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 water deficit stress in a glasshouse experiment. The response of the plants to a progressively severe water stress over three weeks 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 competitive 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, 1986ab; 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 (e.g., 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 competitive 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. This is 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 are also investigated.

Materials and Methods

Plant material

The ten hill country pasture species used were: *Lolium perenne* cv. Grasslands Nui, *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°C and a mean night temperature of 18°C. Each pot was supplied with water and full basic Rorison nutrient solution (Hendry and Grime, 1993) was 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 and the other 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 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 found by calculating the difference between the logarithm of the dry mass data. 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.

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 (Fig 1.). 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 *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*. *Agrostis castellana*, *Holcus lanatus*, *Plantago lanceolata* and *Agrostis capillaris* showed no extension after the resumption of water.

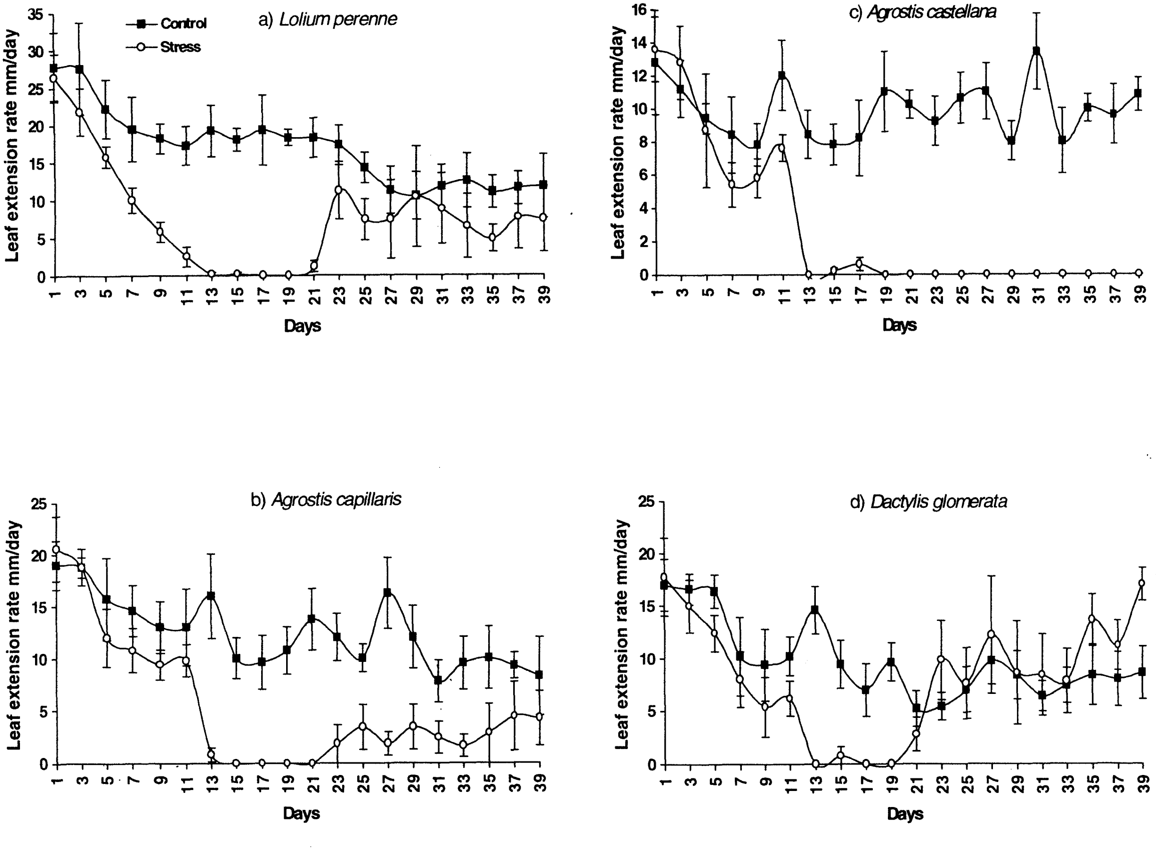
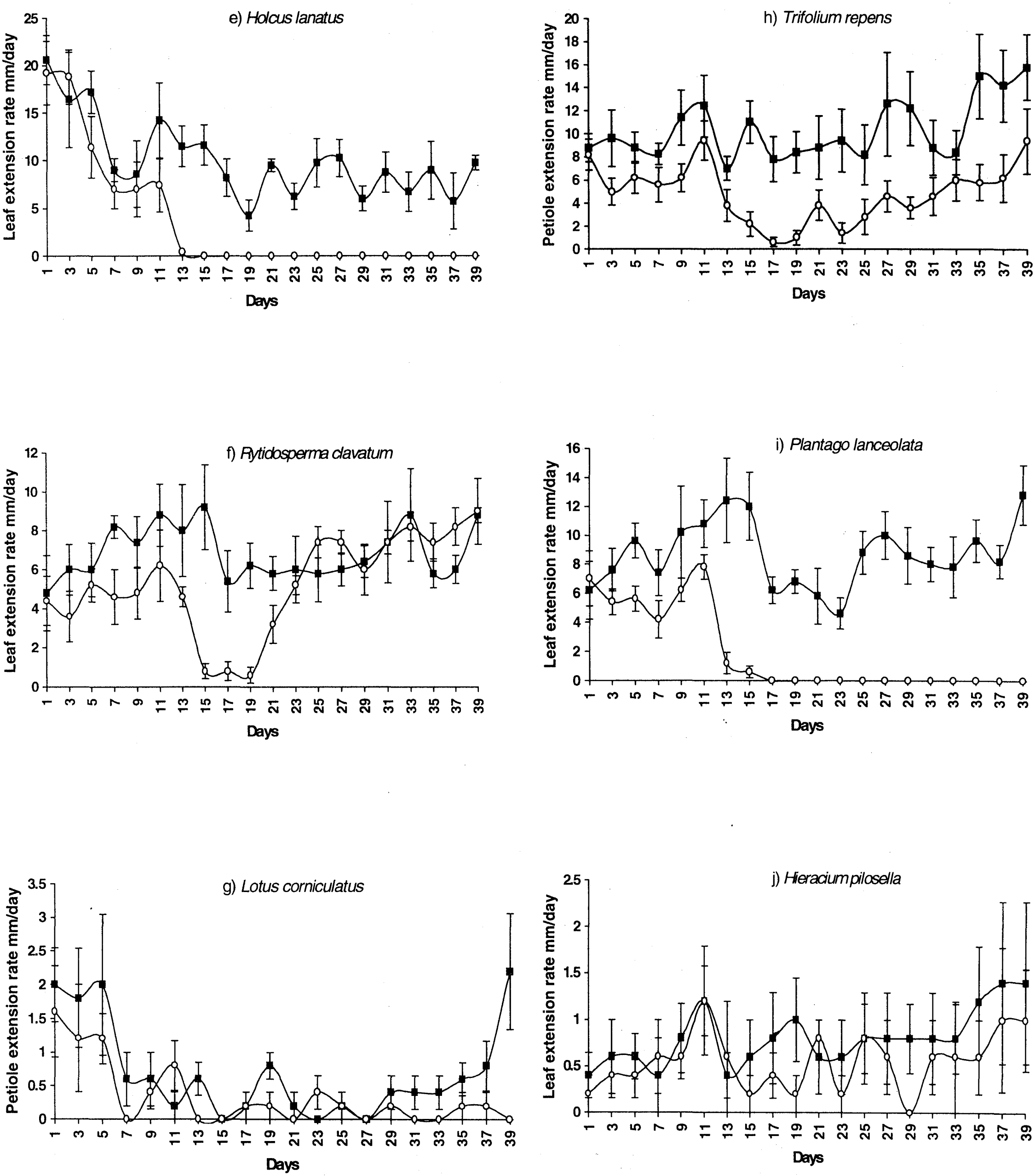


Figure 1. a-j) The leaf and petiole extension rate of different grassland species exposed to water stress. No water supplied from day 12 to 20, then water and nutrients were resupplied on day 20. Error bars indicate standard error of the mean.


e) Holcus lanatus
Leaf extension rate mm/day
Days
h) Trifolium repens
Petiole extension rate mm/day
Days
f) Rytidosperma clavatum
Leaf extension rate mm/day
Days
i) Plantago lanceolata
Leaf extension rate mm/day
Days
g) Lotus corniculatus
Petiole extension rate mm/day
Days
j) Hieracium pilosella
Leaf extension rate mm/day
Days

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 ratio was also significant for *Agrostis capillaris, Lotus corniculatus*, *Lolium perenne*, *Plantago lanceolata*, *Trifolium repens*, *Hieracium pilosella*, *A. castellana*, and *Holcus lanatus* ($P < 0.05$) at the end of the stress period in terms of total dry mass. *Rytidosperma clavatum* had no response. 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 *Holcus lanatus*, that also did not recover, 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. *Trifolium repens* had the lowest ratio while *Rytidosperma clavatum*, *Hieracium pilosella*, and *Lotus corniculatus* had no significant change in the ratio between control and stress treatments at the end of the recovery period, form that at the end of the stress.

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 known for occupying moist habitats (Levy, 1970) and would be expected to show the greatest response to water stress.

Dactylis glomerata is considered to be amongst the most able to withstand drought and recover afterwards (Thomas, 1986b), 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 with other resident species in its habitat like *Agrostis capillaris*, and it is concluded that *Hieracium pilosella* shows a relatively wide edaphic-climatic tolerance.

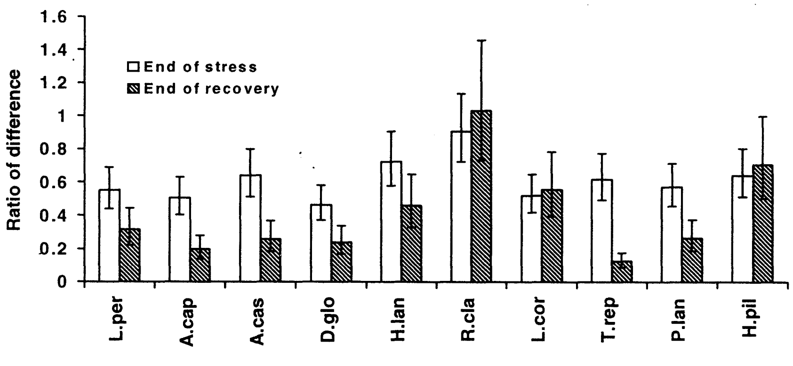


Figure 2. Ratio of difference in total dry mass between control and stress treatments immediately after the water stress and after three weeks of recovery. Vertical lines indicate the 95% confidence interval.

Between the extremes of response are the 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). The response of the species in terms of leaf/petiole extension rate during the stress and recovery period has enabled us to identify a pattern of response, that fits the understanding of the species in terms of plant strategy theory. The ratio of the difference in total dry mass between control and stress treatments identified the distinct strategies, especially those of the C and S types.

Acknowledgments

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