry matter production compared to other resident species in its habitat such as *Agrostis capillaris*, it was concluded that *Hieracium pilosella* showed a relatively wide edaphic-climatic tolerance giving it greater abundance and higher dry matter production than other *Hieracium* species within the same growth habitat. The low growth rate is one characteristic of stress tolerator type species that have developed in a chronically unproductive but relatively undisturbed environment (Grime 1988).

4.11 Division of dry mass between shoot and root at end of recovery

The two main groupings that were found at the end of the stress period remained distinct but there was a notable increase in the relative difference in above ground dry mass in the species *Rytidosperma clavatum*. Of the surviving species *Lolium perenne* and *Dactylis glomerata* were the only species to have a root:shoot ratio in the stress treatment above one. The control and stress treatments for *Rytidosperma clavatum* and the control treatment for *Trifolium repens* were below one and the other surviving species, *Lotus corniculatus* and *Hieracium pilosella* were close to one. The root:shoot ratio at the end of the recovery showed some changes from those at the end of the stress period. *Lolium perenne* was the only species in which the stress treatment had a higher ratio than the control at the end of the recovery. *Dactylis glomerata* had an increase of the control ratio from what it was at the end of the stress.

The difference in the root:shoot ratios in the stress treatments from the end of the stress to the end of the recovery in the surviving species increased in only *Lolium perenne* and *Hieracium pilosella*, indicating post-stress growth being allocated to the roots. *Trifolium repens* and *Rytidosperma clavatum* allocated more growth to above ground material, especially in the species *Rytidosperma clavatum* which is being recognised as a S-SR strategist.

4.12 Dead material percentage at end of recovery

The results at the end of the recovery period showed the observed continued loss of live dry mass in all the affected species because of the continued loss of material due to irreversible plastic responses to the stress in tissue death (Levitt 1972). This was especially important in the species that showed no sign of recovery, but a large relative difference still occurred in the species that did recover due to continued tissue death. The levels of dead material in above-ground material at the end of the recovery period show the continued death and accumulation of dead material after the stress was over and indicates the inability of recovering plants to produce new material at the same rate. The species that showed no recovery from the stress, therefore, show the highest percentage of dead material at the end of the recovery. High levels of dead material were also observed in plants that lost most of their original above ground material and replaced it with new growth during the recovery period as in *Lolium perenne* and *Dactylis glomerata*. *Trifolium repens* also had an observed high leaf death rate but this is not reflected as a percentage of total dry mass as the stolon material was not observed to be dead. The higher dead material concentration in the *Hieracium pilosella* control is of significance, the reason for this is not known but could be associated with the control being at a more developed age then the stress treatment, at the end of the recovery.

4.13 Resistance and resilience

To relate the plants response to the water stress and the subsequent recovery period to Plant Strategy theory and to assist in the comparison between species the plants with similar patterns of response were grouped together. To do this the plants were ranked according to levels of resistance and resilience. The terms resistance and resilience are used to describe both the ability of the plant to continue functioning during the stress (resistance) and the rate of recovery after the stress is removed (resilience). The leaf elongation rates plotted against time were used to help in the assessment of the groupings through a subjective view of the patterns of response, and are illustrated in Figure 22.

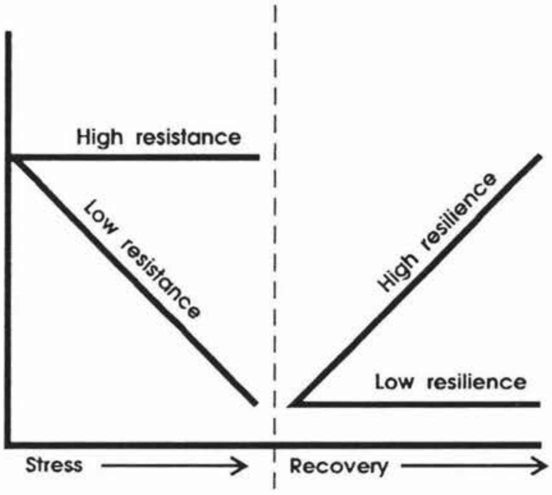


Figure 22 Leaf/petiole elongation rate pattern

The species ranking for resilience and resistance is seen in Table 18. The least resistant species, on the basis of leaf elongation rate, was *Lolium perenne*, more so than *Holcus lanatus* which is the only species considered a moist habitat plant (Levy 1970), and would have been expected to show the greatest response to water stress. The species with the highest resistance in leaf/petiole extension rate were, *Rytidosperma clavatum*, *Lotus corniculatus*, and *Hieracium pilosella*. These are all species which exhibit characteristics of the stress tolerators type (Grime *et al.* 1988), supporting plant strategy theory predictions.

Table 18 Species ranking of resistance and resilience

	Resistance	Resilience
Greatest	*Hieracium pilosella*	*Lolium perenne*
	Lotus corniculatus	*Dactylis glomerata*
	Rytidosperma clavatum	*Rytidosperma clavatum*
	Trifolium repens	*Trifolium repens*
	Agrostis castellana	*Lotus corniculatus*
	Plantago lanceolata	*Hieracium pilosella*
	Agrostis capillaris	*Agrostis capillaris*
	Holcus lanatus	*Agrostis castellana*
↓	*Dactylis glomerata*	*Plantago lanceolata*
Least	*Lolium perenne*	*Holcus lanatus*

The species that showed the highest resistance during the water stress were assessed as having poor resilience because they had no potential for recovery, with the exception of *Rytidosperma clavatum* which had the shortest interval of depressed leaf extension rate of the responsive species, over the last four days of the stress period. This was followed by an immediate recovery in leaf extension rate. The species that showed the highest resilience in recovery of leaf elongation rate were *Lolium perenne*, *Dactylis glomerata* and *Rytidosperma clavatum*. These species of high resilience were characteristic of C-R to C-S-R type species in relation to plant strategy theory (Grime *et al.* 1988).

4.14 Plant tissue nutrient concentration

The analysis of phosphorus and nitrogen concentration in the surviving species in plant material at the end of the stress period and at the end of the recovery were taken to give a possible indication of root function. The difference in total nutrient content at the end of the stress period to the end of the recovery was used to assess resource use as an indication of plant function during the recovery period. The nitrogen concentration in total plant tissue at the end of the stress period was higher in the control plants of *Dactylis glomerata*. Phosphorus concentration was higher in the stress plants for the species *Rytidosperma clavatum* and *Trifolium repens*. At the end of the recovery *Dactylis glomerata* and *Lolium perenne* both had a higher concentration of phosphorus in the control plants than in the stress plants. Plant tissue phosphorus concentration at the end of the stress period was higher in the control plants of *Dactylis glomerata*. The phosphorus concentration was higher in the stress plants treatment in the species *Rytidosperma clavatum*. At the end of the recovery *Lolium perenne* had a larger concentration of phosphorus in the total plant tissue of the control plants than the stress plants.

4.15 Response to water stress - morphological plasticity

This section discusses the changes to particular plant attributes used in the plots of the change in nutrient content against functional attributes (figures 12 to 21). The changes are then discussed in view of the predictions in plant strategy theory (Table 19) relating to; relative growth rate, response to stress and acclimation of photosynthesis, mineral nutrition and tissue hardiness to seasonal change in temperature, light and moisture supply.

4.15.1 Leaf extension index

In the plots of change in phosphorus and nitrogen over the recovery against the leaf extension index (figures 12 and 13), which is the number of days into the stress that the stress treatment plants extension rate went below 15% of the control, three groups can be identified. Those that have a low index but high change in nutrient content, the four non-survivors with moderate extension index and no change in nutrient content, the species that have a higher extension index and a low change in nutrient content. The groups appear to be defined as the more competitor type species in the first group and stress tolerant type species in the third group. *Trifolium repens* is the exception of the competitor type species by responding later in petiole extension rate to the stress possibly because petiole leaf extension rate is not directly comparable or that the species were less plastic in the response of petiole extension rate.

4.15.2 Relative growth rate

The plot of relative growth rate against change in total phosphorus and nitrogen content has a modest and strong correlation (figures 14 and 15). The correlation between nutrient uptake as an indicator of recovery vigour, coupled with strong vegetative growth in the more competitor type species fits plant strategy theory. The immediate response to the stress as seen in the leaf elongation rate and other attributes of the more competitor type species which responded rapidly both to the stress and to the conditions of the recovery enabled the species to survive successfully. Plant strategy theory (Grime *et al.* 1988) suggests that plants with low growth rates and other stress tolerant attributes will be better able to tolerate water stress than faster growing, more competitor type plants, but this is only the case past a particular point. C-S-R strategists such as *Agrostis capillaris*, *A. castellana* and *Plantago lanceolata* neither had the rapid plastic response or the stress tolerant attributes to enable the plant to survive, and did not recover

4.15.3 Root:shoot ratio

The plot of the difference in root:shoot ratio between control and stress at the end of the stress against the change in total phosphorus and nitrogen content over the recovery (Figure 16 and 17) show *Trifolium repens* was the only species to survive that had a higher root:shoot ratio in the stress than the control. The pattern has the dead species with little difference and little response. The difference between stress and control does not indicate the levels of plasticity exclusively due to water stress in the species as in addition there would have been a response to the nutrient deficit by the potential growth rate and is of less importance for the stress tolerator type with lower potential growth rate.

4.16 Response to water stress and plant strategy theory predictions

The indices used in the plots of plant attributes against changes in total phosphorus and nitrogen content (figures 12 to 21) have been placed on the table of predicted responses of the species in terms of their classification in plant strategy theory (Table 19). A comparison can be seen between the predicted behaviour of the primary plant strategies and the species response to the water stress through the indices measured.

Table 19 Comparative characteristics of the ten hill country species

Species	**C-S-R classification**	**Relative growth rate (RGR over recover period)**	**Response to stress (Day of stress that stress treatment at 15% of control), (Difference in R:S between stress and control at end of stress)**	**Acclimation of photosynthesis etc. (Difference in dead material content between stress treatment and control at end of stress)**
Lolium perenne	C-R to C-S-R	High/moderately high (**0.11**)	Rapid/moderate morphological responses (**12**), (**-0.125**)	Weak/moderately developed (**18.13**)
Agrostis capillaris	C-S-R	Moderately high (**0**)	Moderate morphological responses (**14**), (**-0.109**)	Moderately developed (**2.44**)
A. castellana	C-S-R	Moderately high (**0**)	Moderate morphological responses (**13**), (**-0.349**)	Moderately developed (**2.13**)
Dactylis glomerata	C-S-R to C	Moderate high/high (**0.112**)	Moderate/rapid morphological responses (**13**), (**-0.568**)	Moderate/weakly developed (**5.07**)
Holcus lanatus	C-S-R	Moderately high (**0**)	Moderate morphological responses (**13**), (**0.266**)	Moderately developed (**23.97**)
Rytidosperma clavatum	S to S-R	Low/moderately low (**0.123**)	Morphological responses slow and small/diversion of resources into flowering (**17**), (**-0.164**)	Strong/moderately developed (**0.53**)
Lotus corniculatus	S to C-S-R	Low/moderately high (**0.084**)	Morphological responses slow and small/moderate morphological responses (**19**), (**-0.621**)	Strong /moderately developed (**6.15**)
Trifolium repens	C-S-R to C-R	Moderately high/high (**0.014**)	Rapid/moderate morphological responses/diversion of resources into flowering (**16**), (**0.496**)	Moderate/weakly developed (**-0.27**)
Plantago lanceolata	C-S-R	Moderately high (**0**)	Rapid/moderate morphological responses (**14**), (**0.0947**)	Moderately developed (**7.36**)
Hieracium pilosella	S to C-S-R	Low/moderately high (**0.02**)	Morphological responses slow and small/moderate morphological responses (**19**), (**-1.425**)	Strong to moderately developed (**-10**)

The competitor type species *Lolium perenne*, *Dactylis glomerata* had the highest growth rate during the recovery. These species responded early in the stress in leaf elongation rate indicating morphological response to the stress. The three species identified as being of the stress tolerant strategy had characteristically low growth rate during the recovery and were slow to have a morphological response in terms of leaf extension rate. The difference in root:shoot ratio between stress and control treatments at the end of the stress did not appear to reflect the strategy of the species with differences between root and shoot not consistent over any strategy type. The difference in dead material content between stress and control treatment at the end of the stress indicates the large differences for species with weak or moderate acclimation which is characteristic of competitor type species although there is inconsistency due to *Trifolium repens* not behaving as expected. The difference in dead material as an indicator of acclimation was strongly developed for *Rytidosperma clavatum* but was inconsistent for *Lotus corniculatus* and *Hieracium pilosella*. The species that did not survive are all of the C-S-R strategy, they show a moderate morphological response to the stress in terms of leaf extension rate and are the species that had little response in terms of changes in root:shoot ratio. The difference in dead material between stress and control at the end of the stress divides this group into two with *Holcus lanatus* and *Plantago lanceolata* exhibiting generally high amounts of dead material in the stress plants. *Agrostis capillaris* and *A. castellana* did not appear to be dead at the end of stress but rapidly lost living tissue during the recovery. The percentage of dead material at the end of the recovery indicates the continuing death of these species through the recovery period.

4.17 Species coexistence in hill country pasture communities

The coexistence of species which interact competitively has long interested ecologists and the question of what permits so many competitors to coexist has been largely unresolved (Aarson 1983). A central problem of community ecology is to explain the coexistence of plant species within communities (Fitter 1987). The complex array of species found in New Zealand hill country pasture communities is no exception. It is known that the effect of seasonal growth patterns of different species in hill country magnify the competitive interactions, and the effect of seasonal stress such as drought causes large year to year variation in species abundance (Lambert *et al.* 1986). On the basis of the current knowledge of the responses of pasture species to water deficit it is, therefore, not possible to predict with any degree of confidence the effects of water deficit on mixed communities or the effect that a deficit will have on competition between species (Turner and Begg 1978).

Coexistence has been coupled with competition in that it may be defined as the absence of competitive exclusion, much as health is the absence of disease (Aarson 1983). Many species competing for the same limited resources of light, mineral nutrition and moisture have an ability to coexist. The question that is posed for the hill country pasture situation is; do species coexist because of co-evolution leading to niche differentiation, or do they consist of species that have complementary behaviour patterns? Gause (1934) suggests that coexistence implies niche differentiation, although later work (Fitter 1987) states that this is not wholly the case and that powerful external forces will modify species behaviour so as to render niche differentiation unnecessary by suppressing competitive interactions. This implies that for species to coexist they do not necessarily need to have the ability to reduce niche overlap in the utilisation of resources. It is generally believed however that ecological succession consists of the process which begins in a state of great overlap of fundamental niches and ends in a situation in which niches are contiguous but do not overlap (Ares 1971). Figure 23 diagrammatically portrays a general coexistence theory discussed by Fitter (1987). The evolutionary premise has competition an important force in natural selection operating on two components of variation: Fundamental niche requirements and relative competitive ability. This is layered over Gause's principle and developed through three concepts: Gaussian coexistence, ecological combining ability, competitive combining ability.

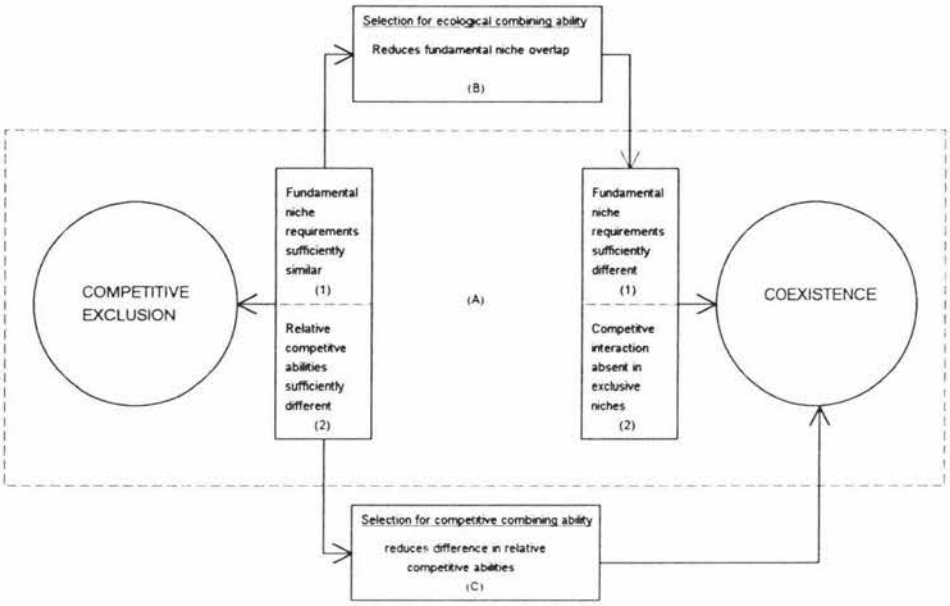


Figure 23 The structure of a general theory of species coexistence

1. Fundamental niche requirements, 2. Relative competitive abilities, A. 'Gaussian' coexistence (dashed box), B. Niche differentiation, C. Balanced competitive abilities (Fitter 1987)

The differentiation of niches and differences in the response of plants to environmental change both work towards the coexistence of species. There is strong evidence of the role that the environment plays in coexistence and the response of species to the environment. Turkington and Harper (1979) in a study of inter and intra-specific contact in pasture species found that the contact between one grass species by *Trifolium repens* varied through the year and that this has an effect on the competition for space which must also vary throughout the year, possibly explaining the ability of the species to coexist. Other examples from work in New Zealand hill country also supports this. It is noted by Gillingham (1973) that variability in the plant environment is very important for changes in pasture composition of species in hill country. Climate and soil fertility are noted by Levy (1970) to be the main determinants of species composition in hill country pastures. Differences are seen to occur on a regional basis and between hillsides and microsites and as a result, diverse plant communities are a common feature of hill environments (Grant and Brock 1974). Differences in botanical composition of pastures can be considered a reflection of the prevailing environment (Lambert *et al.* 1986). The species that are part of the hill country pasture community are of a range of strategy types. The response of these species to the changing environment of the hill country is dependent on their regenerative and established plant strategies. Stress causes plants to have a morphological response to escape the conditions limiting growth (Hutchings and De Kroon 1994), and it is the range of response the species have to stress that enables the species to coexist.

5 CONCLUSION

The differences in the plant strategies of the species studied were evident in the different responses to the water deficit stress. Although the broad differences between plants with S-type and C-type attributes were consistent with plant strategy theory, there is however within the CR-CSR classification several different types of response to water deficit stress. In particular, the CR-CSR strategists *Lolium perenne* and *Dactylis glomerata* showed a well developed capacity to cease leaf elongation early and senescence leaf material so as to preserve meristems in a viable state to allow recovery when water supply resumed. Other CR-CSR strategists did not have this capacity and several species died as a result of water stress. This suggests that secondary functional types may be recognised within the primary types of CSR theory.

The response of species in terms of leaf/petiole extension during the stress period and the recovery period enabled us to identify a pattern of response, that fitted our understanding of the species in terms of plant strategy theory. The leaf/petiole extension measurements indicated differences in species sensitivity to water stress. The ranking of species for resistance to water stress (defined as the ability of the plant to continue functioning during the stress) based on the measurements of leaf/petiole extension rate, was (lowest to highest): *Lolium perenne* < *Dactylis glomerata* < *Holcus lanatus* < *Agrostis capillaris* < *Plantago lanceolata* < *Agrostis castellana* < *Trifolium repens* < *Rytidosperma clavatum* < *Lotus corniculatus* < *Hieracium pilosella*. *Lolium perenne*, *Dactylis glomerata* and *Rytidosperma clavatum*, followed by *Trifolium repens* showed the highest resilience (defined as the rate of recovery after the stress is removed) again measured by leaf/petiole extension rate. *Dactylis glomerata* was the only species that showed a higher leaf extension rate in water stressed plants than the control.

The difference in total dry mass between control and stress treatments was used to assess the effect of the stress on biomass accumulation. The distinct strategies of the species, especially between the C-type and S-type were able to be identified. Those species classified with C attributes according to plant strategy theory survived the water stress through rapid plastic adjustments in leaf extension and senescence and hence developed a large difference in dry mass between the stress and control treatments. The stress tolerant type species had the least response in terms of difference in biomass accumulation and senescence, consistent with strategy theory predictions.

The levels of dead material at the end of the stress and recovery related closely to the predicted strategies of the species in the experiment. The loss of leaf material is a characteristic of the more competitor type species with rapid leaf turnover and rapid morphogenetic response to stress (Grime *et al.* 1988). The more stress tolerant species exhibited low loss of material to death with a characteristic longer leaf longevity and slow morphogenetic responses.

The species that did not survive were: *Holcus lanatus*, *Agrostis capillaris*, *Agrostis castellana*, *Plantago lanceolata*. They are all species of the C-S-R strategy. The deaths of the species that are more commonly found in dry habitats, *Agrostis capillaris*, *Agrostis castellana* and *Plantago lanceolata*, were not expected. It is assumed that these species have particular characteristics that is part of their strategy that enables them to survive in dry habitats that were not able to be utilised under the experimental conditions. The main difference between the experimental conditions and field conditions is that the medium was selected to not retain any soil moisture so that any advantage of having deep roots or the ability to conserve soil moisture was removed.

The differentiation of niches and differences in the response of plants to environmental change both work towards the coexistence of hill country pasture species. There is strong evidence of the important role environment plays in coexistence through the response of species to changes in that environment. The environment in which the hill country communities exist has a profound effect on the dynamics of hill country pasture communities and the range of species that coexist in such an environment which do so through both fine scale niche differentiation and a range of strategies and response to large scale environmental permutations. As an example of this it is suggested that the persistence of *Lolium perenne* and *Dactylis glomerata* in hill country pastures may be partly related to a capacity for rapid plastic adjustments in leaf extension and leaf area so preserving dormant vegetative meristems during water stress, allowing rapid recovery in the cooler period of the year with adequate water.

This study has given a comparative overview of the response to water stress in the selected species and has enabled the identification of the possible range of strategies that these hill country pasture species have. In addition it has also investigated a novel technique of screening plants to a uniform water deficit.

REFERENCES

Aarson, L.W. 1983: Ecological combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. *American naturalist 12(6):* 707-731

Acevedo, E.; Hsiao, T.C.; Henderson, D.W. 1971: Immediate and subsequent response of maize leaves to changes in water status. *Plant physiology 48:* 631-636

Ares, J.O. 1971: Equitability, competition and seasonal succession in a plant community. *Journal of ecology 60:* 325-331

Boyer, J.S. 1973: Water stress and plant growth. *Proceedings of soil and plant water symposium*. New Zealand department of scientific and industrial research information series no 96: 10-11

Booth, R.E.; Mackey, J.M.L.; Rorison, I.H.; Spencer, R.E.; Gupta, P.L.; Hunt, R. 1993: ISP germination and rooting environments: sand, compost and solution culture. *In* Hendry, G.A.F.; Grime, J.P. (*ed.*), *Methods in comparative plant ecology: A laboratory manual.* Chapman & Hall, Melbourne.

Bradshaw, A.D. 1965: Evolutionary significance of phenotypic plasticity in plants. *Advances in genetics 13:* 115-155

Bradshaw, A.D.; Chadwick, M.J.; Jowett, D.; Lodge, R.W.; Snaydon, R.W. 1960: Experimental investigations into the mineral nutrition of several grass species Part III. Phosphate level. *Journal of ecology 48:* 631-637

Campbell, B.D.; Grime, J.P. 1989: A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. *New phytologist 112:* 261-267

Charlton, J.F.L; Belgrave, B.R. 1992: The range of pasture species in New Zealand and their use in different environments. *Proceedings of the New Zealand grassland association 54:* 99-104

Dale, J.E. 1988: The control of leaf expansion. *Annual review of plant physiology and plant molecular biology 39:* 267-295

Donald, C.M. 1958: The interaction of competition for light and for nutrients. *Australian journal of agricultural research 9:* 421-432

Doughty, C.T. 1973: *Proceedings of soil and plant water symposium.* New Zealand department of scientific and industrial research information series no 96: 12-16

Fitter, A.H. 1987: Spatial and temporal separation of activity in plant communities: prerequisite or consequence of coexistence? *in* Gee, J.H.R.; Giller, P.S. *(ed.), Organization of communities past and present.* The 27th symposium of the British ecological society, Aberystwyth 1986. Blackwell scientific publications, London.

Fitter, A.H.; Hay, R.K.M. 1987: *Environmental physiology of plants.* (second edition) Academic press, London.

Fowler, J.; Cohen, L. 1992: *Practical statistics for field biology.* John Wiley & Sons Ltd, Brisbane.

Garwood, E.A.; Sinclair, J. 1979: Use of water by six grass species 2. Root distribution and use of soil water. *Journal of agricultural science, Cambridge 93:* 25-35

Gause, G.F. 1934: *The struggle for existence.* Hafner, New York (reprint 1964)

Gillingham, A.G. 1973: Influence of physical factors on pasture growth on hill country. *Proceedings of the New Zealand grasslands association 35(1):* 77-85

Grant, D.A.; Brock, J.L. 1974: A survey of pasture composition in relation to soils and topography in hill country. *New Zealand journal of experimental agriculture 2:* 243-250

Grime, J.P. 1973^{a}: Competitive exclusion in herbaceous vegetation. *Nature 242:* 344-347

Grime, J.P. 1973^{b}: Competition and diversity in herbaceous vegetation - a reply. *Nature 244:* 310-311

Grime, J.P. 1974: Vegetation classification by reference to strategies. *Nature 250:* 26-31

Grime, J.P. 1977: Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American naturalist 111:* 1169-1194

Grime, J.P. 1979: *Plant strategies and vegetation processes.* John Wily & sons, Chichester.

Grime, J.P. 1988: The C-S-R model of primary plant strategies - origins, implications and tests. *in* Gottieb, L.D.; Jain, S.K. *(ed.), Plant evolutionary biology.* Chapman & Hall, London.

Grime, J.P.; Crick, J.C.; Rincon, J.E. 1986: The ecological significance of plasticity. *in* Jennings, D.H.; Trewavas, A.J. *(ed.), Plasticity in plants.* Symposia of the society of experimental biology, No. xxxx. The company of biologists Ltd., Cambridge.

Grime, J.P.; Hodgson, J.G.; Hunt, R. 1988: *Comparative plant ecology. A functional approach to common British species.* Unwyn Hyman Ltd, London.

Grubb, P.J. 1985: Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization. *in* White, J. *(ed.), The population structure of vegetation.* Junk, Dordrecht.

Harper, J.L. 1977: *Population biology of plants.* Acedemic press, London.

Hart, A.L. 1987: Physiology. *in* Baker, M.J.; Williams, W.M. *(ed.), White clover.* C.A.B. International, Wallingford.

Hsiao, T.C.; Acevedo, E. 1974: Plant responses to water deficits, water use efficiency, and drought resistance. *Agricultural meteorology 14:* 59-84

Hunt, R. 1982: *Plant growth curves. The functional approach to plant growth analysis.* Edward Arnold, London.

Hurd, E.A. 1976: Plant breeding for drought resistance. *in* Kozlowski, T.T. *(ed.), Water deficits and plant growth, Volume IV. Soil water measurement, plant responses, and breeding for drought resistance.* Academic press. London.

Hutchings M.J.; De Kroon, H. 1994: Foraging in plants: The role of morphological plasticity in resource acquisition. *Advances in ecological research 25:* 159-238

Jackson, D.K. 1974: The course and magnitude of water stress in *Lolium perenne* and *Dactylis glomerata*. *Journal of agricultural science, Cambridge 82:* 19-27

Johns, G.G. 1978: Transpirational, leaf area, stomatal and photosynthetic responses to gradually induced water stress in four temperate herbage species. *Australian journal of plant physiology 5:* 113-125

Kozlowski, T.T. 1973: Extent and significance of shedding of plant parts *in* Kozlowski, T.T *(ed.), Shedding of plant parts.* Academic press, London.

Lambert, M.G.; Clark, D.A.; Grant, D.A.; Costall, D.A. 1986: Influence of fertiliser and grazing management on North Island moist hill country, 2. Pasture botanical composition. *New Zealand journal of agricultural research 29:* 1-10

Lancashire, J. A. 1984. The physical boundaries of temperate pasture species in New Zealand. *NZ Agricultural science, Proceedings of the 1984 NZIAS convention. The journal of the New Zealand institute of agricultural science. 18 (3)*, 98-110

Langer, R.H.M. 1982: Grass species and strains *in* Langer, R.H.M. *(ed.), Pastures and pasture plants.* (special edition). Lincoln College. A.H & A.W. Reed. Wellington.

Levitt. J. 1972: *Responses of plants to environmental stresses.* Academic Press, London.

Levy, E.B. 1970: *Grasslands of New Zealand.* (3rd Edition). A.R. Shearer Government Printer, Wellington.

Ludlow, M.M.; Ng, T.T. 1977: Leaf elongation rate in *Panicum maximum* var. *trichoglume* following removal of water stress. *Australian journal of plant physiology 4:* 263-272

Makepeace, W. 1985: Growth, reproduction, and production biology of mouse-ear and king devil hawkweed in eastern South Island, New Zealand. *New Zealand journal of botany 23:* 65-78

McKenzie, H.A.; Wallace, H.S. 1954: The Kjeldahl determination of nitrogen: A critical study of digestion conditions-temperature, catalyst and oxidising agent. *Australian journal of chemistry 7:* 55-70

Meinder, H; Sheriff, D.W. 1976: *Water and plants.* Blackie, Glasgow.

Newman, E.I. 1973: Competition and diversity in herbaceous vegetation. *Nature 244:* 310

Olff, H. 1992: Effects of light and nutrient availability on dry matter an N allocation in six successional grassland species. *Oecologia 89:* 412-421

Oppenheimer, H.R. 1960: Adaptation to drought: xerophytism. *in* UNESCO. *Plant-water relationships in arid and semi-arid conditions: reviews of research.* pg 105

Parker, J. 1968: Drought resistant mechanisms. *in* Kozlowski, T.T. *(ed.), Water deficits and plant growth, Volume I. Development, control, and measurement.* Academic press. London.

Raynal, D.J.; Grime, .J.P.; Boot, R. 1985: A new method for the experimental droughting of plants. *Annals of botany 55:* 893-897

Rook, D.A. 1973: Effects of water stress on plant processes. *Proceedings of soil and plant water symposium.* New Zealand department of scientific and industrial research information series no 96: 10-11

Scott, D.; Robertson, J.S.; Archie, W.J. 1990: Plant dynamics of New Zealand tussock grasslands infested with *Hieracium pilosella.* I. Effects of seasonal grazing, fertilizer and over drilling. *Journal of applied ecology 27:* 224-234

Shantz, H.L 1927: Drought resistance and soil moisture. *Ecology 8:* 145-151

Smetham, M.L. 1982: Pasture legume species and strains. *in* Langer, R.H.M. *(ed.), Pastures and pasture plants.* (special edition). Lincoln College. A.H & A.W. Reed. Wellington.

Steel, R.G.D.; Torrie, J.H. 1981: *Principles and procedures of statistics.* McGraw-Hill International. Auckland.

Stevens, D.R.; Lancashire, J.A.; Barker, D.J.; Molony, S.C.; Pollock, K.; Archie, W.J. 1993: Introduction, production, and persistence of five grass species in dry hill country 1. Introduction, site descriptions, and general methods. *New Zealand journal of agricultural research 36:* 1-10

Thomas, H. 1986: Water use characteristics of *Dactylis glomerata* L., *Lolium perenne* L. and *L. multiflorum* Lam. Plants. *Annals of botany 57:* 211-223

Thomas, H.; Norris, I.B. 1981: Evaluation of drought resistance of grass and clover populations grown in containers. *in* Wright, C.E. *(ed.), Plant physiology and herbage production.* Proceedings of a symposium organised by the British Grassland Society, Nottingham 1981. British Grassland Society, Berks.

Trewas, A.J. 1986: Resource allocation under poor growth conditions. A major role for growth substances in developmental plasticity. *in* Jennings, D.H.; Trewavas, A.J. *(ed.), Plasticity in plants.* Symposia of the society of experimental biology, xxxx. The company of biologists Ltd., Cambridge.

Turkington, R.; Harper, J.L. 1979: The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. *Journal of ecology 67:* 201-218

Turner, L.B. 1990: Water relations in white clover (*Trifolium repens*): water potential gradients and plant morphology. *Annals of botany 65:* 285-290

Turner, L.B. 1991: The effect of water stress on the vegetative growth of white clover (*Trifolium repens* L.): Comparison of long term water deficit and a short term developing water stress. *Journal of experimental botany 42:* 311-316

Turner, N.C.; Begg, J.E. 1978: Response of pasture plants to water deficits. *in* Wilson, J.R. *(ed.), Plant relations in pastures.* Proceedings of a symposium held in Brisbane, 1976. CSIRO, Melbourne.

APPENDICES

Appendix I.

Paper presented at the Agronomy Society session of the NZIAS/NZIHS convention Massey University. August 1994

A comparative study of the resistance and resilience of hill country pasture species exposed to water deficit stress.

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Abstract

Ten hill country pasture species were screened for response to a water deficit stress in a glasshouse experiment. The response of the plants to a progressively severe water stress followed by the resumption of water and nutrient supply for a three-week recovery period was assessed. Resistance is defined as the ability of the plant to maintain function with a stress (such as drought), while resilience is defined as the rate of recovery after the stress is removed. The ranking of species (lowest to highest) for resistance to water stress (based on the measurement of leaf extension rate) was, *Lolium perenne*, *Dactylis glomerata*, *Holcus lanatus*, *Agrostis capillaris*, *Plantago lanceolata*, *A. castellana*, *Trifolium repens*, *Rytidosperma clavatum*, *Lotus corniculatus* and *Hieracium pilosella*. With the exception of *Trifolium repens* the middle order species did not recover. The differences in total dry mass at the end of the water stress period fell into two groups, those that showed no significant difference between the water stress and control plants, and those that were affected by the water stress. Consistent with plant strategy theory, the species showing the highest resistance were characteristic of stress tolerator types. The species *Lolium perenne*, *Dactylis glomerata* and *Rytidosperma clavatum*, followed by *Trifolium repens* showed the highest resilience as measured by leaf/petiole extension rate. *Dactylis glomerata* was the only species that showed a higher leaf extension rate in water stressed plants than the control. The species that showed the highest resilience, with the exception of *Rytidosperma clavatum,* are classified as more competitor types according to plant strategy theory.

Additional key words: Plant strategy theory, drought, *Lolium perenne*, leaf extension.

Introduction

The supply of moisture to plants has been reported as the primary environmental factor limiting the attainment of production potentials in New Zealand pastures (Lancashire 1984). Work by Levy (1970) has broadly described the influence of climate on grassland farming, and work on individual species (Stevens *et al.* 1993; Thomas 1986^{ab}; Turner 1991) has given us some understanding of the response of pasture species to drought, but currently we are unable to predict hill country vegetation responses to most environmental and management disturbances, including the effect of drought.

The screening of species enables a picture to be built up of plant responses to different environmental conditions. One approach that is taken is the screening of large numbers of diverse plant types in an integrated screening programme (Hendry and Grime 1993). The programme is designed to use a range of laboratory-based procedures to find distinctive characteristics and management needs of key plant species under a wide range of environmental conditions. This suggests that by testing a range of species in conditions suitable for the growth of a wide range of plants, that patterns of ecological specialisation in plant traits and strategies in relation to water deficit stress will be detected. Although subjecting pot-grown plants to water stress does not simulate all aspects of a field drought (for a number of reasons, such as eliminating the plants ability to explore for water) it is a useful way of screening a number of different genotypes for drought tolerance and recovery (Norris and Thomas 1982) in a strictly standardised way. The method used in this experiment is based on that used by Raynal *et al.* (1985). Plant strategy theory (Grime *et al.* 1988) suggests that plants with low growth rates and other stress tolerant attributes will be better able to tolerate water stress than fast growing, more competitor type plants.

A range of hill country plant species were screened for response to and recovery from water deficit stress, with a comparison made of the resistance and resilience of the species to severe water stress. The terms resistance and resilience are used to describe both the ability of the plant to continue functioning during the stress (resistance) and the rate of recovery after the stress is removed (resilience). In this paper the differences in the change in leaf/petiole extension rate of the plants during and after the water stress are investigated because many workers have reported that cell expansion is extremely sensitive to water stress (Dale 1988, Hsiao and Acevedo 1974). In addition to leaf/petiole extension rate the differences in total plant dry mass between stressed and control plants is also investigated.

Materials and methods

Plant material

The ten hill country pasture species used were: *Lolium perenne* cv. Grasslands SuperNui, *Agrostis capillaris*, *A. castellana*, *Dactylis glomerata* cv. Grasslands Wana, *Holcus lanatus* cv. Massey Basyn, *Rytidosperma clavatum*, *Lotus corniculatus* cv. Grasslands Goldie, *Trifolium repens* cv. Grasslands Huia, *Plantago lanceolata* and *Hieracium pilosella*. The plants were grown from seed germinated in approximately 5 ml of agar on the surface of the pot media.

Pot design

Plants were grown singly in pots constructed of 300 mm lengths of 110 mm diameter PVC drainage pipe closed off at one end with aluminium fly-screen mesh, containing Grade 6 Manawatu river stone chip of a diameter between 5 to 10 mm. Each pot stood in a 20 mm deep dish flooded to provide a water table. The plants were grown in a controlled glasshouse environment with a mean daily temperature of 25^{o}C and a mean night temperature of 18^{o}C. Each pot was supplied with water and full basic Rorison nutrient solution (Hendry and Grime 1993) fed into the irrigation system, which supplied each pot by an individual whisker. The water regime was set at the end of germination to supply 2.7 litres of water to each pot every 24 hours at set intervals. This amount increased with the demand of the plants to 10.8 litres pot^{-1} day^{-1} at an interval of 60 seconds every 15 minutes at a rate of 0.1125 l minute^{-1}, three weeks before the stress treatment commenced.

Experimental design

Pots were laid out in a randomised complete block design of the ten species, four treatments, and five blocks. The blocking was based on plant size within species. The four treatments consisted of two stress treatments one of which was harvested at the end of the stress period the other harvested at the end of the recovery period, and two control treatments with one harvested at the end of the stress period and the other harvested at the end of the recovery period. The stress treatment commenced 13 weeks after seed germination, with the stress treatment plants exposed to a progressive water deficit by removing the whisker and the dish from the pot and elevating the pot to facilitate drainage, for increasing lengths of time each day. The control plants continued to receive water at the set rate, but without the inclusion of the nutrient solution over the deficit periods, thus the control treatments delivered the same quantity of nutrients as the water stress treatment. The deficit periods began with two hours, increasing by two hours each day until day 12 and then having completely no water for a further nine days. Water and nutrient solution was then reinstated at the previous rate for a recovery period of three weeks.

Measurements

Throughout the experiment leaf/petiole lengths were measured daily. Leaf length of the grasses was measured from the tip of the marked leaf to the collar of the previous leaf, petiole lengths were measured for the two legume species from the base of the leaflets to the petiole junction of the next mature leaf. Leaf length of the forbs was measured from the tip of the leaf to the emerging point on the crown. At the end of the stress period and the recovery period the appropriate treatment plants were harvested and fresh and dry weights of the plant components were measured. The difference between the plant dry mass of the control and stress treatments was calculated by taking the natural log of the data ($x + 1$) and subtracting the stress from the control in their replicate pairs. The mean difference was found and the standard error of the difference (Fowler and Cohen 1992) calculated and multiplied by the appropriate value of t to calculate the confidence interval. The mean difference was back transformed as was the confidence interval. All figures where then multiplied by 100 for interpretation on a per cent scale.

Results

Leaf/Petiole Extension Rate

The leaf and petiole extension rates plotted against time were used to give an indication of the onset and severity of the stress. All species except *Lotus corniculatus* and *Hieracium pilosella* showed a significant difference between the control treatment and the stress treatment in leaf/petiole extension at some stage of the stress period. The earliest and greatest difference in the leaf extension rate between the control and stress treatments was observed for *Lolium perenne*. Species showing a smaller and delayed response were *Dactylis glomerata*, *Holcus lanatus*, *Agrostis capillaris*, *A castellana*, *Rytidosperma clavatum*, *Trifolium repens* and *Plantago lanceolata*. Leaf extension ceased by day 14 (the third day without any water at all) in the species *Lolium perenne*, *Dactylis glomerata*, and *Holcus lanatus*. *Agrostis capillaris* ceased extension by day 16, *Plantago lanceolata* by day 18 and *A. castellana* by day 20. *Trifolium repens* did not cease petiole extension completely, but reached its lowest rate around day 18, as with *Rytidosperma clavatum* which had its lowest rate on days 16-20. *Lotus corniculatus* and *Hieracium pilosella* both showed little response to the water stress in terms of leaf/petiole extension rate, but the overall rates of extension were very small in these species using the measurement technique adopted.

Over the recovery period which began on day 20, the species which showed an immediate increases in leaf extension rate were *Dactylis glomerata*, *Lolium perenne*, *Rytidosperma clavatum*, and to a lesser extent *Trifolium repens*. The species which did not recover *Agrostis castellana*, *Holcus lanatus*, *Plantago lanceolata* and *Agrostis capillaris*, all showed no extension after the resumption of water.

Total Dry Mass

Dactylis glomerata had the greatest difference between stress and control treatments in total dry mass (Fig. 2.) immediately after the stress period. The difference was also significant for *Agrostis capillaris*, *Lolium perenne*, *Plantago lanceolata*, *A. castellana*, *Holcus lanatus* and *Trifolium repens* ($P < 0.05$) to the stress period in terms of total dry mass. *Rytidosperma clavatum*, *Lotus corniculatus* and *Hieracium pilosella* did not respond. At the time the plants were harvested three weeks later a much greater difference had occurred between the stress and control treatments. The greatest differences were evident in the species that did not recover, namely *Plantago lanceolata*, *Agrostis capillaris*, *A. castellana* but for another species that did not recover, *Holcus lanatus*, the difference was not altered from that at the end of the stress period. The variability across the replicates for this species in relation to the difference between control and stress was very large.

Discussion

The species selected show a range of response in terms of the resistance and resilience of leaf extension rate to water stress. The species ranked for resistance to water stress (from lowest resistance to highest) as: *Lolium perenne* < *Dactylis glomerata* < *Holcus lanatus* < *Agrostis capillaris* < *Plantago lanceolata* < *A. castellana* < *Trifolium repens* < *Rytidosperma clavatum* < *Lotus corniculatus* < *Hieracium pilosella*. The least resistant species, on the basis of leaf elongation rate, was *Lolium perenne*, more so than *Holcus lanatus* which is thought of as occupying moist habitats (Levy 1970) and would be expected to show the greatest response to water stress.

Dactylis glomerata is generally considered to be amongst the most able to withstand drought and recover afterwards (Thomas 1986^{b}), but this was not evident in terms of leaf extension rate. It was reported by Jackson (1974) that in this species leaf water status is more sensitive to water deficit than *Lolium perenne* and responds by reducing transpiration rate, conserving the available soil moisture and therefore being apparently more resistant under field conditions. The species with the highest resistance in leaf/petiole extension rate, *Rytidosperma clavatum*, *Lotus corniculatus*, and *Hieracium pilosella*, are all species which exhibit characteristics of the stress tolerators type (Grime *et al.* 1988), supporting plant strategy theory predictions. These species were less responsive to the effect of water stress on biomass accumulation presumably because of their lower growth rates. Makepeace (1985) reported that *Hieracium pilosella* has low dry matter production compared to other resident species in its habitat like *Agrostis capillaris*, and it is concluded that *Hieracium pilosella* shows a relatively wide edaphic-climatic tolerance giving it greater abundance than other *Hieracium* species with higher dry matter production within the same growth habitat. Between the two extremes are species that did have a response, if somewhat delayed, to the stress. In this group are the species that showed no sign of recovery, *Holcus lanatus*, *Plantago lanceolata*, *Agrostis capillaris* and *A. castellana*. Also in this group is *Trifolium repens* that showed an intermediate level of resistance and also resilience.

This is possibly due to selective allocation of water resources from leaves to stem material as reported by Turner (1990).

The species response to the recovery period was more variable than during the stress period, which was also found by Thomas and Norris (1981) where proportional differences between species were greater after a drought than during. The species that showed the highest resilience in recovery of leaf elongation rate were *Lolium perenne*, *Dactylis glomerata* and *Rytidosperma clavatum*. *Dactylis glomerata* was the only species to exhibit any form of compensatory growth in leaf elongation rate. The compensatory or 'stored growth' in leaf elongation is also reported in maize after mild water stress (Hsiao and Acevedo 1974), and indicates continued cell division during the water stress. The species that showed the highest resistance during the water stress had poor resilience because of no potential for recovery, with the exception of *Rytidosperma clavatum* which had the shortest interval of depressed leaf extension rate of the responsive species, over the last four days of the stress period, which was followed by an immediate recovery in leaf extension rate. The species of high resilience were characteristic of C-R to C-S-R type species in relation to plant strategy theory (Grime *et al.* 1988).

Acknowledgments

This research was financially assisted through the Massey University Agricultural Research Foundation.

References

Dale, J.E. 1988. The control of leaf expansion. *Annual review of plant physiology and plant molecular biology* ***39***, 267-295.

Fowler, J. and Cohen, L. 1992. *Practical statistics for field biology.* John Wily & sons, Brisbane.

Grime, J.P., Hodgeson, J.G., Hunt, R. 1988. *Comparative plant ecology: a functional approach to common British species.* Unwin Hyman, London.

Hendry, G.A.F.and Grime, J.P. 1993. *Methods in comparative plant ecology.* Chapman & Hall, Melbourne.

Hsiao, T.C. and Acevedo, E. 1974. Plant responses to water deficits, water-use efficiency, and drought resistance. *Agricultural meteorology* ***14***, 59-84.

Jackson, D.K. 1974. The course and magnitude of water stress in *Lolium perenne* and *Dactylis glomerata. Journal of agricultural science (Cambridge)* ***82***, 19-27.

Lancashire, J. A. 1984. The physical boundaries of temperate pasture species in New Zealand. *NZ Agricultural science, Proceedings of the 1984 NZIAS convention. The journal of the New Zealand institute of agricultural science.* ***18 (3)***, 98-110

Levy, E.B. 1970. *Grasslands of New Zealand.* A.R. Shearer, Government printer, Wellington.

Makepeace, W. 1985. Growth, reproduction, and production biology of mouse-ear and king devil hawkweed in eastern South Island, New Zealand. *New Zealand journal of botany* ***23***, 65-78.

Norris, I.B. and Thomas, H. 1982. The effect of droughting on varieties and ecotypes of *Lolium*, *Dactylis*, and *Festuca*. *Journal of applied ecology* ***19***, 881-889.

Raynal, D.J., Grime, J.P., Boot, R. 1985. A new method for the experimental droughting of plants. *Annals of botany* ***55***, 893-897.

Stevens, D.R., Lancashire, J.A., Barker, D.J., Moloney, S.C., Pollock, K., Archie, W.J. 1993. Introduction, production, and persistence of five grass species in dry hill country. 1. Introduction, site descriptions, and general methods. *New Zealand journal of agricultural research* ***36***, 1-10.

Thomas, H. 1986^a. Effect of rate of dehydration on leaf water status and osmotic adjustment in *Dactylis glomerata* L., *Lolium perenne* L. and *L. multiflorum* Lam. *Annals of botany* ***57***, 225-235.

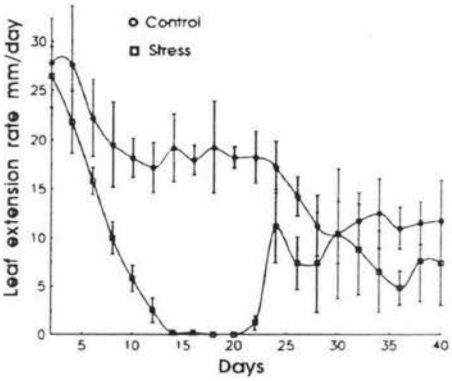
Thomas, H. 1986^b. Water use characteristics of *Dactylis glomerata* L., *Lolium perenne* L. and *L. multiflorum* Lam. plants. *Annals of botany* ***57***, 211-223.

Thomas, H. and Norris, I.B. 1981 Evaluation of drought resistance of grass and clover populations grown in containers. *in* Wright, C.E. *(ed.)*, *Plant physiology and herbage production.* Proceedings of a symposium organised by the British Grassland Society, Nottingham 1981. British Grassland Society, Berks.

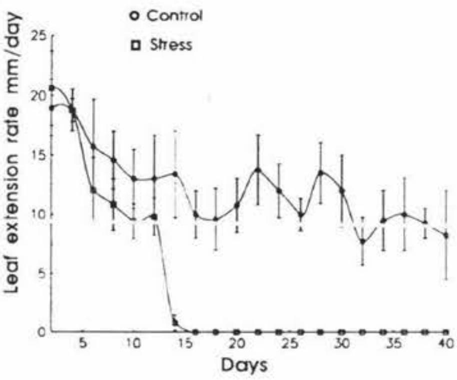
Turner, L.B. 1990. Water relations of white clover (*Trifolium repens*): Water potential gradients and plant morphology. *Annals of botany* ***65***, 285-290.

Turner, L.B. 1991. The effect of water stress on the vegetative growth of white clover (*Trifolium repens* L.): Comparison of long-term water deficit and a short-term developing water stress. *Journal of experimental botany* ***42***, 311-316.

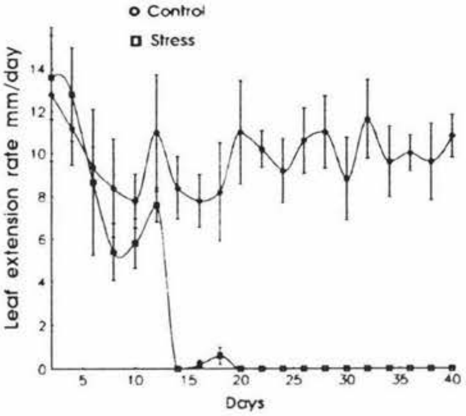
(Fig 1. a-j) The leaf and petiole extension rate of different grassland species exposed to water stress. No water supplied from day 12 to 20, then water and nutrients were resupplied on day 20. Error bars indicate standard error of the mean.



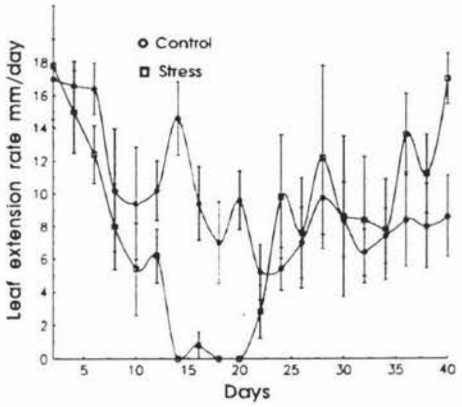
(a). *Lolium perenne*



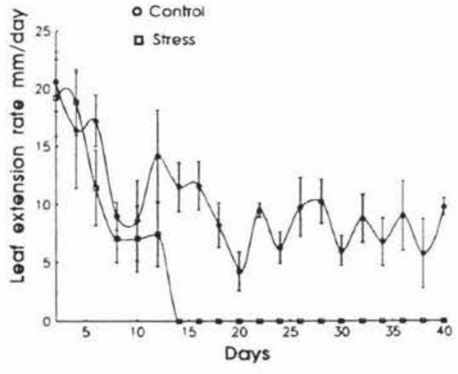
(b). *Agrostis capillaris*



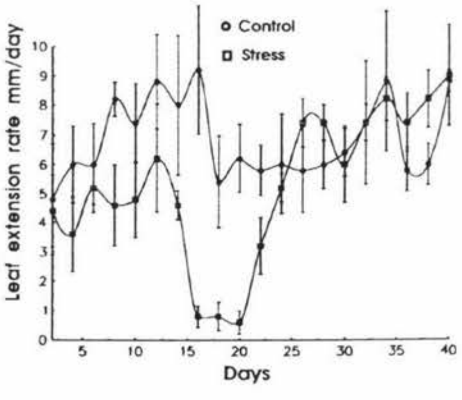
(c). *Agrostis castellana*



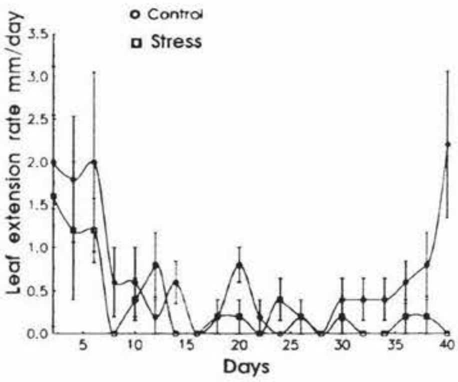
(d). *Dactylis glomerata*



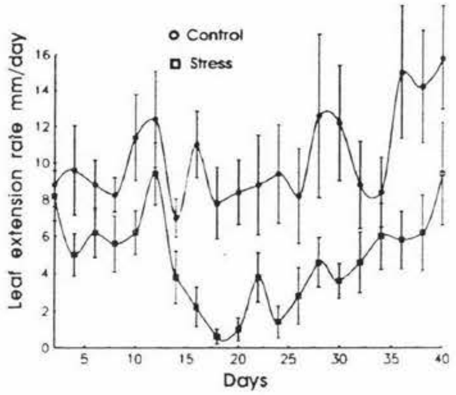
(e). *Holcus lanatus*



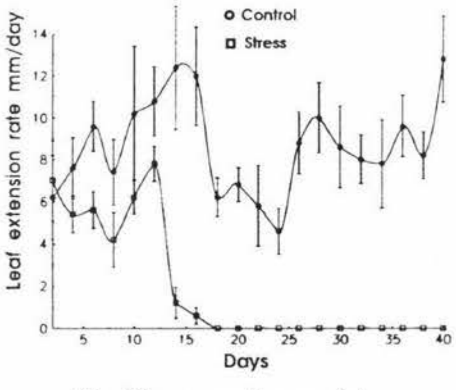
(f). *Rytidosperma clavatum*



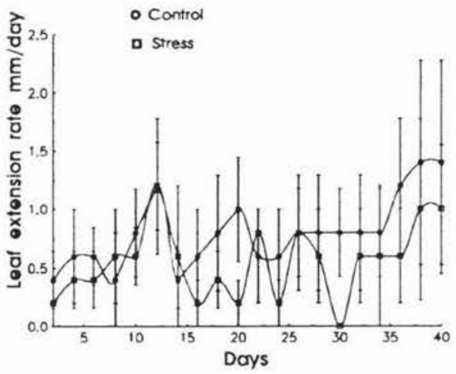
(g). *Lotus corniculatus*



(h). *Trifolium repens*



(i). *Plantago lanceolata*



(j). *Hieracium pilosella*

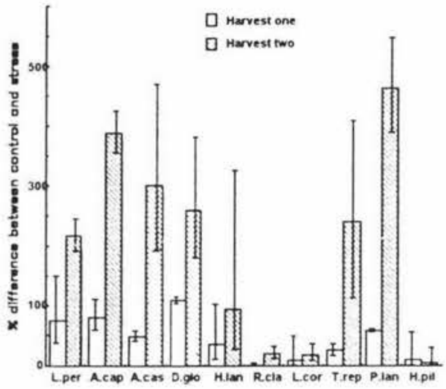


Fig 2. Percent difference in total dry mass between control and stress treatments immediately after the water stress and after three weeks of recovery. Vertical lines indicate the 95% confidence interval.