ASPECTS OF WATER DEFICIT AND VEGETATIVE GROWTH IN SELECTED PASTURE AND FORAGE GRASSES

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ASPECTS OF WATER DEFICIT AND VEGETATIVE GROWTH IN SELECTED PASTURE AND FORAGE GRASSES

ABSTRACT

In this study, the sensitivity of leaf extension to plant water status, the ability of the plant to recover after different periods of water deficit and the plant's reaction to atmospheric pre-conditioning were examined using different pasture and forage grasses.

The sensitivity of leaf extension to plant water status was studied in 3 separate experiments using sudax (SX-6, a forage sorghum hybrid, *Sorghum bicolor* (L) *Moench* x *S. sudanese* (piper) Staff), prairie grass (*Bromus catharticus* Vahl. cv. Grasslands Matua) and 2 cultivars of perennial ryegrass (*Lolium perenne* L. c.v. Grasslands Nui and Grasslands Ruanui). The sudax experiment was conducted in the field, whereas the prairie grass and ryegrass experiments were conducted in the Climate Laboratory, D.S.I.R. The day/night temperatures used in the prairie grass experiment was 22.5°/12.5°C. For the ryegrass, 2 contrasting temperature regimes were used; these were high (H), 27.5°/12.5°C, and low (L) 17.5°/12.5°C day/night temperatures.

It was found that leaf extension was very sensitive to small changes in leaf water potential during the initial stages of desiccation, but the response became less sensitive with increasing levels of desiccation. However, the relationship between leaf water potential and leaf extension rate was not unique. It varied according to the environmental conditions. The true relationship between leaf water potential and leaf extension rate can only be established when the leaf water potential at the site of measurement can be related unequivocally to the leaf water potential at the site of elongation.

The rates of recovery in leaf extension, leaf emergence, tiller

number, green leaf number, leaf area and dry weight per plant were followed after different water deficit treatments in one experiment with prairie grass and in another experiment with 2 cultivars of perennial ryegrass under 2 contrasting temperature regimes. The environmental conditions for these experiments were the same as those used in the leaf extension experiments.

In prairie grass, upon relief of water deficit, the previously desiccated plants showed an "accelerated" rate of leaf extension up to 20% higher than those of the well-watered control plants of the same physiological age. The "accelerated" rate lasted for over 28 days after rewatering during which time 4 to 5 new leaves emerged. However no such "accelerated" rates were observed in the ryegrasses.
The "accelerated" response following rewatering in prairie grass would be consistent with a differential sensitivity of cell division and cell elongation to water deficit. The desiccation treatment was more severe in the ryegrass experiment where both cell division and cell elongation could be suppressed, and this could account for the absence of a similar response in the ryegrasses.

Under well-watered conditions, the mean leaf emergence rate was 4.1 days per leaf for the prairie grass. The corresponding mean leaf emergence rates for Nui and Ruanui were 5.7 and 6.3 days/leaf under the H and 6.6 and 6.6 days/leaf under the L temperature regimes respectively. Within the grass species, post-desiccation leaf emergence rates between the previously desiccated and the well-watered plants were similar.

During desiccation, tiller number was the least sensitive parameter to water deficit, followed by dry weight and leaf number. Leaf area was the parameter most sensitive to desiccation. Amongst the dry weight components, lamina component was the most sensitive followed

by the root component with the sheath component the least sensitive to desiccation.

The pattern of recovery from desiccation was examined to see if positive or negative carryover effects occurred. To enable valid comparison of desiccated and control plants, physiological age was adjusted by removing a number of "drought" days from the chronological age. It was found that when the desiccation was mild e.g., in the prairie grass experiment, reductions in plant dry weights were proportional to the number of "drought" days. On the other hand, under a more severe level of desiccation, e.g., as in the ryegrass experiments, using the same method of adjustment, it was found that the dry weights of the previously desiccated plants were substantially lower than those of the well-watered control plants of the same physiological age. The reduction in dry weight was more pronounced under the H than under the L temperature regime.

After rewatering, in both prairie grass and ryegrass, the relative rates of increase of leaf area were higher in the previously desiccated plants than the well-watered control plants. In contrast to this, the relative rates of increase in dry weight, tiller number and leaf number in the previously desiccated plants were either similar to, or slightly less than those of the well-watered control plants.

Although the pattern of recovery in the leaf extension rates was different between the two experiments, this had no apparent positive or negative carryover effects on the relative rates of recovery in the growth parameters measured (e.g., tiller number, green leaf number, leaf area and dry weight per plant).

The reaction of prairie grass to desiccation following either a "dry"

or a "wet" atmospheric pre-conditioning was compared with those plants that were grown continuously under either the "dry" or the "wet" vapour pressure environments.

Plants with a previously "dry" history were able to grow longer into the desiccation period than those with the "wet" history as well as those under the continuous "wet" or "dry" conditions. This apparent "adaptation" was due to a more efficient rate of water use per unit leaf area by the "hardened" plants. But the mechanism that enabled these plants to use water more efficiently was not known.

Nui had been reported to outyield Ruanui under the summer and autumn conditions in New Zealand. Because of the importance of perennial ryegrass to New Zealand, a comparison of these 2 cultivars was also made in this study. Between the two cultivars of ryegrass, Nui had a higher leaf extension rate (+20%) under the H temperature regime, it also had a heavier mean tiller dry weight (+28%), a larger mean area per leaf (+24%), but a lower tiller number (-24%) and a lower green leaf number (-18%) per plant than Ruanui. All the other paramters measured, including total leaf area and total dry weight per plant, top to root ratio, specific leaf area, leaf area ratio, stomatal resistance and transpiration rates were similar between the two ryegrass cultivars. Some of the possible reasons for the lack of difference on a per plant basis are discussed.

The possibility of using leaf extension rate to predict plant dry weight changes in water deficit studies is also discussed.

CHAPTER 1

INTRODUCTION AND OBJECTIVES

1.1 INTRODUCTION

A greater part of New Zealand has an average annual rainfall of between 635 and 1500 mm, a range generally regarded as favourable for plant growth in a temperate environment (Robertson, 1972). The only areas with under 635 mm are found in the South Island to the east of the ranges, where the climate tends to be more Mediterranean, or even continental (e.g., Central Otago). The rather high rainfall often leads people to believe that moisture is not really a major limiting factor for pasture production in New Zealand.

However, average annual rainfall does not necessarily give a clear indication of the availability of water for plant growth. First, a significant proportion of rainfall may be lost by runoff, surface evaporation and deep drainage. Secondly for maximum plant growth, the supply of water to the roots must be continuous and approximately equal to the rate of loss from the plant. The continuity of supply to the plant depends obviously on much more than the quantity of supply to the soil. It depends on the frequency of supply and on the buffering capacity of the soil. This in turn depends on the soil's water holding capacity, depth and the degree to which the roots explore it. The achievement of balance between the uptake and loss of water by the plant depends on a number of factors including atmospheric conditions (potential evapotranspiration), plant factors (leaf area index, canopy architecture, stomatal control, root characteristics) and soil factors (hydraulic conductivity).

The results of field trials have demonstrated just how much these factors can influence pasture production in practice. For example, even in regions such as the Manawatu where the average annual rainfall is 1002 mm, seasonal shortage of water between October and April can reduce potential pasture production by as much as 40% (Brougham, 1966). Under the drier environment of Canterbury, Rickard and Fitzgerald (1970) reported that lack of soil moisture was the major cause of low pasture production during the warmer months (November - April). In a season with an average of 39 days of Agricultural Drought (for definition of term see section 2.1.1) irrigated pasture produced 88% more dry matter than non-irrigated pasture and this increased to 176% during a season with an Agricultural Drought of 60 days.

It is sometimes said that irrigation can provide the means of overcoming the summer drought problem. The irrigation of pasture is certainly increasing in importance in New Zealand. The area of irrigated grassland, including lucerne, increased from 54,632 hectares in 1958 to 129,120 hectares in 1976, the majority of which was in Canterbury (46%) and Otago (42%) (N.Z. Dept. of Stat. 1958 and N.Z. Official Yearbook 1978). However, for the bulk of the agricultural land in the country, including 70% of which is classified as hill country (Watkin, 1972), livestock production must continue to rely on a system of dryland farming. This points to a continuing need to adopt plant types and management systems for the dryland environment. It should also be recognised that many plant features that are desirable under dryland conditions will also be desirable under irrigation.

Two further features of the New Zealand environment can also influence our views on the importance of drought on pasture production. First, our climatic environment is less extreme than many other countries and it is less likely that any one climatic factor is completely dominant at any one time. This is in contrast, for example, to the semi-arid regions of

Australia where water deficit is clearly the limiting factor, or to North America and Europe were low temperature significantly limits production. As a consequence, in New Zealand, we have to recognise that pasture which is relatively unadapted genetically or phenotypically may suffer more severe reductions in production than the climatic conditions might indicate. In addition, we need to understand the interactive effects of, climatic parameters, such as temperature and rainfall, and not merely the effects of these parameters in isolation.

A second important feature of our pasture environment is the frequent defoliation of our pastures. Frequent removal of herbage during grazing can restrict the development of a vigorous rooting system. This type of grazing practice encourages the occurrence of more severe water deficits in our pastures (Mitchell, 1966).

1.2 OBJECTIVES

It is clear from the above that pasture production in New Zealand can be reduced substantially by water deficit. This provided the general background to the selection of the particular study on plant water relations described in this thesis.

Physiological studies reported during the late 1960's and early 1970's provided a more specific impetus. Physiological evidence showed that leaf growth can be substantially reduced by relatively mild water deficits. In pastures where leaf growth consititutes the bulk of the economic yield, reductions in leaf growth by water deficit can have serious economic consequences to the farmer. Furthermore, water deficit frequently occurs at the time of the year when potential production is at its maximum. In light of the above comments, it was considered

important and worthwhile to examine the physiology and agronomy of water deficit more closely.

The specific objectives of this study were to investigate:-

(a) The sensitivity of leaf extension to plant water deficit. Can there be sub-clinical level of water stress which will substantially restrict pasture production to an extent that we are unaware of?

(b) The effects of duration of water deficit on subsequent recovery growth. How long can pasture grasses withstand desiccation before its growth is adversely affected? And are there positive or negative carryover effects after rewatering?

(c) The reaction of plants to water deficit following atmospheric preconditioning. Does the physiological response of the phenotype to desiccation depend on previous growing conditions?

In New Zealand, Nui ryegrass has been reported to outyield Ruanui (Rumball, 1969; Baars *et al.*, 1976; Sheath *et al.*, 1976). Because of the importance of perennial ryegrass to New Zealand's agriculture, a comparison of these 2 cultivars was also made in this present study.

This thesis presents the results obtained from a series of six experiments. The first was in the field and the remainder under controlled conditions in the Climate Laboratory, Department of Scientific and Industrial Research (DSIR), Palmerston North, New Zealand.

The study started in 1974 and since then significant progress has been made in this field by other workers. Consequently only a brief review of literature is presented in Chapter II, covering relevant

information available at the time when this study was commenced. Where appropriate, further reviews are presented in the introductory section of each chapter to bring the discussion up-to-date. An "overview" summarising results from the experiments conducted under this study and relating them to the current state of knowledge in these fields is presented in the final chapter.

Some of the results presented in this thesis have already been published by the author. These will be indicated in the appropriate sections.

CHAPTER II

REVIEW OF LITERATURE

2.1 INTRODUCTION

The relationship between plant growth and water deficit has been reviewed by many authors. Comprehensive reviews since that presented by Vaadia *et al.* (1961) include Salter and Goode (1967), Slatyer (1967, 1969), Gates (1968), Kozlowski (1968a, 1968b, 1972), Dainty (1969), Kramer (1963, 1969), Weatherley (1970), Hsiao (1973), and Hsiao and Acevedo (1974).

Apart from a brief review of (1) the development of plant water deficit, and (2) the responses by plants to water deficit, the bulk of this review will therefore be centred on the points directly relevant to the objectives of this thesis. These are:

(a) effects of desiccation on leaf growth,

(b) effects of desiccation on vegetative yield, and

(c) reactions of plants to pre-desiccation treatments.

However, because temperature has been found to have some interactive effects with water deficit, a brief review on the effects of temperature and temperature x water deficit on plant growth will be presented in the final section of this Chapter.

2.1.1 Terminology

The following definitions have been adopted for some of the commonly used terms:

1. ACCELERATED RATE - during recovery from a period of water deficit, plant growth rate, for example leaf extension rate, can be faster in the previously desiccated plant than those of the well-watered control of the same physiological age. The term "accelerated rate" is used to describe such a faster rate.

2. AGRICULTURAL DROUGHT - it is a condition that exists when the soil moisture in the root zone is at or below permanent wilting percentage, and which persists until rain falls in excess of the daily evapotranspiration (Rickard, 1960).

3. COMPENSATORY GROWTH - refers to the situation where the growth accumulated by a previously desiccated plant since rewatering exceeds that of a well-watered plant, growing in the same environment, and over the same physiological stage of growth.

4. DESICCATION - unless otherwise stated (e.g. soil desiccation) it refers to the lowering of plant water status.

5. DROUGHT - refers to a meteorological condition during which there is no measurable rainfall. The duration is arbitrary, sometimes 15 days (May and Milthorpe, 1962). It is sometimes used loosely to mean "plant water deficit".

6. DROUGHT ADAPTATION - Refers to the adjustment by plants which can occur as a result of a period of exposure to desiccation, such that they become less sensitive to a subsequent desiccation. The term used in this thesis refers to a change in the phenotype. It is not to be confused with the ability of a plant population to grow well in a range of given environments as in "well adapted cultivar". Two forms of "drought adaptation" are commonly used (Levitt, 1972):-

   Avoidance - refers to the ability of the plant to prevent the lowering of internal plant water content by some physical or morphological means, such as deeper roots or reduced

transpiration.

Tolerance - refers to the plant's ability to survive serious desiccation with a low internal plant water content and able to recover and grow rapidly upon the relief of water deficit.

7. WATER DEFICIT - refers to the lowering of plant water potential from that equal to the free energy of pure water at the same temperature.

8. WATER POTENTIAL - is defined as the difference between the free energy of water in the system and that of pure water at the same temperature. The "water potential" in a plant tissue is the sum of its osmotic potential, matric potential, turgor potential and gravitational potential. Although normally only that of the osmotic and turgor potentials are considered (Slatyer, 1967).

9. WATER STRESS - strictly speaking, this can apply to both a deficit or an excess of water, however, more commonly this term implies the "deficit stress" (Levitt, 1972). In this thesis it refers to a level of water deficit in which an impairment in some plant function has occurred.

2.2 DEVELOPMENT OF PLANT WATER DEFICIT

As water is evaporated from the mesophyll cells during transpiration a gradient of water potential will be developed through the plant from the evaporating leaf surface to the absorbing root surface. Water moves along this gradient from the soil, through the plant to the atmosphere (i.e., the concept of Soil-Plant-Atmosphere-Continuum (SPAC) which was reviewed by Philip (1966)). Two factors of practical importance arise from the nature of this system. First, as a consequence of water movement through the SPAC, all transpiring and/or growing plants will experience some degree of water deficit. Secondly, plant water status depends on the atmospheric factors as well as the more commonly recognised soil factors. Plant factors, such as stomatal control, of course can have important mediating effects.

The amount of water lost to the atmosphere by plants through transpiration is large compared to the amount of water contained in the plant tissue at any one time. Rapidly growing and transpiring plants can use their own weight in water every 2-3 hours, hence the water status of the plant is highly sensitive to any imbalance between the rate of uptake of water and its loss. As the soil dries, the declining soil water potential sets the upper limit for the plant water potential. Although plant water potential can approach the soil water potential at night when there is no transpiration, the rate of recovery in plant water potential becomes slower as the soil becomes progressively drier. As the leaf water content decreases, cell turgor will also decrease and when cell turgor reaches zero, wilting will occur (Slatyer, 1969).

Substantial plant water deficit can develop even when roots are well supplied with water. This situation is most likely to occur under dry conditions. For example, in a sward of pasture grasses and legumes grown in a lysimeter, Shepherd and Dilley (1970) observed that wilting of leaves occurred when potential evapotranspiration, calculated from meteorological data, exceeded 0.5 mm per hr for several hours, even when the plots were "well-watered".

As water deficit will develop in all transpiring plants, the important question is at what level of deficit will plant processes be adversely affected and what are the short and long term effects of this.

2.3 PLANT RESPONSES TO WATER DEFICIT

The plant can be considered to be in a state of "stress" when the level of water deficit is sufficiently large or prolonged, to cause the impairment of plant functions. However, increasing plant water deficit does not have a uniform effect on different physiological and developmental processes. Some processes are more sensitive to water deficit than others. Hsaio (1973) in his comprehensive review on this subject has summarised the relative sensitivity of different plant processes to water stress. The actual levels of desiccation when the processes are first affected will depend on the species, stage of growth and the speed of stress development. By and large, it is accepted that leaf growth, which includes cell expansion and cell division, is the first process to be affected as water deficits develop (Boyer, 1968; Hsiao, 1973). As plant water status decreases further, a number of other processes will be affected, for example, ribonucleic acid and

protein synthesis (Shah and Loomis, 1965) and enzyme levels (Bardzik *et al.*, 1971) will be reduced and abscisic acid level will be increased (Wright and Hiron, 1969).

Further increase in water deficit will result in stomatal closure which leads to reduced transpiration and CO_2 assimilation (Brix, 1962; Boyer, 1971) and reduced translocation (Wardlaw, 1967). More severe stress will cause free proline to accumulate (Singh *et al.* 1972) and eventually accelerated senescence of plant tissues (Hsiao, 1973).

The effects of long term water stress on plant physiological and developmental processes are more complex, since interactive responses between different processes can play a part. For example, in the cambium layer of ash *(Fraxinus excelsior)* cell division can only commence after these cells have expanded to a diameter of 6 μ (Doley and Leyton, 1968). Thus, water deficit that is only sufficient to inhibit cell expansion (-0.10 MPa, in Doley and Leyton's experiment) can indirectly affect cell division. Similarly, reduced cell growth can cause a decrease in the demand for assimilates. The reduced metabolic activity associated with the production and translocation of assimilates can therefore be an indirect effect consequent upon a reduced internal demand, rather than a direct result of water stress on these processes (Wardlaw, 1969; Hsiao, 1973).

In addition to the effects of water deficit on physiological processes *per se*, reactions by the plant as a whole to desiccation will depend on both species and stage of development (Salter and Goode, 1967). Interspecific differences are illustrated by the comparison of sorghum with maize, i.e., sorghums are more drought tolerant than maize.

Even amongst different strains of the same species different responses to water deficit can occur. For example, Cook (1943) in a study of 8 different selections of *Bromus inermis* found that there were drought tolerance differences between different selections. Those drought tolerant strains had higher number of 'large' and 'small' roots and these roots penetrated deeper into the soil than the drought sensitive strains.

The differential sensitivity of plants to desiccation at different stages has been discussed by Salter and Goode (1967). For cereals, during the vegetative stages, the sensitive stages are: during tillering and during early shooting; whereas for the reproductive stages the sensitive stages are: latter part of shooting, during heading and during flowering.

In cereals, while the period when the reproductive organs are developing is normally regarded as the most sensitive period to water deficit, the final grain yield at the end of the season may also depend on the less moisture sensitive vegetative stage. For instance, even if water is not limiting during the reproductive stages, grain yield can be reduced as a result of lower tiller numbers due to water stress during the tillering phase.

On the other hand, in lucerne, the vegetative yield has been reported to be more sensitive to water stress than reproductive yield (Taylor *et al.*, 1959). Taylor *et al.* reported that seed yield in lucerne was highest when the soil moisture was between -0.2 to -0.8 MPa, whereas forage yield was maximum when the soil was at field capacity. Similarly, growth rates of vegetative organs tended to be more sensitive to moisture deficit than growth rates of the reproductive

organs (Stanhill, 1957). Stanhill, in a survey of 80 papers on the effects of different soil moisture conditions on plant growth concluded that the response by the vegetative parameters to water deficit was greater than the reproductive parameters, thus reflecting the more sensitive nature of the vegetative parameters to desiccation.

From the agronomic point of view the important measure of response is the economic yield. In the case of pasture grasses the leaf component constitutes the bulk of this yield. Reductions in leaf growth may therefore result in economic losses to the farmer. Although it is known that leaf growth is sensitive to mild levels of water deficit, the extent to which reduction in this process impedes the responses of other growth parameters such as the rate of tillering and dry matter yield, is largely unknown.

2.4 THE EFFECT OF WATER DEFICIT ON LEAF GROWTH IN PASTURE GRASSES

In order to review the effects of water deficit on the process of leaf growth in grasses, it is desirable to review briefly, the process of leaf extension in grasses.

2.4.1 Leaf extension in grasses

Descriptive accounts of leaf growth in Graminae have been presented by Sharman (1942), Soper and Mitchell (1956), Gregory (1956), Barnard (1964), Evans *et al.* (1964), Jewiss (1966), Silsbury (1970) and Langer (1972). In this section of the review, only aspects related to leaf extension will be discussed.

Leaf extension involves both cell division and cell expansion. At its inception the whole leaf primordium is meristematic, but cell division soon becomes localised to a basal zone of cells. As a result of transverse division, files of cells will be produced towards the distal end of the primordium and cause it to elongate. In ryegrass, when the primordium is about 1 cm long, the intercalary meristem will be differentiated (Barnard, 1964). This band of cells separates into an upper region which develops into the lamina and a lower region which develops into the sheath. In grasses, cell division in the lamina is completed by the time the ligule (an outgrowth of the epidermis on the adaxial side of the intercalary meristem) is differentiated (Langer, 1972). Leaf extension at this stage comes from the expansion of the cells in the lamina and cell division and cell expansion in the sheath. This will continue until the ligule is fully exposed which then marks the end of leaf extension process.

In grasses, the zone of leaf extension is limited to the lower region of the leaf. For example Wardlaw (1969) found that in leaf 8 of the ryegrass plant the zone of extension was within the basal 4 cm of the leaf. Thus, the region of leaf extension in grasses is within the zone enclosed by the leaf sheath of the preceding leaf, with cell division confined more to the basal region (Langer, 1972).

2.4.2 The effects of water deficits on leaf extension

Cell expansion, an essential component of leaf expansion, has been recognised as being one of the most sensitive plant processes to desiccation both in the field and in the laboratory (Slatyer, 1969; Hsiao, 1973). Boyer and his colleagues (Boyer, 1968, 1970a; Meyer and Boyer, 1972) reported that under controlled environments leaf enlarge-

ment was severely reduced as leaf water potential reached about -0.4, -1.1 and -1.3 MPa for sunflower, maize and soybean respectively. The major changes in leaf enlargement occurred within a very narrow range of 0.2 to 0.3 MPa leaf water potential. Similarly, Hsiao *et al.* (1970) and Acevedo *et al.* (1971) demonstrated that extension growth of young maize leaves stopped completely at -0.65 MPa and this occurred before visible wilting was evident.

Such results suggested that restriction in leaf growth may occur quite frequently in the field as leaf water potential of -0.4 to -0.6 MPa represents a relatively "wet" leaf. Lower leaf water potentials (more negative) are normally reached under the evaporative demand experienced in the field. For example from maize, wheat, barley, beans, peas, potatoes, sugar beet and lucerne grown in the field, Cary and Wright (1971) found that maximum (least negative) leaf water potential measured in the morning with freezing point meter seldom rose above -0.50 MPa and for most crops it was nearer to -1.00 MPa. Similar field results have been reported by others (Klepper, 1968; Kanemasu and Tanner, 1969; Jackson, 1974).

On the basis of these physiological findings it seems worthwhile to establish whether the usual degree of desiccation experienced in the field will depress yield, particularly in the case of pastures where the leaf component constitutes most of the economic yield.

2.5 THE EFFECTS OF WATER DEFICIT ON VEGETATIVE YIELD IN PASTURE GRASSES

A number of growth components are involved in pasture herbage production. Among these are the rates of leaf and tiller production and the size to which each will attain.

Desiccation can influence vegetative yield through the reduction in leaf area by restricting the rate of leaf expansion and by accelerated senescence of older leaves. Under conditions where Leaf Area Index (LAI) is low enough to limit dry matter accumulation, restrictions in leaf area can reduce yield (Hsiao and Acevedo, 1974).

Desiccation can also influence vegetative yield by reducing the number and size of leaves and tillers per plant. Luxmoore and Millington (1971) reported that in perennial ryegrass the variation in total tiller number was the major morphological parameter associated with variations in total plant dry weight and leaf area.

The rate and amount of tillering are generally reduced under desiccation (Langer, 1963). For example, in sideoat grama *(Bouteloua curtipendula)* both the number of tillers and the mean dry weight per tiller were found to be correlated directly with the amount of water supplied (Olmsted, 1941). Similarly, in Marquis wheat the number of tillers was significantly higher when the soil moisture was at 50% than at 25% saturation (Gardner, 1942).

These experiments were done with repeated waterings of different amounts and/or frequencies. Plants can respond differently to different numbers of drying and rewatering cycles. For example, Aspinall

et al. (1964) reported that in barley the number of elongating tiller buds following rewatering depended on the number of rewatering cycles and also on the stage of development when stress was applied. Under a single, short water stress more tiller buds were induced to elongate following rewatering than control plants. However, under more than one cycle of stress, control plants tended to have more tillers than stressed plants.

Fresh weight is more sensitive to water deficit than is dry weight (Denmead and Shaw, 1960; May and Milthorpe, 1962). In the field, under a mild water deficit condition, percentage dry matter of sudax, a forage sorghum, was up to 5% higher than the 'irrigated' plants and this had partially compensated for the decrease in fresh weight in the "stressed" plants. (Chu and Tillman, 1976).

Although water stress reduces the growth of the whole plant the differential effects of water stress on different plant parts, such as shoot and root growth, can result in a lower shoot to root ratio during desiccation (El Nadi *et al.*, 1969; Hoffman *et al.*, 1971).

The differential effects of water deficit on different plant parts will also influence the quality of the herbage. For example, Gates, (1955a, 1955b) found that in tomato plants the effect of water stress was greater in the laminae component than the stem. As protein and mineral content is normally higher in the leaf component than stem or roots, reduced leaf growth will indirectly reduce the quality of the herbage. Water deficit will also hasten the maturation of forage crops and lead to reduced quality, because quality of forage crops usually decreases with increasing maturity (Richards and Wadleigh, 1952).

A frequently observed effect during the recovery phase following desiccation is the apparently more rapid rate of plant growth and development compared with the well-watered plants. Such higher growth rates have been reported for tomato (Gates, 1955a, 1955b) sugar beet (Owen and Watson, 1956) and tobacco (Hopkinson, 1968). Gates (1955b) attributed the higher post-desiccation growth rate as "a tendency towards a more juvenile form". Owen and Watson (1956) found that although the absolute dry weight and LAI of a sugar beet crop was lower without irrigation, Net Assimilation Rate, Relative Leaf Growth Rate and Relative Dry Weight increases were temporarily higher in the unirrigated plots as the result of a small amount of rain falling after a prolonged drought. Hopkinson (1968) observed that the stimulated growth rate in tobacco was slow to develop but prolonged in duration. In Hopkinson's experiment, the higher rates in the stressed plants caused an accelerated recovery leading to a greater final total leaf area and dry weight in the stressed plants than the well-watered control.

Similarly, higher rates of leaf extension upon relief of water stress have been reported for young maize leaves (Acevedo *et al.* 1971), but the accelerated growth lasted only a fraction of an hour. On the other hand, Lawlor (1972) reported a fourfold increase in the rate of leaf extension in young ryegrass leaves 3 days after rewatering. This significant effect persisted, although declining, for a period of 8 days.

There are numerous reports of pasture dry matter yield responses to irrigation. For example, under New Zealand conditions, Rickard and his colleagues (Rickard, 1968; Rickard and Fitzgerald, 1970; Rickard, 1972) reported varying degrees of pasture responses under different frequencies of irrigation in Canterbury. The responses depended on climatic conditions which influenced the severity and duration

of water stress, soil type, species and timing of stress. However, many of these reports do not describe plant water status and the short term plant responses during the drought and recovery phases. In plant water relation studies it is important to relate final yield performance to basic physiological principles so that information obtained can be interpreted and extrapolated to other conditions.

2.6 REACTION OF PLANTS TO WATER DEFICIT FOLLOWING "DROUGHT HARDENING" PRE-TREATMENTS.

It is generally believed that exposure to a period of moderate desiccation can allow some plants, to "harden" or become less sensitive to a subsequent and perhaps more extreme water deficit. Such "hardening" or "adaptation" to drought can be induced in the seed, during the pre-sowing stage (May *et al.*, 1962; Henckel, 1964; Woodruff, 1969), as well as on the whole plant (Todd and Webster, 1965; Levitt, 1972; McPherson and Boyer, 1974).

For example, Woodruff (1969) reported up to 20% higher grain yield in pre-sowing drought-hardened wheat seed. The higher yield was due to a slower rate of relative water content decline during periods of water deficit by the pre-treated plants. There was also an interaction between the rate of relative water content decline and the growth stage when water deficit occurred. Although the mechanism whereby the seed adapted to drought was not fully understood, May *et al.*, (1962) in their review of the Russian work on this subject concluded that "there is considerable evidence to show that the drought resistance of plants can be induced by subjecting seeds to a cycle of wetting and drying prior to sowing".

Similarly on the whole plant level, higher photosynthetic rates at a lower water content were observed in a number of wheat and oat varieties after the plants were subjected to a single drought period (about 1 week)(Todd and Webster, 1965). However, the reason for the higher photosynthetic rates by the hardened plants was not given. Under controlled environments, McPherson and Boyer (1974) demonstrated substantial advantage in final maize grain yield by plants that had been "pre-treated" in dry atmosphere (air vapour pressure deficit (VPD) of 2.6 kPa). When these "pre-treated" plants were subjected to soil desiccation during the grain filling stage, their grain production was greater because their rate of water use was 33% lower than the plants which had been "pre-treated" with more humid atmosphere (VPD 0.5 kPa).

Drought adaptation in plants can take two forms. It can be either an avoidance or a tolerance to low internal water content. Drought avoidance has also been described as "drought endurance with high internal water content" by May and Milthorpe (1962). A comprehensive review on the possible mechanisms of drought avoidance and tolerance had been presented by Levitt (1972). Briefly, adaptative reactions by plants can be grouped according to the nature of the response, i.e., whether it is morphological or physiological.

Some examples of the morphological adaptations include:

i. Reduction in leaf area during desiccation through reduced leaf growth and accelerated leaf senescence. The reduction in the evaporative surface will help to conserve water.

ii. Parahelionasty, or the positive orientation of leaves parallel to the incident radiation, will help to reduce the energy load upon the leaf surface (e.g., in beans, (Dubetz, 1969)).

iii. The development of wax bloom on sorghum leaves will help to reduce transpiration (Chatterton *et al.*, 1975).

iv. The development of a high root to shoot ratio which will allow the plants to grow further into the drought period (e.g., in beans (El Nadi *et al.*, 1969) and cotton (Hoffman *et al.*, 1971)).

Some examples of physiological reactions include:

i. Stomatal closure

Jordan and Ritchie (1971) found that stomatal resistance of the adaxial surface in field grown cotton were low even at leaf water potential of -2.7 MPa, whereas stomata of greenhouse grown cotton plants were closed at -1.6 MPa leaf water potential. They attributed this difference to the adaptation of the field grown cotton to prolonged drought conditions. Such adaptation by stomata was also found later by McCree (1974) using "pre-stressed" (plants subjected to 5 cycles of mild soil desiccation) sorghum plants in the growth room. McCree found that at a given leaf water potential the stomatal conductance of "pre-stressed" sorghum leaves was consistently higher than those of the previously "unstressed" control.

ii. Osmotic adjustment

As a consequence of water loss during desiccation the concentration of solute in the cells must increase. However, water deficit can also induce a net increase in solute concentration, i.e., osmoregulation or osmotic adjustment (Levitt, 1972).

There is some evidence of osmotic adjustment as a reaction to increasing water deficit. Under desiccation, etiolated but intact soybean hypocotyls showed some degree of osmotic adjustment resulting in constant turgor. The adjustment involved the movement of solute from the cotyledons to the hypocotyl (Meyer and Boyer, 1972). Few studies have been made for pasture species. Only some indirect evidence reported by Gavande and Taylor (1967) had suggested that a change in the osmotic potential under a low evaporative demand condition (21^{o}C, 60% Relative Humidity) was of some advantage in maintaining turgor potential in cocksfoot *(Dactylis glomerata)*, when the plants were subjected to different levels of soil moisture deficit.

2.7 INTERACTIVE EFFECTS OF TEMPERATURE AND WATER DEFICIT ON PLANT GROWTH

As the emphasis in this section of the review will be placed on the interactive effects of temperature and water deficit, it will also be necessary to review briefly the direct effects of temperature on leaf growth.

2.7.1 The effects of temperature on leaf growth

The effects of temperature on leaf growth and development had been very intensively studied and reviewed, (amongst others: Mitchell, 1953a, 1953b, 1954, 1956; Gregory, 1956; Milthorpe, 1956, 1959; Blackman, 1956; Evans *et al.*, 1964; Leopold, 1964; Silsbury, 1970). More recently studies on the effects of temperature on maize by Kleinendorst and Brouwer (1970, 1972) and Watts (1972, 1974), on ryegrass by Peacock (1975a, 1975b) and on tall fescue by Robson (1972, 1973, 1974) have contributed greatly to our understanding of the responses by grass leaves to temperature.

Although Festucoid grasses will grow well between 10°C and 27°C, for most the optimum is between 15°C and 25°C. The optimum for top growth is higher than for root growth (Evans *et al.*, 1964). For grass leaf growth, the site of temperature perception has been shown to be around the stem apex rather than there being a general effect of soil or air temperature (Peacock, 1965b).

That there are differences in plant responses between constant temperature and different day/night temperatures has been demonstrated by Robson (1972, 1973, 1974). In general, day temperature has a greater influence on plant growth than night temperature. Robson (1973) found that in tall fescue, under a daily mean temperature of 20°C, all growth parameters reached their maximum value when the day temperature was 4° to 10°C higher than the night temperature.

Depending on the location of temperature influence, leaf responses can be affected by different processes. For example, Kleinendorst and Brouwer (1972) examining the effect of local cooling on growth and water content of maize leaves concluded that responses by leaf elongation growth in maize leaves depended on the site of cooling. Cooling in the root medium caused a reduction in leaf elongation by a lower water content which retarded cell extension. The plant adjusted for the lower water content by increasing its osmotic potential which allowed the water potential to recover followed by the recovery in cell extension. Cooling at the meristemic region caused a more permanent reduction in leaf elongation and there was no recovery. Cooling above the meristemic region on the other hand, temporarily retarded leaf growth by a reduction in translocation. Leaf growth then recovered when the concentration of carbohydrate above the stem apex increased.

2.7.2. The interactive effects of temperature and water deficit on plant growth

A number of workers have reported the interactive effects of temperature and water deficit on plant growth (e.g., Abdelhafeez and Verkerk, 1969; Gates *et al.*, 1971; Sharma, 1976). It seems in general that the detrimental effects of water deficit are greater under

the "high" than under the "low" temperature conditions.

For example, Abdelhafeez and Verkerk (1969) compared the rate of tomato seedling emergence under 3 temperature regimes (24^{o}, 19^{o} and $9^{o}C$) and 3 moisture regimes (wet, between 0 and 10% of field capacity; medium, between 0 and 20% of field capacity; dry, water to field capacity after plants had shown severe wilting). They showed that the best emergence rate was for a treatment combination of the highest temperature and the wettest moisture regime. A similar trend was also observed for plant growth under 2 different temperature regimes ($35^{o}/18^{o}$ and $20^{o}/15^{o}C$, day/night temperature), with the same 3 levels of moisture regimes (Abdelhafeez and Verkerk, 1969). Maximum growth and fruit set in tomato was influenced more by moisture regimes than by temperature. Under the lower temperature regime, differences in growth and fruit set due to moisture deficit was less pronounced than that under the higher temperature regime.

Similarly, Gates *et al.*, (1971) using low temperature (chilling stress) and moisture stress to examine their effects on maturation and chemical composition of townsville stylo *(Stylosanthes humilis)* reported that the major effect was due to the moisture stress. Temperature participated as a small temperature-moisture stress interaction, in that under the cold temperature conditions growth was reduced and proline concentration was higher under the moist but not under the dry condition.

Temperature and moisture interaction was also reported in the rate of germination of different semi-arid plant species. Sharma (1976) studied the interaction of different incubation temperatures with matric potentials (induced by using polyethylene glycol 20,000)

and osmotic potentials (induced by using sodium chloride) on the rate of germination of *Danthonia caespitosa*, *Atriplex mummularia* and *Atriplex vesicaria*. Moisture deficit reduced percentage germination in all 3 species under all the temperature regimes. The best germination rate for all species was at the lower water potentials in the vicinity of the optimum temperature (20^{o} - 25^{o}C). There were significant temperature x water potential interactions for all species in that inhibition of germination was less at the lower temperature regime.

CHAPTER III

SENSITIVITY OF LEAF EXTENSION TO PLANT WATER DEFICIT

3.1 INTRODUCTION

As discussed in the earlier section (Section 2.4.2) the sensitivity of leaf extension to small changes in leaf water potential has been demonstrated (e.g. Boyer, 1968; Hsiao *et al.*, 1970; Acevedo *et al.*, 1971) and leaf extension can be severely restricted under the normal range and magnitude of leaf water potential found in the field (e.g. Cary and Wright, 1971; Jackson, 1974). Plants can also experience water stress even under well watered situations (Shepherd and Dilley, 1970) suggesting that sub-clinical levels of water deficit can occur in the field long before wilting is evident. This physiological finding implies that plants can experience levels of water deficit sufficient to reduce leaf growth which may lead to reductions in green herbage yield. Maize plants have been observed to cease growth entirely during highly evaporative daytime conditions, growing only under the lower evaporative demand conditions of the night time environment which tends to support the significance of this physiological finding (Loomis, 1934; Boyer 1968).

These reports in the literature led to the suggestion that using overhead mist irrigation to reduce the atmospheric evaporative demand and consequently lower plant water deficit could increase crop yield (Kramer, 1963; Hanan, 1972; Jackson, 1972). Similarly, high frequency irrigation had been suggested as a means of increasing crop yield (Salter and Goode, 1967; Rawling and Raats, 1975).

Kramer (1963) in his review quoted an example where light sprinkling during mid-day increased growth more than the same amount

of water applied to the soil (Stocker *et al.*,1954). Under horticultural conditions, frequent overhead sprinkling did increase tomato yields (Carolus *et al.*, 1965). Similarly, during a dry summer, the dry matter yield of a ryegrass and white clover pasture increased with increasing frequency of irrigation (irrigate at 12 mm soil moisture deficit with 12 mm of water), but the total quantity of water applied was also increased (Stiles and Williams, 1965).

The most convincing evidence that frequent irrigation would increase dry matter yield came from the report by Snaydon (1972). In lucerne, Snaydon found that a total water supply equal to 0.2 E_{pan} (class A pan evaporation) frequent small applications of water (5 mm per application) produced 50% more dry matter than less frequent but larger applications (20 and 80 mm per application) during the summer at Canberra, Australia. However, application of water in amounts greater than 0.5 E_{pan} produced no significant differences between frequencies in terms of dry matter yield.

If plants do frequently experience levels of water deficit sufficient to reduce leaf growth and consequently green herbage yield, it is important, in the study of plant water relations, to identify the extent of this restriction and the frequency of its occurrence.

In the following 3 sections of this Chapter, the relationships between leaf water potential and leaf extension rate for 3 forage species (viz, sudax, prairie grass and ryegrass) collected from different experiments, are presented. Some of these data (sections 3.2 and 3.3) have already been published (Chu and Kerr, 1977, and Chu and McPherson, 1977 respectively). The third section 3.4 will be published as part of another paper.

The implications of the findings from these experiments relative to the objectives as stated at the beginning of this thesis will be discussed under the "Overview and Conclusion" section in Chapter VI.

3.2 EXPERIMENT 1 - LEAF WATER POTENTIAL AND LEAF EXTENSION IN A SUDAX CROP

3.2.1. Abstract

Leaf water potentials were measured on leaves at three canopy heights in dryland and irrigated sudax plots. Basal tiller leaf water potentials ranged from -0.20MPa to -0.50 MPa while those of upper leaves on the main stem fell to -1.30 MPa during the daytime. Mid-canopy leaf water potential ranged from -0.40MPa to -0.70MPa. Removal of the main canopy immediately caused the basal tiller potentials to approach those of the upper canopy leaves. Under irrigation, night time leaf extension rates were 1.5 ± 0.2 mm h^{-1} compared with daytime rates of 3.1 ± 0.1 mm h^{-1}.

3.2.2. Introduction

In this experiment a forage sorghum hybrid (*Sorghum bicolor* (L) Moench X *S. sudanese* (piper) Staff.), Sudax, was used. Where grown as a summer greenfeed crop, sudax is normally cut or grazed a number of times during the season. Subsequent production depends largely on the regrowth of the basal tillers. Field observations on sudax showed that wilting and senescence of leaves under stress first occurred in the lower leaves and basal tillers.

Diurnal changes in leaf water potential, leaf resistance and canopy irradiance measured at different heights within a canopy have been reported in undefoliated crops of maize, sorghum and tobacco (Turner and Begg, 1973). Until 1973 there was no information on the simultaneous measurements of leaf water potential and leaf extension rate from field experiments. The reported restriction on leaf growth

by low leaf water potential was mainly from experiments conducted under controlled conditions. Hence it was important that the relationship between leaf water potential and leaf extension rates be checked in the field.

This report describes the variation of leaf water potential at various heights within a sudax crop grown under two different soil moisture regimes, and basal tiller leaf water potential before and after removal of the main canopy. In addition, diurnal measurements of leaf water potential and leaf extension of the youngest leaf during regrowth are presented.

3.2.3 Materials and Methods

Sudax SX-6 *(Sorghum bicolor* X *S. sudanese)* was planted on 16 November 1973 in a 0.06 ha field on a recent alluvial soil (Manawatu fine sandy loam) at Massey University, Palmerston North. Two experimental plots, each 2.5 m X 4 m and 1 m apart, were sited in the centre of the field. The plots were hand planted in 15 cm rows with 6 cm spacing within rows. The rest of the field was drilled at the rate of 27 kg ha^{-1} in 15 cm drills and was used as a guard area.

The plots were covered with black polythene sheets which were buried at the edges in a 75 cm deep surrounding trench. The trench prevented any surface movement of water. Different soil moisture regimes were established on each plot. The "irrigated" plot was trickle-irrigated weekly to return soil water content to "field capacity". The "dryland" plot was not irrigated and was covered with clear polythene shelters during rain.

Leaf water potentials were measured on at least 2 leaves at each sampling time using a pressure chamber (Boyer, 1969). All samples were taken from the distal end of exposed laminae.

The diurnal course of leaf water potential was determined in both soil moisture regimes on 26 January 1974. Leaves were randomly selected from the following positions:

1. Upper canopy (1.6 - 1.8 m): the youngest mature leaf (i.e., youngest leaf with exposed ligule) on the main stem was selected. This was either leaf 8 or 9.
2. Mid canopy (0.8 - 1.0 m): the third youngest mature leaf on the main stem.
3. Lower canopy (0.2 - 0.4 m): the youngest mature leaf on a basal tiller. There were 2-3 basal tillers on each plant.

The average soil moisture content of the top 37.5 cm was 29% and 18% (w/w dry soil basis) for the irrigated and dryland plots respectively, on 26 January 1974.

The change in leaf water potential of leaves on the basal tillers induced by sudden increases in evaporative demand was determined by cutting the plants on both treatments and a 3 m border at ground level to expose the basal tillers. This was done between 1430 and 1445 hours on 28 January 1974. A control area of 2 m^2 on the irrigated plot was not cut. The leaf water potential of the basal tillers and of the upper canopy of the control area were measured before and after main canopy removal.

The leaf length of the youngest leaf of the basal tillers were measured with a ruler placed on a fixed reference point on the ground

beginning at 1800 hours on 13 February 1974. Measurements were made at 3-hourly intervals during daylight on five and three leaves for the irrigated and dryland treatments respectively. Leaf water potentials were also measured on the youngest leaves of adjacent plants.

Net radiation data were collected over an adjacent paspalum sward. These indicate the diurnal change in the major energy input to the crop canopy. Air temperature was measured at 1.2 m with a screened thermometer adjacent to the experimental plots.

3.2.4 Results and Discussion

3.2.4.1 Diurnal changes in leaf water potential within the canopy

Within a crop the energy input varies among leaves and is normally least on the lower leaves where net radiation flux densities are smallest. (Begg *et al.*, 1964). This was reflected in the leaf water potential of the upper canopy leaves which had lower values than either the middle or lower canopy leaves (Figure 3.1). The diurnal change in the upper canopy leaves were similar to those reported for other field crops, e.g., cotton (Jordan and Ritchie, 1971), maize, sorghum and tobacco (Turner and Begg, 1973) and cocksfoot and ryegrass (Jackson, 1974).

Although the diurnal range of leaf water potential in the basal tiller leaves was much less than higher in the canopy, basal tillers may experience water stress before the main tiller. Leaf water potential of the basal tillers of the dryland plots was lower (more negative) than the irrigated plot and this difference was apparent earlier in the day than at the other canopy heights. This could explain field observations in a nearby plot that wilting and senescence under moisture

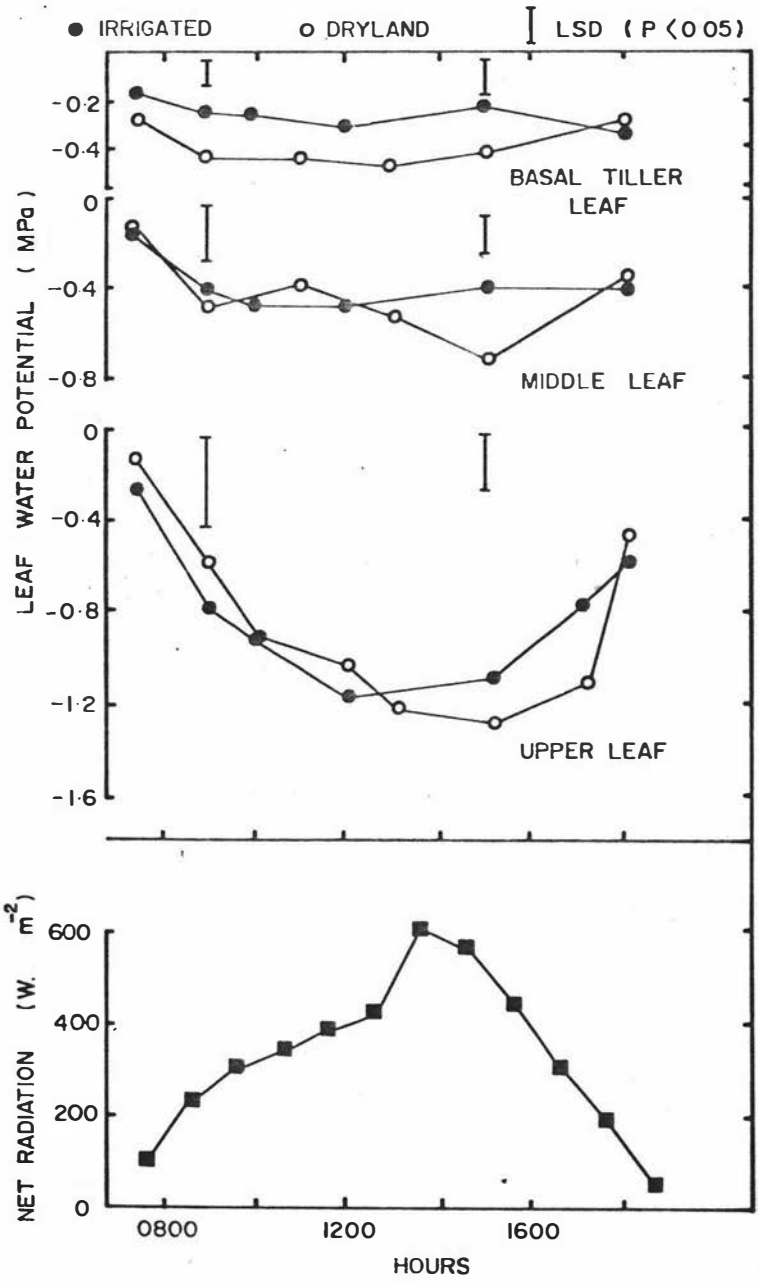


Figure 3.1. Leaf water potentials (ψ_l) measured at three heights in the canopy of field-grown sudax and net radiation taken over an adjacent plot of paspalum (26 Jan 1974).

stress initially occur on the basal tillers.

For the leaves on the main stem, between treatment differences in leaf water potential did not occur until mid-afternoon, when the higher net radiation would indicate a correspondingly higher evaporative demand.

Variability among the leaf water potential measurements made on 6 similar leaves was high. In the dryland plots differences up to 0.40 MPa were recorded in the upper canopy, but variations were less in the irrigated plots. This was probably associated with plant to plant variability which Cary and Wright (1971) reported to be as high as 0.20 to 0.30 MPa for field grown wheat and barley. Short term changes in radiation flux density would also contribute to variability between successive measurements especially in mid canopy positions.

3.2.4.2 Changes in leaf water potential of basal tillers after removal of canopy

Leaf water potentials for the basal tiller leaves and the upper canopy taken on 28 January before canopy removal were similar to those two days earlier. For example, between 1030 and 1100 hours leaf water potential values of -1.08 ± 0.25 MPa, -0.35 ± 0.10 MPa and -0.52 ± 0.05 MPa were recorded for upper canopy (irrigated), irrigated and dry land basal tiller leaves respectively. Immediately after cutting, basal tiller leaf water potentials in both treatments fell quickly (within 5 minutes) to -0.96 ± 0.26 and -0.94 ± 0.04 MPa for the irrigated and dryland treatments respectively. Leaf water potentials in a crop can decrease in response to the increasing evaporative

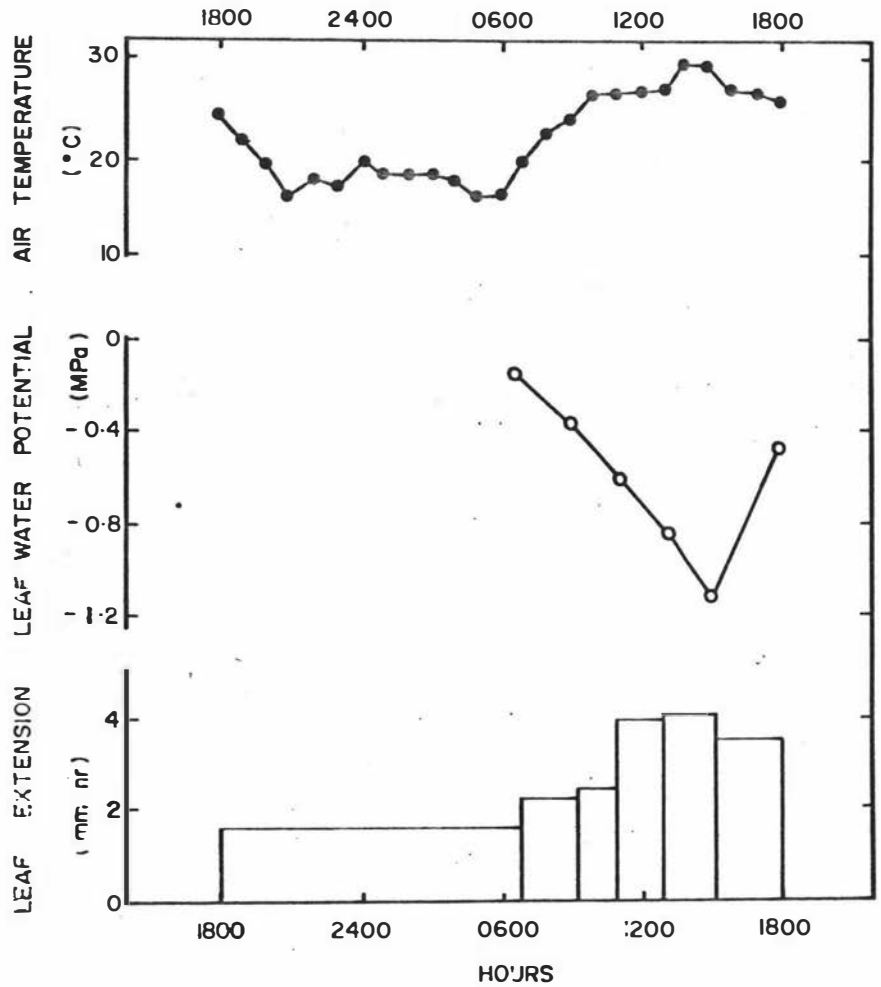
demand and drying soil (Kanemasu and Tanner, 1969). The sudden exposure of the basal tillers to much higher net radiation fluxes with a consequent increased evaporative demand could explain the rapid drop in leaf water potentials. By 1700 hours basal tiller leaf water potentials were similar to the upper canopy leaf water potential on the uncut control (irrigated) area (-0.78 ± 0.07, -0.77 ± 0.16 and -0.78 ± 0.26 MPa for the upper canopy, irrigated and dryland basal tiller leaves respectively).

3.2.4.3 Leaf extension rate and leaf water potential

The plant heights were 0.69 ± 0.05 m and 0.65 ± 0.02 m on the irrigated and dryland plot respectively. Differences in leaf extension rate and leaf water potential were not statistically significant. This could be due to (a) the large variation between samples as reported earlier or (b) the possible horizontal movement of water along the coarse layer/fine sandy loam interface thus effectively "irrigating" the dryland plots below the 75 cm dividing trench (Clothier, pers. comm), hence delaying the onset of the dryland treatment. Consequently results from the irrigated plot only are presented in Figure 3.2 to illustrate the relationship between leaf water potential and leaf extension rate. Two main points emerge from the data:-

(i) The minimum leaf water potential of -1.17 ± 0.05 MPa was reached at 1500 hours and the corresponding leaf extension rate was 4.0 ± 0.4 mm h^{-1}.

(ii) The mean "night" (1800 - 0600 hours) and "day" (0600 - 1800 hours) leaf extension rates were 1.6 ± 0.2 mm h^{-1} and 3.1 ± 0.1 mm h^{-1} respectively.



3.2 Diurnal course of air temperature, leaf water potential (ψ_l) and leaf extension rate in a stand of field grown sudax (13-14 Feb 1974).

In growth room experiments on maize, Boyer (1970a) and Acevedo *et al.*, (1971) found that leaf extension rate ceased when leaf water potential was between -0.40 and -0.65 MPa. Hsaio and Acevedo (1974) have suggested that leaf extension may occur mainly at night when evaporative demand will be lower and the internal plant water status is more favourable for growth. In the present experiment daytime leaf extension rates were approximately double the nightime rates. Maximum rates coincided with maximum air temperature and occurred when leaf water potential was less than -0.65 MPa. One possible explanation for this apparent discrepancy between the results obtained from the present experiment and those reported in the literature is that the water potential of the shaded meristemic region where extension occurs is much higher than leaf water potential measured on the distal end of the exposed lamina, and that it is the meristemic water potential rather than leaf water potential that affects extension growth. Although in the present experiment it is not possible to separate actual leaf extension from possible internode elongation, the magnitude of the overall growth would not have been predicted from the studies reported above (i.e. Boyer, 1970a; Acevedo *et al.*, 1971; Hsiao and Acevedo, 1974).

The findings of the present experiment will be discussed further, in relationship to reports by other workers published about the same time in the "overview" section (section 6.1).

3.3 EXPERIMENT 2 - SENSITIVITY TO WATER DEFICIT OF LEAF EXTENSION IN PRAIRIE GRASS.

3.3.1 Abstract

The short-term response of leaf extension rates and leaf water potential to controlled diurnal changes in the environment of a pasture species, prairie grass *(Bromus catharticus)*, was followed over a soil drying cycle.

Consistent relationships between rates of leaf extension and leaf water status were found only when measurements had been made under a common environment or when the effects of the environmental differences were allowed for by comparing the response of desiccated plants to that of well-watered control plants under the same conditions.

In the early stages of desiccation leaf extension rates were extremely sensitive to reduction in leaf water potential. Water potentials of only 0.20 to 0.30 MPa below that of well-watered control plants were sufficient to depress leaf extension rates by 50%. However, as desiccation became more severe, leaf extension rates became much less responsive to further reductions in leaf water potential.

It is inferred from the results that it will be possible to resolve some of the apparent discrepancies which exist among various reports on the sensitivity of leaf extension rates to desiccation when allowance can be made for the actions of other important influences, such as temperature in this experiment, and when leaf water potential at the site of measurement can be related unequivocally to water potential at the region of elongation.

3.3.2 Introduction

Leaf enlargement is thought to be more sensitive to desiccation than most other physiological processes and can be severely inhibited at relatively high leaf water potentials (see under Review of Literature). For example, leaf water potential at which leaf enlargement was reduced to 50% of well-watered rates was -0.20 MPa in one study of maize (Boyer, 1970a) and -0.40MPa in other (Acevedo *et al.*,1971). Other similar results include: -0.30 MPa for sunflower (Boyer, 1968); -0.20 MPa for soybean (Boyer, 1970a); and -0.40 MPa for potatoes (Gandar, 1975). Such evidence suggests that leaf extension will be inhibited at a relatively high plant water status.

However, there has been some controversy regarding the dependence of leaf extension on high plant water status. Watts (1974) concluded from field measurements of maize that leaf water potentials greater than -0.80 to -0.90 MPa had little effect on leaf extension rate. In controlled environment studies of sorghum, McCree and Davis (1974) found that leaf expansion continued day and night despite a diurnal change of about 0.80 MPa in leaf water potential. Similarly in the field experiment with sudax reported in section 3.1, it was found that peak diurnal rates of leaf extension coincided with a leaf water potential of -1.17 MPa.

The data reported in this section describe the short-term response of leaf extension and leaf water potential to controlled diurnal changes in the environment of prairie grass over an entire soil drying cycle.

3.3.3 Materials and Methods

Prairie grass (*Bromus catharticus* Vahl. c.v. Grasslands Matua -

a perennial pasture species) was grown from seed in 2.3 litres of soil mixture (Opiki peaty loam 70 parts: sand 30 parts by volume) with an air temperature of 22.5/12.5 ± 0.5° C day/night and a 2.0/0.2 kPa air vapour pressure deficit (VPD) day/night (equivalent to relative humidity 26/86 ± 5% day/night). The diurnal change in temperature and VPD occurred gradually over 4 hours immediately inside the day period. Details of diurnal changes are shown in Figure 3.3. The 12 hour photoperiod started at 0900 hour N.Z. Standard time with a photosynthetically active radiation flux of 170 W m^{-2}(0.4 - 0.7 μm waveband from Sylvania "Metal-arc" and Philips tungsten iodide lamps) throughout the day period. The carbon dioxide concentration was uncontrolled.

Plants were fed with modified Hoagland's solution at 200 ml per pot 30 minutes before the dark period. The plants were thinned from 9 to 2 per pot by week 5, selecting for evenness of height and leaf number.

Water was withheld from the soil when the sixth leaf (youngest leaf) was 10-20 mm clear of the preceding leaf sheath (designated day 0). The plants were rewatered on day 10 by standing the pots in a tray of water for 2 hours to fully saturate the soil.

Changes in leaf length (the sum of lamina and sheath extension) were measured over 4 periods for each day during the drying cycle (see figure 3.3 for details). The mean extension rate of the youngest visible leaf and the second youngest visible leaf of the main tiller was used. The rates for the two leaves were within 1.5% of each other. As soon as the next leaf (leaf 7) appeared, leaf 6 became the second youngest leaf and measurements on leaf 5 ceased. The plants remained vegetative

(checked by apical dissections) throughout the duration of the experiment. The leaf extension measurements were made with a ruler placed against the base of the plant using the soil surface as a reference point. Ten replicates were used for the leaf extension measurements.

Leaf water potentials were measured with a pressure chamber (Boyer, 1969) and were taken, where possible, during the middle of each leaf increment measurement period (for details of timing of leaf water potentials and extension measurements relative to diurnal changes in temperature and VPD see Figure 3.3). On a number of occasions leaf water potentials were also taken at 2200 hours. Each leaf water potential measurement was made on the entire exposed portion of the lamina of the second youngest leaf of the main tiller. Up to 5 samples were taken for each sampling period.

3.3.4 Results and Discussion

3.3.4.1 Diurnal trends in leaf water potential and leaf extension during the drying cycle

(i) Leaf water potential

Diurnal changes in leaf water potentials of both well-watered and desiccated plants showed similar patterns until an advanced state of desiccation (Figure 3.4). Recovery of leaf water potential during the last 4 hours of the photoperiod was presumably a response to reducing VPD. Significant differences between leaf water potentials in well-watered and desiccated plants only became apparent 4 days after water was withheld from the latter. Thereafter the differences increased until the end of the experiment.

On day 6 the leaves of a number of plants were visibly wilted by the middle of the day. The leaf water potentials of these plants were all lower than -1.40 MPa. By day 10 the leaf water potentials of the droughted plants had reached -2.10 MPa late in the day, and the leaves were all severely

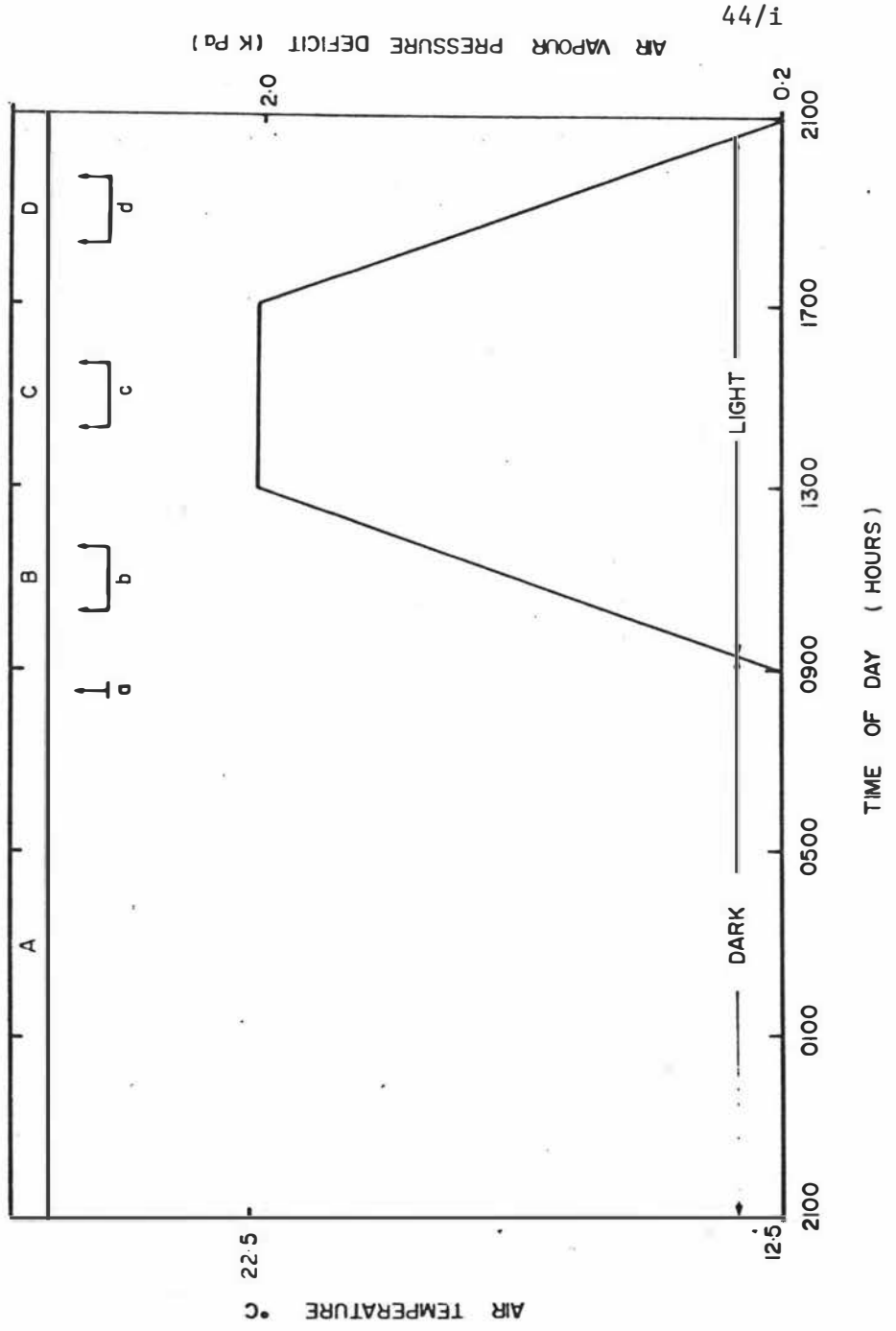


Figure 3.3 Timing of measurements of leaf extension rate (A to D) and ψ_l (a to d) relative to diurnal changes in temperature and air vapour pressure deficit. The leaf length measurements used to compute extension rates were taken at each end of the periods indicated. Leaf water potential measurements were taken during the periods indicated by arrows.

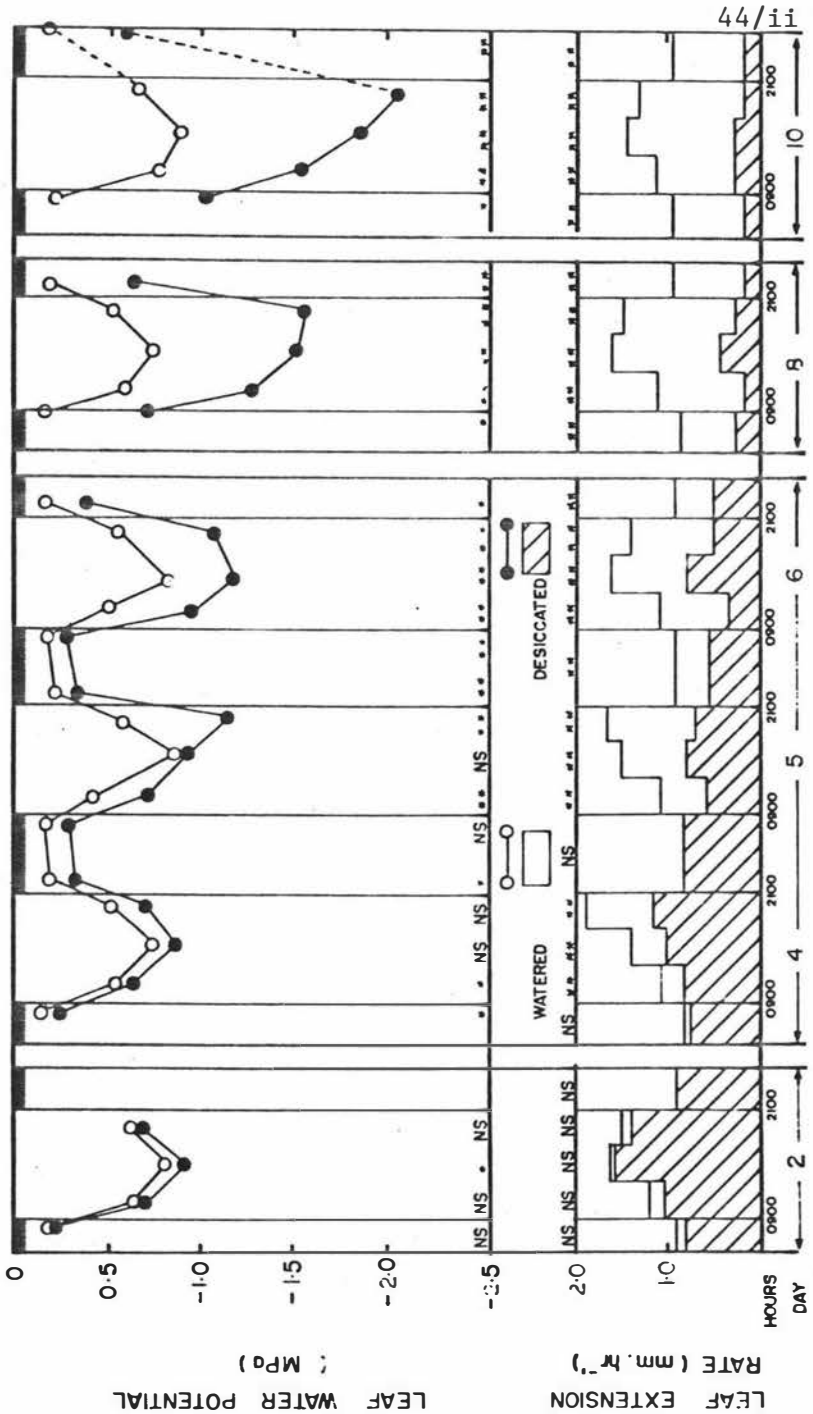


Figure 3.4 Diurnal time course of ψ_l and leaf extension rate for prairie grass during several days of a drying cycle. Statistical significance of differences between treatments are shown for each time period (*P < 0.05; **P< 0.01).

wilted. The droughted plants were rewatered at the end of day 10, 1½ hours prior to darkness. The pre-dawn leaf water potentials of the droughted plants on day 11 showed overnight recovery but was still 0.50 MPa below control plants.

(ii) Leaf extension rates

The rate of daytime leaf extension differed significantly between treatments for the first time also on day 4 when a reduction in extension rate of 23% to 41% occurred (Figure 3.4). Treatment differences in night-time leaf extension rate did not occur until a day later on day 5.

As desiccation proceeded, the afternoon extension rates became more similar to the morning. By day 10 there was little change in rate throughout the 24 hour period. It is notable that from day 5 through to day 8 the morning rate of extension fell below the night-time rate. The reason for this is not clear. One would expect an increase in temperature early in the day to enhance rather than reduce growth. Although VPD is increasing and might decrease growth by causing desiccation, leaf water potential measurements were in fact higher than the last period of the day when elongation was occurring at a faster rate.

The general diurnal pattern of leaf water potential and leaf extension rates is similar to the field experiment of Watts (1974) using maize and that of the sudax experiment (Experiment 1) reported in Figure 3.1.

3.3.4.2 Relationship between leaf water potential and leaf extension rate

In analysing the sensitivity of leaf extension to leaf water potential it is useful to distinguish between relative changes in water status, and absolute changes in water status.

(i) Relative changes in leaf water status

When the performance of desiccated plants is considered relative to well-watered plants measured at the same time the depression in the rate of leaf extension can be seen to follow a similar pattern to the depression in leaf water potential, regardless of absolute leaf water potential (Figure 3.4). For example, on day 6 differences in both leaf water potential and leaf extension rate during the day are relatively stable despite a 1.00 MPa diurnal change in absolute leaf water potential. This can be seen more clearly in Figure 3.5 when the trend in daily leaf extension is shown relative to daily maximum and minimum leaf water potentials over all days of the soil drying cycle. Similar patterns are evident in the field measurements of Gandar (1975), for potatoes and that of the sudax data presented in section 3.1.

(ii) Absolute leaf water status

The relationship between rate of leaf extension and leaf water potential measured at various times of day over the soil drying cycle are shown in Figure 3.6. The pattern is consistent only within each time of day showing an effect of the diurnal changes in temperature and/or VPD (and perhaps light). The difference in response curves B and D (Figure 3.6) could be due to different leaf water potential/time and temperature/time relations over these respective periods which the measurements made in the middle of each period would not reveal. In addition, because these environmental variables were changing simultaneously in this experiment it is not possible to determine what their individual influence was. It does seem likely however that both temperature and VPD were involved.

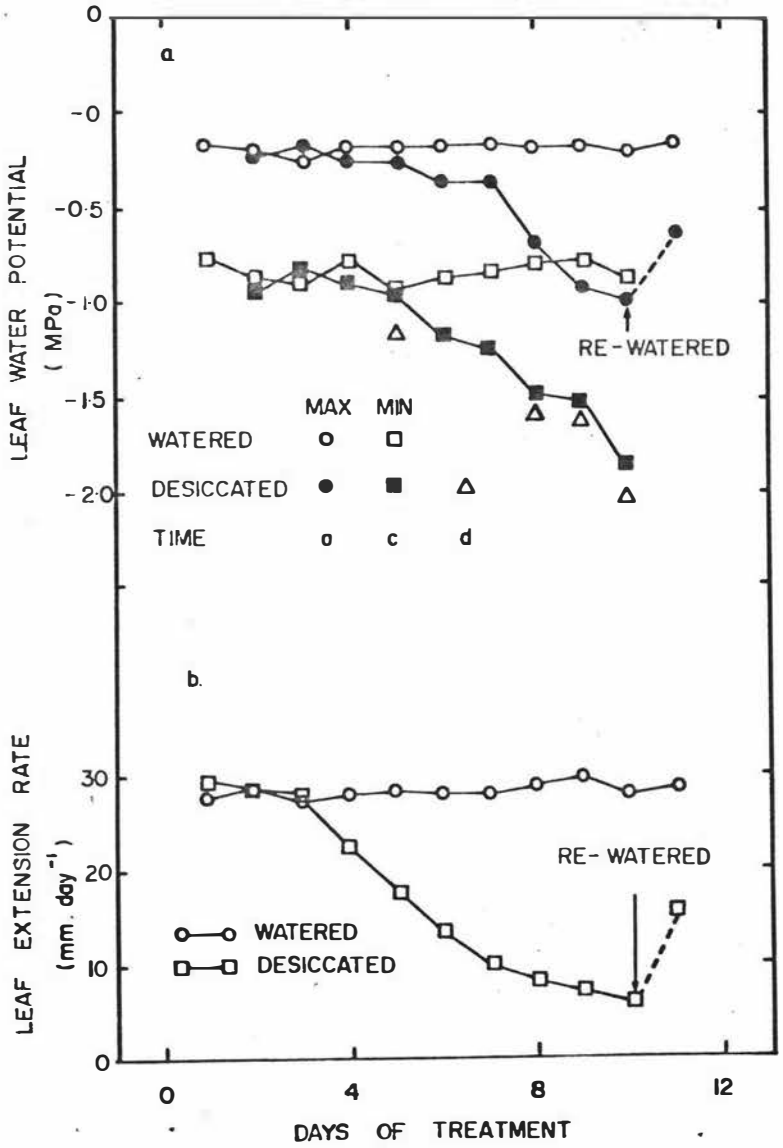


Figure 3.5 Daily maximum and minimum ψ_1 (a) and daily leaf extension rate (b) for prairie grass during a drying cycle. Arrows indicate time of rewatering.

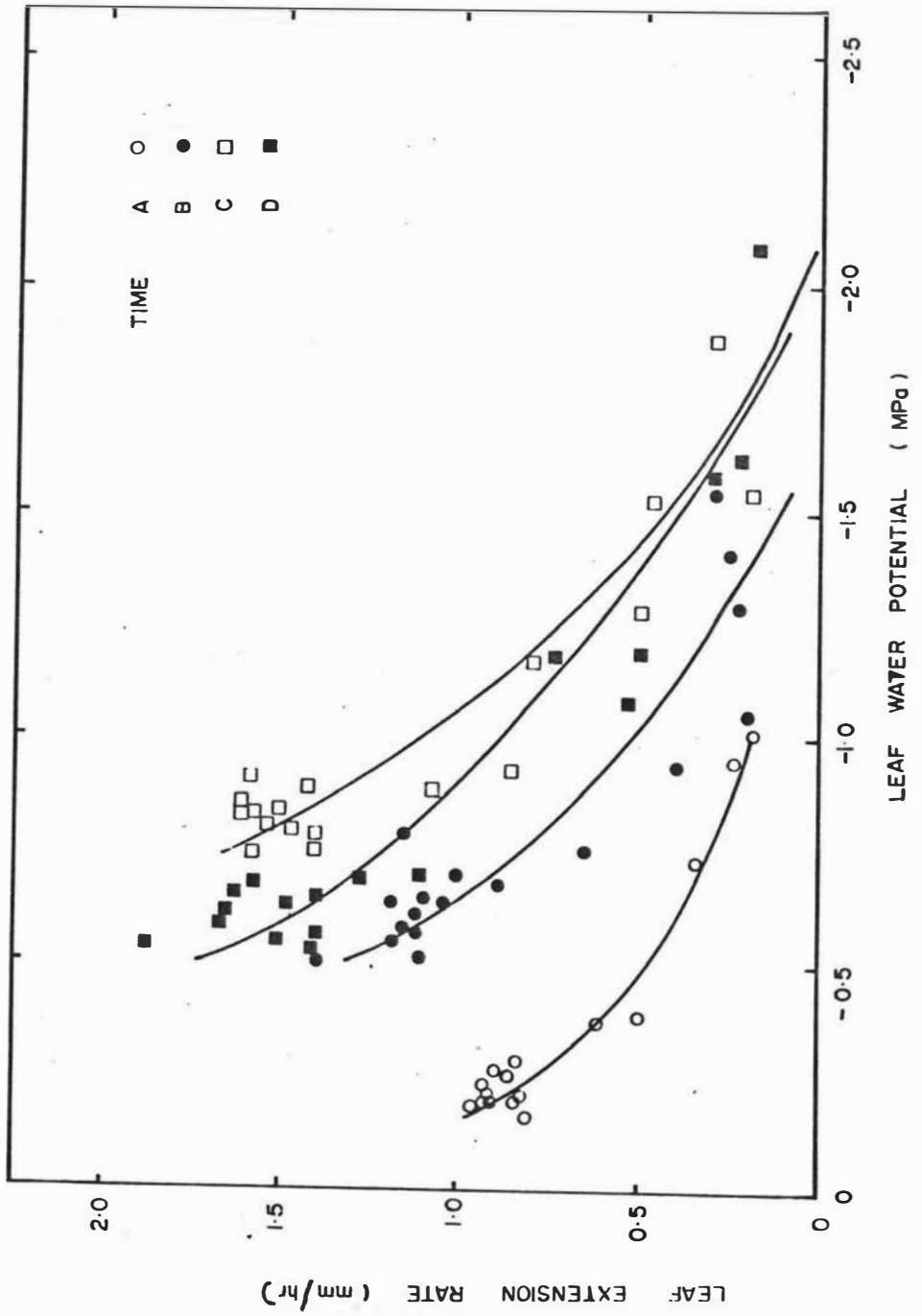
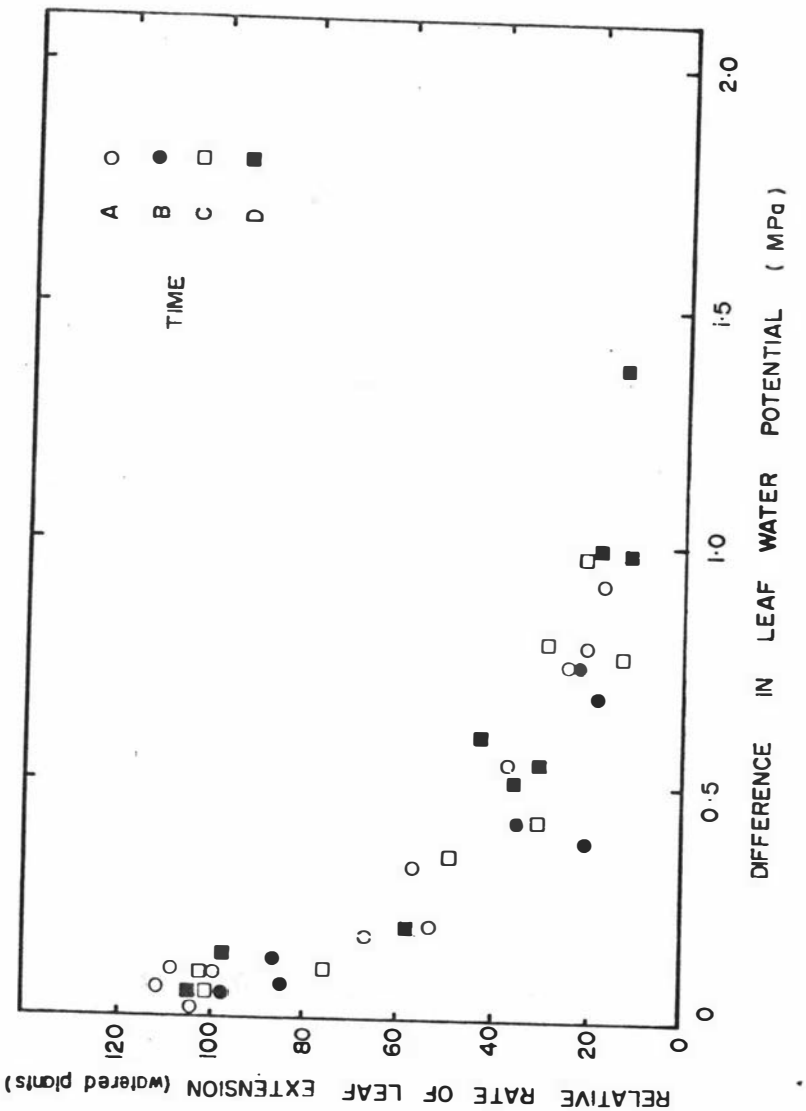


Figure 3.6 Relationship between leaf extension rate and ψ_l at four different times of day during a drying cycle in prairie grass. Curves were fitted using $y = a + b \log_e X$.

The temperature dependence of leaf extension rate has been demonstrated for maize (Kleinendorst and Brouwer, 1970; Watts, 1972, 1974) and ryegrass (Peacock, 1975a, 1975b). Temperature effects on the rate of leaf extension can be large. Watts (1972) for example, measured a Q_{10} of 2 in maize over a 0-30^{o}C range in the temperature of the zone of cell expansion. In the present experiment the diurnal variation on leaf extension rate of well-watered control plants was consistent with such a temperature effect and yield a Q_{10} of 1.6 using soil temperature at 2-4 mm, corresponding to the approximate region where most of the leaf extension was occurring.

Air VPD could affect results by changing transpiration rates which would, in turn, affect gradients in leaf water potential between the site of measurement near the tip of the exposed lamina and the actual site of elongation near the base of the leaf. That significant gradient can exist along leaves is known. Yang and de Jong (1971) measured gradient in leaf water potential of up to 1.90 MPa between the tip and the base of a wheat leaf.

From the above it can be seen that consistent relationshipsbetween leaf extension rates and leaf water potential do exist but only when measurements were made under a common environment (Figure 3.6), or when the effects of environmental differences are allowed for by comparing the response of desiccated plants with those of well-watered control plants under the same conditions. It is interesting to note that normalisation of the results shown in Figure 3.6 produces a single relationship between rates of leaf extension and leaf water potentials (Figure 3.7). In the absence of more complete information this relationship could assist in relating rates of leaf extension and leaf water potentials across different environments. Rates of



Relative to control rates (1.0)

Figure 3.7 Normalised relationships with rates of leaf extension for each time of day expressed relative to the well watered control plants measured at the same time, and with ψ_l expressed as a difference from the ψ_l of the control plants measured at the same time of day.

leaf extension were expressed as a percentage of the mean of well-watered control plants measured at the same time. This has the effect of allowing for any variables such as temperature which may influence absolute growth rates. Leaf water potentials for the desiccated plants at each time of day were expressed as a difference from the leaf water potentials of control plants measured at the same time. In effect a constant equal to the absolute leaf water potential of the control mean for each group was removed from each measurement.

The normalisation procedure would have to be tested with other species and under more diversed conditions in the field before the relationship between leaf water potential and leaf extension can be quantitatively defined.

(iii) Sensitivity of leaf extension rates and degree of desiccation

Whether comparisons are made on an absolute basis (Figure 3.6) or a relative basis (Figure 3.5) it is clear that in the early stages of desiccation leaf extension rates are extremely sensitive to desiccation. For example, on day 4,maximum and minimum leaf water potential of the desiccated treatment were within approximately 0.10 MPa of the control plants but a 20% difference in leaf extension rate was measured (Figure 3.5). By day 6 differences in maximum and minimum leaf water potentials ahd increased to only 0.20 MPa and 0.30 MPa respectively yet the difference in rates of leaf extension was by then 52%.

On the other hand, as desiccation became more severe, rates of leaf extension became much less responsive to further reductions in leaf water potential. Although the plants were continuously wilted by day 10 an average extension rate of 5 mm per day was recorded and this was still 18% of control rates.

Published data in general show a similar pattern of high, then declining sensitivity of leaf extension rates to progressive reduction in leaf water potential (e.g., for glasshouse grown *Lolium perenne*, Lawlor, 1972; and controlled environment grown maize, Watts, 1974). The implications of this for crop management are that relatively small differences in leaf water potential at early stages of desiccation are likely to have large effects on leaf growth, whereas in an already desiccated crop leaf growth will be relatively insensitive to further change in water potential.

The results show that the relationship between leaf elongation rate and measured leaf water potential is not unique but can vary dramatically within one group of plants over short periods depending on environmental conditions. It is inferred from the results that it will be possible to resolve some of the apparent discrepancies which exist among various reports on the sensitivity of leaf extension to desiccation when allowance can be made for the action of other influences, such as temperature, and when leaf water potential at the site of measurement can be related unequivocally to water potential at the site of elongation.

3.4 EXPERIMENT 3 - SENSITIVITY TO WATER DEFICIT OF LEAF EXTENSION IN TWO RYEGRASS CULTIVARS UNDER DIFFERENT TEMPERATURE REGIMES.

3.4.1 Abstract

The relationship between leaf water potentials and leaf extension rates for Nui and Ruanui ryegrass under a high (H) (27.5°/12.5°C, day/night) and a low (L) (17.5°/12.5°C) temperature regime were compared.

The diurnal time course of leaf water potential and leaf extension rate responses were similar to that reported for prairie grass under a 22.5°/12.5°C, day/night temperature (section 3.3). The strong influence of temperature on leaf extension rate was again evident.

Under the H temperature regime well watered Nui had a 20% higher leaf extension rate than Ruanui, however over a period of 7 days, this difference was not apparent under the L temperature regime.

There was no difference in the relationship between leaf water potential and leaf extension rate for the two ryegrass cultivars under different temperatures. The normalisation procedure suggested in section 3.3 was more suitable for the data collected under the H temperature regime. Under the L temperature conditions the data did not follow a single relationship upon normalisation.

3.4.2 Introduction

The relationship between leaf water potential and leaf extension rate in prairie grass was discussed in section 3.3. The results

showed an initially high, then declining sensitivity of leaf extension rate to progressive reduction in leaf water potential. However this relationship was not unique but varied according to the environmental conditions. In section 3.3.4.2, a method to normalise the data was suggested. The normalization was intended to allow for less ambiguous comparison between the relationship between leaf water potential and leaf extension rate taken from different environments. As suggested in section 3.3.4.2 other species and environmental conditions should also be tested before such a procedure can be adopted.

Because of the importance of perennial ryegrass to New Zealand's agriculture, two cultivars of ryegrass (Grasslands Nui and Grasslands Ruanui) were selected as the experimental plants. One of the cultivars (Nui) has been reported to outyield a number of other ryegrass cultivars, including Ruanui, under the summer and autumn conditions in New Zealand (Rumbell, 1969; Baars *et al.*, 1976; Sheath *et al.*, 1976).

The data reported in the present section were part of another experiment designed to investigate the physiological and plant growth parameters which might reflect drought tolerance/avoidance differences between the 2 ryegrass cultivars. The comparison was also made under two temperature regimes because it was thought that the reported superiority of Nui over that of Ruanui could be related to a temperature response.

In the present section only the leaf water potential and leaf extension rate data of these two cultivars are presented. The physiological parameters (viz stomatal resistance, transpiration rate and relative leaf water content) have been summarised and presented in Appendix 3.

The plant growth parameters such as tiller number, leaf number, leaf area and dry weights are presented in section 4.3.4.

3.4.3 Materials and Methods

Two cultivars of ryegrass (*Lolium perenne* L. c.v. Grasslands Nui and Ruanui) were sown in 2.3 litre of soil mixture (Manawatu silt loam 50% and river sand 50% by volume) in controlled climate rooms.

There were two air temperature treatments: $27.5^{o}/12.5^{o}C \pm 0.5^{o}C$ (day/night) designated as high (H) temperature and $17.5^{o}/12.5^{o} \pm 0.5^{o}C$, designated as low (L) temperature treatments. The air vapour pressure deficit (VPD) was 0.7/0.2 kPa (day/night) for both treatments, equivalent humidity of 80.8/86.2 ± 5% and 64.9/86.2 ± 5% for the H and L temperature regimes respectively. The diurnal changes in temperature and VPD occurred gradually over 4 hours immediately inside the day period. The 12 hour photoperiod started at 0900 hour N.Z. standard time (NZST, the times in hours referred to in this section are all NZST), with a photosynthetically active radiation flux of 170 W/m^2 (0.4 - 0.7 μm wave band from Sylvania "metal arc" and Philip tungsten iodide lamps) throughout the photoperiod. Carbondioxide concentration was uncontrolled.

Plants were fed with modified Hoagland's solution at 200 ml per pot per day 30 minutes before the dark period. The plants were thinned from 15 to 6 per pot by week 4 and 3 by week 5. Selection was based on evenness of height and leaf number.

Soil desiccation treatment started when the sixth leaf (youngest leaf) was about 20-30 mm clear of the preceding leaf sheath and the time designated as day 0. Desiccation treatment consisted of withholding

water from the soil until the mean daily leaf extension rate of the youngest leaf had ceased for 24 hours. Control treatment consisted of plants watered daily with 200 ml of nutrient solution per day. For each treatment (i.e. 2 cultivars and 2 soil moisture treatments) 4 plants were tagged and used for leaf extension rate measurements.

Changes in leaf length (sum of lamina and sheath extension) were recorded 4 times per day at 0900, 1300, 1700 and 2100 hours. The leaf extension rates were made with a ruler placed against the base of the plant using the soil surface as a reference point and measured to the tip of each leaf. Measurements of each leaf started when it first appeared and continued until the ligule appeared.

Leaf water potentials were measured with a pressure chamber (Boyer 1969). Samples for leaf water potentials were taken from the entire lamina of the youngest mature leaf. Up to 6 samples were taken for each treatment per sampling time. Leaf water potential measurements were taken at 0830, 1100, 1500, 1900 and 2200 hours. Details of the timing of leaf extension rate and leaf water potential measurements relative to the diurnal changes in temperature and VPD was similar to the experiment on prairie grass (Figure 3.3) however the values of air temperature and VPD were different.

3.4.4 Results and Discussion

3.4.4.1 Diurnal pattern of leaf extension rate and leaf water potential

The diurnal time course of leaf extension rate for the 2 temperature regimes are presented in Figure 3.8a and b. Although there was no consistent pattern, especially at the lower temperature (L)

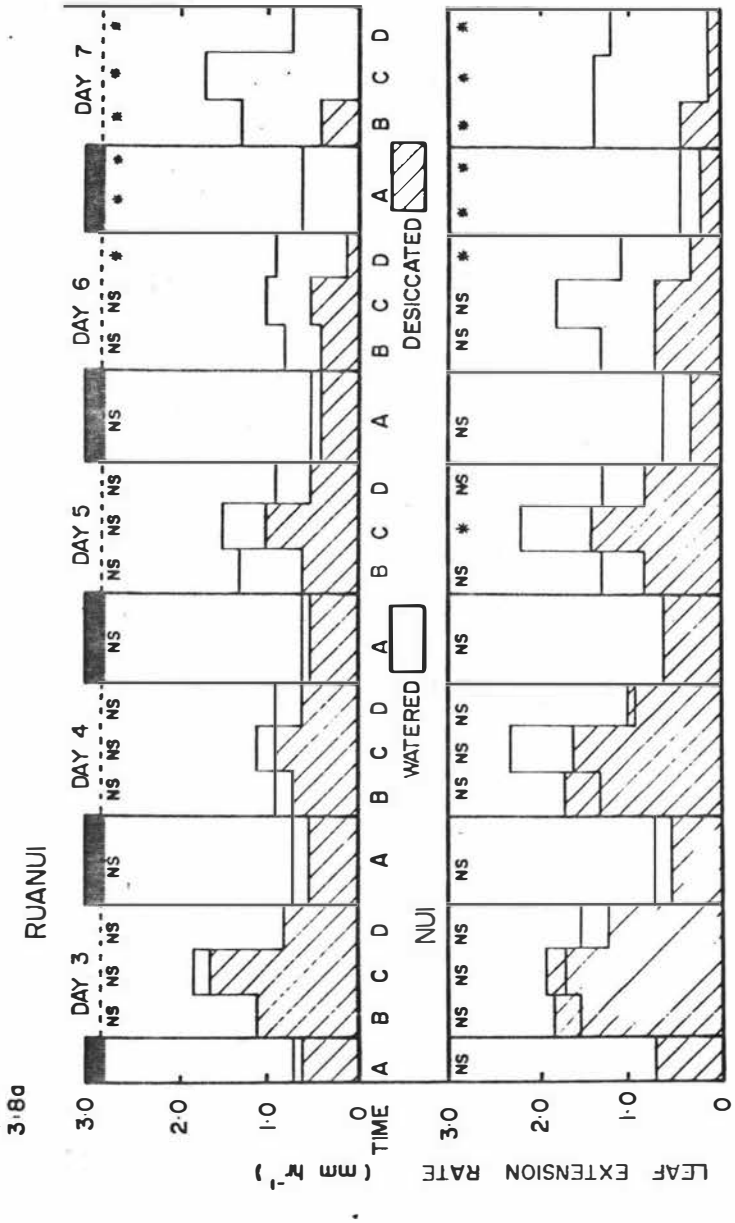


Figure 3.8 Diurnal time course of leaf extension rate (LER) for Ruanui and Nui ryegrasses during several days of a drying cycle.
(a) under high temperature regimes (27.5°/12.5°C)

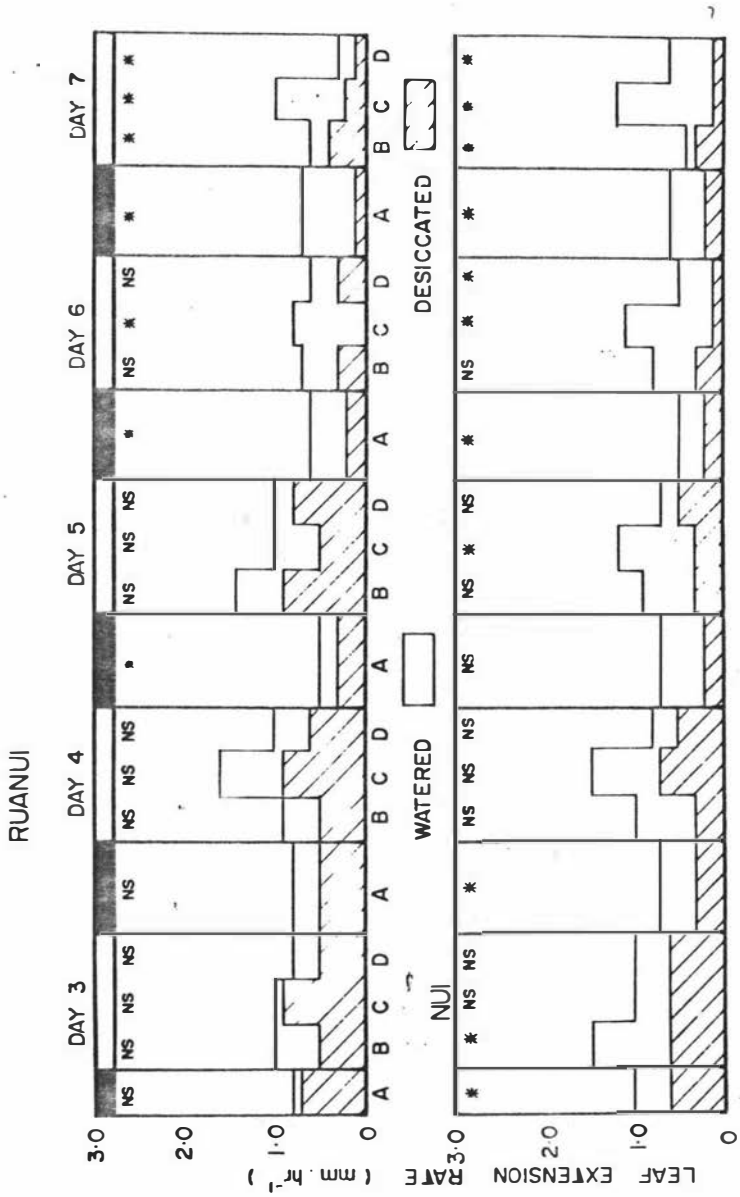


Figure 3.8 Diurnal time course of leaf extension rate (LER) for Ruanui and Nui ryegrasses during several days of a drying cycle.

(b) under low temperature regime ($17.5^{o}/12.5^{o}C$).

(Figure 3.8b), generally speaking during Time C (maximum temperature) leaf extension rate in the well-watered control plants for both cultivars tended to be highest and for Time A (minimum temperature) leaf extension rate was the lowest. The uneven nature of the diurnal leaf extension rate in the control plants could be due to the technique used in recording leaf extension. Normally, in ryegrass when a leaf emerges, leaf extension will reach its highest rate and will be followed by a fairly steady rate, over a period of about 3 to 4 days, before a rapid decline when the ligule emerges (Wardlaw, 1969). In this experiment leaf extension rate was measured on leaf 6 on day 0 and by day 7 it would have become necessary to transfer the measurement to leaf 7. The changing over from leaf 6 to leaf 7 could account for this "noise".

Although by and large, control rates were higher than the stress rates from day 3 onwards in L treatment and from day 4 onwards in H treatment, statistically significant differences between the water deficit treatments were not consistent. This was due mainly to the small number of replicates used and also to the fact that there were greater between replicate variations varying, for example, from 10 to 32 mm per day even for control rates in Ruanui. That ryegrass leaf extension growth is far less uniform than Grasslands Matua prairie grass has also been noticed by Rumball (Pers. Comm.).

The diurnal time course of leaf water potential is presented in Figure 3.9 a and b. The overall pattern of leaf water potential response was similar to that of prairie grass reported in section 3.3 (Figure 3.4). Minimum values for leaf water potentials in the well-watered control plants were normally reached when both temperature and VPD were highest (i.e., Time C) and the maximum leaf water potential of about -0.20 MPa occurred only during the dark period (i.e., Time A).

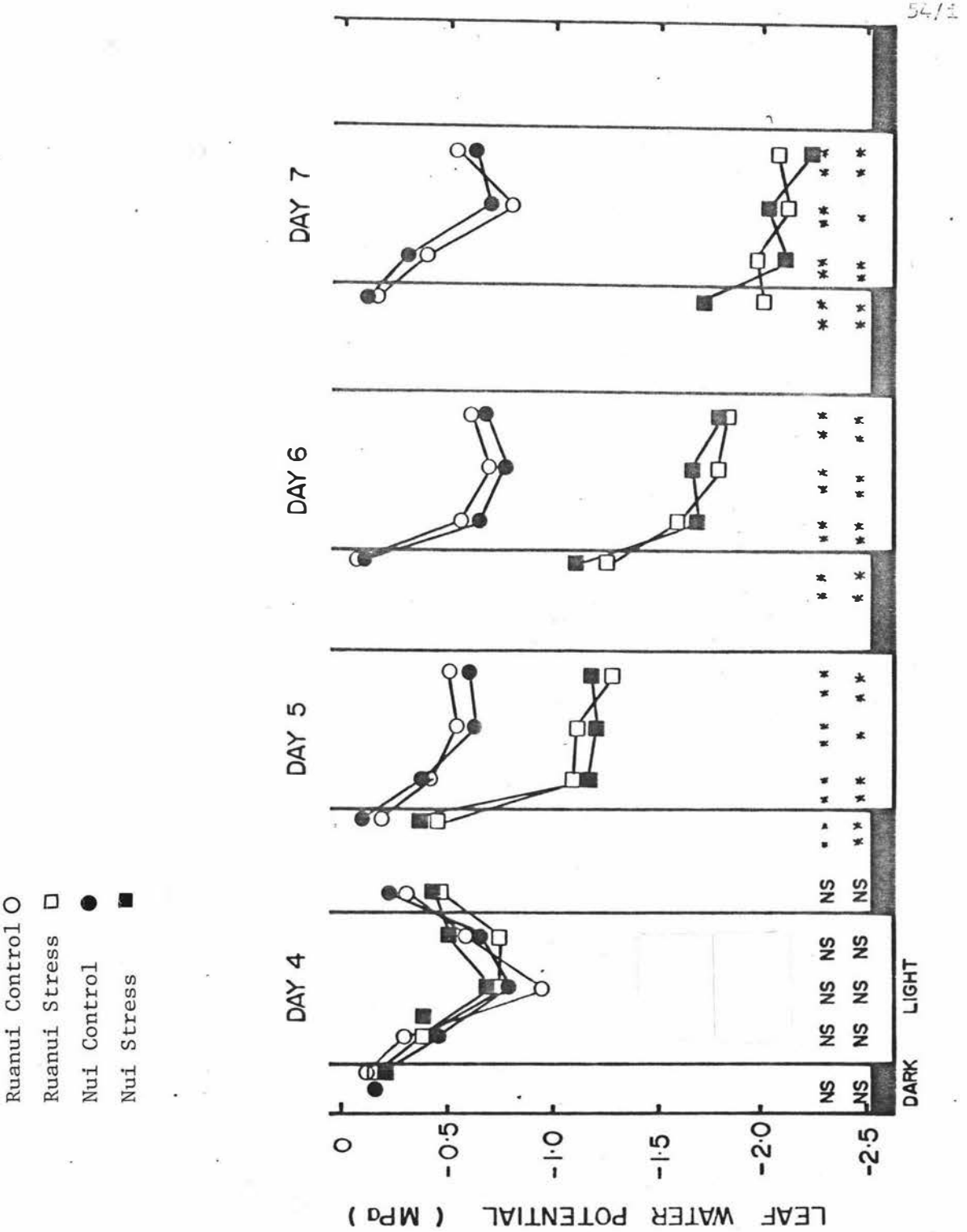


Figure 3.9 Diurnal time course of leaf water potential for Ruanui and Nui ryegrass during several days of a drying cycle.

(a) under high temperature regime (27.5°/12.5°C)

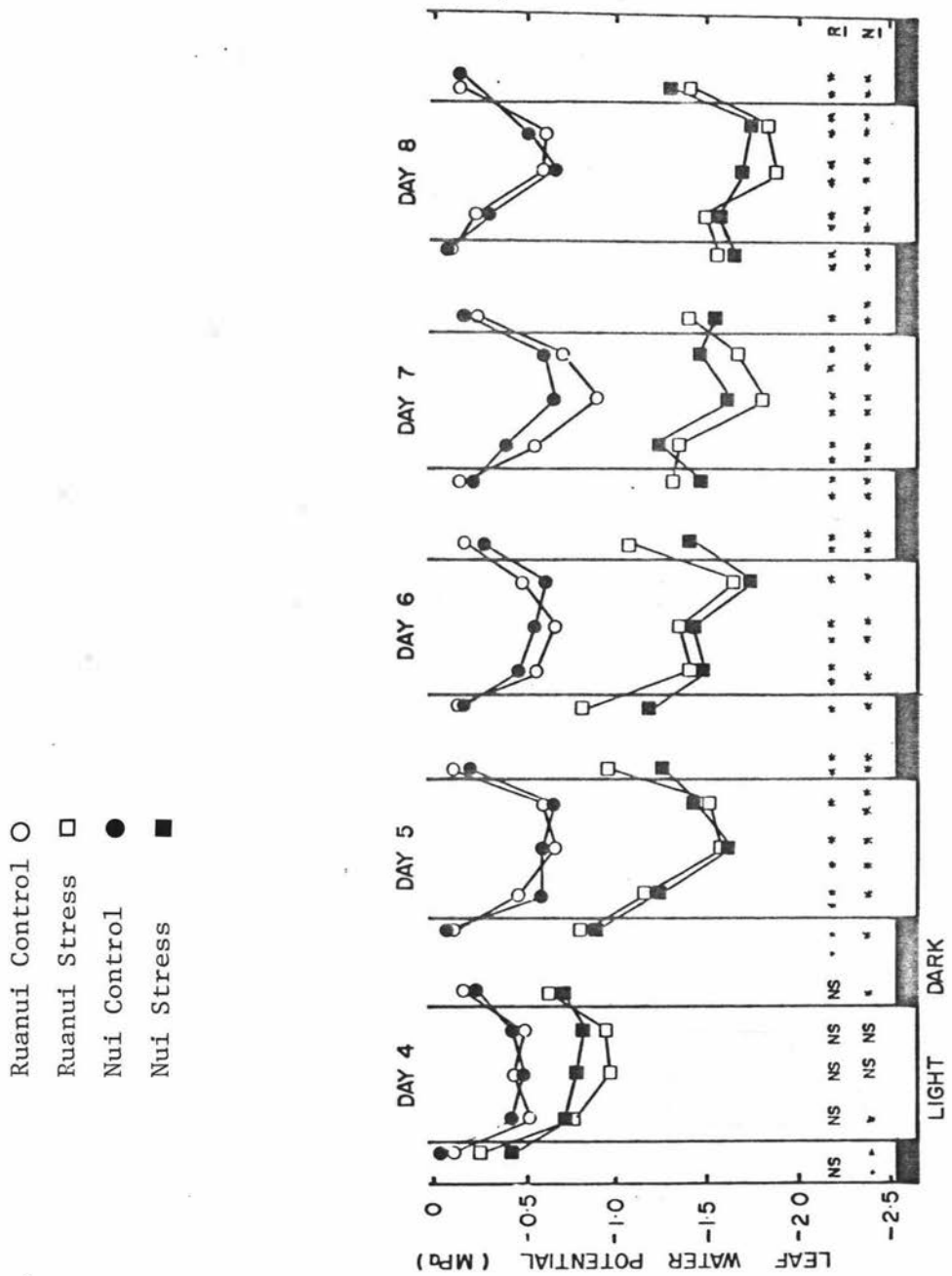


Figure 3.9 Diurnal time course of leaf water potential for Ruanui and Nui ryegrass during several days of a drying cycle.

(b) under low temperature regime (17.5°/12.5°C)

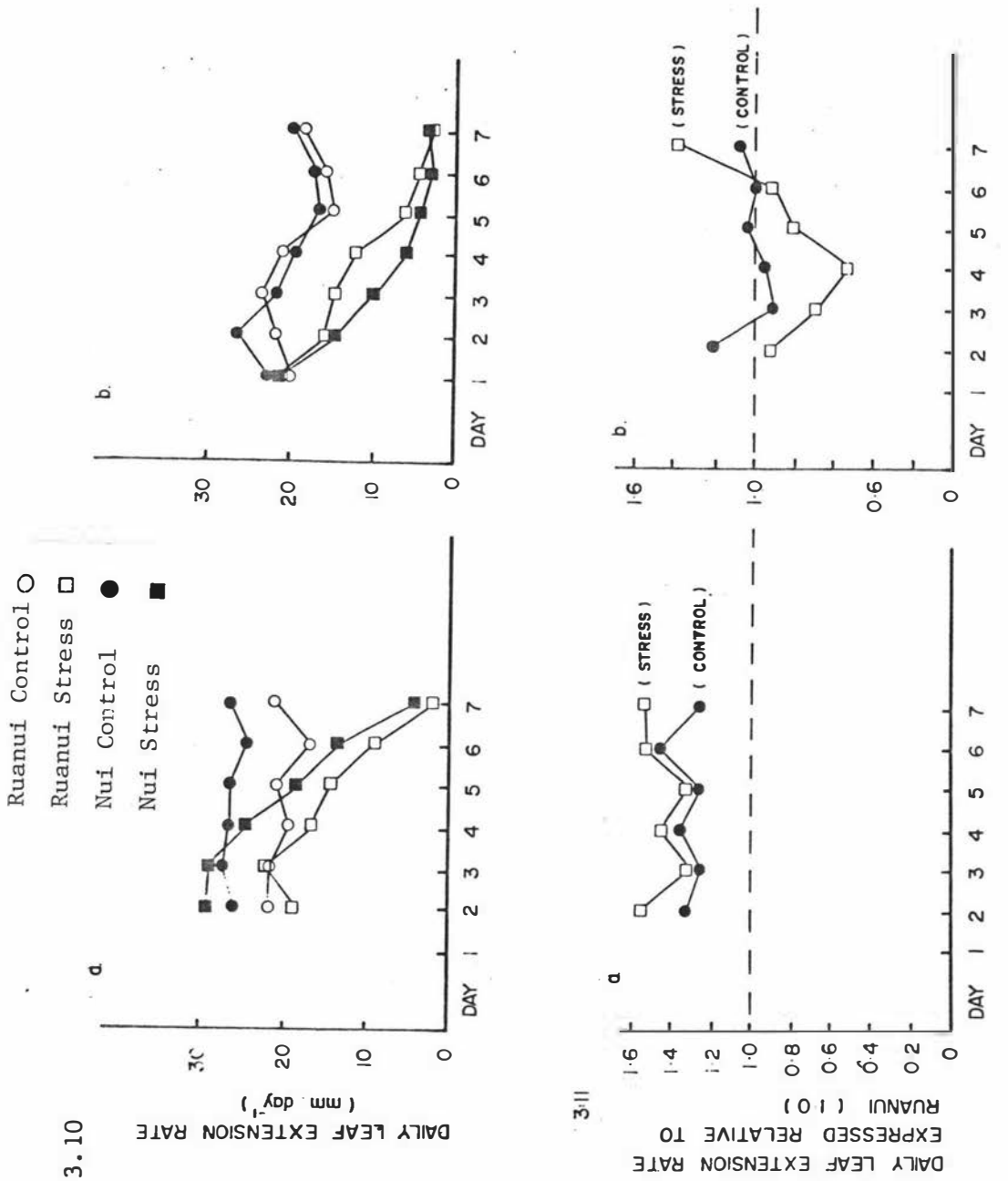
By and large, significant differences between well-watered control and stress treatments became consistent after day 5 in both temperature regimes.

Although differences between control and stress reached 0.20 - 0.30 MPa on day 4 in the low temperature regime (Figure 3.9b), most of these were not significant because of large between sample variations.

Under severe desiccation conditions, as was the case from day 6 onwards, stomata were closed (Appendix 3.1) and transpiration rates were much reduced (Appendix 3.2). The reduced transpiration rate could cause an increase in leaf temperature. Although the closing of stomata can be considered as a means of reducing water lost through higher stomatal resistance the increase in leaf temperature may offset the increased stomatal resistance (Cowan and Troughton, 1971). The extent to which plants can prevent further water losses under high temperature conditions is not clear. When Figure 3.9 (a) was compared with Figure 3.9 (b) an apparent effect due to temperature was evident after day 6.

3.4.4.2 Mean daily leaf extension rate

Figure 3.10 a and b present the mean (24 hour) leaf extension rates for the two cultivars under the two temperature regimes over the first 7 days. It was clear that the higher (approximately 20%, $P < 0.05$) leaf extension rate of Nui was only evident under the higher temperature treatment. Furthermore, this advantage in leaf extension rate was maintained under desiccation (Figure 3.11a). Whereas under the lower temperature regime (Figure 3.11b) the leaf extension rate of Ruanui was similar to that of the higher temperature at about 20 mm per day, and that of Nui was similar to Ruanui. These values were



3.10

3.11

Figure 3.10 Mean daily leaf extension rates for Ruanui and Nui ryegrasses during a drying cycle.

(a) under high temperature (27.5°/12.5°C)

(b) under low temperature (17.5°/12.5°C)

Figure 3.11 Mean daily leaf extension rate of Nui expressed relative to Ruanui (1.0) during a drying cycle.

(a) under high temperature (27.5°/12.5°C)

(b) under low temperature (17.5°/12.5°C)

the average of 7 days. As will be discussed later, when averaged over 26 days (section 4.3.4.2) Nui had a 27% greater leaf extension rate under the H and 13% greater under the L temperature regimes than Ruanui.

3.4.4.3 The relationship between leaf water potential and leaf extension rate

The relationship between leaf water potential and leaf extension rate for the 4 time periods was scattered and the pattern was very similar to that of the unadjusted prairie grass data (Figure 3.6). The normalisation procedure as suggested was used to adjust the data set from this experiment, and the normalised values were presented in Figure 3.12 a and b. Normalisation had only improved the data from the high temperature regime (Figure 3.12a). In the case of ryegrass the relationship between leaf water potential and leaf extension rate was more linear than the relationship reported for prairie grass. In the low temperature regime the relationship was far from consistent. This was mainly due to the responses of the diurnal leaf extension rate under the lower temperature conditions (Figure 3.8b). The small maximum-minimum temperature difference ($5^{o}C$) for the L treatment could be the reason for the inconsistent pattern of leaf extension rate response. It seems, at least from the results of this experiment, the normalisation procedure suggested earlier is more suitable when leaf extension rate in desiccated plants is proportional to the well-watered control rate. It also emphasises the importance of temperature in influencing leaf extension rates.

There were marked differences between prairie grass and ryegrass in the leaf water potential at which 50% depression of leaf extension rates occurred. Leaf extension rate in prairie grass fell to 50% of control rates when leaf water potential fell to approximately -0.25 MPa lower than the control

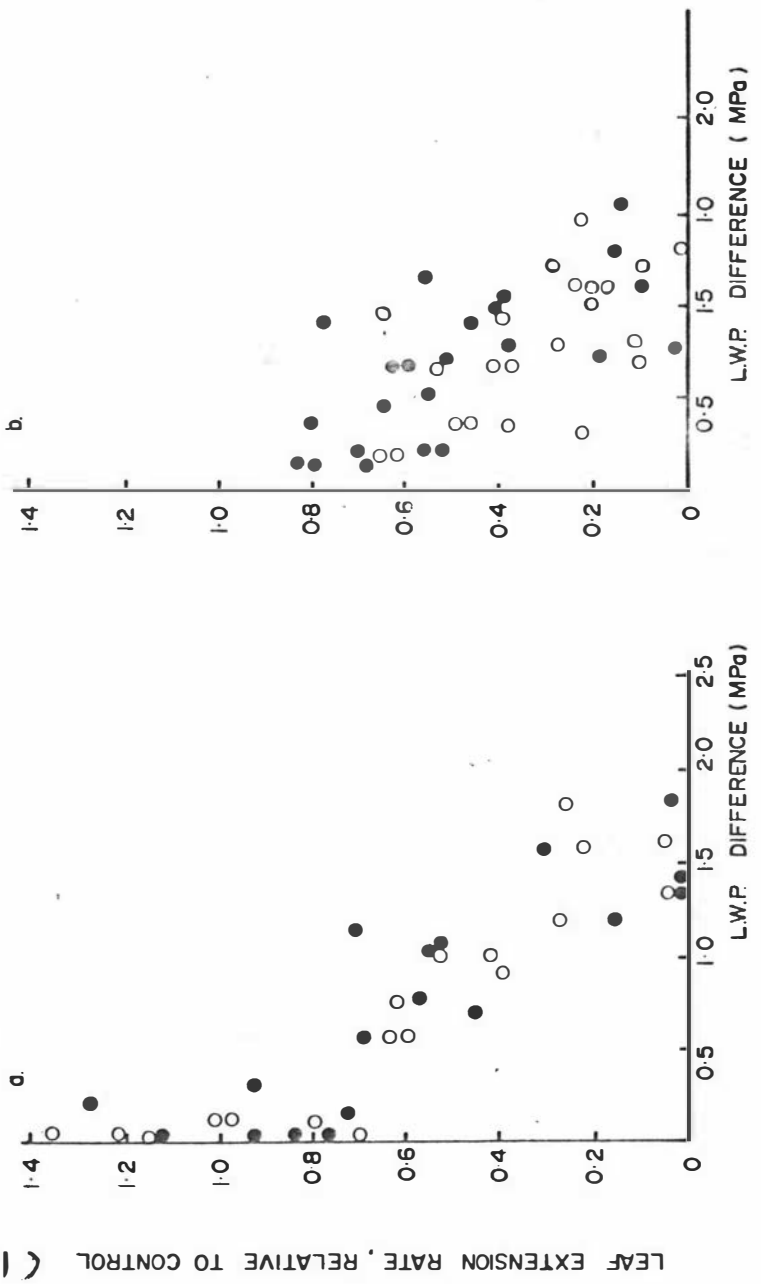


Figure 3.12 Normalised relationships with rates of leaf extension for each time of day expressed relative to the well watered conrol plants measured at the same time, and with ψ_l expressed as a difference from the ψ_l of the control plants measured at the same time of day, for Ruanui (o) and Nui (●).

(a) under high temperature regime (27.5°/12.5°C)

(b) under low temperature regime (17.5°/12.5°C)

TABLE 3.1 Comparison of regressions between leaf water potential (LWP) and leaf extension rates (LER) for two ryegrass cultivars under different temperature regimes.

$y = a + b \log_e X$, where y = LER (mm/day)

x = LWP (bars)

Temperature regime	Cultivars	Regression Equation	R^2
H (27.5°/12.5°C)	Nui	$y = 4.93 - 1.54 \log_e X$	0.80
	Ruanui	$y = 3.75 - 1.14 \log_e X$	0.67
L (17.5°/12.5°C)	Nui	$y = 3.08 - 1.01 \log_e X$	0.67
	Ruanui	$y = 2.85 - 0.91 \log_e X$	0.73

(Units of LWP in bars, 10 bars = 1 MPa)

F test between cultivars (F test according to Snedecor and Cochran, 1968: see Appendix 4.1 for details) (d.f.: 1 : 24).

for slope H temp F = 1.57 NS

L temp F = 0.15 NS

for elevation (constant)

H temp F = 7.90*

L temp F = 0.02 NS

(* = P <0.05)

values (Figure 3.7), whereas the 50% leaf extension rate in ryegrass occurred when leaf water potential of the desiccated plants was approximately -0.70 MPa lower than the control values (Figure 3.12a). This indicated that the leaf extension rate - leaf water potential relationship was not unique but varied with 'time' (Figure 3.6) as well as with species. On the evidence presented here, one is tempted to speculate that ryegrass leaf extension rate is less sensitive to increasing water deficits than prairie grass. The extent to which leaf water potential can be different between these 2 species at the stem base or nearer to the actual zone of leaf extension is not known.

To compare the two ryegrass cultivars, only the leaf water potential and leaf extension rate values collected during Time C are presented in Figure 3.13 a and b. Regression equations ($Y = a + b \log_e X$) were fitted through the data sets and these are shown in Table 3.1. Although no significant difference was detected between the slopes of the regression lines for the two cultivars under both temperature regimes, a significant ($P < 0.05$) difference was detected for the constant (a) between Nui and Ruanui ryegrass cultivars under the higher temperature regime. This again reflected a temperature response by Nui under the H treatment.

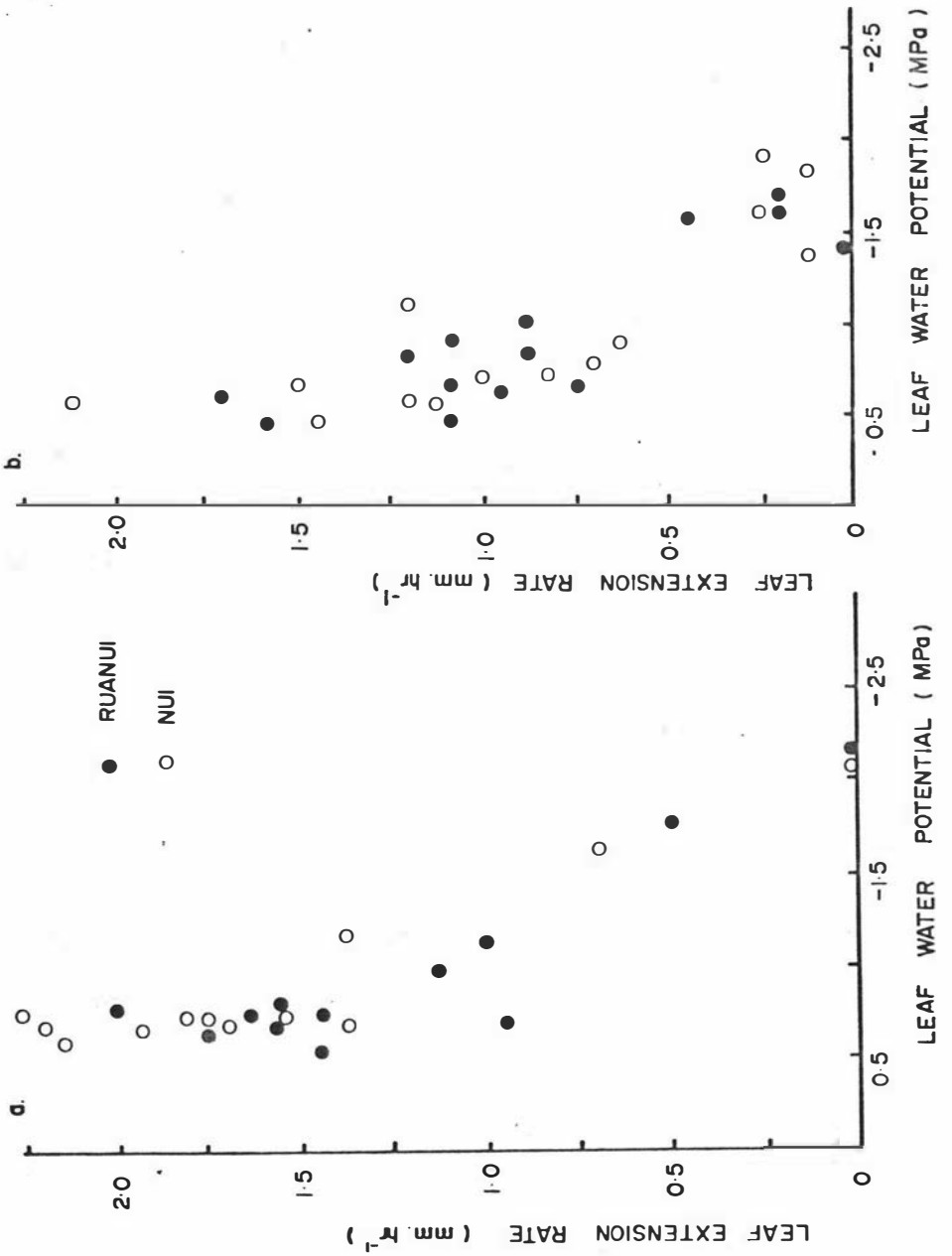


Figure 3.13 The relationship between leaf water potential (ψ_l) and leaf extension rate (LER) measured at time C for Ruanui (o) and Nui (●) ryegrass during a drying cycle.

(a) under high temperature regime (27.5°/12.5°C)

(b) under low temperature regime (17.5°/12.5°C)

CHAPTER IV

THE EFFECTS OF WATER DEFICIT ON SUBSEQUENT RECOVERY GROWTH IN PASTURE GRASSES

4.1 INTRODUCTION

The rapid formation of new leaf tissue is desirable in pasture grasses both to maximise the amount of light energy trapped by the canopy for dry matter production (Brougham, 1956; Watson, 1956) and because the leaf tissue itself constitutes the economic yield. The rate of growth of leaf and tiller during the period of drought and also the speed of their recovery will influence the productivity and perenniality of pastures.

Little appears to be known about the recovery of leaf growth following rewatering on the subsequent plant performance, even though physiological evidence indicates that relatively small reductions in leaf water status can have substantial effects on leaf growth (Boyer, 1968, 1970a; Hsiao, 1973; Experiment 2 and Experiment 3 of this study). The rate and amount of tillering is generally reduced under water stress (Langer, 1963) but again little is known about the rates of tiller recovery after the water status returns to normal.

A knowledge of the responses of leaf and tiller recovery growth following different durations of water deficit may help towards a better understanding in grassland productivity under dryland situations. Furthermore, this information may also be useful in any irrigation-pasture growth model, where at present, recovery growth after a period of water deficit is often assumed to return immediately to well-watered rates.

(Wright and Baars, 1975).

In the following two sections of this Chapter, the effects of water deficit on the rates of recovery in leaf emergence, leaf extension, tiller number, leaf number, leaf area and plant dry weights, in two pasture grasses, are presented. Section 4.2 (Experiment 4) has been submitted as a paper (Chu *et al.*, 1979).

4.2 EXPERIMENT 4 - RECOVERY GROWTH FOLLOWING WATER DEFICITS OF DIFFERENT DURATION IN PRAIRIE GRASS

4.2.1 Abstract

The recovery of rates of leaf emergence, leaf extension, tiller number, leaf number, leaf area and shoot dry weight per plant following water deficits lasting for between 10 and 28 days was measured in prairie grass *(Bromus catharticus)* in a controlled environment.

The rate of leaf extension recovered to the rate of control plants within 4-6 days of rewatering. Rates in rewatered plants then exceeded control plants for up to 28 days. During this time 4 or 5 new leaves emerged. The maximum rate of leaf extension for individual leaves during recovery was up to 20% higher than rates typical for leaves of the same insertion on well watered control plants.

Similarly elevated rates occurred during the recovery phase for several other components of yield. After rewatering, following the 28 day water deficit, the rate of increase in tiller number, leaf number, and leaf area per plant was greater than control rates by up to 38%, 48% and 51% respectively. Rates for these components of yield then normalised 20 days after rewatering.

There was no comparable response upon relief from desiccation in the case of rate of shoot dry matter accumulation. Final shoot dry weight was approximately proportional to the number of "non-drought" days which was defined as those days on which the leaves showed no sign of wilting. This also corresponded to day time leaf water potentials higher (less negative) than -1.40 MPa.

4.2.2 Introduction

There are suggestions that during the period when leaf area is important in determining growth rates e.g., in newly sown or recently defoliated pasture, the reduction in the rate of leaf area expansion due to water deficit can adversely affect green herbage dry matter yield (Hsiao, 1973). Since leaf extension in grasses can be affected by relatively low levels of water deficit, the question is whether there is a critical duration of suspension in leaf extension growth during which the ability of the plant to recover is affected, i.e. whether there is a positive or negative carryover effect due to the suspension of leaf extension growth.

Growth rates higher than well-watered control rates have been reported in desiccated plants upon rewatering, for example in tomato by Gates (1955a, 1966b), in sugar beet by Owen and Watson (1956) and in tobacco by Hopkinson (1968). However the extent to which the effect of duration of water deficit have on the ability of pasture grasses to recover, and whether there is true compensatory growth, is largely unknown.

This section reports the effects of different durations of water deficit on the recovery rates of leaf emergence, leaf extension, tiller number, leaf number, leaf area and dry weight per plant in prairie grass.

4.2.3 Materials and Methods

Prairie grass (*Bromus catharticus* Vahl, c.v. Grasslands Matua - a perennial pasture grass) was grown from seed under controlled environmental conditions. The air temperature was $22.5^{o}/12.5^{o} \pm 0.5^{o}C$ day/night, with a 2.0/0.2 kPa air vapour pressure deficit (VPD) day/night (equivalent to

relative humidity 26/86 ± 5% day/night). The diurnal change in temperature and VPD was programmed to occur at a constant rate of change over 4 hours immediately inside the day period. The photosynthetically active radiation flux density was 170 W/m^2(0.4 - 0.7 μm waveband from Sylvanis "metal-arc" and Philip tungsten iodide lamps) throughout a 12 hour photoperiod. The carbon dioxide concentration was uncontrolled.

The seeds were sown into 2.3 litre pots with a mixture of Opiki peaty loam (70% by volume) and sand (30%). The plants were thinned from 9 to 2 per pot by week 5, selecting for evenness of height and leaf number. During the experiment plants were watered with modified Hoaglands solution at 200 ml per pot per day, 30 minutes before the beginning of dark period.

Treatment started when the sixth leaf (youngest leaf) was 10-20mm clear of the preceding leaf sheath, this was designated as day 0. Treatments will be referred to in the following manner:

Control (C) plants watered daily, 200 ml per pot.

Stress 1 (S1) water deficit was imposed by withholding water from the soil until day 10, when mean daily leaf extension rate reached approximately 20% of the control rates. Rewatering was done by standing the pots in a tray of water for 2 hours to saturate the soil fully. Thereafter, watering was continued as for control plants.

Stress 2 (S2) water withheld as in S1, but the leaf extension rate was maintained at less than 20% of control for 9 days by giving 10 ml of water per day injected through a funnel which had the spout buried 3 cm into the soil. The procedure of rewatering on day 19 was similar to that of S1.

Stress 3 (S3) water withheld and low leaf extension rate maintained as in S2 for 18 days. Rewatering on day 28 was similar to S1.

A low level of desiccation was maintained and was just sufficient to reduce leaf area expansion to a very low rate relative to the control without causing excessive leaf senescence.

Ten replicate plants were used for the leaf emergence and leaf extension measurements. The same plants were used for these measurements throughout the duration of the experiment.

A leaf was counted as "emerged" when it could first be seen projecting beyond the preceding leaf sheath. Each leaf on the main tiller was tagged with a coloured wire loop and the number of leaves on the main tiller was counted daily.

Changes in leaf length (lamina and sheath) were recorded daily, this was measured with a ruler placed against the base of the plant using the soil surface as a reference point.

Both the youngest and the second youngest leaves were measured. As soon as the next leaf (e.g. leaf 7) appeared, leaf 6 became the second youngest leaf and measurement on leaf 5 ceased 24 hours later. The mean extension rate of the youngest and second youngest leaves were within $\pm$ 1.5% of each other.

Five replicates were used for the destructive harvests which were made on days 0, 10, 19, 28, 38 and 47, where days 10, 19 and 28 represented the end of desiccation for S1, S2 and S3 respectively.

Within each replicate the treatments were arranged at random on the trollies, but with at least 10 cm between pots after day 28 to minimise shading. There were 2 plants per replicate, hence treatment means were the means of 10 plants.

At harvest, plants were cut below the crown without breaking the tillers. The tiller and leaf number per plant were counted. The laminae were separated from the sheath and the immature leaves cut at the ligule of the youngest mature leaf. The sheath category therefore included all unexposed immature leaf tissue. Laminae area were measured with an electronic leaf area meter. Dry weights were recorded for the laminae, sheaths and dead components. Dead laminae and dead sheaths were bulked as dead matter. Dry weights of each component were taken after drying at 35^{o}C for 24 hours, in a vacuum assisted oven. Relevant statistical methods and procedures are presented in Appendix 4.1.

4.2.4 Results and Discussion

4.2.4.1 Rate of leaf emergence

The rate of leaf emergence on the main tiller is shown in Figure 4.1. Most of the control plants reached leaf 16 by the end of the experiment. Leaf emergence rate in the desiccated plants started to slow down after day 5, by then most of the desiccated plants had reached leaf 7. From then on no further leaf appeared in the stress treatments until rewatering.

The leaf emergence rate for the control plants between leaves 8 and 12 was relatively constant, averaging 4.1 ± 0.5 (standard error of the mean) days per leaf. The rate for leaves of the same

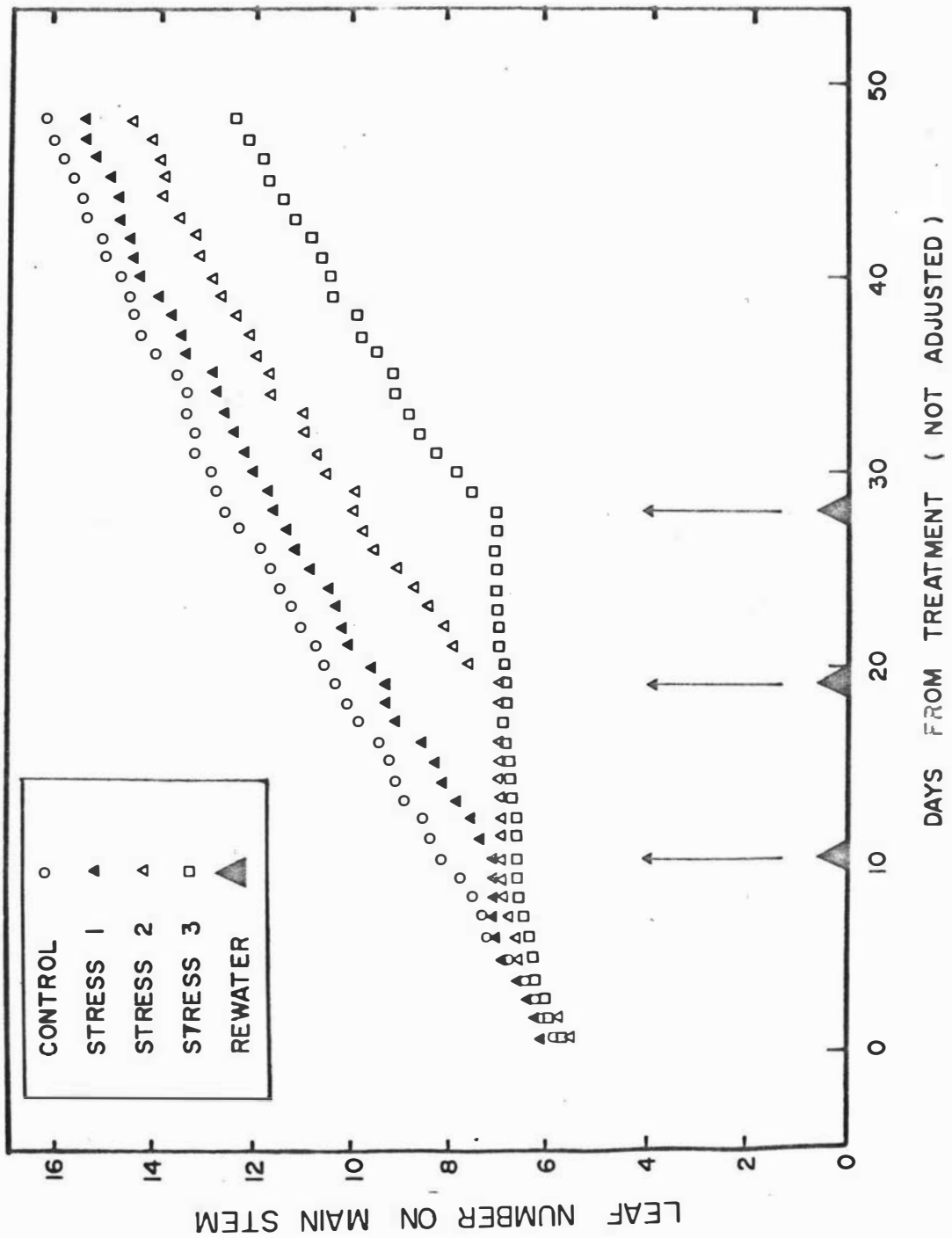


Figure 4.1 Time course of main tiller leaf emergence in prairie grass after water deficits of different duration.

insertion in plants which had been desiccated were slightly faster during their recovery phase. The mean leaf emergence rates were 3.9 ± 0.4, 3.7 ± 0.2 and 3.8 ± 0.4 days per leaf for S1, S2 and S3 treatments respectively (Figure 4.1).

The slightly faster, although statistically non-significant, rate of leaf emergence in the stressed plants was due mainly to a shorter interval between leaves 8 and 9, the first leaves to emerge following rewatering. The rates were about 3 days per leaf as compared with 4 days per leaf in the control treatment. For many pasture grasses the rate of leaf emergence appears to be constant with time when grown under controlled environments (Silsbury, 1970).

4.2.4.2 Rate of leaf extension

The rate of leaf extension began to fall three days after water was withheld and continued to fall rapidly until day 10 when rates were approximately 15% of those in control plants (Fig. 4.2). Leaf extension rates had fallen to 7% of control rates by day 28 in the longest desiccation treatment (S3).

Some wilting of leaves was observed by day 6. Most of the leaf extension in the desiccated plants occurred during the dark period (between 2-5 mm per day). This degree of inhibition of leaf growth was just sufficient to prevent accelerated senescence of the old leaves. By day 19 some leaf tips in the S2 and S3 plants were dead. These plants were wilted during the mid-day period but did regain some turgidity at night.

Within 2-3 hours of rewatering a response of leaf extension rate was measurable. Even earlier responses were detected by Acevedo *et al.*

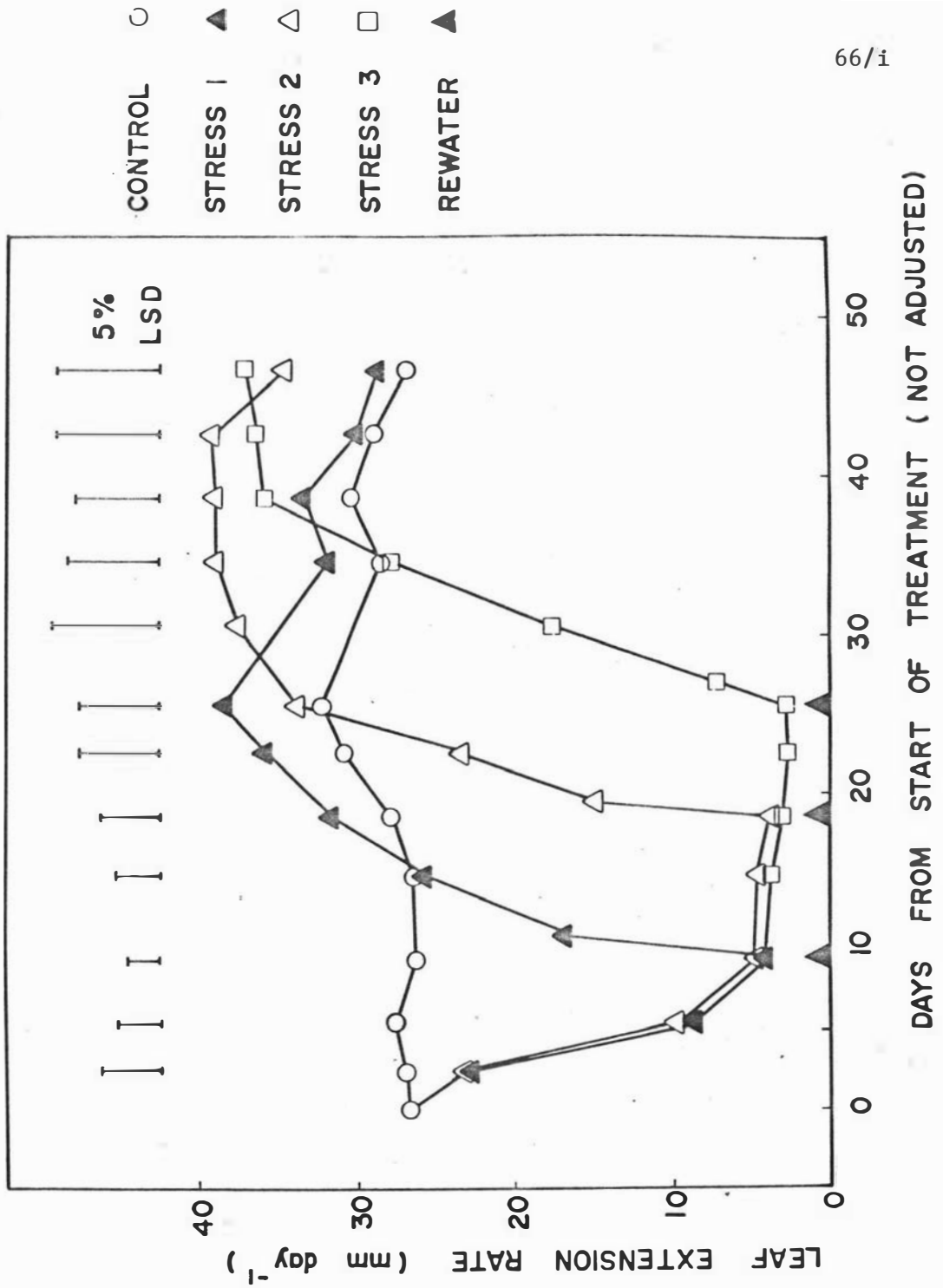


Figure 4.2. Leaf extension rate of prairie grass after water deficits of different duration. Four-daily means are shown.

TABLE 4.1 Mean leaf extension rates for each leaf insertion level on the main stem measured from its appearance until the appearance of the next leaf (mm/day).

Treatments	Control	Stress 1	Stress 2	Stress 3
Leaf 7	27.6 ± 0.6†	16.0 ± 2.4†*	14.0 ± 2.6†*	9.1 ± 4.1†*
8	26.2 0.4	27.1 1.2	20.1 4.4	15.1 3.6
9	26.5 0.7	31.7 1.4	32.6 1.8	27.7 3.3
10	28.0 1.3	35.9 1.9	35.4 1.3	35.7 0.7
11	30.9 1.3	38.2 1.5	38.2 2.2	36.7 0.7
12	32.1 1.8	31.6 1.8	39.1 2.1	37.1 3.1

† standard error of the mean

* leaf extension rate on first day of rewatering

(1971). Using a linear variable differential transformer they detected an increase in leaf extension rate within less than a minute of rewatering mildly desiccated young maize leaves.

Because desiccation delays leaf ontogeny (Fig. 4.1) it is useful to make comparisons between control plants and those recovering from desiccation on physiologically comparable leaves and not just leaves which happen to be undergoing elongation at the same time (Fig. 4.2). Table 4.1 presents mean rates of leaf extension for each individual leaf insertion level on the main stem.

On the first day of rewatering leaf extension in the S1 plants (leaf 7) increased to 58% of control rates and took 4 days to reach levels similar to the rate of extension of leaves of the same insertion on control plants (i.e. leaf 8, Table 4.1). Recovery of leaf extension on the first day of rewatering was 51% and 33% of controls for S2 (leaf 7) and S3 plants (leaf 7) respectively. It took 5 days for S2 and 6 days for S3 plants to reach control rates and in both cases this occurred as leaf 9 emerged (Table 4.1).

Leaf water potential measured during the predawn period on the first day of rewatering showed overnight recovery but was still 0.50 MPa below those of control plants (Section 3.3.4.1). As no further leaf water potential measurements were taken it was not known whether the lower rates observed in leaf 7 (for S1, S2 and S3) and leaf 8 (for S2 and S3) (Table 4.1) were due to leaf water potential or some other reasons. One possible explanation was that of advancing physiological age in these leaves. During desiccation leaf extension, up to 15% of control rates, did occur (Figure 4.2), hence these leaves would be physiologically older than when stress was first

effective (day 6). Upon rewatering they could be in the region of lower growth rate. Extension rate of grass leaves fall off rapidly after an initial high and relatively constant rate of 3-4 days (Wardlaw, 1969). Under mild but prolonged desiccation cell walls could become hardened even in the poorly expanded cells, thus leading to an overall reduced leaf extension rate upon rewatering.

For four weeks or so after first regaining control rates, leaf extension rates in the S1, S2, and S3 treatments were higher than control rates (Fig. 4.2). Higher rates of leaf extension upon relief of water deficit have been reported for young maize leaves (Acevedo *et al.*, 1971), but the faster extension growth in that case lasted only a fraction of an hour. In *Lolium perenne*, Lawlor (1972) reported that leaf extension rates in desiccated plants was 1.8 times faster than control 14 h after rewatering. The rate increased to 4 times faster by day 3 and only returned to levels similar to control plants 8 days after rewatering. In the present experiment the faster leaf extension rate occurred only after 4-6 days and lasted over an extended period during which 4 or 5 new leaves emerged.

The higher extension rates of leaves 9, 10 and 11 for S1; leaves 9, 10, 11 and 12 for S2 and leaves 10, 11 and 12 for S3 (Table 4.1) are more difficult to explain. In prairie grass, during the vegetative stage, normally only 3 leaf primordia were found to be present at the stem apex, with 3 immature leaves in various stages of expansion(Karim, 1961). A similar number of leaves were recorded by Hill (1971) before the onset of "double-ridging" stage in prairie grass. In this experiment the plants were maintained in the vegetative state (checked by apical dissection during the experimental period). This meant the youngest leaf primordia would be 6 plastochrons from the fully expanded leaf i.e., the youngest mature leaf.

Using S1 plants as an example, an attempt will be made to explain these observed higher rates. When stress was effective (day 6) the youngest mature leaf for S1 plants was leaf 4. The youngest leaf primordia would therefore be leaf 10. Although the rate of leaf primordia initiation and the rate of leaf appearance could be different, under uniform conditions these two parameters can be relatively constant (Silsbury, 1970). Assuming that the rates of appearance of these two parameters are similar at 4 days per primordium or leaf, leaf 11 would have been initiated by day 10 (day of rewatering). If this assumption was correct, by day 10, in S1 plants the 3 leaf primordia would be that of leaves 9, 10 and 11. The differential effect of water deficit on cell division and cell elongation (Clough and Milthorpe, 1975) could then have allowed cell division in the primordia while expansion remained suppressed. In this event, rapid cell expansion in these primordia could occur following rewatering, giving rise to the observed high rates. However, as no leaf primordia count was conducted in this experiment, this explanation can only be speculative.

A fall in leaf extension rates occurred in the control and S1 treatments between days 29 and 32 because insufficient water had been added to allow for the increased transpiration that accompanied the rapid increase in leaf area over that period. Nutrient application was increased to 200 ml twice daily but it took 3-4 days before the response returned to normal. The data for these days have been omitted for Fig. 4.2.

Leaf extension rates were measured only on leaves which were in their most rapid phase of elongation. A more complete picture of the significance of the period of water deficit and the recovery phase can be obtained from changes in the whole plant growth components.

4.2.4.3 Rate of increase in growth components

The rate of increase in tiller number, leaf number, leaf area and shoot dry weight per plant were all depressed within the first few days of water being withheld (Fig. 4.3). During the period of water deficit the number of tillers per plant continued to increase slowly. There was also a small increase in the leaf number per plant and leaf area per plant during the first 19 days. By day 28 a subsequent decline due to senescence had partially offset this increase. The amount of dead material on day 28 was not great however, representing only 3%, 2%, 3% and 5% of control, S1, S2 and S3 plant dry weights respectively.

On an unadjusted basis, the overall effect of the desiccation treatment was least for tiller numbers and the greatest for shoot dry weights. By the end of the experiment S3 plants had 64%, 48%, 32% and 27% of control values for tiller number, leaf number, leaf area and shoot dry weight per plant respectively.

A simple and reliable relationship between the duration of water deficit and the degree of dry matter yield depression that results, would be a useful tool for pasture management. The essential question is whether there are significant positive or negative carryover effects or whether the loss of yield is proportional to the duration of water deficit. This was tested using a plant based criterion to determine the effective duration of water deficit and then adjusting for the number of these "drought days" to allow comparison among treatments of the recovery pattern. A "drought day" was defined as any day for which all the leaves were wilted during the day period. During this period, leaf water potentials measured with a pressure chamber 2 to 3 hours into the photoperiod averaged -1.41 ± 0.25 MPa.

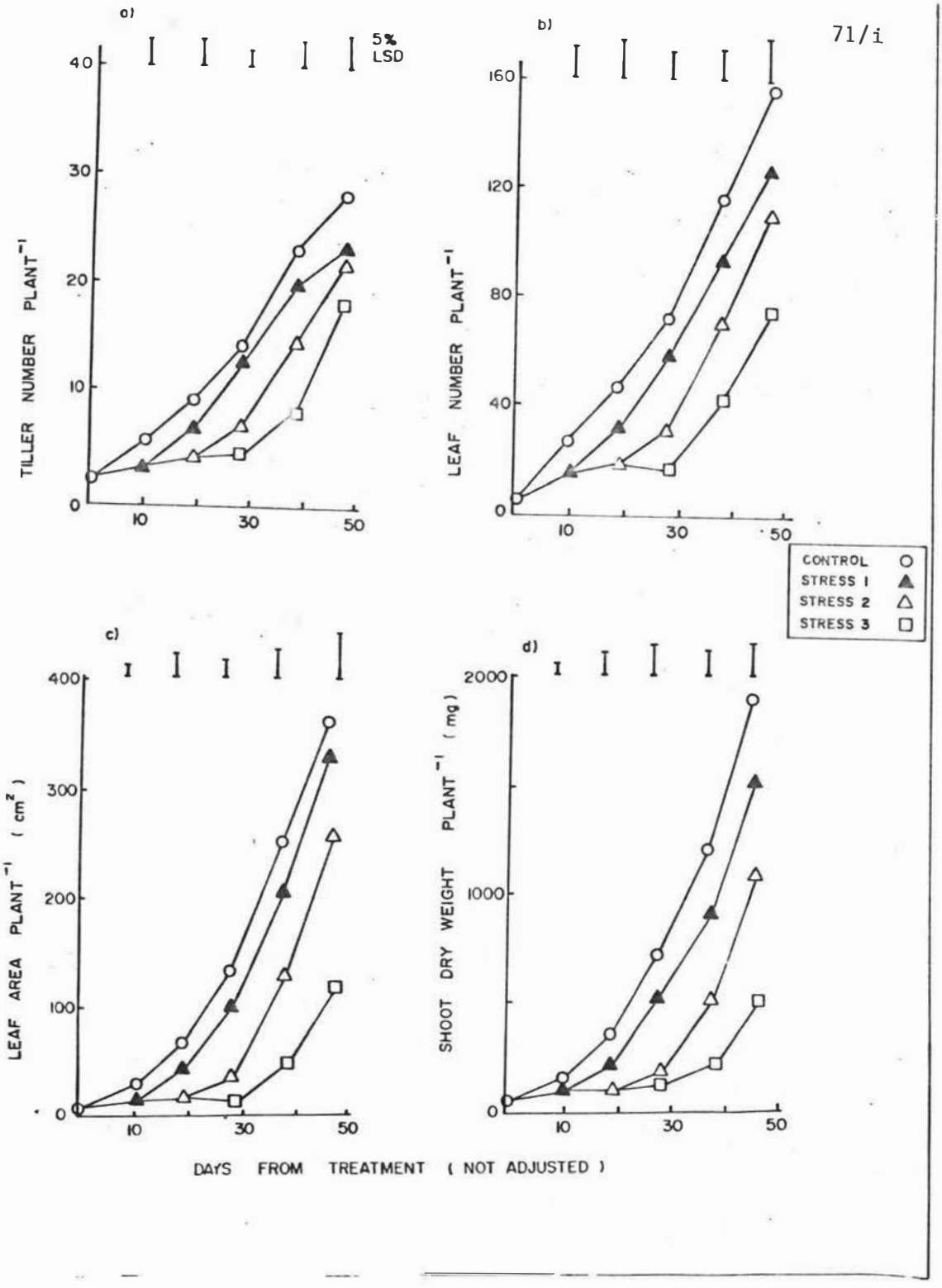


Figure 4.3 Patterns of recovery of growth components in prairie grass after water deficits of different duration.

(a) tiller number per plant

(b) leaf number per plant

(c) leaf area per plant

(d) shoot dry weight per plant.

Wilting was first evident at about -1.40 MPa on day 6 and at this stage the mean daily leaf extension rate was less than 40% of control rates (section 3.3.4.1).

By removing the "drought days" from the chronological time scale, the pattern of recovery growth relative to the control over the "non-drought days" will indicate any carryover effects. Figure 4.4 shows the changes in growth components with respect to the number of "non-drought days" which numbered 47, 43, 34 and 24 for C, S1, S2 and S3 treatments respectively. At a first approximation, at least for the shoot dry weight per plant data, the S1, S2 and S3 treatments followed the curve drawn through the values for the control plants. This indicated that the suppression of shoot dry weight per plant was proportional to the duration of the period of water deficit. However the rate of increase in tiller number, leaf number and leaf area per plant showed less suppression due to desiccation reflecting the accelerated growth that occurred during the recovery period.

In order to follow the recovery phase of the growth component more closely, regression equations of the form $\text{Log}_e Y = a + bX$ were fitted through the data set. The value of each replicate for the first 4 harvests (except for S3 where only 3 harvests were used) in Figure 4.4 was used as an observation in the regression calculation. The results are summarised in Table 4.2. Comparisons of regression slopes were based on the F test by Snedecor and Cochran (1968).

The rates of shoot dry weight increase following desiccation became lower as the duration of desiccation increased. The differences were small (16% faster than controls to 11% slower) and non-significant among all treatments. Larger differences between control

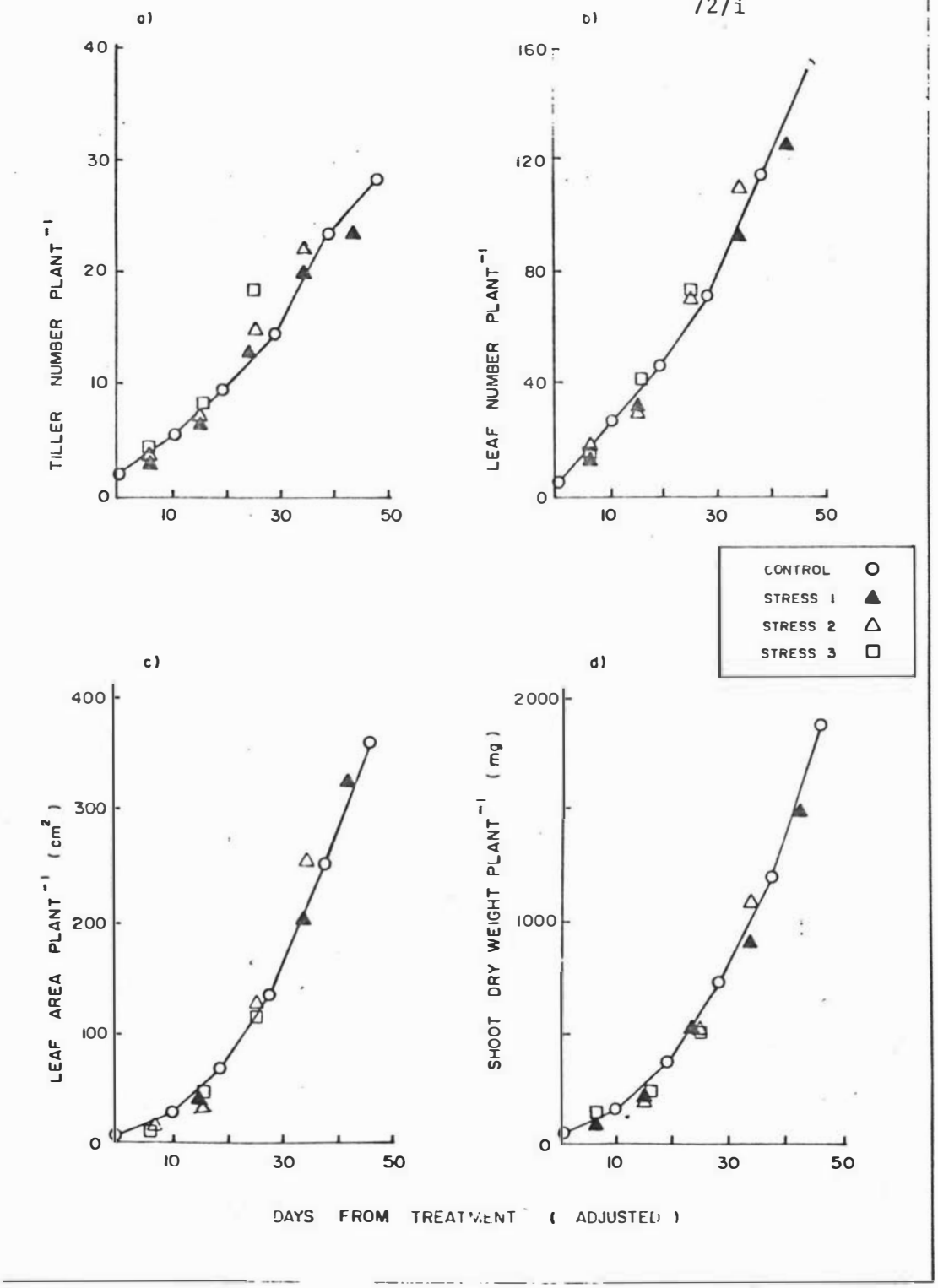


Figure 4.4 Growth component data from Figure 4.3 expressed as a function of "non-drought" days.

(a) tiller number per plant

(b) leaf number per plant

(c) leaf area per plant

(d) shoot dry weight per plant

TABLE 4.2 Linear regression analysis ($\log_e Y = a + bx$) for growth components during the recovery phase in prairie grass, where Y = growth component and X = time in days. (up to 29 days for C, S1 and S2; 20 days for S3)

Growth component	Treatment	Regression Coefficient	Constant	R^2	F test between regression coefficients
Tillers number	C	0.0547	1.10	0.82	a*
per plant	S1	0.0676	0.79	0.91	ab
	S2	0.0626	1.03	0.93	ab
	S3	0.0754	0.98	0.93	b
Leaf number	C	0.0939	2.73	0.82	a
per plant	S1	0.0673	2.35	0.95	ab
	S2	0.0670	2.47	0.97	ab
	S3	0.0797	2.36	0.94	b
Leaf area	C	0.0795	4.86	0.90	a
per plant	S1	0.1015	4.30	0.97	b
(cm^2)	S2	0.1065	4.28	0.96	b
	S3	0.1190	4.10	0.98	b
Shoot dry	C	0.0777	4.23	0.85	a
weight per plant	S1	0.0901	3.80	0.83	a
	S2	0.0892	3.93	0.95	a
mg	S3	0.0694	4.38	0.84	a

* Values with common letters are statistically non-significant at 5% level of probability.

plants and desiccated plants were found for the other growth components. During the recovery from desiccation the rate of tiller formation was between 14-38% faster than controls. The rate of leaf number increase was 24-48% faster than controls. Only the longest desiccation treatment gave differences that were statistically significant ($P < 0.05$). The rate of leaf area increase was between 28-51% faster than controls and the differences were significant ($P < 0.05$) for all three treatments, reflecting the higher leaf extension rates measured during the recovery phase (Fig. 4.2 and Table 4.1).

It is of interest to note that the longer duration stress treatments had a higher rate of leaf area expansion but a slower rate of dry weight increase. Differential responses of leaf area and dry weight have been reported by others. For example, Meads (1975) observed that in a sward of field grown perennial ryegrass during recovery from severe defoliation, leaf area recovered immediately whereas dry weight decreased initially over the first 3 to 5 days before increasing. The utilization of reserves during regrowth could cause the reduction in dry weights (Milthorpe and Davidson, 1966).

The choice of the criterion used for determining the number of drought days was arbitrary. The implication that growth stopped instantly on the first drought day and returned to control rates on the first non-drought day was an oversimplification. Nonetheless, a simple relationship such as the one used above would be useful if it were found to apply in a wide enough range of conditions.

A similar suspension of physiological activity during periods of water deficit with resumption soon after rewatering at rates which were normal for the stage of ontogeny for the tissue was found for apparent

photosynthetic rates in *Panicum maximum* by Ludlow and Ng (1974).

Other workers have reported enhanced growth rates upon recovery from a period of water deficit, for example in tomato (Gates, 1955a, 1955b) sugar beet (Owen and Watson, 1956) and tobacco (Hopkinson, 1968). However, it is not clear whether this indication of enhanced growth is real in physiological terms or simply due to the interactive effect with stage of plant development. The importance of such interaction in interpreting results has been clearly indicated by Ludlow and Ng (1974) and Ng *et al.* (1975) in their work with *Panicum maximum* where water deficits delayed ontogeny in terms of apparent photosynthesis, stem elongation and flowering.

In the present experiment, recovery growth at higher than control rates did occur over several days in the rate of leaf extension (Figure 4.2 and Table 4.1) and in the rate of tiller number, leaf number and leaf area increases (Table 4.2). The overall effects of these accelerated responses on plant dry weight were however minimal (Figure 4.4d). The loss in yield, as represented by shoot dry weight per plant was approximately proportional to the duration of the period of water deficit.

4.3 EXPERIMENT 5 - RECOVERY GROWTH FOLLOWING DIFFERENT LEVELS OF WATER DEFICIT IN TWO CULTIVARS OF RYEGRASS UNDER TWO DIFFERENT TEMPERATURE REGIMES.

4.3.1 Abstract

The rates of leaf emergence, leaf extension, tiller number, leaf number, leaf area and plant dry weight increases were measured following different levels of water deficit lasting up to 12 days in two cultivars of ryegrass (Nui and Ruanui) under two controlled temperature regimes. The levels of water deficit were C, representing well-watered control; S1, representing stress duration lasting until 24 hours after the cessation of leaf extension growth in the youngest leaf and S2, representing a further stress period of 6 days from S1. Stress was applied by withholding water from the soil. The temperatures were $27/5^{o}/12.5^{o}C$ (day/night) designated as H temperature treatment and $17.5^{o}/12.5^{o}C$ designated as L temperature treatment.

Significant differences were detected for leaf emergence rates between temperature treatments and between different leaves depending on the order of insertion on the main stem. However, there was no difference in leaf emergence rates between cultivars.

Under well-watered conditions, over a period of 26 days, Nui had approximately 27% faster rate of leaf extension than Ruanui under the H temperature, but was only 13% faster under the L temperature treatment. Within 2 days of rewatering, leaf extension rate in S1 under both temperature treatments, returned to rates similar to those of the control. In S2, under the H temperature regime, no new leaves emerged until 3 days after rewatering, but once emerged the extension rate was similar to that of S1. During a period of up to 12 days after rewatering

there was no evidence of leaf extension rates being slower than control rates in any treatment.

Leaf area per plant, mean leaf size, number of dead leaves and dead matter per plant were all significantly greater under the H temperature than under the L temperature regime. The major differences between cultivars were in Ruanui having about 24% more tillers and 18% more green leaves than Nui, but with Nui having heavier mean tiller dry weight (28%), a larger mean leaf size (24%) and less dead leaves (34%) than Ruanui.

As expected, desiccation reduced all the parameters measured, with the magnitude of reduction dependent on the degree of desiccation. Final tiller number, leaf number, leaf area and dry weight per plant, 12 days after rewatering for S1 were, 92%, 91%, 90% and 77% that of control plants respectively. For S2 the corresponding values were 79%, 73%, 42% and 59% that of control plants.

The rates of recovery, over 12 days after rewatering, for tiller number, green leaf number, leaf area and dry weight per plant were compared by fitted regressions. The rates of recovery of leaf area in the previously desiccated plants were higher than those of the well-watered control, whereas the rates of recovery for tiller number, leaf number and dry weight were similar to those of the control. Senescence of tissues during desiccation rather than a lower rate of recovery was the major cause of a lower "final" dry weight in the previously desiccated plant.

4.3.2 Introduction

In the prairie grass experiment reported in the previous section

(Experiment 4), recovery growth exceeded control rates over several days in the rate of leaf extension, rates of recovery in tiller number, leaf number and leaf area per plant. However, the overall effect of this on plant dry weight was minimal. Losses in dry weight were roughly proportional to the duration of water deficit.

In the field, under prolonged drought, the plants will most likely experience both the effect of the duration as well as that of the "intensity" or degree of water deficit. The combined effects of duration and "intensity" may have a more detrimental effect on plant performances than that due to the effect of duration alone.

Furthermore, in the field, water deficit is frequently associated with high temperature conditions. Plant responses to water deficit may be quite different under different temperature regimes. In the experiment reported in this section plant response to water deficit are compared under two contrasting temperature regimes.

Because of the importance of perennial ryegrass as the major pasture component in New Zealand, a comparison of Grasslands Nui and Grasslands Ruanui was included in this experiment. From the results of many trials conducted in New Zealand, it has been demonstrated that Grasslands Nui can outyield Grasslands Ruanui, especially during the dry summer-autumn conditions (Rumball, 1969; Baars *et al.*, 1976; Sheath *et al.*, 1976; Armstrong, 1977; Vartha, 1978). These trials were conducted under grazing (Rumball, 1969; Baars *et al.*, 1976; Armstrong 1977) or mowing (Sheath *et al.*, 1976) and the dry matter yields were scored (Rumball, 1969) or calculated from dry matter samples (Sheath *et al.*, 1976). However, the reason for Nui's superiority is still not known. In addition, the extent to which high temperature may have influenced the response of Nui during the warmer months is also not known. A knowledge of their relative

performance under different water deficit and temperature conditions may throw some light on the reasons why Nui can perform better than the other ryegrass cultivars.

The following section presents data collected from controlled environment experiments designed to investigate the responses of two cultivars of ryegrass during and after different periods of water deficit under two temperature regimes.

4.3.3 Materials and Methods

Plant materials and growing conditions for this experiment were the same as that reported in Section 3.4.3.

Grasslands Nui and Grasslands Ruanui ryegrasses were sown in 2.3 litres of soil mixture (50% Manawatu silt loam and 50% river sand by volume) in two controlled climate rooms.

The two air temperature treatments were $27.5^{o}/12.5^{o} \pm 0.5^{o}C$ (day/night) designated as high (H) temperature and $17.5^{o}/12.5^{o} \pm 0.5^{o}C$ designated as low (L) temperature regimes. The other environmental conditions were the same for both rooms:

Air vapour pressure deficit (VPD) 0.7/0.2 kPa (day.night) equivalent to relative humidity of 80.9/86.2 ± 5% and 64.9/86.2 ± 5% for the H and L temperature regimes respectively.

Photoperiod 12 hours with a photosynthetically active radiation flux of 170 W/m^2 (0.4 - 0.7 μm wave band)

Carbondioxide concentration was uncontrolled.

Diurnal changes in temperature and VPD occurred gradually over 4 hours immediately inside the day period.

The plants were thinned from 15 to 6 per pot by week 4 (from sowing) and to 3 by week 5, selecting on the basis of evenness of height and leaf number. Soil desiccation treatmentsstarted when the sixth leaf was about 20-30 mm clear of the preceding leaf sheath and the time was designated as day 0. Desiccation treatment consisted of withholding water from the soil and treatments will be referred to as follows:

Control (C) plants watered daily with modified Hoagland's solution, 200 ml per pot 30 minutes before the dark period.

Stress 1 (S1) desiccation was imposed by withholding water from the soil until the mean daily leaf extension rate of the youngest leaf has ceased for 24 hours.

Rewatering was done by standing the pots in a tray of water (nutrient solution) for 2 hours, plus repeated watering from the top to ensure full saturation.

Stress 2 (S2) water withheld as in S1 and rewatered 6 days after the end of S1. Procedure of rewatering was the same as in S1.

For each treatment, 4 plants were tagged and used for leaf appearance and leaf extension rate measurements. To aid identification each leaf on the main tiller was marked with a number enclosed in a strip of cellotape. A leaf was counted as 'emerged' when first visible from the preceding leaf sheath, and 'matured' when the ligule was fully exposed.

The interval between appearance of successive leaves was used as a measure of the rate of leaf emergence. For example, the interval (in days) between the appearance of leaf 6 and leaf 7 was treated as the leaf emergence rate for leaf 7.

Changes in leaf length (sum of lamina and sheath extension) were recorded daily. Leaf extension measurements were made with a ruler placed against the base of the plant using the soil surface as a reference point. The height of the youngest mature ligule was also recorded during each reading and the length of each leaf was recorded from the time when it first appeared until matured.

Destructive harvests were taken at 3 day intervals from day 0. Days 9 and 15 represented the end of S1 and S2 treatments respectively. Thereafter 4 more harvests were taken during the recovery phase for each treatment.

During harvest, roots were washed with a high pressure hose. Some fine roots were lost during washing but the bulk of the roots were retained. However it was not possible to distinguish visually between dead and alive roots. The leaf number and tiller number per plant were counted. Each of these components was divided into two categories as follows:

Tiller: mature ----tiller with at least 1 mature leaf showing
immature----tiller with only the immature leaf showing

Leaf: mature ---- where the ligule is fully exposed
immature --- where the ligule is not exposed.

The laminae were separated from the sheath at the junction of the youngest matured ligule. The "sheath" therefore included the unexposed immature leaves and the sheath of the matured leaves. The leaf laminae component represented the photosynthetically active tissue. Dry weights were recorded for each component after drying at 35°C for 24 hours in a vacuum assisted oven. The dead matter component included both dead laminae and sheath. Leaf area for the mature and immature leaves were taken with an electronic leaf area meter.

Relevant statistical methods and procedures are presented in Appendix 4.1.

In this section, the H and L Temperature regime are also compared on the degree-hour weighted mean basis. The H temperature 27.5°/12.5oC is equivalent to 17.5°C = [(12hr x 12.5°C) + (8 hr x 20.0°) + (4 hr x 27.5°)] /24 hr = 17.5°C and the L temperature 17.5/12.5°C is equivalent to 14.3°C [(12h x 12.5°) + (8 hr x 15.0°) + (4hr x 17.5°)] /24 hr = 14.3°C

4.3.4 Results and Discussion

4.3.4.1 Rate of leaf emergence

(a) The well-watered control plants

No significant difference in mean leaf emergence rate was detected between the 2 ryegrass cultivars (Table 4.3). Although under the H temperature regime, Ruanui had a slightly faster rate (5.7 days/leaf) than Nui (6.3 days/leaf).

Under the H temperature conditions, leaf emergence rate was approximately 10% faster than those of the L temperature conditions (i.e., 6.0 days/leaf and 6.6 days/leaf respectively). The difference was significant ($P < 0.01$). In prairie grass under a day/night temperature treatment of $22.5^{o}/12.5^{o}C$ the mean leaf emergence rate was 4.1 days/leaf (section 4.2.4.1).

(b) The desiccated plants

During the period of desiccation no new leaf emerged in the stress treatments and for S2 the existing leaves were all senesced on the day of rewatering. Hence comparison on the effects of desiccation on leaf emergence rates between the different desiccation treatments during the recovery phase could only be done on leaf 9, the first leaf to appear in S2 following rewatering.

Withholding water so that leaf growth stopped for 7 to 8 days (i.e., S2) had no more adverse effects on the rate of emergence of leaf 9 following rewatering than only stopping for 1 day (i.e., S1) (Table 4.4). The response of leaf emergence to temperature after a period of desiccation was similar to that of the control. The emergence rate was 13% faster in the H temperature than the L temperature regime (6.1 days/leaf and 6.9 days/leaf respectively). Although

TABLE 4.3 Mean interval (days) between appearance of successive leaves in well-watered control plants of Ruanui and Nui Ryegrass under 2 temperature regimes. (Details of analysis of variance are presented in Appendix 4.2a).

(days per leaf)

Temperature	27.5/12.5°C(H)		17.5/12.5°C(L)		Means for
Cultivars	Ruanui	Nui	Ruanui	Nui	leaf No. (P < 0.01)
Leaf No. 7	5.8	6.3	6.0	6.3	6.1 a
8	5.5	6.0	6.0	5.8	5.8 a
9	5.5	6.5	7.5	6.8	6.6 b
10	6.0	6.3	7.0	7.5	6.7 b
Means for temp x cultivar (P <0.05)	5.7	6.3	6.6	6.6	

TABLE 4.4 Mean interval (days) between appearance of leaves 8 and 9 (i.e., leaf 9) in Ruanui and Nui ryegrass during the recovery phase for control, Stress 1 and Stress 2 plants under 2 temperature regimes (Details of analysis of variance is presented in Appendix 4.2b)

(Days per leaf)

Temperature	27.5/12.5°C		17.5/12.5°C		Means for
Cultivar	Ruanui	Nui	Ruanui	Nui	water stress (N.S.)
Water C	5.5	6.5	7.5	6.8	6.6
Stress S1	6.5	6.5	7.3	6.3	6.6
S2	5.8	6.0	6.8	7.0	6.4
Means for temp x cultivar (P <.05)	5.9	6.3	7.2	6.7	

averaged across the two temperature regimes the cultivars were similar in their leaf emergence rate (Nui = 6.5 days/leaf and Ruanui = 6.6 days/leaf), there was a significant temperature x cultivar interaction ($P < 0.05$). Ruanui had a faster emergence rate under the H temperature regime but a slower emergence rate under the L temperature regime than Nui (Table 4.4).

4.3.4.2 Rate of leaf extension

(a) The well-watered control plants

Under well-watered conditions, the effects of both temperature and cultivar on the rate of leaf extension were highly significant ($P< 0.01$) (Table 4.5). The rates were measured over a period of 26 days.

When averaged across the temperature treatments Nui had a 20% faster leaf extension rate than Ruanui. However, under the H temperature conditions, Nui leaf extension rate was 27% faster than Ruanui, whereas it was only 13% faster under the L temperature regime (Table 4.5). This interaction was significant ($P< 0.01$),

(b) The desiccated plants

During the period of desiccation the leaf extension rates of the desiccated plants fell quickly and ceased totally on day 8 and day 9 for the H and L temperature treatments respectively (Figure 4.5).

Temperature had little effect on the rate of recovery from the shortest period of desiccation (S1). It took 2 days for the leaf extension rates in the desiccated plants to reach control rates (Figure 4.5a & b). The pattern was similar for both cultivars. On

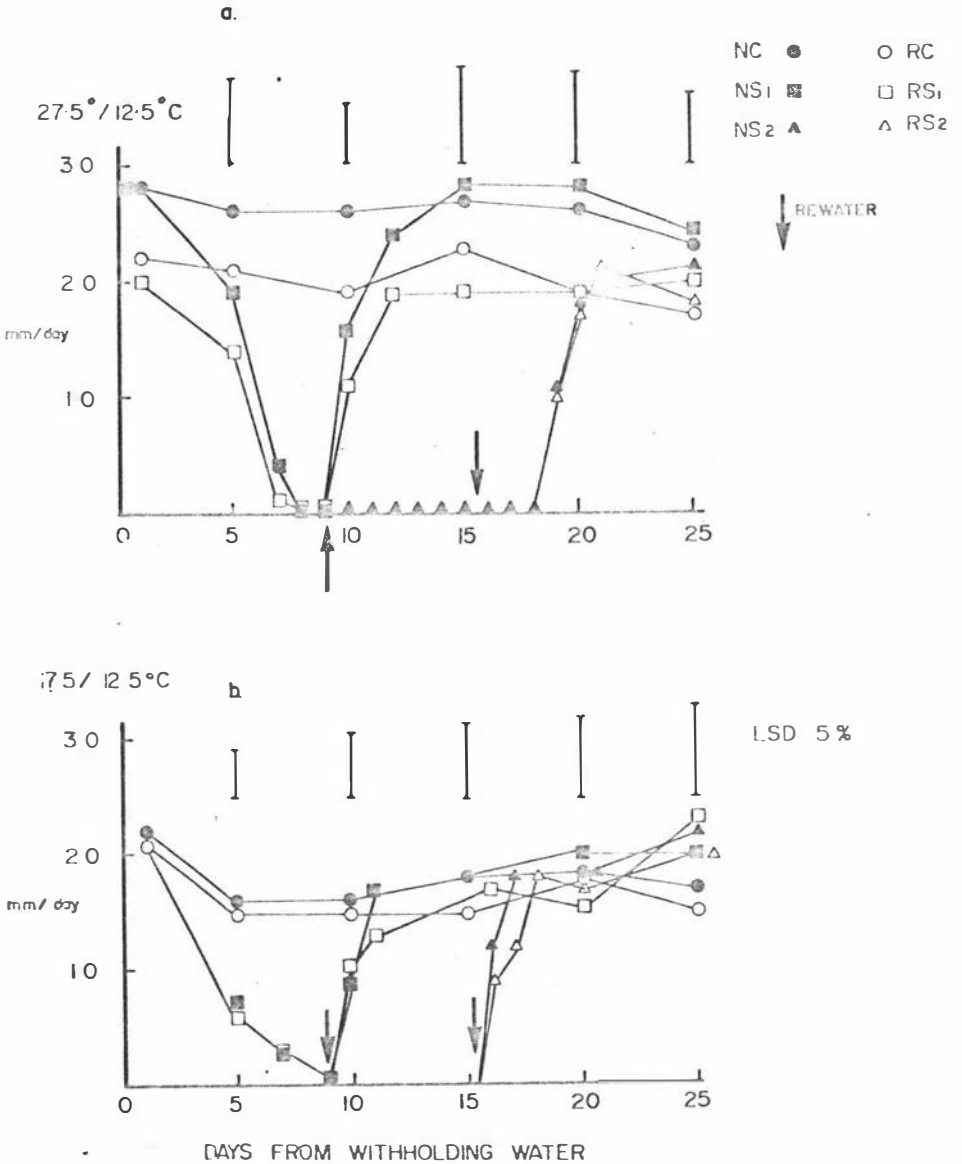


Figure 4.5 Time course of leaf extension rate in Ruanui (R) and Nui (N) for well watered control (C), stress 1 (S1) and Stress 2 (S2) plants: (a) under H temperature regime, and (b) under L temperature regime.

TABLE 4.5 Comparisons of the rates of leaf extension (mm/day) between well-watered Ruanui and Nui ryegrass under 2 temperature regimes (Details of analysis of variance is presented in Appendix 4.4)

	Temperature		Means for
Cultivars	27.5°/12.5°C	17.5°/12.5°C	cultivar (P<0.01)
Ruanui	19.9	16.5	18.2
Nui	25.3	18.6	21.9
Means for temperature	22.6	17.5	

(P<0.01)

(Temperature x cultivar interaction P < 0.01)

the first day of rewatering all treatments reached to between 50% and 65% of control rates. The rates on the first day of recovery were similar to those of the S1 treatment in the prairie grass experiment (section 4.2.4.2), but in the case of the ryegrass it took 2 days for the desiccated plants to recover to control rates compared with 4 days in prairie grass (Figure 4.2). In Lawlor's experiment with ryegrass (Lawlor, 1972), leaf extension rate of the previously desiccated plants was 1.8 times faster than the control rate 14 hours after rewatering.

In contrast with the L temperature regime, the H temperature regime had a significant effect on the rate of recovery of leaf extension rate under the longer period of desiccation (S2). Under the H condition all the leaves were dead by the end of S2, and new leaves appeared 3 days after rewatering (Figure 4.5a). Under the L temperature condition although the leaves were severely wilted and the tips were dead, they recovered quickly and were measurable within 24 hours after rewatering (Figure 4.5b). Once the new leaves emerged, the rates of leaf extension recovery relative to their respective controls were again similar for both temperature and cultivar comparisons. The recovery rates in S2 took 2 days to reach control rates, and these were similar to those recorded under the milder desiccation treatment (S1).

The influence of temperature on leaf extension rate is well documented (Evans *et al.*,1964; Silsbury, 1970; Langer, 1972; Robson, 1972; Peacock, 1975a, 1975b). In general, leaf extension rate is faster under the higher temperature regime. For instance, in tall fescue *(Festuca arundinacea)* leaf extension rate at 25^{o}C was 4 times as fast as that under 10^{o}C, but for only half the time (Robson, 1972). However, there were species differences, for example, in the prairie grass experiment (Expt. 4) leaf extension rates were higher than

those of the ryegrasses under the H temperature treatment of the present experiment (Expt. 5), even though the temperature of the prairie grass experiment was lower.

Upon rewatering, leaf extension rates of previously desiccated plants sometimes were much higher than the rates of the well-watered control plants. This "accelerated" rate had been reported in ryegrass by Lawlor (1972), in *Panicum maximum* by Ludlow and Ng (1977) and in prairie grass (Expt. 4 of this study). However, in the present experiment on ryegrass (Expt. 5), no evidence of an "accelerated" rate was detected (Figure 4.5).

The lack of such an "accelerated" rate in this experiment even at the S1 level of desiccation could be due to the more severe desiccation imposed in Expt. 5. In S1 of the present experiment leaf extension growth stopped completely, whereas in S1 of Expt. 4 leaf extension rate was maintained at between 7 and 15% of control rates (Figure 4.2). Ludlow and Ng (1977) suggested that the higher leaf extension rate in *Panicum maximum* after rewatering was due to the differential levels of sensitivity by cell division and cell elongation to water deficit. This could result in an accumulation of newly divided but yet poorly expanded cells at the zone of leaf expansion. A similar explanation was put forward in the prairie grass experiment (Expt. 5). The lack of an "accelerated" rate in this experiment would be consistent with the explanation that both cell division and cell elongation had been suspended.

4.3.4.3 Growth data from the destructive harvests

For convenience of discussion, plant growth data collected from

the destructive harvests will be presented under the following headings:

1. Responses during the desiccation phase.

2. Responses during the recovery phase.

4.3.4.3.1 Responses during the desiccation phase

The pattern of esponse exhibited by the 4 growth parameters that were measured, viz., tiller number, green leaf number, leaf area and dry weight per plant, were quite different during desiccation (Figure 4.6). By day 9 (i.e., end of S1) tiller number, green leaf number and dry weight per plant were all significantly higher than those on day 3 ($P < 0.05$). Only leaf area was significantly lower on day 9 than day 3 ($P < 0.05$). This demonstrated further the very sensitive nature of leaf area responses, relative to other parameters, to desiccation. By day 15 (i.e., end of S2) green leaf number and leaf area per plant were reduced to a greater extent than were tiller number and dry weights. Tiller number and dry weight per plant were lower on day 15 than on day 9 but were still higher than those on day 3.

Upon closer examination of the data the following points emerged:

1. Mature and immature tiller numbers responded to desiccation in a similar manner. No death of tillers were noted, all the tillers had some green tissues within the inner layers of the leaf sheath even on day 15.

2. Mature leaves were more "sensitive" to desiccation than immature leaves. During S1 (i.e., between day 3 and day 9), the increase in mature leaf number was less than immature leaf number. In the case of the mature leaf number this would be due to both the senescence of existing mature leaves and the lack of development of immature

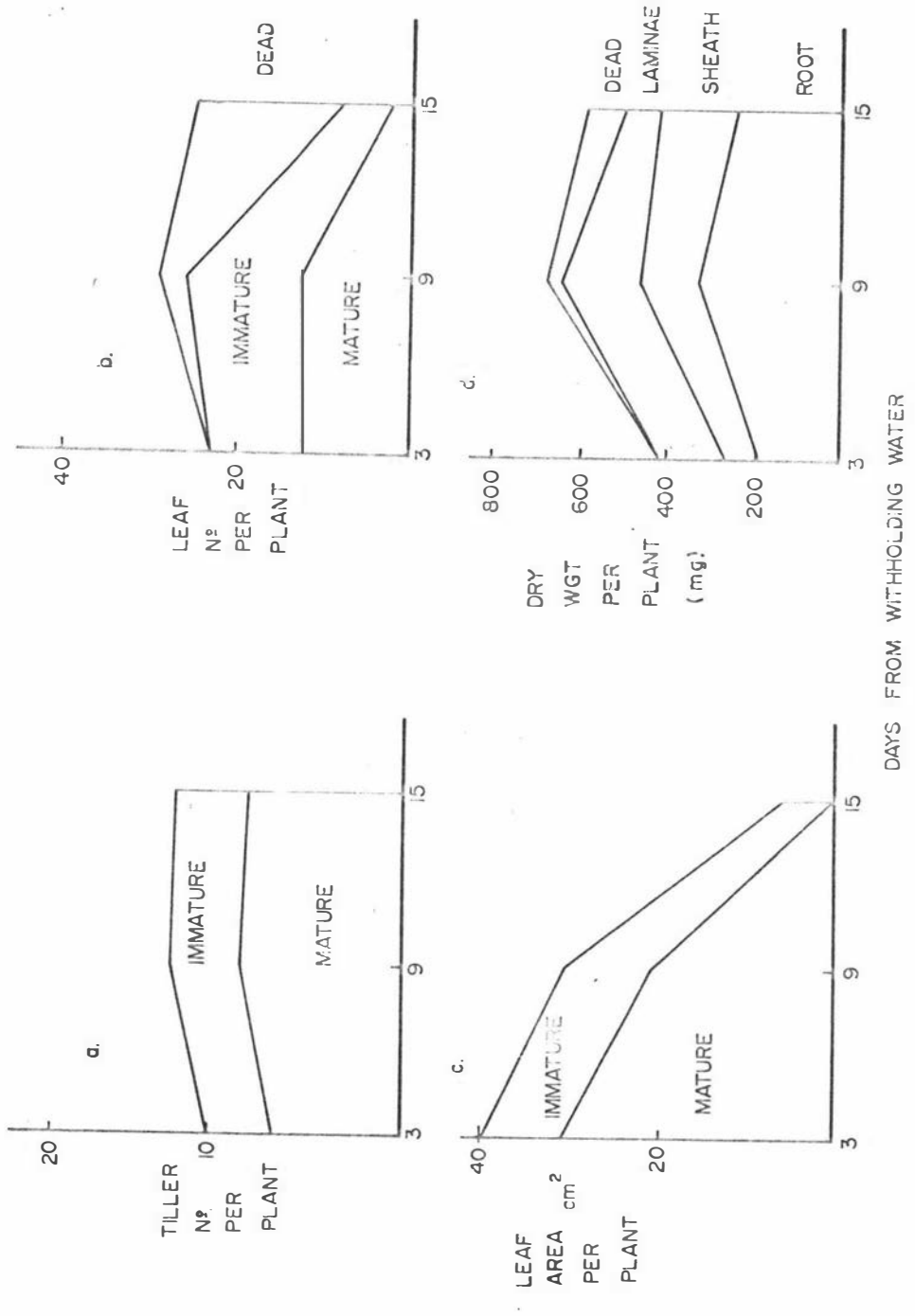


Figure 4.6 Changes in plant growth parameters during the desiccation period.

(a) tiller numbers per plant (mature and immature tillers)

(b) leaf number per plant (mature, immature and dead leaves)

(c) leaf area per plant (mature and immature leaves)

(d) dry weight components (root, sheath, laminae and dead matter).

TABLE 4.6 Growth parameters comparisons between Nui and Ruanui at the end of the desiccation phase

Growth Parameters	Nui	Ruanui	Significance Level
Tiller number per plant	12	15	**
Green leaf number per plant	21	24	NS
Dead leaf number per plant	6.0	7.3	**
Leaf area per plant (cm^2)	34	32	NS
Dry weight per plant (mg)	624	620	NS
Mean dry weight per tiller (mg)	51.7	41.0	**

leaves into the mature leaf category. At this stage of desiccation all the senesced leaves were from the mature leaf category. During S2 (i.e., between day 9 and 15), the relative reduction was again greater in mature leaves. The relative sensitivity of tissues of different maturity status to water deficit had also been noted by Cates (1968). Cates concluded that younger tissues had features common to embryonic tissues and were more resistant to desiccation than older tissues.

3. Leaf area was the growth parameter most sensitive to desiccation. Both mature and immature leaf areas were reduced during S1 and S2, and the reduction was greater under the H than under the L temperature regime (Appendix 4.3a).

4. All dry weight components showed an increase during S1. During S2, lamina dry weight was reduced to a greater extent than was root dry weight, with sheath dry weight showing an increase (Figure 4.6). The increase in sheath weight during S2 was due to the accumulation of unexposed leaves within the sheath. Reduction in dry weight under the H temperature regime started during S2, whereas under the L temperature regime, plant dry weight actually increased during S2 (Appendix 4.3a).

5. Nui had a heavier mean tiller dry weight than Ruanui, but Ruanui had a larger tiller number and dead leaf number per plant than Nui (Table 4.6). On a per plant basis, total dry weight, total leaf area and total green leaf numbers were similar between the cultivars.

4.3.4.3.2 Responses during the recovery phase

The growth parameters measured during the recovery phase were compared on the basis of similar physiological age. The procedure of

physiological adjustment was similar to that used in the prairie grass experiment (Expt. 4). The number of "drought" days was taken as 3 and 9 days for S1 and S2 treatments respectively. A "drought" day was defined as "any day for which all the leaves were wilted during the day period" (section 4.2.4.3).

Responses of the 4 growth parameters during the recovery phase will be discussed under the main treatment effects. Where major interactions occur, they will also be discussed.

Details of the analysis of variance are presented in Appendix 4.6. The means of the various components of the growth parameters are presented in Appendix 4.7.

The chronological age of the S1 and S2 plants had been adjusted for physiological age. Harvest number 1, 2, 3, 4 and 5 represents physiological age of 6, 9, 12, 15 and 18 days from the commencement of desiccation treatment or 0, 3, 6, 9 and 12 days from rewatering.

A. Water deficit comparison

The responses of the 4 growth parameters following different desiccation treatments are presented in Table 4.7. The following are the major points of interest:-

1. After 12 days of recovery growth, the values of S1 plants, expressed as percentages of the control for tiller number, green leaf number, leaf area and dry weight per plant were 92%, 91%, 90% and 77% respectively. The corresponding values for S2 were 79%, 73%, 42% and 59% (Table 4.7). After the relatively severe S2 treatment, tiller number and leaf number recovered much more quickly than leaf area and

TABLE 4.7 Influence of previous water deficit treatments on plant growth parameters during the period of recovery

(C = control; S1 = Stress 1; S2 = Stress 2)

Plant growth parameters	Previous water deficit treatments	Harvest No. 1	2	3	4	5	Final value as % of control
Tiller No per	C	15 a	20 a	28 a	35 a	38 a	100
plant	S1	13 b	17 b	23 b	27 b	35 a	92
	S2	13 b	17 b	20 b	24 b	30 b	79
		*	**	**	**	**	
Leaf No per	C	33 a	45 a	61 a	74 a	89 a	100
plant	S1	26 b	36 b	48 b	61 b	81 a	91
	S2	8 c	27 c	36 c	47 c	65 b	73
		**	**	**	**	*	
Leaf area per	C	62 a	96 a	128 a	171 a	218 a	100
plant	S1	31 b	53 b	82 b	109 b	196 b	90
(cm^2)	S2	6 c	27 c	53 c	69 c	91 c	42
		**	**	**	**	**	
Dry weight per	C	705 a	1145 a	1359 a	1691 a	2152 a	100
plant	S1	651 b	712 b	893 b	1252 b	1655 b	77
(mg)	S2	509 c	489 c	663 c	918 c	1279 c	59
		**	**	**	**	**	

dry weight. By contrast, after a relatively short period of desiccation (S1), leaf area recovered almost as quickly as tiller number and leaf number, but dry weights did not. This relatively quicker leaf area response after S1 treatment was due to a greater leaf area response under the H temperature regime (Appendix 4.8 a).

2. The detrimental effects of desiccation on plant dry weight were less under the L temperature than under the H temperature regime (Appendix 4.8b). A similar interactive effect of water deficit and temperature on plant growth was reported by Abdelhafeez and Verkerk (1969). They found that under the low temperature regime ($20^{o}/15^{o}C$) the difference in growth and fruit set of tomatoes due to water deficit (up to severe wilting) was less pronounced than that under the higher temperature regime ($35^{o}/19^{o}C$).

3. Plant dry weights after 12 days of recovery growth were much lower for both S1 and S2 plants than those of the control plants of similar physiological age (Table 4.7). This differed from the prairie grass experiment (Expt. 4) where the dry weights recorded after a period of recovery growth were comparable to plants of the same physiological age. The lower dry weights in S1 and S2 plants of the present experiment was due to senescence and the possibility of the use of reserves for respiration during desiccation. Furthermore, recovery in plant dry weight in S1 was slow, and in S2 there was an actual decrease in dry weight immediately following rewatering (harvest 2, Table 4.7). The reduction in plant dry weight in S2 was due to the reduction in root and lamina components and not the sheath component (Appendix 4.7a IX, X, XI). Such reduction in plant dry weight soon after rewatering could be due to the utilization of reserves for respiration and regrowth (Milthorpe and Davidson, 1966).

TABLE 4.8 The influence of temperature on plant growth parameters during the period of recovery.

(H - high temperature; L = low temperature).

Plant growth parameters	Temperature treatments	Harvest No 1	2	3	4	5	Mean over 5 harvests
Tiller No per	H	14	18	25	30	34	24
plant	L	14	17	23	28	36	24
		NS	NS	NS	NS	NS	
Leaf No per	H	19	35	50	62	75	48
plant	L	26	36	48	60	82	50
		*	NS	NS	NS	*	
Leaf area per	H	33	65	109	136	205	110
plant	L	33	52	67	96	132	76
(cm^2)		NS	**	**	**	**	
Dry weight per	H	618	724	950	1279	1583	1031
plant	L	626	824	994	1295	1808	1113
(mg)		NS	*	NS	NS	*	

B. Temperature comparison

Temperature had no influence on the number of tillers per plant nor the number of green leaf numbers per plant in this experiment (Table 4.8). In undefoliated perennial and short rotation ryegrass plants, Mitchell (1954) also reported no difference in tiller number per plant between mean temperatures of 22°C and 14°C. These temperatures represented the mean temperatures measured inside and outside of the glasshouse respectively.

In contrast to the tiller and green leaf number data, temperature had a major incluence on the leaf area per plant (Table 4.8). Plants in the H temperature regime had approximately 45% larger leaf area than those in the L temperature regime when meaned across all harvests (Table 4.8). Most of this difference in leaf area could be attributed to a difference in mean leaf size which was 38% greater in the H than the L temperature regime (Appendix 4.7b VIII). Both mature and immature leaf components contributed towards this difference (Appendix 4.7b VI, VII).

On weighted mean basis, the daily degree-hour mean temperature for the H temperature was equivalent to 17.5°C and that of the L temperature was equivalent to 14.3°C. This rather narrow range of temperature between the 2 temperature treatments could be the main reason for the lack of difference between the dry weights (Table 4.8). The only significant difference was in the dead matter component which was higher under the H temperature regime, due to a higher number of dead leaves (Appendix 4.7b V, XII).

In general, Festucoid grasses have a range of optimum temperature for growth at between 10° and 27°C (Evans *et al.*, 1964). In perennial

ryegrass, the optimum dry weight increment per tiller per day was just below 15°C but the percentage increase was fairly small between 10°C and 25°C (Mitchell, 1956).

C. Cultivar comparison

The major difference between Nui and Ruanui were in mean tiller dry weight, tiller number, green leaf number, mean leaf size and dead leaf number per plant (Table 4.9 and Appendix 4.7c). When averaged across the 5 harvests Ruanui had 24%, 18% and 34% more tiller number, green leaf number and dead leaf number than Nui respectively. But Nui had a 28% heavier mean tiller dry weight and a 24% larger mean leaf size than Ruanui. The larger mean leaf size in Nui could be the result of a faster leaf extension rate (Table 4.5) and a longer interval betwen emergence of 2 successive leaves (Table 4.4) than Ruanui.

However on a per plant basis there was no significant difference between Nui and Ruanui in total leaf area and total dry weight (Table 4.9); nor was there any significant difference in specific leaf area, leaf area ratio and top:root ratio between the cultivars (Appendix 4.7c VII; VIII; XIII).

Nui might have a higher dry matter after a period of severe desiccation (S2) as shown in Figure 4.7, but again on a per plant basis the differences failed to reach statistical significance.

Although results reported in the present experiment indicated that Nui and Ruanui were similar in dry weight on a per plant basis, there was unequivocal evidence that Nui was much heavier, by about 28%, than

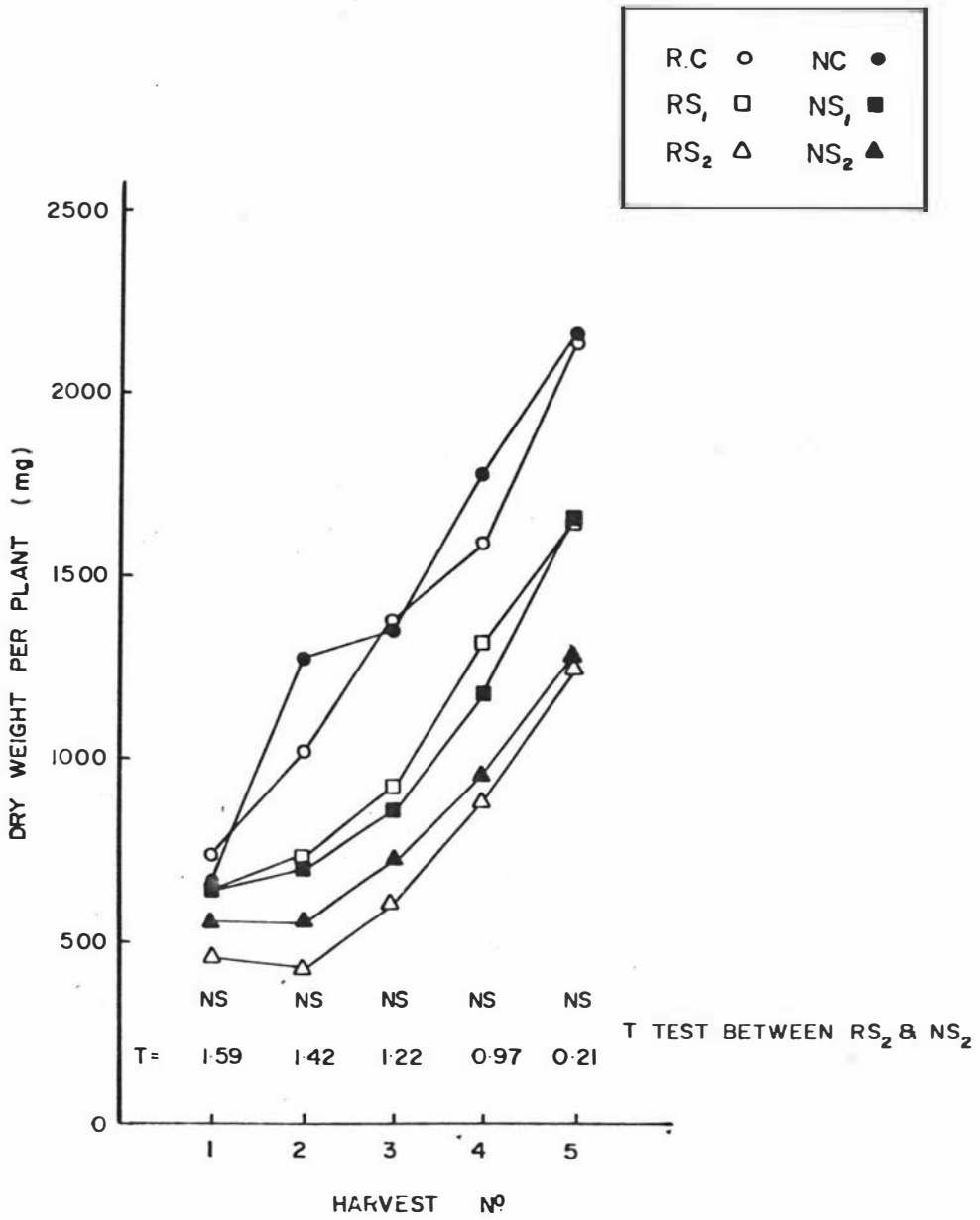


Figure 4.7 Nui and Ruanui dry weight per plant for control, Stress 1 and Stress 2 during the recovery phase. The means were averaged across the two temperature regimes. (mg/plant).

TABLE 4.9 The difference between ryegrass cultivars during the period of recovery (R = Ruanui, N = Nui)

Plant growth parameters	Cultivars	Harvest 1	2	3	4	5	Mean over 5 harvests
Tillers per plant	R	15	19	26	32	39	26
	N	12	16	21	26	31	21
		**	**	**	**	**	
Leaf No per plant	R	24	38	53	67	85	53
	N	21	34	45	55	71	45
		NS	**	**	**	**	
Dead leaf No per plant	R	7.3	6.6	8.7	7.7	9.0	7.9
	N	6.0	5.8	5.6	6.0	6.0	5.9
		**	NS	**	*	**	
Leaf area per plant (cm^2)	R	32	56	87	116	167	92
	N	34	61	89	116	169	94
		NS	NS	NS	NS	NS	
Mean leaf size (cm^2)	R	1.15	1.37	1.57	1.65	1.91	1.53
	N	1.40	1.70	1.94	2.05	2.36	1.89
		**	**	**	**	**	
Dry weight per plant (mg)	R	620	726	968	1263	1687	1053
	N	624	838	976	1311	1704	1091
		NS	*	NS	NS	NS	
Mean tiller dry weight (mg)	R	41.0	37.8	36.4	39.1	44.0	39.7
	N	51.5	49.8	46.2	51.0	55.2	50.8
		**	**	**	**	**	

Ruanui on a per tiller basis, both during desiccation and during recovery.

Many reports cited in the introductory section of this present experiment (section 4.3.2) had commented on the observation that Nui can persist better than Ruanui especially during the dry summer and autumn months and this resulted in Nui having a higher dry matter production in the subsequent seasons. However apart from Sheath *et al.*, (1976), none of the other reports had provided information on tiller density. In Sheath *et al.'s* dryland experiment the tiller density (per m^2) of Ruanui and Nui, 3 years after the commencement of their trial, were 8600 and 18400 for the frequently defoliated and 8400 and 19400 for the infrequently defoliated treatments respectively. It was apparent that under the dryland condition the superiority of Nui over that of Ruanui was the result of this higher tiller density in the Nui sward. The higher mean tiller dry weight recorded in the present experiment (Table 4.9) together with a higher tiller density as reported by the field trials cited above could therefore be the major reason why Nui outyielded Ruanui.

The conclusions from the present experiment together with the conclusions from experiment 3 will be discussed in more detail in the "overview" section (section 6.3).

4.3.4.4 The rate of increase on growth parameters

As discussed in the earlier section (section 4.3.4.3.2A), even after adjusting for physiological age, there were still considerable differences in the growth parameters between the control plants and the desiccated plants by harvest 5. For example, in the case of dry weight per plant, this could be due to senescence during the period of desiccation and

TABLE 4.10 Regression coefficients (b) and coefficient of determination (R^2) for the rate of increase in the four major growth components. (Log_e Y = a + bx).

			Tiller no/ plant		Leaf no/ plant		Leaf area/ plant (cm^2)		Dry weight/ plant (mg)	
Temp.	Cult.	Wtr.	b	R^2	b	R^2	b	R^2	b	R^2
H	Ruanui	C	0.0891	0.85	0.0883	0.86	0.1208	0.86	0.0948	0.90
		S1	0.0834	0.88	0.1000	0.90	0.1870	0.88	0.0778	0.76
		S2	0.0521	0.66	0.1103	0.85	0.1633	0.67	0.0863	0.67
H	Nui	C	0.0850	0.85	0.0892	0.85	0.1101	0.88	0.0847	0.66
		S1	0.0759	0.81	0.0856	0.86	0.1552	0.92	0.0673	0.66
		S2	0.0667	0.87	0.0854	0.77	0.1397	0.77	0.0940	0.77
L	Ruanui	C	0.0741	0.83	0.0738	0.89	0.0837	0.71	0.0752	0.74
		S1	0.0895	0.88	0.0977	0.95	0.1168	0.88	0.0859	0.83
		S2	0.0813	0.85	0.0986	0.89	0.1218	0.85	0.0953	0.88
L	Nui	C	0.0782	0.90	0.0819	0.97	0.0861	0.92	0.0943	0.86
		S1	0.0742	0.88	0.0864	0.93	0.1229	0.88	0.0945	0.83
		S2	0.0783	0.83	0.0967	0.89	0.1213	0.81	0.0620	0.74

TABLE 4.11 Comparisons of regression coefficients from Table 4.10. using F test according to Snedecor and Cochran (1968).

Comparison for	Tiller No/plant		Leaf No/plant		Leaf area/plant		Dry wt/plant	
	F Ratio	P	F ratio	P	F ratio	P	F ratio	P
(a) Water stress								
(C:S1:S2)								
Between H - R	5.59	*	1.25	NS	4.26	*	0.61	NS
H - N	1.09	NS	0.06	NS	3.90	NS	1.12	NS
L - R	0.84	NS	2.41	NS	2.88	NS	1.18	NS
L - N	0.11	NS	0.64	NS	4.26	*	4.31	*
2:54 d.f.								
(b) Cultivar (R:N)								
Between H C	0.10	NS	0.01	NS	0.57	NS	0.37	NS
H S1	0.45	NS	1.59	NS	2.67	NS	0.46	NS
H S2	1.13	NS	2.06	NS	0.42	NS	0.18	NS
L C	0.11	NS	0.64	NS	0.03	NS	1.98	NS
L S1	2.40	NS	1.02	NS	0.16	NS	0.41	NS
L S2	0.06	NS	0.01	NS	0.01	NS	7.70	**
1:36 d.f.								
(c) Temperature (H:L)								
Between R C	1.36	NS	1.46	NS	4.76	*	2.35	NS
R S1	0.34	NS	0.05	NS	13.48	**	0.35	NS
R S2	5.82	*	0.41	NS	1.57	NS	0.31	NS
N C	0.39	NS	0.53	NS	4.72	*	0.31	NS
N S1	0.03	NS	0.01	NS	4.33	*	3.16	NS
N S2	0.86	NS	0.39	NS	0.50	NS	4.70	*
1:36 d.f.								

the use of reserves during the early phase of regrowth. However, the lower values in the previously desiccated plant after 12 days of recovery growth could also be due to a lower rate of recovery relative to the control.

The relative growth rates of the 4 major growth parameters were compared using the regression coefficients of the regression equation ($\log_e Y = a + bX$). The regression coefficients and coefficient of determinations are presented in Table 4.10. The F test between pairs of regression coefficients and their significance levels (P) are presented in Table 4.11.

When the regression coefficients were compared across different treatments (Table 4.11) the following points emerged:

1. The recovery rates for leaf number and tiller number were by and large similar across all the treatments. The two significant tests ($P < 0.05$) for the tiller number comparisons were due to the low values in Ruanui S2 plants under the H temperature regime with a regression coefficient of 0.0521 (Table 4.10).

2. The recovery rates for plant dry weight were similar in most cases except in 3 occasions due to the low rates of recovery in Nui S2 in the L temperature regime with a regression coefficient of 0.0620 (Table 4.10).

3. The most obvious difference in the rates of recovery growth among the 4 growth parameters was in the rate of increase in leaf area. There was no overall difference between the cultivars, but significant differences were found in the temperature and water deficit comparisons.

A closer examination of the leaf area regression coefficients revealed that:

a. recovery rates in the previously desiccated plants were higher than the well-watered control rates, and
b. the rate of increase was higher in the H than in the L temperature treatments.

The pattern of response in the 4 growth parameters was similar to the response recorded for prairie grass experiment (Table 4.2) particularly for leaf area and dry weight parameters. The evidence from this experiment further confirms the suggestion in section 4.2.4.3 that upon rewatering leaf area and dry weight will respond differently.

That leaf area expansion was more severely depressed during desiccation but was strongly stimulated during recovery than was dry weight had also been noted by Hopkinson in tobacco (Hopkinson, 1968). In Hopkinson's study, the experiment was conducted over the entire growing season of the tobacco plant, and the accelerated leaf area expansion was one of the reasons given for the greater final dry weight and leaf area in the previously desiccated plants.

In this experiment, at harvest 1, the leaf area of the S1 plants was 50% that of the control plants (Table 4.7). It reached 90% by harvest 5 (12 days), consequently rates that were higher than those of control plants must have occurred during the recovery phase. If the experiment had continued longer the leaf area of the S1 plants might have reached values similar to, or even greater than those of the control plants.

However, the same could not be said for plant dry weights. The relative dry weights between S1 and control plants changed from 92% during

harvest 1 to 77% by harvest 5, and those of S2 and control plants changed from 72% to 59% over the same period.

CHAPTER V

THE REACTION OF PLANTS TO WATER DEFICIT FOLLOWING ATMOSPHERIC PRE-CONDITIONING

5.1 EXPERIMENT 6 - THE REACTION OF PRAIRIE GRASS TO WATER DEFICIT FOLLOWING ATMOSPHERIC PRE-CONDITIONING

5.1.1 Abstract

In a controlled environment study, the reaction of prairie grass *(Bromus carthariticus)* to desiccation following evaporative demand pre-treatments was compared over a period of 3 weeks. One group of plants were grown under a high (H) vapour pressure deficit (VPD) pre-treatment (2.0/0.2 kPa VPD) for 5 weeks before half of the plants were transferred to a low (L) VPD environment (0.5/0.2 kPa VPD). The plants under the continuous high VPD were designated as HH and those that were transferred to the low VPD at week 5 as HL plants. A second group of plants were grown initially at low VPD before half were transferred to high VPD conditions. These were designated as LL or LH accordingly. After transfer, water was withheld from some of the plants until the extension growth of the youngest leaf ceased for 3 hours (S1) or 24 hours (S2). The growth responses of these plants were compared with those of the well-watered control.

Under well-watered conditions the leaf area of the individual leaves followed closely that of the environment under which they were unfolding rather than previous environments. Leaf area and plant dry weight of the desiccated plants was lower than those of the control. However, there was no difference which could be attributed to the pre-treatments.

Leaf water potentials when wilting was first evident were between -1.30 and -1.40 MPa for all treatments. In all the treatments the plants reached the S1 level of desiccation in about the same number of days. By contrast, the HL plants took 4 days longer to reach the S2 level of desiccation than the other treatments. This could be due to its more efficient rate of water use as a result of adaptation. Under well-watered condition the transpiration rates per unit leaf area of the LL, HH and LH plants relative to the HL plants (100%) were 159%, 250% and 309% respectively. No statistically significant differences were detected in the pattern of wax deposition, stomatal density, epidermal cell numbers and the slope of the moisture release curve between plants of different pre-treatments.

5.1.2 Introduction

Drought hardening refers to the exposure of plants to a moderate level of water deficit which results in the development of an apparent "adjustment" in the plant. This "adjustment" enables the plant to grow and function better than it normally would when desiccated again. In most cases so far reported drought adaption in higher plants is by avoidance rather than actual tolerance of low water potential.

There are a number of reports of the ability of higher plants to adapt to drought conditions by hardening (Levitt, 1972). It varies from the development of drought hardening by pre-treating wheat seeds (Woodruff, 1969) to a more efficient water usage by pre-conditioned maize plants (McPherson and Boyer, 1974). Similarly, in pasture grasses, the reduction in leaf area through the reduction in leaf growth and accelerated leaf death can also be regarded as an adaptative mechanism (Turner and Begg, 1978). These adaptative mechanisms allow the plants to last longer under

a condition of limited soil moisture supply by means of drought avoidance. In contrast, examples of adaptation through the development of drought tolerance, such as osmotic adjustment in higher plants (e.g. in sorghum leaves (Jones and Turner, 1978))are few (for discussion see Section 2.6).

However, not all plants will harden. For example millet and one variety of wheat showed no sign of adaptation after a pre-droughting period of 2 to 6 weeks, whereas another variety of wheat and two varieties of barley adapted by becoming more drought tolerant (Levitt, 1972). Whether this is related to a function of degree or duration of stress or both, is not known.

Severe desiccation can be induced via a high evaporative demand, such as that under a hot, dry Föhn wind on the east coasts of both islands in New Zealand. Low humidities under controlled conditions had been used to induce adaptation (McPherson and Boyer, 1974). They grew two groups of maize, one under a low humidity (VPD of 2.6/0.5 kPa, day/night) and the other under a high humidity (VPD of 0.5/0.2 kPa) during the vegetative stage. At tassel emergence, the low humidity room was changed to high humidity conditions. Both groups were well watered until fertilisation was completed. Water stress was imposed by withholding water from the soil. The desiccated plants were given small quantities of water which maintained the leaf water potentials at approximately -2.00 MPa during the grain filling stage. Final dry matter yield was 27% higher in the low humidity pre-treatment plants. The authors claimed that the adaptative mechanism was mainly related to the plant's ability to conserve water. The low humidity pre-treated plants used 33% less water per unit leaf area than the high humidity pre-treated plants.

In this chapter the adaptation of prairie grass to different vapour pressure pretreatments is reported.

5.1.3 Materials and methods

Prairie grass (*Bromus catharticus* Vahl. c.v. Grasslands Matua) were grown from seed in controlled climate rooms. The plants were grown in 2.25 litre pots in a mixture of Opiki peaty loam (70% by volume) and river sand (30%). The plants were thinned from 15 to 3 per pot by week 5. Selection was based upon evenness of leaf development and size.

Two climate rooms, one with high (H) and one with low (L) evaporative demands were used. All other environmental conditions were similar. The conditions were:

Temperature (day/night) $22.5^{o}/12.5^{o} \pm 0.5^{o}C$

Carbon dioxide concentration uncontrolled

Light (Photosynthetically active irradiance)

170 W/m^2 (0.4 - 0.7 μ m wave band from Sylvania metal arc and Philips tungsten iodide lamps)

Duration 12 hours photoperiod.

Relative humidity (day/night)

High evaporative demand (H) 26/86 ± 5%, equivalent to 2.0/0.2 kPa air vapour pressure deficit (VPD)

Low evaporative demand (L) 81/86 ± 5%, equivalent to 0.5/0.2 kPa VPD.

Diurnal changes in temperature and VPD occurred gradually over 4 hours immediately inside the photoperiod. Plants were fed with

modified Hoagland's solution at 200 ml per pot 30 minutes before the dark period.

At 5 weeks from sowing (beginning of leaf 6, designated day 0) half of the plants (72 pots) in the H room were exchanged with half of the plants (72 pots) in the L room. Plants that were grown continuously under the high evaporative demand were termed HH and plants grown continuously under the low evaporative demand were termed LL. Those that were exchanged were termed either HL (from H to L rooms i.e., a dry pre-treatment) or LH (from L to H rooms i.e., a wet pre-treatment).

For each group of plants (viz. the LL, HL, HH and LH) the following soil desiccation treatments were imposed.

Control (C)-- well watered, each pot receiving 200 ml nutrient per day.

Stress 1 (S1)-- water withheld from day 0 until the extension growth of the youngest leaf between 2 consecutive measurements 3 hours apart had ceased. Thereafter watered as in control.

Stress 2 (S2) -- water withheld from day 0 until the extension growth of the youngest leaf had ceased over a period of 24 hours. Thereafter watered as in control.

Changes in the length of the youngest leaf (sum of lamina and sheath extension) were measured at 3 hourly intervals during the day period. The measurements were taken with a ruler placed against the base of the plant using the soil surface as a reference point. There were eight replicates in each treatment. The same plants were used for each successive leaf length measurement.

Measurements of leaf water potentials (LWP) and relative leaf water content (RLWC) commenced when 50% of the leaves used in leaf extension measurements had reached the defined stress levels. For S1 this occurred 5 to 6 hours into the day period and for S2 this was at the beginning of the day period. Measurements of LWP and RLWC were taken over the next 24 hours.

Leaf water potentials were measured with a pressure chamber (Boyer, 1969) and RLWCs were measured according to the method described by Barrs and Weatherley (1962) after floating the leaf segments in distilled water for 2 hours under laboratory light and temperature conditions.

Samples for LWP and RLWC were taken from the second youngest leaf of the plant. The upper half of the laminae (distal) was used for LWP measurements and the lower (basal) half used for RLWC determinations. Leaf water potentials and RLWCs were measured within the period from the last 30 minutes of the night period until the end of the day period (i.e., 12½ hours). During each sampling time at least 2 sets of samples were taken at random from each of the treatments. The values presented are the means of these samples.

Except for days 2, 3 and 4 of the transpiration experiment, all leaf area measurements were taken with the electronic leaf area meter. For days 2, 3 and 4 of the transpiration experiment the laminae area (LA) for each plant was determined by using the pre-determined regression equation (Appendix 5.1).

$$LA = -26 + 0.802\ (l \times w) \quad (R^2 = 0.91)$$

where LA = lamina area of leaf

l = length of leaf

w = width at ½ l.

For each plant, all the exposed leaves were measured.

Water use for the control plants were measured by weighing the pots 24 hours after watering to a pre-determined weight. Eight "soil only" pots were used as "blank-controls". Transpiration rates per unit leaf area over 24 hours were calculated from the water use per pot (less the "blank-control") and the sum of the laminae area of all the leaves of that pot. Plant dry weights (excluding roots) were determined after drying at 35^{o}C for 24 hours in a vacuum assisted oven. One group of the plants (4 replicates) were harvested at the end of the desiccation treatment (between week 6 and 7 depending on the treatment), designated as the first harvest. The other group of plants (4 replicates) were harvested 1 week after the plants were rewatered (between week 7 and 8), designated as the final harvest.

All secondary tillers were removed as soon as they appeared. Measurements were taken only on the main plant. The effect of removing the secondary tillers on the performance of the main plant was investigated in a separate experiment (Appendix 5.2). As concluded in Appendix 5.2, removing the secondary tillers had no apparent influence on the performance of the leaves of the main plant.

5.1.4 Results and Discussion

The effects of different vapour pressure deficit (VPD) on dry weight and leaf area of the well watered control plants were evident throughout the duration of the experiment (Table 5.1a). By the final harvest (week 7-8), LL plants were twice as heavy as the HH plants.

TABLE 5.1 Effects of different evaporative demands on plant dry weight (DW) and lamina area (LA) of well-watered control plants

(a) DW and LA per plant

Treatments		LL	HL	HH	LH	LSD 5%	CV%
First harvest (wk 6-7)	DW (mg)	58.7	54.1	36.7	53.3 **	10.9	14
	LA (cm^2)	11.2	11.1	6.6	11.9 *	3.1	19
Final harvest (wk 7-8)	DW (mg)	116.1	104.2	59.5	92.2 **	18.8	12
	LA (cm^2)	20.6	19.3	11.8	15.1 *	5.1	19

(b) Mature lamina area of individual leaves at final harvest

Treatments	LL	HL	HH	LH	LSD 5%	CV%
Leaf No. 2	1.1	1.2	1.2	1.1 NS	-	17
3	1.8	1.5	1.8	1.7 NS	-	19
4	2.7	1.9	1.9	2.4 **	0.4	13
5	3.4	2.4	2.4	3.0 **	0.5	13
6	4.3	3.3	3.1	3.4 **	0.6	11
7	4.5	4.1	2.9	3.6 *	0.9	15

NS = non-significant at 5% level of probability

** = $P < 0.01$

* = $P < 0.05$

The influence of the VPD treatments started from leaf 4 (Table 5.1b), with the pre-transfer low evaporative demand plants (LL and LH) having a significantly larger ($P < 0.05$) leaf area than those of the pre-transfer high evaporative demand plants (HH and HL). The plants were transferred at week 5, when leaf 4 had just matured (i.e., when its ligule had emerged from the preceding leaf sheath), leaf 5 was about 2/3 emerged and leaf 6 just emerging. By the time leaf 7 matured, its leaf area had been influenced mainly by the new environment in the transferred treatments (i.e., HL and LH).

That leaf growth will adjust quickly to the new environment and will reflect characteristics typical of the new environment has been demonstrated in tall fescue by Robson (1974). Although the plants were grown from seed in the controlled conditions, it was not known why leaves 2 and 3 did not also show characteristics of the respective rooms (Table 5.1b).

Within each of the soil desiccation treatments (i.e., S1 and S2) no difference in plant dry weights and leaf areas were detected among evaporative demand treatments (Table 5.2a). Similarly, different evaporative demands did not cause any significant difference between leaf areas of leaves 5 and 6 (Table 5.2b). In the stress treatments leaf 7 was not matured when the plants were harvested.

In the present experiment although leaf tips were wilting, leaf extension rates still continued but at a much lower rate. This could be due to the fact that the region of leaf extension at the base of the leaf might have a higher leaf water potential than the exposed distal end where leaf water potential measurements were taken (Experiment 2).

TABLE 5.2 Effects of different evaporative demands on plant dry weight (DW) and lamina area (LA) of desiccated plants.

(a) DW and LA per plant at first harvest

Treatments	LL	HL	HH	LH	LSD 5%	CV%
Stress 1 DW (mg)	35.6	31.1	23.5	29.6 NS	-	18
LA (cm^2)	6.0	5.1	5.2	5.4 NS	-	21
Days to reach	5	5	4	5		
Stress 2 DW (mg)	31.2	32.7	23.8	27.1 NS	-	18
LA (cm^2)	5.7	6.9	4.8	5.9 NS	-	22
Days to reach	6	10	5	6		

(b) Mature lamina area of individual leaves at final harvest

Treatments		LL	HL	HH	LH	LSD 5%	CV%
Stress 1	Leaf No. 4	2.6	1.7	1.7	2.3 *	0.5	20
	5	2.6	2.2	1.8	2.5 NS	-	22
	6	2.1	2.1	1.6	2.2 NS	-	15
Stress 2	Leaf No. 4	2.2	1.7	1.7	2.4 *	0.3	10
	5	2.7	2.0	2.0	2.3 NS	-	23
	6	2.5	2.0	1.6	1.6 NS	-	34

The leaf water potential where wilting was just visible (leaf tips just started to lose turgidity) were similar for all treatments at about -1.30 to -1.40 MPa. These values were similar to the upper limits of the "critical leaf water potentials" - leaf water potential when turgor potential was zero - reported for maize and sorghum by Neumann *et al.*, (1974).

The minimum leaf water potentials at which leaf extension stopped for 24 hours (i.e., S2) were between -1.50 and -3.10 MPa depending on treatments and time of the day when the samples were taken. Using only measurements collected during the dark period (30 minutes before the day period) the leaf water potentials were -1.50, -1.50, -1.50 and -2.00 MPa for LL, HL, HH and LH treatments respectively.

The longer interval required for the HL plants to reach S2 desiccation level (10 days) relative to the other pre-treatment plants (ranging from 5 to 6 days), and its higher although statistically non-significant dry weight and leaf area per plant at S2 (Table 5.2a) suggested that the HL plants could have developed some degree of drought adaptation.

Drought adaptation can take 2 forms. It can be a tolerance to, and/or an avoidance of, low internal plant water content. The relationship between leaf water potential and relative leaf water content, termed the moisture release curve (Jarvis and Jarvis, 1965), could be used as a means of measuring drought tolerance in plants. Jarvis and Jarvis (1965) claimed that the slope of the moisture release curve could be used to indicate relative drought tolerance because under water deficit conditions, plants that lost a smaller volume of water for a given unit reduction in leaf water potential would have an advantage over those with a steeper gradient. This was supported by Sanchez-Diaz and Kramer

TABLE 5.3 Linear regression equations (Y = a + bX) fitted through the data sets in Figure 5.1. (where Y = Relative leaf water content (RLWC), and X = leaf water potential (LWP) in bars).

Treatments	Regression equations	R^2
LL	RLWC = 99 - 1.04 LWP	0.85
HL	RLWC =101 - 0.94 LWP	0.84
HH	RLWC =100 - 1.01 LWP	0.78
LH	RLWC =103 - 1.18 LWP	0.85

F test (according to Snedecor and Cochran, 1968) for regression coefficients between treatments, was non-significant.

TABLE 5.4 Effects of different evaporative demands on the transpiration rates of well watered control plants (μg H_2O $cm^{-2}s^{-1}$).

Treatments	Days from transfer				Mean over 4 days	% relative to HL
	2	3	4	5		
LL	0.9	1.0	1.1	1.3	1.08	159
HL	0.7	0.6	0.6	0.8	0.68	100
HH	1.4	1.6	1.9	1.9	1.70	250
LH	1.6	1.9	2.4	2.5	2.10	309
Significance	**	**	**	**		
LSD 5%	0.4	0.5	0.4	0.4		

(1971) who found that maize lost more water than sorghum at the same leaf water potential, this the authors claimed, reflected the drought tolerant characteristics of sorghum. More recently, Jones and Turner (1978) have shown that changes in the relationship of the moisture release curve will depend on the plant's previous stress history. Using 2 cultivars of sorghum, they reported that during a quick drying cycle, previously stressed plants were able to maintain higher tissue water content than control plants at the same leaf water potential.

The relationship between leaf water potential and relative leaf water content for the 4 treatments are presented in Figure 5.1. Linear regressions of the form (Y=a + bX) were fitted through the data sets in order to compare their respective slopes. As shown in Table 5.3, no statistically significant difference was detected.

In the present experiment, although the HL plants (Figure 5.1b), had the lowest slope of 0.94 (Table 5.3) the data were not sufficiently consistent to detect whether or not differences in drought tolerance occurred.

The relationship between leaf water potential and relative water content can be different depending on species (Ehlig and Gardner, 1964), plant age and environmental conditions (Knipling, 1967; Millar *et al.*,1968). Furthermore, some workers (e.g., Whiteman and Wilson, 1963; Knipling, 1967) found that the scattered nature of the data made the errors too large for useful comparisons.

Drought adaptation can also occur through a mechanism of avoidance. For example, McPherson and Boyer (1974) found that grain yield in maize plants subjected to a soil desiccation cycle during the grain filling

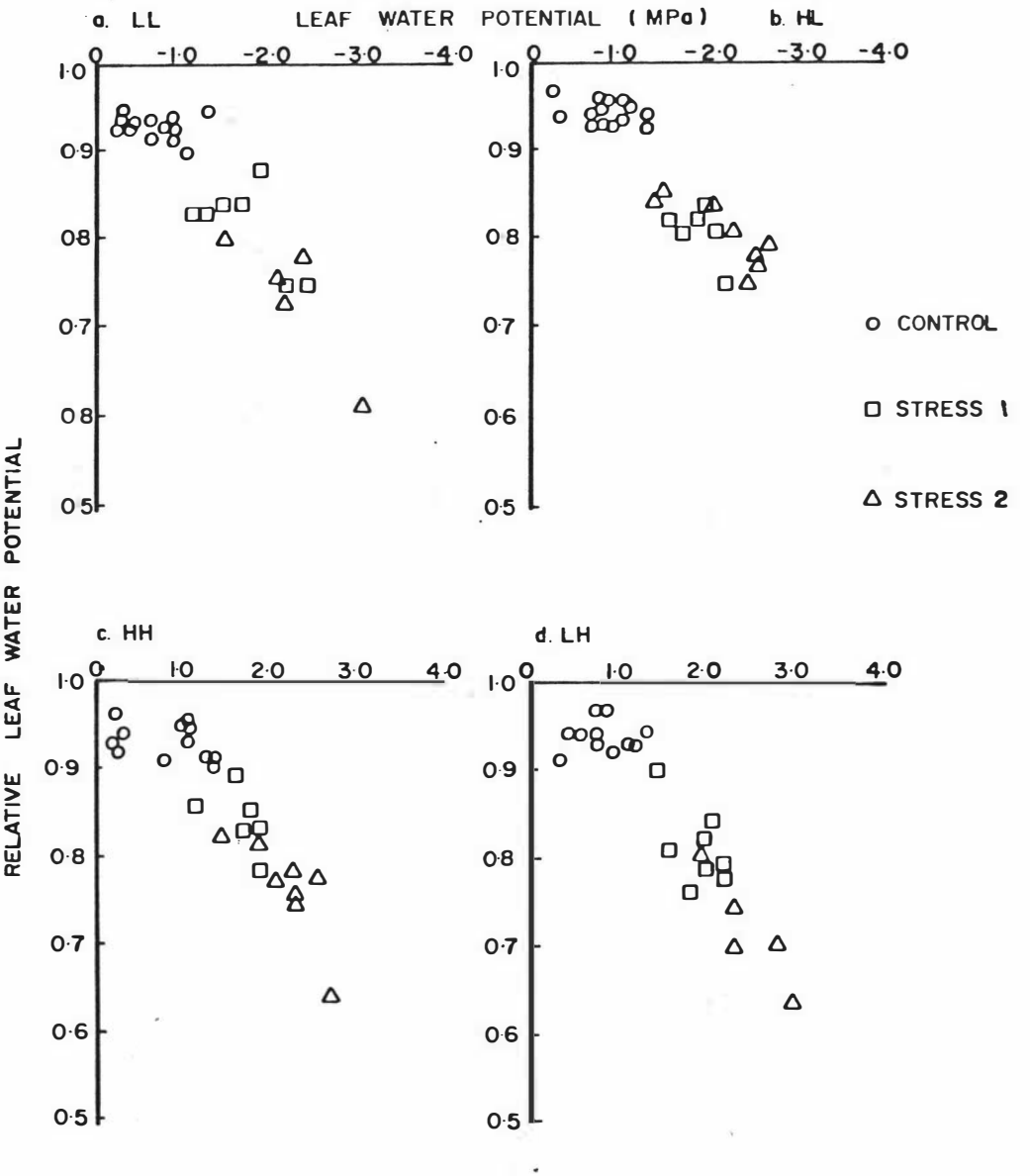


Figure 5.1 Relationships between leaf water potential and relative leaf water content of the 4 different environments. (a) LL, (b) HL, (c) HH and (d) LH.

period was 27% higher in the plants that had a high evaporative demand (dry) history than those plants with a low evaporative demand (wet) history. The pre-conditioning was done during the vegetative phase. The authors claimed that the higher grain yield was due to the more efficient rate of water use by the plants with the dry pre-treatment history.

In the present experiment, supportive evidence for drought avoidance was demonstrated from a separate experiment conducted at the same time and in the same rooms. Transpiration rates ($\mu g\ H_2O/cm^2/sec$) of the well-watered plants were compared across the 4 treatments during the first 5 days after transfer (Table 5.4). The mean transpiration rates per unit leaf area (averaged over 4 days) for the LL, HH and LH plants relative to the HL plants (100%) were 159%, 250%, and 309% respectively.

Although the transpiration rate response recorded in this present experiment was similar to that reported by McPherson and Boyer (1974), the extent to which the transpiration rates could be different during the soil drying cycle is not known.

At the end of week 8, leaf samples were taken from the mid section of leaf 6, and these were examined under a scanning electron microscope. Counts made on 20 fields (2 plant replicates, 10 fields each) failed to detect any significant difference in stomatal density and epidermal cell numbers between the treatments (Table 5.5). Nor was there any consistent difference in the pattern or thickness of wax deposition on the leaf surfaces between the treatments.

TABLE 5.5 Effects of different evaporative demands on stomatal density and epidermal cell numbers of well-watered plants. Using scanning electron microscopy. 200 x magnification.

Treatments	Stomatal density No/field	Epidermal cell No/diameter
LL	16.7	30.5
HL	26.0	31.7
HH	18.5	28.7
LH	16.5	28.7
Significance	NS	NS
c.v.	28%	11%

Values are means of 20 counts (2 replicates of 10 fields each)

The value of water potential can be influenced by adjustments in osmotic potential and many reports have emphasised the importance of osmotic adjustment (e.g. Meyer and Boyer, 1972; Neumann *et al.*, 1974; Turner, 1974; Jones and Turner, 1978). Since osmotic potential was not measured in this present experiment, its influence in the HL leaf water potentials was not known.

In summary, the present experiment has demonstrated that adaptation, in the form of avoidance, can develop in prairie grass after a period of "dry" atmospheric pre-conditioning. The lower rate of transpiration per unit area has allowed these "hardened" plants to grow longer into the desiccation period. However, the actual mechanism (s) of the avoidance action by these plants is not known.

CHAPTER VI

OVERVIEW AND CONCLUSION

In this chapter results and conclusions from experiments reported in the earlier chapters will be discussed in relation to the objectives as stated in Chapter I, and to the current stage of knowledge in this field. Possible future experimentation to resolve some of the queries arising from this research will also be presented.

6.1 THE SENSITIVITY OF LEAF EXTENSION TO PLANT WATER DEFICIT

Between 1968 and 1971 a number of papers illustrated that leaf extension growth is very sensitive to changes in plant water status. Leaf extension/enlargement declined rapidly at leaf water potential below -0.2 MPa and for the species studied, leaf extension stopped at potentials between -0.7 and -0.9 MPa (Boyer, 1968, 1979a; Hsiao *et al.*, 1970; Acevedo *et al.*, 1971). These reports together with the observation made by Loomis (1934) that in Iowa, maize growth occurred mainly at night when evaporative demand was lower rather than during the day, implied that plants might experience levels of water deficit which could restrict green herbage production. This led to the suggestion that using light sprinkling or mist irrigation during periods of high evaporative demand, could increase growth (Kramer, 1963; Salter and Goode, 1967; Hanan, 1972; Jackson, 1972; Rawling and Raats, 1975). Thus, the idea of increasing growth by reducing evaporative demand appeared to have some application in the field.

A number of papers reporting on the magnitude of the diurnal leaf water potentials of some crop and pasture species indicated that the day-time leaf water potential would be near to if not actually

inhibiting leaf extension growth (Cary and Wright, 1971; Jordan and Ritchie, 1971; Dougherty, 1972; Jackson, 1974). However in none of these studies were leaf water potential and leaf extension rate measured simultaneously. In order to confirm that leaf extension growth would actually stop at the low leaf water potentials indicated by Boyer (1968, 1970a), Hsiao *et al.*,(1970) and Acevedo *et al.*,. (1971), a field experiment was conducted in 1973/74 with the aim of defining the relationship between leaf water potential and leaf extension rate. As concluded in section 3.2.4.3, the results from the sudax experiment (Experiment 1) would not have been predicted from the evidence available in the literature at that time.

At about the same time (1974/1975) a number of papers were publishd reporting results which were similar to those of the sudax experiment (McCree and Davis, 1974; Watts, 1974). McCree and Davis (1974) reported that under laboratory conditions sorghum leaf expansion continued day and night at the same rate despite a diurnal change in leaf water potential of -0.1 to -0.9 MPa. In the field, sorghum leaf growth did not cease until about -1.7 MPa (McCree and Davis, 1974). Similarly, Watts (1974) using field grown maize reported that leaf water potential of -0.8 to -0.9 MPa had no apparent effect on leaf growth, whereas leaf extension in maize grown in a controlled climate room was almost nil at that same level of leaf water potential.

The apparent discrepancy between these reports and those of Boyer, Hsiao *et al.* and Acevedo *et al.* mentioned earlier might be due to the different environmental conditions when measurements of leaf water potential were made.

Results from the prairie grass experiment (Experiment 2) clearly indicated that there was a family of curves for the relationship

between leaf water potential and leaf extension rate (Figure 3.6) depending on the environmental conditions at the time of measurement.

For grasses, at least, where the normal site of leaf water potential measurement differed from the site of elongation, the measured leaf water potential could be influenced by 2 factors.

(i) osmotic adjustment, and/or
(ii) leaf water potential gradient along the leaf.

Stress induced change in solute concentration or osmotic adjustment had been reported by a number of workers (e.g., Gavande and Taylor, 1967; Meyer and Boyer, 1972; Brown *et al.*, 1976; Jones and Turner, 1978). Hence in water stress studies it is important that osmotic potential should also be measured. The decrease in leaf water potential may be matched by a similar reduction in osmotic potential leading to an apparently lower leaf water potential with no change in turgor potential.

The possibility of a leaf water potential gradient between the tip and the base of graminae leaf had been discussed in section 3.3.4.2.

More recently, Wiebe and Prosser (1977) examined mature maize leaves at tasselling and detected a gradient of 0.2 to 0.4 MPa from the tip to the base of the leaf under either dry or wet conditions. From the soil to the base of the leaf there was another gradient of approximately 0.4 MPa.

In addition to those factors discussed above, other factors such as the size of pots and the levels of irradience frequently used in growth rooms could also contribute towards this discrepancy (Begg and Turner 1976).

In the absence of adequate information such as temperature and turgor potential, the normalisation procedure suggested in section 3.3.4.2 could assist in relating rates of leaf extension and leaf water potential across different environments.

Although results from experiment 2 fitted the normalisation procedure nicely, only results from the high temperature treatment of experiment 3 followed a similar pattern. The data from the low temperature treatment of Experiment 3 did not follow a single relationship upon normalisation.

From the evidence obtained so far it can be concluded that:-

1. In the early stages of desiccation, leaf extension rates are extremely sensitive to desiccation but are less sensitive when desiccation becomes more severe.

2. The relationship between leaf extension rate and measured leaf water potential in grasses is not unique, but will vary dramatically within one group of plants over short periods depending on environmental conditions.

3. Although some discrepancies can be resolved by allowing for the action of other influences, such as temperature, unless the water potential and its components (osmotic potential and turgor potential) at the site of measurement can be related unequivocally to the water potential and its components at the zone of elongation, no firm conclusions can be drawn.

6.2 THE EFFECTS OF WATER DEFICIT ON SUBSEQUENT PLANT RECOVERY GROWTH

In this section the following 2 aspects will be discussed:-

1. The relative sensitivity of different growth parameters to desiccation.

2. The effects of water deficit on subsequent recovery from different growth parameters.

6.2.1 The relative sensitivity of different growth parameters to water deficit

The pattern of response in the prairie grass and the ryegrass experiments was similar, hence only results from the ryegrass experiment (Experiment 5) will be used to illustrate the relative sensitivity of the different growth parameters to water deficit. The growth parameters measured, viz., tiller number, leaf number, leaf area and dry weight per plant, will be grouped into the following 3 categories for discussion.

(a) that associated with "survival" of the plant, as represented by tiller numbers,

(b) that associated with the photosynthetic areas, as represented by leaf numbers and leaf area, and

(c) that associated with green herbage production, as represented by the different dry weight components.

(a) Tiller numbers

Tiller number was the least sensitive to desiccation. Even at the relatively severe water deficit level of S2, no death of tillers was recorded. At the end of 15 days of desiccation (i.e., end of S2) the number of viable tillers was the same as that of S1, and was only 13% less than that of the control plants of similar physiological age (Table 4.7). In this experiment, reductions in tiller numbers were from the suspension of tiller production rather than accelerated death of existing tillers. Within each existing tiller, the immature leaves were still green. This indicated that tillers, once formed, could survive a fairly severe level of desiccation by remaining "dormant".

Following the dry summer conditions in the field, plants with a greater number of viable tillers will be better able to respond to the autumn rain. Sheath *et al.*, (1976) observed that in North Otago the persistancy of Nui was related to the number of viable tillers or tiller buds at the end of the summer drought

(b) Leaf numbers and leaf area

Leaf number and leaf area parameters responded similarly to desiccation. They were both reduced soon after the start of the desiccation period, particularly the leaf area (Figure 4.5), reflecting its very sensitive response to water deficit. However, both parameters recovered quickly upon rewatering (Table 4.7 and Table 4.10).

That tissues of different maturity status could have different ability to tolerate drought was further demonstrated (Table 6.1). The values used to calculate the mature to immature ratios were taken from Harvest 1, Table 4.7. For leaf numbers, this ratio was approximately 1:1 and for leaf area this ratio was approximately 2:1, for both the control and Stress 1 treatments. On the other hand, in S2 plants, the ratios were much lower, thus reflecting a greater "tolerance" to desiccation by the immature leaf components.

Reductions in leaf area during desiccation can be regarded as a means of drought adaptation by the plant (Begg and Turner, 1976; Turner and Begg, 1978). The reduced leaf area will help the plant to conserve soil water. The rapid expansion of leaf area upon relief of water deficit can also be regarded as an advantage. The sooner the plant draws on current photosynthate for regrowth the lesser the dependence it will have on reserves.

TABLE 6.1 Ratio of mature to immature leaf components at the end of the desiccation periods (values were from Harvest 1, Table 4.7).

		Control	Stress 1	Stress 2
Leaf number per plant	Mature (M)	17.3	13.3	2.5
	Immature (I)	16.1	12.9	6.1
	Ratio M/I	1.07	1.03	0.41
Leaf area per plant (cm^2)	Mature (M)	40.3	20.9	2.4
	Immature (I)	19.6	10.5	3.5
	Ratio M/I	2.06	1.99	0.69

(c) Plant dry weights

Sensitivity of green herbage dry weight per plant to desiccation was intermediate between those of tiller number and leaf parameters. Dry weight reductions at the end of S1 and S2 treatments were 8% and 28% of control plants respectively (Table 4.7). The reduction in dry weights during desiccation was mainly due to senescence and possibly also to respiratory losses.

Although water deficit reduced the dry weight of the whole plant, different plant parts had different degrees of sensitivity to desiccation. For example, roots were reduced during desiccation but the reduction was less than the reduction in the laminae component. On the other hand, sheath dry weight actually increased during desiccation, even under S2 treatment (Harvest 1, Appendix 4.7a).

6.2.2 The effects of water deficit on subsequent recovery of different growth parameters

In this section, the following parameters will be used to illustrate the different patterns of recovery growth recorded in the experiments:

(a) the rate of dry weight increase,
(b) the rate of leaf area expansion,
(c) the rate of leaf extension.

(a) The rate of dry weight increase

Within 3 days of rewatering, in both Experiment 4 (Figure 4.3) and Experiment 5 (Table 4.7), there was a reduction in dry weight in the previously desiccated plants. This initial reduction in dry weight could be due to the mobilisation of reserves for regrowth (Milthorpe and Davidson, 1966). A similar pattern of reduction in plant dry weight was recorded for severely defoliated ryegrass swards during the first 3 days of regrowth by Meads (1975).

Considering that rates of net photosynthesis are usually depressed following desiccation, the dependence of reserves for regrowth may be greater in plants recovering from desiccation than from defoliation. Although Vartha (1979) has indicated the possibility of carbohydrate reserves being important during the recovery from water deficit in ryegrass, the extent to which carbohydrate reserves are related to desiccation responses, such as drought resistance and the speed of recovery, are largely unknown. Further work should be done to establish this relationship.

In order to compare the direct response to water deficit between different treatments during the recovery phase, it was necessary to adjust for the delay in ontogeny in the previously desiccated plants. The importance of such physiological adjustment had been indicated and discussed by Ludlow and Ng (1974).

In this study (Experiment 4 and Experiment 5) physiological adjustment was made by using the criteria of "drought" days, which was defined as "any day for which all the leaves were wilted during the day period" (section 4.2.4.3). The "drought day" adjustment method is a simple model using wilting as the criterion. The implication that growth stops when wilting is evident and will return to control rate on the first "non-drought day" is an over-simplification. However, if this simple relationship can be used in a wide enough range of conditions, it will be useful, at least as a first approximation to see whether a "positive" or "negative" carryover effects have occurred.

As concluded in Experiment 4, after allowing for "drought" days the dry weights of the previously desiccated plants followed closely to those of the control plants (Figure 4.4). This indicated that in Experiment 4 there was no "positive" nor "negative" carryover effects.

The model fitted the data of Experiment 4 because the dead matter component was relatively small (5% of total herbage yield for S3). In contrast, using the same adjustment method for Experiment 5, the dry weights of previously desiccated plants were much lower than those of the control plants of similar physiological age (Table 4.7). In this case, the model had detected a "negative" carryover effect due to severe desiccation. The reduction in dry weights of the previously

desiccated plants was due to senescence. In Experiment 5, dead matter reached 31% that of total herbage at the end of the S2 desiccation treatment.

The "drought day" adjustment method is useful as a first approximation but it does not compare the relative rates of recovery. One of the ways to compare relative rates of recovery is to compare the relative growth rates of plants from different treatments. In the present experiment, relative growth rates were calculated by using the regression equation, $\log_e Y = a + bX$, where b, the regression coefficient, represents the relative growth rate (Hughes and Freeman, 1967; Radford, 1967). Although this technique will not reveal short term responses, such as that of the initial reduction reported in Experiment 5 it has the advantage that it is independent of the position on the "time" axis (X-coordinate).

As concluded in Experiment 4 and Experiment 5, there was no statistically significant difference between the different treatments for the relative rates of dry weight increases. Dry weight results from the present study were in agreement with the conclusion of Ng *et al.*, (1975), in that after allowance was made for physiological age, there was no real evidence of higher relative growth rates in the previously desiccated plants than those of the well-watered control.

(b) The rate of leaf area expansion

In contrast to the relative rates of dry weight increase, the relative rates of leaf area expansion in the previously desiccated plants, for both Experiment 4 and Experiment 5, were higher than those of the control plants of similar physiological age (Table 4.2

and Table 4.10). In experiment 4 the relative rates of leaf area expansion were between 28% and 51% faster, and in Experiment 5 the rates were between 27% and 55% faster than their respective control rates.

Higher rates of leaf area expansion after a period of water deficit had also been reported by Hopkinson (1968) in tobacco. Hopkinson found that the "accelerated" rates were slow to develop but were prolonged in duration. By the end of the growing season, the plants that had been subjected to the most severe desiccation acquired the greatest final total leaf area and dry weight.

In the present study, the duration of the recovery periods for both Experiment 4 and Experiment 5 was not long enough to see whether the accelerated leaf area expansion rate would eventually lead to a higher "final" dry weight in the previously desiccated plants. Such response, if occured, would represent a true "compensatory" growth.

(c) The rate of leaf extension

An accelerated rate of leaf extension was recorded on relief of desiccation in the prairie grass experiment (Experiment 4) but not in the ryegrass experiment (Experiment 5) (Figure 4.2 and Figure 4.5).

Upon relief of mild water deficit, higher rates of leaf extension/enlargement in the desiccated plants than the well-watered control were reported in sunflower (Boyer, 1970a), maize (Hsiao *et al.*, 1970;

Acevedo *et al.*, 1971), ryegrass (Lawlor, 1972) and *Panicum maximum* (Ludlow and Ng, 1977). The duration of this "higher" rate varied considerably. For example, in the cases reported by Boyer, Hsiao and Acevedo *et al.*, the higher rates were only transitory, lasting for a fraction of an hour. In Ludlow and Ng's experiment the higher rates lasted 33 hours and in Lawlor's experiment the higher rates lasted 8 days. By comparison, the higher rates reported in Experiment 4 lasted over 28 days during which 4 to 5 new leaves had emerged.

Whether the accelerated rates will occur and for how long, will probably depend on the duration and severity of water deficit. For example, in maize, when the deficit was brief, full recovery was possible, but if the deficit was severe or prolonged, full recovery would not occur (Acevedo *et al.*, 1971).

The relative sensitivity of cell division and cell enlargement to water deficit was suggested as the reason for the accelerated leaf extension rate recorded in the prairie grass experiment. A similar explanation was also offered by Ludlow and Ng (1977) for their results. The lack of accelerated response in the ryegrass experiment was probably due to the more severe level of water deficit imposed rather than a species difference. That accelerated leaf extension rate could occur in previously desiccated perennial ryegrass plants was shown by Lawlor (1972).

From the evidence presented in this section it may be concluded that:

1. Tiller numbers were the least sensitive to desiccation and this was followed by dry weights. Leaf area was more sensitive to desiccation than was leaf number.

2. The plant dry weight component most sensitive to desiccation was laminae dry weight, followed by roots and then sheath dry weights. In the case of sheath component it actually increased in dry weight during desiccation, possibly due to the accumulation of immature leaves within the sheath.

3. The pattern of recovery from desiccation was different for the relative rates of increase in leaf area and dry weight. The relative rates of leaf area increase in the previously desiccated plants were higher than the well-watered control rates. By contrast, the relative rates of dry weight in the previously desiccated plants were similar or slightly less than those of the well-watered control plants.

4. Accelerated leaf extension rates were recorded in the prairie grass experiment and these rates were maintained for over 28 days. However, no accelerated rates were recorded in the ryegrass experiment. This difference was probably due to the different water deficit levels imposed between the prairie and the ryegrass experiments rather than a species difference.

5. The different patterns of suspension and recovery in leaf extension rates between prairie grass and ryegrass had no apparent positive or negative carry-over effects on the relative rates of leaf area and dry weight recovery in the two pasture species.

In the present study although no compensatory growth in plant dry weight was recorded, a faster rate of leaf area recovery was evident. Further experimentation with a much longer time period for recovery growth should be conducted to see whether the faster rate of leaf area expansion upon relief of water deficit will lead to a higher "final" dry weight per plant than that of the well-watered control over a longer time scale.

6.3 COMPARATIVE RESPONSES OF NUI AND RUANUI TO DESICCATION AND DURING SUBSEQUENT RECOVERY

There is no question that Nui can produce more dry matter and persist longer under the dry summer and autumn conditions than Ruanui in New Zealand (Rumball, 1969; Baars *et al.*, 1976; Sheath *et al.*, 1976; Armstrong, 1977; Vartha, 1978).

When compared with Ruanui, the higher dry matter yield in Nui ranged from about +12%, over a period of 18 months in Waikato (Baars *et al.*, 1976) to approximately +54% over a period of 12 months under an infrequently defoliated dryland regime in North Otago (Sheath *et al.*, 1976). The most significant comment from these reports was that Nui could persist better than Ruanui and that the higher dry matter yield in Nui during the subsequent seasons was the result of a higher tiller population per unit area in the Nui sward (Sheath *et al.*, 1976). However, none of the reports cited above provided quantitative data on a per plant or per tiller basis. It was not known whether the surviving Ruanui plants were similar in dry weight and tiller numbers to those of the surviving Nui plants.

As reported in Experiment 5 of the present study, on a per tiller basis Nui tillers were about 28% heavier than those of the Ruanui tillers (Table 4.9). However, because of a 24% greater number of tiller per plant in Ruanui, the total dry weight per plant did not differ significantly between the two cultivars.

In the present study a range of other parameters, were measured. The results can be summarised as follows:

1. Nui had a higher leaf extension rate than Ruanui, especially under the high temperature regime (Table 4.5). The higher rate was maintained under desiccation (Figure 3.11).

2. Nui had a larger mean leaf size (24%) and a heavier mean tiller dry weight (28%), but a lower tiller number per plant (24%), hence a lower green leaf number per plant (18%) than Ruanui (Table 4.9).

3. For all the other parameters measured there were no statistically significant differences between the two cultivars. These parameters were: dry weight and leaf area per plant (Table 4.6 and Table 4.9), top to root ratio, specific leaf area, leaf area ratio (Appendix 4.7c), leaf water potentials (Figure 3.9), stomatal resistance (Appendix 3. 1), transpiration rates (Appendix 3. 2) and the relationship between leaf water potential and relative leaf water content (Appendix 3. 3).

The lack of difference in dry weight and leaf area per plant could be due to the following reasons:

1. Under growth room conditions, using small pots spaced evenly on the trolley, Ruanui may have a larger tiller population (i.e., single plants with light available on all sides) than it would have in a closed sward situation in the field. A similar lack of difference in pot experiments between Nui and Oregon ryegrass in one experiment and between Nui and Ariki in another experiment, was also observed by Vartha (pers. comm.).

2. In the field trials cited above, defoliation had always been one of the treatments, whereas no defoliation was imposed in the

present study. That there were significant defoliation x water deficit interaction had been shown by Vartha (1979) in Nui ryegrass. After rewatering, leaf dry weights increased in the "cut" but not in the "uncut" treatments over the first 21 days.

3. The rooting pattern of the two cultivars could be different in the field or with a larger pot. Differences in the depth of rooting and the number of different categories of roots were some of the reasons given for differences in drought tolerance between strains of *Bromus inermis* (Cook, 1943).

Evidence from the present study together with those reported by others (as cited earlier) have emphasised the importance of the persistency of Nui relative to the other ryegrasses. An experiment has been conducted in the Climate Laboratory, DSIR, by the author to investigate the ability of Nui and Ruanui to persist under a prolonged desiccation situation. Observations during the trial indicated that large variations in the ability of individual plants to survive prolonged desiccation occurred within both cultivars. However, the data has yet to be analysed.

A further point of interest emerged from the report by Sheath *et al.*, (1976), in that the dry matter production and tiller density of Nui was higher than Ruanui under the irrigation treatment as well as under the dryland treatment. This suggested that the response of Nui during the warmer months of summer and autumn, was more than just to water deficit but possibly to high temperature as well. That there was difference in temperature response between the two cultivars was also evident from the leaf extension growth results presented in Experiment 3 and Experiment 5 of the present study. If the superior performance

recorded in Nui is related to a high temperature response, it may be possible to select for a higher producing summer pasture grass based on high temperature response rather than water deficit response. This is an area which should be investigated further.

6.4 THE RELATIONSHIP BETWEEN LEAF EXTENSION RATE AND PLANT GROWTH RATE

In grasses, variation in leaf length is the major determinant of leaf area (Ryle, 1964). This made leaf extension rate potentially useful as an index of leaf area expansion. Under conditions where dry matter yield is limited by leaf area, for example young or recently defoliated pasture, the rate of leaf area expansion, as represented by leaf area index have been shown to influence sward productivity (Brougham, 1956). This indirect relationship between leaf extension rate and dry matter production could also make leaf extension rate a possible index of crop growth rate. However, the degree to which extension rate is related to dry matter production is not fully understood.

Scott (1961) using 3 tussock species compared 4 different methods of estimating growth under controlled conditions. He concluded that the method using the leaf extension rate of the youngest leaf in the tiller reflected the same proportional changes in the amount of growth as that obtained by the total yield method. The leaf extension rate was considered by Scott as a potentially useful method for estimating total yield in the field.

Roy and Peacock (1972) used leaf extension rate to predict changes in the leaf area index of spring pastures, and Peacock (1975a) considered that leaf extension rate would be useful for predicting the temperature effects on changes in plant dry weights. Similarly, Thomas (1975) found in a simulated sward of perennial ryegrass, that leaf extension rate had the greatest influence on sward growth rate in the field. The response observed by Thomas was mainly related to temperature. The highly sensitive response of leaf extension rate to temperature had been well established (Kleinendorst and Brouwer,

TABLE 6.2 Summary of linear regression information between (i) the rate of dry weight increases (R_W) as the dependent variable with leaf extension rate (LER) as the independent variable and (ii) the rate of leaf area increases (R_L) as the dependent variable with LER as the independent variable.

$$Y = a + bX$$

(i) Relationship between R_W and LER (R_W = Y; LER = X)

Treatment*	Regression coeff.	constant	R^2	F test
Control	2.71	-39.02	0.17	N.S.
Stress 1	2.07	-35.31	0.54	**
Stress 2	2.45	-45.81	0.55	**
Stress 3	1.47	-22.41	0.69	**

(ii) Relationship between R_L and LER (R_L = Y; LER = X)

Treatment*	Regression coeff.	constant	R^2	F test
Control	9.13	-178.7	0.41	*
Stress 1	3.38	-37.8	0.30	*
Stress 2	6.34	-124.0	0.70	**
Stress 3	2.35	-12.7	0.75	**

* treatment from that of Experiment 4.

1970; Robson, 1972, 1973, 1974; Watts, 1972, 1974; Peacock 1975a, 1975b). However, the extent to which leaf extension rate is suitable as a growth rate indicator under moisture deficit condition is largely unknown.

Data collected during the present study provided the opportunity to assess the relationship between leaf extension rate and the rates of increase in leaf area and dry weight during the period of recovery from water stress. Data from the prairie grass experiment (Experiment 4) collected after rewatering until the end of the experiment had been analysed and used for this comparison.

Details of the regression information between the rates of dry weight increases (R_W), leaf area increases (R_L) and leaf extension rate (LER) are presented in Table 6.2. The regressions were based on the rate of increase rather than their absolute values. For R_W and R_L the standard method of calculating rates was used (i.e., $X_2 - X_1 / t_2 - t_1$; where X_2 and X_1 were the absolute values of the parameter at times t_2 and t_1 respectively.). The values of each replicate was used as a data point for the regression calculation. For leaf extension rate the geometrical mean calculated over the same time interval as that of the growth rate was used.

As can be seen from Table 6.2, in the well-watered control plants the usefulness of LER as an index for predicting either R_W or R_L under a "constant" environmental condition is very poor. The low coefficient of determination (R^2) of 0.17 and 0.41 for R_W and R_L respectively was due to the fact that LER was more or less constant under the temperature regime used in this experiment (Figure 4.2)

whereas R_W and R_L were increasing with time (Figure 4.3). However, in the stress treatments LER increased rapidly upon rewatering and so did R_W and R_L hence the higher R^2 values during the recovery phase.

The rate of leaf extension measurement because of the technique was limited to the region of relatively constant growth in the newly emerged leaf (Wardlaw, 1969; Wilson, 1975). Whereas, leaf area expansion of the whole plant should depend on the rate from all the leaves. Furthermore, the rate of leaf area expansion will also depend on the rate of emergence of new leaves, the rate of senescence of expanded leaves and the duration of leaf extension growth of different leaves.

From the evidence collected in this study, it looks unlikely that leaf extension rate will be a suitable index for plant dry weight changes under severe moisture deficit. Furthermore, the greater depression of leaf growth relative to plant dry weights during desiccation and the opposite response during recovery makes it even less suitable. However, because of its sensitivity to mild desiccation, it may be a useful index for evaluating mild moisture deficits.

6.5 REACTION OF PLANTS TO WATER DEFICIT FOLLOWING " DROUGHT HARDENING" PRE-TREATMENT

One of the objectives outlined in Chapter I was to investigate the evidence of drought adaptation by pasture plants by using low air vapour pressure pre-conditioning. As concluded in Experiment 6, plants with a low vapour pressure history (HL) were able to persist longer in the desiccation period than the other pre-treatments. This apparent "adaptation" was probably due to the more efficient rate of water use per unit leaf area by these plants. But as transpiration rates were not recorded for the desiccated plants, this conclusion could only be tentative. Furthermore, the mechanism (s) that enable the HL plants to be more efficient in their water use is not known.

A number of recent publications have indicated the importance of osmotic adjustment as the mechanism of drought adaptation (Boyer and McPherson, 1975; Begg and Turner, 1976; Brown *et al.*, 1976; Simmelsgaard, 1976; Jones and Turner, 1978; Turner and Begg, 1978). In Jones and Turner's experiment (1978) with 2 cultivars of sorghum, they reported evidence of drought adaptation after subjecting the plants to slow soil desiccation. Adaptation was the result of osmotic adjustment of up to -1.6 MPa, as well as a 50% reduction in tissue elasticity. However, Jones and Turner prevented further adaptation during the drying phase by severing the stem at soil level. The adaptation response in their experiment was recorded over a relatively short interval of 8 hours. This points to the question of persistency of the drought adaptation response.

In McPherson and Boyer's experiment with maize (McPherson and Boyer, 1974), the effects of the low vapour pressure pre-treatment imposed from sowing to tassel emergence, persisted long enough to influence grain yield during the period of desiccation at the grain filling stage. Adaptation, the authors claimed, was due to the plant's ability to regulate water loss rather than changes in photosynthesis under desiccation. On the other hand, Rawson *et al.*, (1977) using 2 varieties of barley and 3 varieties of wheat found that upon rewatering, the previously desiccated plants became "prodigal" in their water use. The authors concluded that there was little evidence to indicate that drought adaptation would improve the overall water use efficiency in grain production. Any adaptation that might have developed during the initial drying cycle over the vegetative phase, did not persist long enough to influence grain yield during subsequent drying at the grain filling stage.

In most reported adaptation studies, the adaptative responses are related to the reproductive yields (Woodruff, 1969; Henckel, 1964; Levitt, 1972; McPherson and Boyer, 1974; Rawson *et al.*, 1977). The author is not aware of any work on adaptative responses by pasture plants. From the pasture production point of view, where the vegetative yield is important, unless drought adaptation can persist long enough to result in a higher dry matter production or a more efficient water usage, it will be of little agronomic value. Furthermore, it will be more desirable to be able to induce adaptation by using soil desiccation, as this can be easily implemented by the farmer.

Further field experiments with rainout shelters should be conducted to determine the extent to which vegetative yields can be influenced through drought adaptation.

APPENDIX 3.1

Time course of stomatal resistance in 2 cultivars of ryegrass under 2 temperature regimes

Stomatal resistance (R_s) is expressed as stomatal conductance ($1/R_s$) in cm/sec, and the daily time course of the stomatal conductance for the 2 ryegrass cultivars (Ruanui and Nui) under the 2 temperature regimes are presented in Figure A1.

By and large under well-watered conditions, control plants of both cultivars had similar values, with those in the H temperature regime having a slightly higher stomatal conductance value than those under the L temperature regime (0.65 cm/sec and 0.60 cm/sec for the H and L temperature regimes respectively).

In contrast, under desiccation Ruanui tended to have a slightly higher but statistically non-significant difference than Nui. The trend was consistent for both temperatures.

During desiccation, the decrease in stomatal conductance was detected by day 3, and by day 6 it had reached the level (0.1 cm/sec) where the stomata could be considered as closed (Hansen, 1974).

Stomatal resistance data was collected by Mr P. Rollinson, P.P.D. using a diffusion porometer.

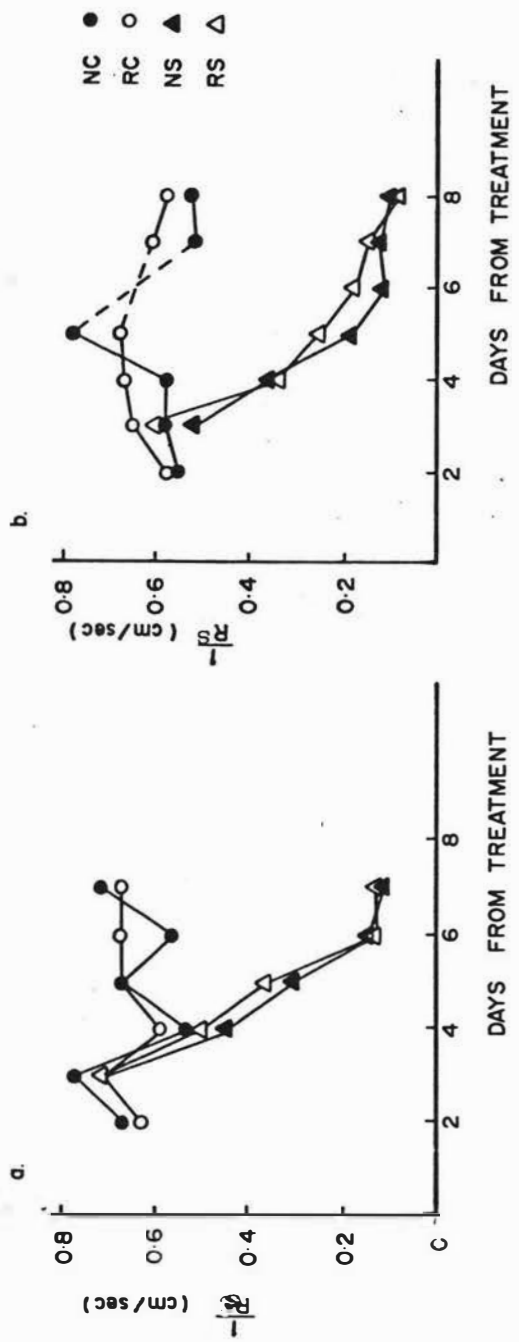


Figure A1 Stomatal conductance for Nui and Ruanui during desiccation.

(a) Under high temperature regime (27.5°/12.5°C)

(b) Under low temperature regime (17.5°/12.5°C)

APPENDIX 3.2

Time course of transpiration rates in 2 cultivars of ryegrass under 2 temperature regimes

The diurnal time course of transpiration rates for days 2, 5 and 8 are presented in Figure A.2. The times A,B,C and D were the same as that illustrated in Figure 3.3, under section 3.3.3. Days 2,5 and 8 represented the 24 hour period immediately preceeding the destructive harvests on days 3, 6 and 9 respectively.

Although transpiration rates in the well-watered plants were significantly higher than those of the desiccated plants ($P < 0.01$), there was no detectable difference at the 5% level of probability between the 2 cultivars under both temperature regimes. Under well-watered conditions, the day-time transpiration rates were between 2 and 5 $\mu g\ H_2O/cm^2/sec$ depending on the temperature and vapour pressure deficit at the time of measurement. By and large, maximum transpiration occurred during time C (except for day 5 in H temperature regime, where time D was the maximum).

Transpiration rates of the desiccated plants during time C on day 8 were approximately 30% and 33% of control rates for the H and L temperature regimes respectively. There was no statistically significant difference between the cultivars.

N.B. The pots of the transpiration experiment were covered with a layer of black polythene at the soil level plus a layer of gravel 1-2 cm thick to prevent evaporation from the soil surface. Eight pots covered in this way, but without plants, were used as "blank control". Leaf areas of the sample plants were measured destructively by an

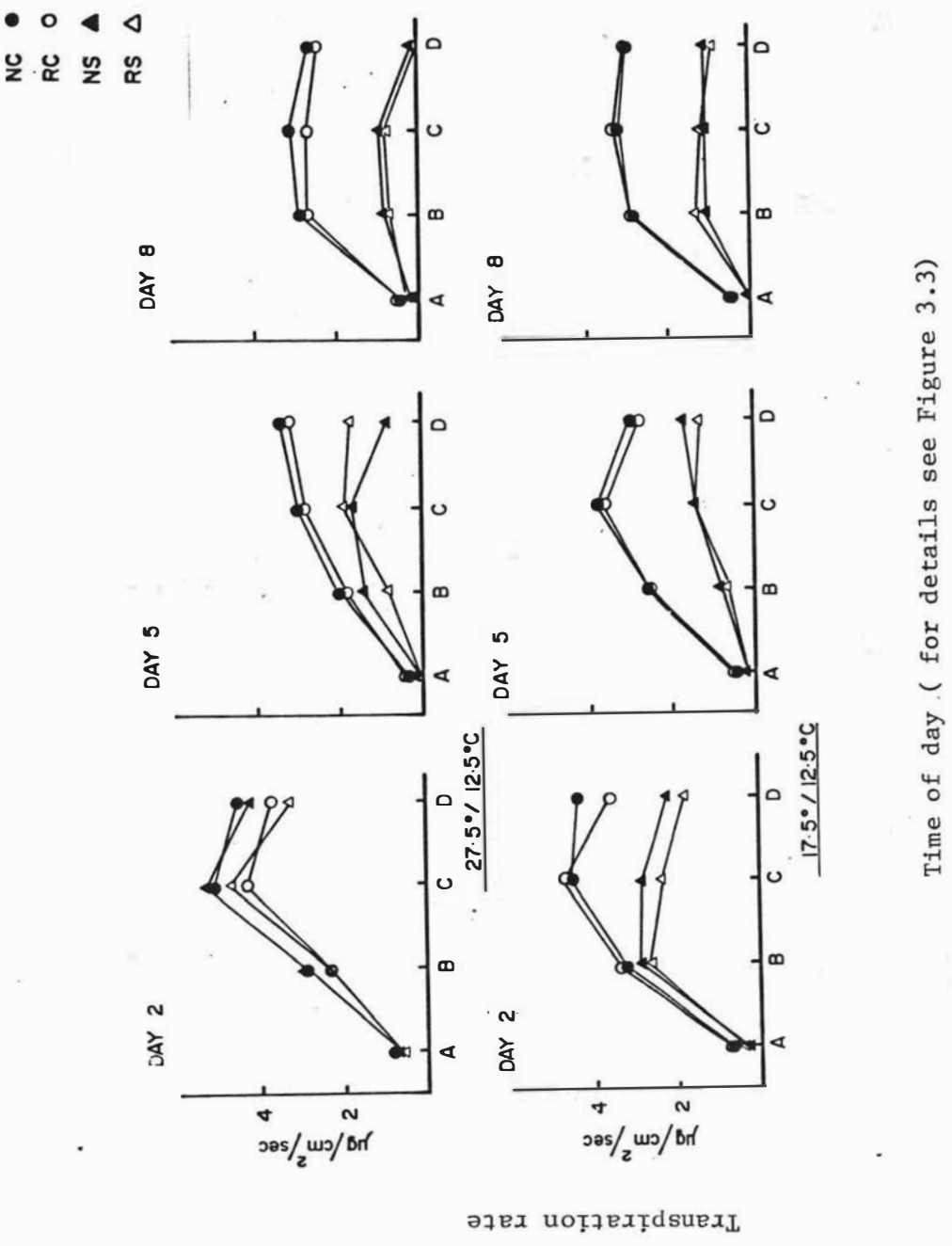


Figure A2 Transpiration rate for Nui and Ruanui during desiccation.

electronic leaf area meter at the end of the 24 hour measurement period.

APPENDIX 3.3

Relationship between leaf water potential and relative leaf water content for Ruanui and Nui ryegrass under 2 temperature regimes

The relationship between the leaf water potential and relative leaf water content curve can be used to detect drought tolerance in plants (Jarvis and Jarvis, 1965 ; Sanchez-Diaz and Kramer, 1971; Jones and Turner, 1978). The relationship of the leaf water potential-relative leaf water content curve (Figure A3 a & b) is similar to others reported in the literature (Slayter, 1967; Neumann *et al.*, 1974; Experiment 6 of the present study). By and large, for both Nui and Ruanui, relative leaf water content values lower than 0.80 corresponded to leaf water potential values between -1.20 and -1.40 MPa, which coincided with the onset of visible wilting in both temperature regimes. This is in agreement with published data, for example, in barley first visible wilting occurred between 0.75 and 0.80 relative content (Millar *et al.*, 1968) and for a range of species (viz., pepper, birdsfoot trefoil and sunflower) this occurred between 0.80 and 0.85 relative water content (Ehlig and Gardner, 1964).

Regression equations of the form (Y = a + bX) fitted through the data sets (Table A.1) showed no statistically significant difference between the two cultivars in both temperature regimes.

TABLE A.1 Regression equations for the relationship between the leaf water potential (LWP) and relative leaf water content (RLWC) for Nui and Ruanui and 2 temperature regimes.

Temperature	Cultivars	Regression equations	R^2
27.5°/12.5°C	Ruanui	RLWC = 121.9 - 3.41 LWP	0.87
	Nui	RLWC = 122.2 - 3.21 LWP	0.89
17.5°/12.5°C	Ruanui	RLWC = 120.1 - 3.34 LWP	0.52
	Nui	RLWC = 115.6 - 3.21 LWP	0.65

F test for regression coefficients were all non-significant (LWP in bars

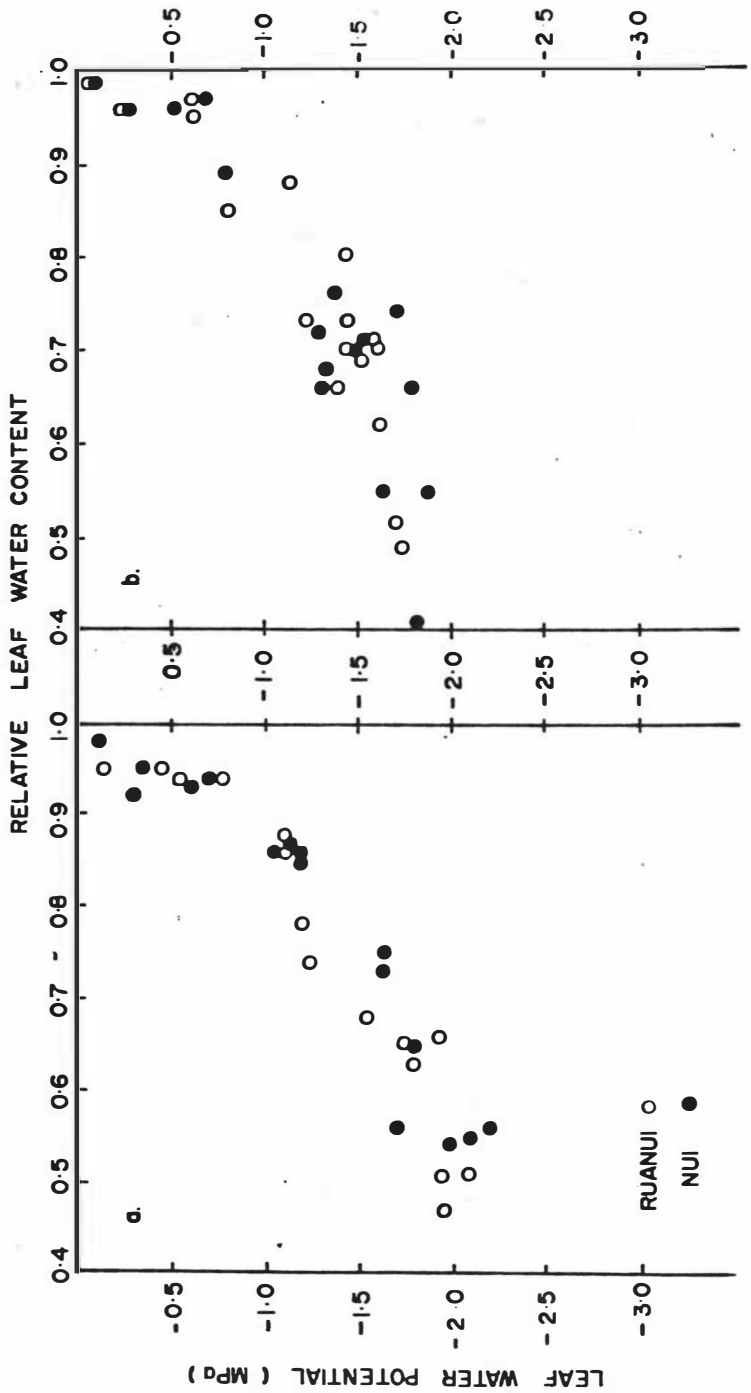


Figure A3 Relationship between leaf water potential and relative leaf water content for Nui and Ruanui under two temperature regimes.

(a) Under high temperature regime ($27.5^{o}/12.5^{o}$)

(b) Under low temperature regime ($17.5^{o}/12.5^{o}$C)

APPENDIX 4.1

Statistical methods and procedures

4.1.1 Preliminary organisation of data

The Massey University computer B6700 was used to process all the data inputs for this study. Raw data (e.g. leaf area/plant and leaf number per plant) were punched on to cards and individual programmes written as required to calculate the "secondary" data (e.g., mean area per leaf) for further analysis.

4.1.2 Analysis of variance

The standard forms of analysis of variance (Snedecor and Cochran, 1968) were used to detect significant differences between means. In this thesis only the Fixed-effect model, (Model I) was used. Where samples were not true replicates, e.g., leaf water potential measurements, the "one-way" classification of analysis of variance according to Snedecor and Cochran (1968, pp. 277) was used. Where more than one replicate was involved the complete factorial designed (e.g., 2-way, 3-way and 4-way) analysis of variance, again according to Snedecor and Cochran (1968, pp 299) was used. The necessary computer programmes were written to analyse the data. During the later part of the study some of the data were analysed by using a package statistical programme "TEDDY-BEAR" written by J.B. Wilson, Botany Department, University of Otago (Technical Report T.5, edition 2.4, July, 1978).

Where transformation is required it is indicated in the appropriate table with letters within paranthesis e.g., with (LN) representing $\log_e$ transformation and with (SQRT) representing square root transformation. Untransformed data is used by default.

4.1.3 Regression analysis

Computer programmes were written to calculate the regression equations according to Snedecor and Cochran (1968, pp 135). Comparison of regression coefficients, using F test, was also according to Snedecor and Cochran (1968, pp 432-436.)

4.1.4 Statistical symbols

Throughout this thesis, unless otherwise stated, the following symbols were used:

NS = non-significant at 5% level of probability

* = $P < 0.05$

** = $P < 0.01$

LSD = least significant difference at 5% level of probability.

$\bar{x} \pm y$, where " $\pm$ y" represents the standard error of mean "$\bar{x}$".

Where the term "statistical significance" is used, unless otherwise specified, refers to the 5% level of probability.

APPENDIX 4.2a

Analysis of Variance for leaf emergence rate in well-watered control plants.

Source	d.f.	Sums of squares	Mean squares	F ratio
Replicates	3	2.82	0.94	2.88*
Leaf number (L)	3	8.19	2.73	8.37**
Cultivars (C)	1	1.00	1.00	3.07NS
Temperature (T)	1	6.25	6.25	19.16**
Interactions				
L X T	3	4.00	1.33	4.09*
L X C	3	0.25	0.08	0.26NS
C X T	1	1.57	1.57	4.81*
L X T X C	3	2.18	0.73	2.23NS
Errors	45	14.68	0.33	

CV = 13%

APPENDIX 4.2b

Analysis of variance for leaf emergence rate between control, Stress 1 and Stress 2 plants for leaf 9

Source	d.f.	Sums of squares	Mean squares	F ratio
Replicates	3	1.40	0.47	0.80NS
Temperature (T)	1	7.52	7.52	12.82**
Cultivar (C)	1	0.02	0.02	0.03NS
Water regimes (H)	2	0.54	0.27	0.46NS
Interactions				
T X C	1	2.52	2.52	4.30*
R X W	2	1.79	0.90	1.53NS
C X W	2	1.29	0.65	1.11NS
T X C X W	2	1.55	0.77	1.31NS
Error	33	19.35	0.59	

APPENDIX 4.3

Means for temperature x water deficit interaction during the period of desiccation

Plant Characters	Days from withholding water						
	3		9		15		
	H	L	H	L	H	L	Significance
Leaf area per plant (cm^2)	42	39	28	35	0.1	11	**
Dry weight per plant (mg)	383	465	728	574	413	605	**

APPENDIX 4.4

Analysis of variance for the rate of leaf extension between well-watered Ruanui and Nui ryegrass under different temperature regimes

Source	d.f	Sums of squares	Mean square	F ratio
Replicates	25	253.93	10.16	1.44 NS
Temperature	1	669.14	669.14	94.64 **
Cultivar	1	357.42	357.42	50.55 **
T X C	1	75.48	75.48	10.68 **
Error	75	530.47	7.07	

APPENDIX 4.5

Summary of F ratios and F tests on plant parameters during the desiccation period

(W = water deficit effects, T = temperature effects, C = cultivar effects)

Source	df	Total tiller No.	Mature tiller No.	Immature tiller No.	Total green leaf No.	Mature green leaf No.	Immature green leaf No.
W	2	9.8 **	6.09 **	4.62 **	3662 **	172 **	49.5 **
T	1	0.01NS	1.3 NS	1.65 NS	2889 **	19 **	61.2 **
C	1	25.5NS	11.4 NS	9.54 **	1.20 NS	0.2 NS	1.4 NS
WT	2	1.1 NS	0.77 NS	1.30 NS	2657 **	5.76**	42.5 **
WC	2	0.69NS	0.96 NS	3.62 *	9.7 **	6.26**	0.74 NS
TC	1	2.77NS	0.36 NS	1.65 NS	14.3 **	10.4**	0.76 NS
WTC	2	1.11NS	0.27 NS	1.30 NS	0.60 NS	0.41NS	0.97 NS
Rep	3	2.10NS	0.86 NS	2.65 NS	1.60 NS	1.34NS	2.55 NS
CV%		6	19	29	5	19	20
		(SQRT)			(LN)		

Source	df	Dead leaf area	Total leaf area	Mature leaf area	Immature leaf area	Mean leaf size	Specific leaf area
W	2	295 **	1380 **	181 **	30.7 **	156 **	225 **
T	1	76.2**	664 **	1.47NS	3.18 NS	8.93**	0.13NS
C	1	24.6**	3.20 NS	8.92**	0.27NS	10.9**	0.84NS
WT	2	55.1**	588 **	16.1**	6.91**	16.6**	49.4**
WC	2	18.8**	0.60 NS	0.72NS	0.96NS	3.56*	2.65NS
TC	1	0.46NS	0.70 NS	1.22NS	3.00NS	1.60NS	3.81*
WTC	2	0.31NS	0.60 NS	0.02NS	1.31NS	0.24NS	0.41NS
Rep	3	0.60NS	0.50 NS	0.29NS	0.92NS	0.70NS	0.32NS
CV%		29	9	23	38	21	18

Source	df	Leaf area ratio	Total dry weight	Root dry weight	Sheath dry weight	Laminae dry weight	Top:Root ratio
W	2	212 **	18.1 **	15.3 **	75.1 **	91.4 **	3.24 *
T	1	1.56NS	1.60 NS	2.44 NS	11.9 **	62.5 **	19.3 **
C	1	0.33NS	1.12 NS	0.75 NS	0.17 NS	2.85 NS	1.54 NS
WT	2	21.0**	10.7 **	10.1 **	11.6 **	20.3 **	1.08 NS
WC	2	0.88NS	0.89 NS	1.95 NS	1.03 NS	2.37 NS	4.32 *
TC	1	0.02NS	3.91 NS	1.78 NS	2.25 NS	3.83 NS	0.22 NS
WTC	2	0.07NS	1.01 NS	0.49 NS	0.24 NS	1.04 NS	0.20 NS
Rep	3	1.23NS	0.20 NS	0.08 NS	0.86 NS	1.06 NS	0.50 NS
CV%		23	20	28	4 (LN)	5 (LN)	26

APPENDIX 4.6

Summary of F ratios and F tests for plant parameters during the recovery phase

(A) Tiller data

(i) Total tiller number/plant

		Harvest No				
Source	d.f	1	2	3	4	5
W	2	8.66 **	7.04 **	19.09 **	26.32 **	9.89 **
T	1	0.14 NS	1.45 NS	3.35 NS	1.44 NS	1.35 NS
C	1	43.51 **	12.54 **	23.69 **	22.47 **	27.13 **
WT	2	2.14 NS	0.49 NS	0.82 NS	2.50 NS	3.76 *
WC	2	1.62 NS	0.01 NS	3.22 NS	4.64 *	0.02 NS
TC	1	1.81 NS	0.10 NS	4.37 *	0.05 NS	0.11 NS
WTC	2	0.39 NS	0.01 NS	0.57 NS	1.50 NS	1.85 NS
Rep	3	5.93 **	0.54 NS	0.60 NS	0.66 NS	1.07 NS
CV%		6 (SQRT)	15	15	15	15

(ii) Mature tiller no/plant

Source	d.f.	Harvest No. 1	2	3	4	5
W	2	2.38 NS	4.62 *	8.13 **	16.22 **	5.29 **
T	1	1.48 NS	0.52 NS	7.59 **	1.51 NS	0.004NS
C	1	7.73 **	13.24 **	14.55 **	29.66 **	14.58 **
WT	2	0.93 NS	2.29 NS	4.28 *	0.58 NS	1.14 NS
WC	2	0.39 NS	0.58 NS	0.76 NS	5.47 **	0.69 NS
TC	1	0.27 NS	1.58 NS	1.35 NS	1.32 NS	3.64 NS
WTC	2	0.36 NS	0.71 NS	0.25 NS	0.73 NS	1.48 NS
Rep	3	0.95 NS	0.82 NS	0.40 NS	1.11 NS	0.90 NS
CV%		17	17	16	17	17

(iii) Immature tiller no/plant

Source	d.f.	Harvest No. 1	2	3	4	5
W	2	2.23 NS	4.75 *	24.89 **	17.48 **	5.70 **
T	1	1.65 NS	1.23 NS	0.38 NS	0.08 NS	3.99 NS
C	1	20.83 **	3.76 NS	18.78 **	0.51 NS	12.65 **
WT	2	1.91 NS	4.63 *	1.32 NS	13.93 **	3.45 *
WC	2	0.53 NS	4.05 NS	6.48 **	2.84 NS	0.94 NS
TC	1	1.10 NS	2.76 NS	7.52 **	2.96 NS	4.39 *
WC	2	0.86 NS	2.25 NS	2.35 NS	3.10 NS	0.46 NS
Rep	3	3.30 *	0.53 NS	0.73 NS	0.11 NS	0.67 NS
CV%		28	19	22	25	30

(B) Leaf number data

(i) Total leaf no/plant

Source	d.f.	Harvest No. 1	2	3	4	5
W	2	163.93 **	53.84 **	35.33 **	34.00 **	25.26 **
T	1	40.31 **	1.28 NS	0.74 NS	0.30 NS	6.53 *
C	1	4.05 *	9.45 **	11.29 **	19.56 **	25.03 **
WT	2	17.39 **	3.70 *	6.93 **	6.88 **	2.24 NS
WC	2	6.61 **	0.005 NS	3.81 *	2.64 NS	0.53 NS
TC	1	2.13 NS	3.05 NS	1.30 NS	0.13 NS	1.48 NS
WTC	2	0.10 NS	0.64 NS	1.01 NS	0.67 NS	1.79 NS
Rep	3	0.72 NS	0.77 NS	0.48 NS	2.08 NS	1.43 NS
CV%		18	14	17	15	12

(ii) Mature leaf no/plant

Source	d.f.	1	2	3	4	5
W	2	150.24 **	105.45 **	46.71 **	46.07 **	30.27 **
T	1	8.45 **	5.74 *	1.77 NS	0.81 NS	0.52 NS
C	1	0.96 NS	7.37 *	2.24 NS	17.34 **	21.23 **
WT	2	3.52 *	5.95 **	10.69 **	13.07 **	1.08 NS
WC	2	5.60 **	0.13 NS	1.85 NS	2.43 NS	0.91 NS
TC	1	4.11 *	0.81 NS	0.15 NS	0.30 NS	2.15 NS
WTC	2	0.56 NS	1.57 NS	0.51 NS	0.14 NS	0.19 NS
Rep	3	0.90 NS	0.23 NS	0.87 NS	2.44 NS	0.80 NS
CV%		22	15	21	15	13

(iii) Immature leaf no/plant

Source	d.f.	Harvest No 1	2	3	4	5
W	2	87.49 **	13.65 **	16.77 **	14.63 **	10.79 **
T	1	66.27 **	0.03 NS	0.01 NS	0.06 NS	14.89 **
C	1	5.68 *	8.67 **	31.85 **	14.72 **	17.06 **
WT	2	28.36 **	2.01 NS	2.48 NS	1.60 NS	3.47 *
WC	2	4.56 *	0.19 NS	6.24 **	1.99 NS	0.19 NS
TC	1	0.21 NS	4.56 *	3.84 NS	1.19 NS	0.49 NS
WTC	2	0.31 NS	0.30 NS	2.02 NS	1.35 NS	3.84 *
Rep	3	0.80 NS	1.85 NS	0.09 NS	1.28 NS	1.12 NS
CV%		19	14	14	17	15

(iv) Dead leaf no/plant

Source	d.d.	1	2	3	4	5
W	2	424.39 **	324.36 **	278.6 **	73.4 **	102.8**
T	1	84.66 **	150.30 **	106.40 **	29.55 **	15.79 **
C	1	6.41 *	0.44 NS	37.16 **	3.55 NS	10.42 **
WT	2	37.71 **	19.78 **	12.05 **	7.79 *	3.54 *
WC	2	3.34 *	0.22 NS	5.09 *	0.51 NS	6.08 **
TC	1	4.33 *	10.21 **	0.02 NS	0.75 NS	0.32 NS
WTC	2	4.22 *	2.21 NS	1.06 NS	0.09 NS	0.46 NS
Rep	3	0.10 NS	0.96 NS	2.09 NS	0.99 NS	0.56 NS
CV%		17	16	14	23	17
		(SQRT)	(SQRT)	(SQRT)	(SQRT)	(SQRT)

(C) Leaf area data

(i) Total leaf area/plant

		Harvest No.				
Source	d.f.	1	2	3	4	5
W	2	286.1 **	104.9 **	62.8 **	112.7 **	139.3 **
T	1	0.04 NS	9.80 **	57.6 **	15.8 **	121.5 **
C	1	1.56 NS	1.88 NS	0.15 NS	2.18 NS	0.12 NS
WT	2	26.12 **	10.56 **	18.92**	46.48 **	36.99 **
WC	2	0.43 NS	1.55 **	1.18 NS	5.28 **	1.26 NS
TC	1	0.53 NS	7.69 **	0.15 NS	0.06 NS	0.97 NS
WTC	2	0.10 NS	1.41 NS	0.22 NS	3.96 NS	5.89 **
Rep	3	0.66 NS	2.78 NS	0.15 NS	0.45 NS	2.56 NS
CV%		20	23	22	4	14
					(LN)	

(ii) Mature leaf area/plant

Source	df	1	2	3	4	5
W	2	159.24 **	75.55 **	59.03 **	92.18 **	122.35 **
T	1	0.08 NS	12.33 **	34.39 **	28.98 **	68.31 **
C	1	5.66 *	2.22 NS	0.14 NS	0.11 NS	0.03 NS
WT	2	12.10 **	5.51 **	20.47 **	55.92 **	24.56 **
WC	2	0.46 NS	1.30 NS	1.30 NS	0.75 NS	1.70 NS
TC	1	0.09 NS	5.73 *	0.38 NS	0.34 NS	0.72 NS
WTC	2	0.24 NS	0.68 NS	0.28 NS	1.47 NS	3.32 *
Rep	3	0.25 NS	2.56 NS	0.23 NS	0.92 NS	0.99 NS
CV%		28	24	25	20	15

(iii) Immature leaf area/plant

		Harvest No.				
Source	df	1	2	3	4	5
W	2	106.83 **	86.39 **	17.63 **	46.99 **	20.51 **
T	1	0.49 NS	1.11 NS	44.82 **	38.24 **	40.73 **
C	1	0.07 NS	0.26 NS	0.03 NS	0.19 NS	0.64 NS
WT	2	12.80 **	13.91 **	2.66 NS	17.74 **	10.83 **
WC	2	0.05 NS	0.96 NS	0.31 NS	3.02 NS	0.39 NS
TC	1	0.41 NS	6.26 *	0.08 NS	1.01 NS	0.20 NS
WTC	2	0.002 NS	3.06 NS	0.92 NS	4.70 *	2.12 NS
Rep	3	1.55 NS	1.37 NS	1.10 NS	0.94 NS	0.34 NS
CV%		27	32	28	20	31

(iv) Mean leaf size

Source	df	1	2	3	4	5
W	2	161.3 **	80.6 **	15.0 **	35.43 **	60.6 **
T	1	0.005 NS	16.26 **	65.46 **	27.22 **	149.8 **
C	1	12.42 **	18.81 **	20.13 **	23.59 **	27.86 **
WT	2	37.46 **	14.15 **	3.52 *	28.13 **	24.69 **
WC	2	4.50 *	2.68 NS	2.97 NS	0.24 NS	1.17 NS
TC	1	0.86 NS	8.00 **	1.22 NS	0.01 NS	2.93 NS
WTC	2	0.07 NS	1.30 NS	0.34 NS	1.20 NS	2.12 NS
Rep	3	0.33 NS	3.11 *	1.03 NS	3.78 *	0.22 NS
CV%		22	17	16	16	14

(v) Specific leaf area

Source	df	Harvest No 1	2	3	4	5
W	2	242.6 **	0.75 NS	10.10 **	0.73 NS	38.3 **
T	1	0.01 NS	109.5 **	174.2 **	84.3 **	264.5 **
C	1	1.34 NS	0.02 NS	0.04 NS	0.12 NS	3.94 NS
WT	2	68.3 **	5.11 *	14.32 **	0.50 NS	14.03 **
WC	2	3.78 *	0.09 NS	0.40 NS	1.09 NS	0.40 NS
TC	1	2.20 NS	0.05 NS	0.48 NS	0.23 NS	3.22 NS
WTC	2	0.16 NS	0.20 NS	0.09 NS	0.55 NS	4.06 *
Rep	3	0.18 NS	1.18 NS	1.27 NS	0.15 NS	1.38 NS
CV%		16	15	13	12	8

(vi) Leaf area ratio

Sourcw	df	1	2	3	4	5
W	2	256.3 **	23.9 **	3.43 *	12.03 **	57.02 **
T	1	1.66 NS	24.98**	76.56 **	26.30 **	146.01 **
C	1	5.92 *	0.42 NS	0.30 NS	0.13 NS	2.37 NS
WT	2	33.85 **	13.44 **	2.20 NS	9.71 **	26.57 **
WC	2	2.17 NS	0.38 NS	0.51 NS	2.61 NS	0.65 NS
TC	1	0.72 NS	4.86 *	0.03 NS	1.24 NS	4.03 NS
WTC	2	0.53 NS	0.43 NS	0.005NS	1.39 NS	4.73 *
Rep	3	0.46 NS	0.37 NS	0.59 NS	1.43 NS	0.94 NS
CV%		19	18	18	16	13

(D) Plant dry weight data

(i) Total plant dry weight/plant

Source	df	Harvest No. 1	2	3	4	5
W	2	12.77 **	96.38 **	72.65 **	65.11 **	31.03 **
T	1	0.05 NS	24.56 **	3.54 NS	0.10 NS	5.98 *
C	1	0.01 NS	6.94 NS	0.25 NS	0.68 NS	0.02 NS
WT	2	9.37 **	9.37 **	6.00 **	23.84 **	0.55 NS
WC	2	2.10 NS	3.79 *	1.95 NS	2.62 NS	0.01 NS
TC	1	4.73 *	1.32 NS	0.01 NS	1.70 NS	4.11 *
WTC	2	0.73 NS	0.26 NS	0.47 NS	1.18 NS	3.62 *
Rep	3	1.34 NS	1.39 NS	0.32 NS	0.24 NS	1.73 NS
CV%		18	3 (LN)	3 (LN)	15	19

(ii) Root dry weight/plant

Source	df	1	2	3	4	5
W	2	4.64 *	46.09 **	28.62 **	10.47 **	3.75 *
T	1	6.50 **	1.97 NS	1.78 NS	1.79 NS	4.68 *
C	1	0.08 NS	8.76 **	0.17 NS	0.03 NS	0.02 NS
WT	2	7.08 **	2.87 NS	0.19 NS	4.37 *	0.07 NS
WC	2	2.21 NS	4.88 *	1.78 NS	0.83 NS	0.07 NS
TC	1	3.22 NS	0.11 NS	0.44 NS	2.90 NS	2.69 NS
WTC	2	0.19 NS	0.66 NS	0.59 NS	0.59 NS	2.02 NS
Rep	3	0.31 NS	0.47 NS	0.35 NS	0.85 NS	1.57 NS
CV%		27	25	22	27	34

(iii) Sheath dry weight/plant

Source	df	Harvest No. 1	2	3	4	5
W	2	23.18 **	40.50 **	38.32 **	52.78 **	51.08 **
T	1	12.95 **	11.80 **	5.95 *	36.45 **	14.03 **
C	1	0.22 NS	4.23 *	1.04 NS	7.68 **	0.64 NS
WT	2	19.11 **	2.15 NS	3.23 NS	16.44 **	1.45 NS
WC	2	0.25 NS	0.66 NS	0.13 NS	1.08 NS	1.59 NS
TC	1	3.09 NS	2.92 NS	0.33 NS	0.001NS	1.87 NS
WTC	2	1.05 NS	0.83 NS	0.36 NS	0.23 NS	4.69 *
Rep	3	4.97 **	2.95 NS	1.71 NS	0.44 NS	1.19 NS
CV%		15	4 (LN)	4 (LN)	3 (LN)	16

(iv) Laminae dry weight/plant

Source	df	1	2	3	4	5
W	2	112.28 **	70.00 **	83.39 **	83.66 **	82.34 **
T	1	20.67 **	10.29 **	0.47 NS	0.08 NS	0.17 NS
C	1	0.70 NS	0.64 NS	0.39 NS	0.71 NS	0.09 NS
WT	2	1.76 NS	6.37 **	18.86 **	34.38 **	6.17 **
WC	2	2.97 NS	0.91 NS	0.47 NS	1.22 NS	1.39 NS
TC	1	3.77 NS	6.33 *	0.01 NS	0.08 NS	3.66 NS
WTC	2	1.42 NS	0.47 NS	0.26 NS	1.05 NS	2.89 NS
Rep	3	1.91 NS	2.18 NS	0.86 NS	0.16 NS	1.87 NS
CV%		19	24	20	17	15

(iv) Dead matter dry weight/plant

Source	df	Harvest No 1	2	3	4	5
W	2	180.47 **	183.75 **	319.8 **	63.30 **	94.71 **
T	1	79.58 **	160.45 **	89.42 **	29.73 **	31.04 **
C	1	12.58 **	0.93 NS	4.23 *	0.62 NS	2.89 NS
WT	2	29.71 **	64.02 **	25.79 **	4.93 *	9.89 **
WC	2	6.80 **	0.39 NS	3.11 NS	1.08 NS	1.54 NS
TC	1	0.37 NS	2.95 NS	0.002 NS	0.49 NS	0.47 NS
WTC	2	1.18 NS	2.07 NS	1.57 NS	0.95 NS	0.90 NS
Rep	3	1.98 NS	1.11 NS	0.29 NS	1.08 NS	2.14 NS
CV%		32	35	18 (SQRT)	32 (SQRT)	37

(v) Top:root ratio

Source	df	1	2	3	4	5
W	2	2.65 NS	0.01 NS	4.57 *	4.28 *	7.60 **
T	1	35.71 **	3.94 NS	0.15 NS	8.41 **	0.64 NS
C	1	0.17 NS	3.74 NS	0.81 NS	0.25 NS	0.11 NS
WT	2	0.72 NS	4.44 *	7.06 **	1.07 NS	1.89 NS
WC	2	3.16 NS	2.49 NS	0.85 NS	0.07 NS	0.27 NS
TC	1	0.01 NS	8.45 **	1.03 NS	2.42 NS	1.58 NS
WTC	2	0.50 NS	0.60 NS	0.35 NS	0.16 NS	0.33 NS
Rep	3	0.79 NS	0.82 NS	0.61 NS	0.71 NS	0.63 NS
CV%		23	26	26	31	31

APPENDIX 4.7a

Influence of previous water deficit treatments on plant growth parameters during the period of recovery

Plant growth parameters	Previous water deficit treatments	Harvest No 1	2	3	4	5
(i) Mature tiller No. per plant	C	10.1	13.9a	18.7a	25.1a	27.7a
	S1	9.3	11.9b	15.7b	19.3b	24.6ab
	S2	8.9	11.8b	15.1b	18.4b	22.7b
		NS	*	**	**	*
(ii) Immature tiller per plant	C	4.9	5.9a	9.4a	10.3a	10.8a
	S1	4.2	5.1b	7.1b	7.8b	10.7a
	S2	4.0	4.9b	5.2c	6.1b	7.7b
		NS	*	**	**	**
(iii) Mature leaf No. per plant	C	17.3a	24.3a	33.6a	39.7a	50.4a
	S1	13.3b	19.3b	23.8b	30.9b	43.7b
	S2	2.5c	10.6c	15.9c	22.9c	34.5c
		**	**	**	**	**
(iv) Immature leaf No. plant	C	16.1a	20.4a	27.9a	34.3a	38.6a
	S1	12.9b	16.7b	24.6a	30.7a	37.3a
	S2	6.1c	16.1b	20.6b	24.6b	30.4b
		**	**	**	**	**
(v) Dead leaf No. per plant	C	0.2a	0.3a	1.0a	1.9a	2.7a
	S1	2.9b	4.9b	7.0b	5.4b	5.0b
	S2	16.9c	13.3c	15.5c	13.2c	14.8c
		**	**	**	**	**
(vi) Area of mature leaves per plant (cm^2)	C	40.3a	68.8a	92.8a	123.4a	164.9a
	S1	20.9b	41.0b	53.3b	69.6b	133.7b
	S2	2.4c	21.9c	34.0c	46.5c	61.8c
		**	**	**	**	**

(vii)Area of	C	19.6a	27.0a	35.1a	47.6a	53.4a
immature leaves per	S1	10.5b	12.1b	29.2b	39.5b	62.0a
plant (cm^2)	S2	3.5c	5.3c	18.6c	22.1c	28.9b
		**	**	**	**	**
(viii) Mean leaf size	C	1.93a	2.14a	2.03a	2.03a	2.47a
	S1	1.21b	1.47b	1.76b	1.81b	2.47a
(cm^2)	S2	0.34c	0.99c	1.48c	1.44c	1.47b
		**	**	**	**	**
(viiib) Specific leaf area (cm^2/g)	C	243a	242	248a	247	262a
	S1	168b	230	261a	246	300b
	S2	51c	227	302b	235	229c
		**	NS	**	NS	**
(viiic) Leaf area	C	89a	82a	92a	95a	101a
ratio	S1	50b	75a	91a	87a	117a
(cm^2/g)	S2	10c	51b	79b	72b	69b
		**	**	*	*	**
(ix) Root DW	C	332a	518a	557a	625a	759
per plant	S1	330a	326b	376b	505b	594
(mg)	S2	252b	225c	317b	401b	562
		*	**	**	**	NS
(x) Sheath	C	123a	236a	308a	402a	571a
D.W. per	S1	134a	146b	203b	310b	421b
plant	S2	174b	128c	153c	217c	316c
(mg)		**	**	**	**	**
(xi) Laminae	C	260a	391a	496a	665a	824a
D.W. per	S1	187b	240b	315b	450b	640b
plant (mg)	S2	84c	136c	193c	301c	402c
		**	**	**	**	**

(xii) Dead matter	C	1a	1a	1a	12a	17a
per plant	S1	30b	27b	40b	32b	35b
(mg)	S2	81c	92c	106c	117c	116c
		**	**	**	**	*
(xiii) Top:root	C	1.30a	1.24	1.48a	1.80a	2.04a
ratio	S1	1.09b	1.22	1.41a	1.61a	1.90a
	S2	1.06b	1.23	1.14b	1.31b	1.34b
		*	NS	*	*	*

APPENDIX 4.7b

The influence of temperature on plant growth parameters during the period of recovery

Plant growth parameters	Temperature	Harvest No. 1	2	3	4	5	Means across 5 harvests
(i) Mature tillers per plant	H	9	13	18	22	24	17.4
	L	10	12	15	20	25	16.4
		NS	NS	**	NS	NS	
(ii) Immature tiller per plant	H	5	6	7	8	9	7.0
	L	4	5	7	8	11	7.0
		NS	NS	NS	NS	NS	
(iii) Mature leaf No. per plant	H	10	17	25	32	42	25.2
	L	12	19	23	31	44	25.8
		**	*	NS	NS	NS	
(iv) Immature leaf No. per plant	H	9	18	24	30	33	22.6
	L	14	18	24	30	38	24.8
		**	NS	NS	NS	**	
(v) Dead leaf No per plant	H	9.7	9.3	9.9	9.3	9.1	9.5
	L	3.6	3.0	4.4	4.4	5.9	4.3
		**	**	**	**	**	
(vi) Mature leaf area per plant (cm^2)	H	21	49	73	93	143	76
	L	22	38	47	67	97	59
		NS	**	**	**	**	
(vii) Immature leaf area per plant (cm^2)	H	11	16	35	43	62	33
	L	12	14	20	30	34	22
		NS	NS	**	**	**	
(viii) Mean leaf size cm^2	H	1.38	1.68	2.09	2.07	2.66	1.98
	L	1.16	1.39	1.43	1.63	1.61	1.44
		**	**	**	**	**	

(viiib) Specific leaf	H	153	287	338	284	318	276
area (cm^2/g)	L	154	178	202	202	210	189
			**	**	**	**	
(viiic) Leaf area	H	48	79	107	95	118	89
ratio (cm^2/g)	L	51	60	67	74	73	65
		**	**	**	**	**	
(iv) Root d.w. per	H	331	338	399	537	570	435
plant (mg)	L	272	374	435	483	706	454
		*	NS	NS	NS	NS	
(x) Sheath d.w. per	H	132	159	210	273	397	234
plant (mg)	L	155	182	233	345	474	277
		**	NS	NS	**	**	
(xi) Laminae d.w.	H	155	227	341	469	616	361
per plant (mg)	L	199	284	328	475	628	382
		**	**	NS	NS	NS	
(xii) Dead matter per	H	52	67	71	77	73	68
plant (mg)	L	22	15	27	30	39	27
		**	**	**	**	**	
(xiii) Top:Root	H	0.90	1.14	1.32	1.37	1.82	1.31
ratio	L	1.33	1.32	1.36	1.77	1.70	1.50
		**	NS	NS	**	NS	

APPENDIX 4.7c.

The difference between ryegrass cultivars during the period of recovery after removal of water deficit (Ruanui = R; Nui = N)

Plant growth parameters	Cultivar	Harvest No 1	2	3	4	5	Means over 5 harvests
(i) Mature tiller No. per plant	R	10	14	18	24	27	19
	N	9	11	15	18	23	15
		**	**	**	**	**	
(ii) Immature tiller No. plant	R	5	6	8	9	11	8
	N	4	5	6	8	8	6
		**	NS	**	NS	**	
(iii) Mature leaf No per plant	R	11	19	26	34	46	27.2
	N	11	17	23	28	39	23.6
		NS	**	NS	**	**	
(iv) Immature leaf no per plant	R	12	19	27	33	39	26.0
	N	11	17	21	27	32	21.6
		*	**	**	**	**	
(v) Mature leaf area per plant (cm^2)	R	19	42	59	79	121	64.0
	N	23	46	61	81	120	66.2
		*	NS	NS	NS	NS	
(vi) Immature leaf area per plant (cm^2)	R	11	14	27	37	46	27.0
	N	11	15	28	36	50	28.0
		NS	NS	NS	NS	NS	
(vii) Specific leaf area (cm^2/g)	R	150	234	269	244	257	231
	N	158	232	271	241	270	235
		NS	NS	NS	NS	NS	
(viii) Leaf area ratio (cm^2/g)	R	46	71	86	84	93	76
	N	53	68	88	85	99	79
		NS	NS	NS	NS	NS	

(ix) Root dry	R	305	319	422	514	633	439
weight per	N	298	394	411	507	642	450
plant (mg)		NS	**	NS	NS	NS	
(x) Sheath dry	R	142	159	217	288	427	247
weight per	N	145	182	225	331	444	265
plant (mg)		NS	NS	NS	*	NS	
(xi) Laminae Dry	R	173	249	328	462	626	368
Wt. per plant	N	181	263	341	482	618	377
(mg)		NS	NS	NS	NS	NS	
(xii) Dead matter	R	44	39	52	55	61	50
dry weight	N	31	43	45	52	51	44
plant		**	NS	NS	NS	NS	
(xiii) Top:root	R	1.10	1.32	1.30	1.54	1.73	1.40
ratio	N	1.13	1.14	1.39	1.61	1.78	1.41
		NS	NS	NS	NS	NS	

APPENDIX 4.8a

Temperature x water deficit interaction means. Leaf area per plant (cm^2)

Harvest No	C		S1		S2		
	H	L	H	L	H	L	
1	72	52	28	35	0	11	**
2	111	81	62	43	20	33	**
3	171	84	99	66	56	50	**
4	234	108	117	101	57	80	**
5	276	161	252	140	87	95	**

APPENDIX 4.8b

Temperature x water deficit interaction means. Dry weight per plant (mg)

Harvest No	C		S1		S2		
	H	L	H	L	H	L	
1	712	699	728	574	413	605	**
2	1181	1109	625	799	367	611	**
3	1425	1293	863	924	561	765	**
4	1954	1428	1124	1380	758	1078	**
5	2054	2252	1593	1717	1102	1456	**

APPENDIX 5.1

Estimation of leaf area from leaf length and leaf width measurements

The regression equation between leaf area (LA) measured by electronic leaf area meter, and the product of leaf length (l) by leaf width (w) at ½ l of the lamina has been used to estimate the leaf areas in Experiment 6.

It was thought that the predictive equation might vary for the different treatments, hence samples were collected separately from the 4 treatments (viz., LL, LH. HL and HH - for definition of treatments see section 5.1.3). All the leaves of the test plants were used and there were between 20 and 30 plants for each group of samples depending on treatments.

Table A.1 summaries the regression information for each treatment. The regression equations were calculated using a package program -- "BASIS" (Burroughs Advance Statistical Inquiry System, 1973) on the B6700 computer at Massey University. The regression coefficients were tested using T test according to Snedecor and Cochran (1968) pp 432. There was no significant difference between the regression coefficients , the data was therefore pooled and a single regression equation calculated (Table A.2).

TABLE A.2 Regression information for the leaf area and leaf length x leaf width relationships

Treatments	Regression equations	R^2	Number of samples
LL	Y = -31.55 + 0.8121 X	0.93	277
HH	Y = -39.60 + 0.7728 X	0.93	263
LH	Y = -32.21 + 0.8039 X	0.89	151
HL	Y = 45.03 + 0.8142 X	0.90	147
All Treatments combined	Y = -25.99 + 0.8029 X	0.91	838

Y = leaf area X = leaf length x leaf width

APPENDIX 5.2

The effect of removing secondary tillers on the performance of the main tiller in prairie grass

A.5.2.1 Introduction

In experiments involving measurements of the length and number of individual leaves on the main tiller, it is desirable to remove the secondary tillers as they appear, so as to make identification of the individual main stem leaves easier. For example, Wardlaw (1969) removed all the secondary tillers and the first 3 leaves on the main culm, before applying treatments in his experiment with ryegrass.

However, it is not known whether the removal of the secondary tillers will influence the growth of the leaves on the main tiller. The following experiment was conducted in the growth rooms at the same time as that of Experiment 6, to check this.

A.5.2.2 Materials and Methods

Prairie grass (*Bromus catharticus* Vahl. cv Grasslands Matua) were grown from seed in the Controlled Climate Rooms, DSIR. The soil medium, growing conditions and treatments were identical to that reported for Experiment 6 (section 5.1.3).

Briefly, the treatments were:

LL plants grown continuously under the low (L) evaporative demand (ED) conditions.

LH plants grown under the L ED conditions until leaf 6 (week 5) and were transferred to the high (H) ED conditions until the end of the experiment at week 8.

HH plants grown continuously under the H ED conditions

HL plants grown under the H ED conditions until week 5 and transferred to the L ED rooms until week 8.

There were 8 replicates for each treatment.

The plants were thinned from 15 to 2 by week 5. Within each pot, i.e., a replicate, one of the two plants was left intact, while the other had all its exposed secondary tillers removed as they appeared.

Removal of secondary tillers started when leaf 6 was just emerging (i.e., the same starting time as that of Experiment 6) at the beginning of week 5 from sowing. The tiller removal operation was done daily by cutting as close as possible to the base of the secondary tillers. Cutting in this manner only removed the exposed laminae without damaging the growing points of the secondary tillers.

A.5.2.3 Results and Discussion

Removal of the secondary tillers did not affect the performance of the leaves of the main tiller in terms of leaf area, leaf numbers and dry weight per main tiller (Table A.3). By the end of the experiment at week 8 the intact plants had 9.9 ± 2.2, 10.5 ± 1.6, 11.9 ± 1.9 and 10.0 ± 2.7 tillers for the HL, LL, LH and HH treatments respectively.

One would expect by removing the laminae of the secondary tillers there must be a greater drain on the photosynthate from the leaves of the main tiller. However this has not been reflected in any adverse effect on the performance of the leaves of the main tiller.

TABLE A.3 Comparison between plants with their secondary tillers removed and those with their secondary tillers intact.

Mean across 4 rooms

Treatments	Leaf area per main tiller (cm^2)	Leaf number per main tiller	Dry weight per main (mg)
Tillers removed	15.2	9.3	838
Tillers intact	14.0	9.4	894
	NS	NS	NS
CV%	16	5	15

There was no room x tiller treatment interaction.

APPENDIX 6.1

Origins of the planting materials used in the present study

Sudax - SX - 6, a forage sorghum hybrid, *Sorghum* bicolor (L) Moench x *S. sudanese* (piper) Staff. seed purchased from Dalgety Ltd., Palmerston North, 89% germination.

Prairie grass - *Bromus catharticus* Vahl. c.v. Grasslands Matua prairie grass. Seed from Dr W. Rumball, Grasslands Division, DSIR, Palmerston North.

Nui ryegrass - *Lolium perenne* L. c.v. Grasslands Nui perennial ryegrass. Seeds from Mr I.M. Ritchie, MAF, originally from DSIR No A 3524, 98% germination.

Ruanui ryegrass - *Lolium perenne* L. c.v. Grasslands Ruanui perennial ryegrass seed from Mr I.M. Ritchie, MAF. Basic seed Reg No. OT1725B (7.10.75), 98% germination.

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