The effects of summer moisture stress and its interaction with spring cutting managements on the production and persistence of a ryegrass (*Lolium perenne* L.) sward

A thesis presented in partial fulfilment of the requirements for the degree of Master of Agricultural Science in Plant Science at Massey University, Palmerston North, New Zealand.

DAVID JOHN BARKER
1983

Table of Contents

Acknowledgements

I would like to acknowledge the assistance given to me by the following:

Dr A.C.P. Chu, my supervisor, for his assistance in many aspects throughout my course and especially for his work (in the wider sense) in obtaining the research contract which made this study possible.

Dr C.J. Korte, my co-supervisor, for his advice and discussion during the experiment and thesis preparation and also for his assistance with computer programming.

Grasslands Division DSIR for a) providing the seed used in the experiment; b) allowing me time during work to complete this study, and c) providing computing facilities.

Dr H.G. McPherson for helpful discussion and comment during the preparatory stages of the project.

Dr B. Clothier, DSIR, for lending the neutron probe.

Mr A. Green and Mr J. Gordon, DSIR, for their electronic and mechanical expertise in setting up and maintaining the rain-out shelter.

Dr I. Gordon, Massey University, for statistical assistance.

Mr A. Hall, DSIR, for computing assistance.

The technical and field services staff of the Agronomy Dept, Massey University, particularly Flora Bartholomew and Marc Hancox for technical assistance.

Fellow post graduate students, members of the Agronomy Department, Massey University, and staff of the Grasslands and Plant Physiology Divisions, DSIR, for their discussions and comments.

And finally to Miss D. Rosvall for her time and effort in typing this thesis.

Financial assistance from the following is acknowledged:

Leonard Condell Scholarship 1981
Leonard Condell Scholarship 1982
Johannes August Anderson 1981
DSIR contract SIR UV/4/45

List of Figures

page

page

List of Tables page

List of Plates

List of Appendices

Abstract

The effect of an increasing water deficit during summer, achieved by means of an automatic Rain-Out Shelter, on the production and persistence of a perennial ryegrass (Lolium perenne L. "Grasslands Nui") was compared to that under irrigation. In addition, the effect and interaction with water deficit, of 2 different cutting intensities (i.e. heights of 2.5 and 7.5 cms) during spring were also investigated.

The responses of perennial ryegrass to an imposed drought, compared to those under irrigation, were related to measurements of soil and plant water status; where the soil and plant water status were measured by soil water deficit and leaf water potential respectively. It was found that the growth of the components of pasture production (particularly tiller and leaf dynamics) was reduced when the soil water deficit exceeded a critical point of 104-111 mm, which could be predicted for the Tokomaru silt loam soil type, according to the soil water balance of Scotter, Clothier and Turner (1979). At this point the soil water potential was approximately equal to -0.1 MPa and had not reached the permanent wilting point (-1.5 MPa). This critical point was characterised by a sharp 0.6 MPa decrease in dawn leaf water potential which contrasted with a more gradual decline in mid-afternoon leaf water potential. Such a change in leaf water potential (particularly at dawn) was found to be a very sensitive indicator showing that this change in water status had occurred. At deficits exceeding the critical point reductions in pasture yield were attributable to a reduction in the rate of tiller appearance, an increase in the rate of tiller death, and a reduction in the rate of leaf production (i.e. extension and appearance).

Furthermore it was found that spring managements to increase tiller density will result in a greater tiller density at the end of drought, but will not give an advantage in dry matter yield during the drought. Any benefit which might result from a management system to prepare a sward for drought is unlikely to be in summer production but may be in the potential for faster recovery after drought.

Keywords perennial ryegrass, water stress, leaf water potential, cutting intensity, tiller dynamics, leaf dynamics, Rain-Out shelter.

CHAPTER I

INTRODUCTION

New Zealand has a humid climate ideally suited to pastoral agriculture, however although annual rainfall in most areas exceeds 1000 mm (N.Z. Official Yearbook 1982) variability between years is high, with 19.9% of years being considered "wet" and 15.1% of years being considered "dry" (Salinger 1979). The increased prevalence of drought since 1968 (58 year average 1920/21-77/78) (Salinger 1979) combined with the uneven geographical distribution of rainfall, tending to be drier in the east than the west (N.Z. Official Yearbook 1982), has prompted researchers to consider the effects of water stress on Agricultural and more specifically pastoral production in New Zealand.

In some areas of New Zealand relief from summer droughts can be achieved by irrigation, however large areas of the country must continue to rely on a system of dryland farming. In these areas, optimum management systems need to be developed from an understanding of the responses of the individual pasture species to summer water stress and their recovery from that stress.

There is considerable evidence that different cutting and grazing treatments will influence subsequent pasture composition and productivity in the summer (Brougham 1959, 1960, 1970; Hunt and Brougham 1967). Differences in the relative effect of a particular treatment from one season to the next, suggest there is a definite interaction between the management of a pasture and its summer drought tolerance. This led Brougham (1959) to state that "the differences between the seasonal growth patterns produced by the different treatments were determined by species tolerance to the grazing systems and the modified action of weather factors on growth because of differences in herbage cover and botanical composition". As yet, there has not been a detailed study of this interaction nor of the possibility of using spring grazing to prepare a pasture for drought.

At the international level, research into water stress has been widespread, however most of the detailed research investigating the mechanisms involved has been restricted to glasshouse and growth-room studies. In general, the water stress was imposed with unnatural rapidity which frequently did not give the same result as experiments performed in the field (Baker and Jung 1968, Ritchie 1974, Johns 1978, Turner and Begg 1978, Jones, Leafe and Stiles 1980(a)).

This experiment therefore had the specific objectives of:

1. Measuring the response of perennial ryegrass to an imposed drought (compared to irrigation) and relating this to measurements of soil and plant water status under field conditions
2. Studying the effect of spring cutting managements on the patterns of tiller and leaf growth on a sward of perennial ryegrass during summer under two contrasting moisture regimes

CHAPTER II

REVIEW OF LITERATURE

2.1 Introduction

The literature contains a wealth of information describing the vast range of effects of water stress on plant growth. This information has accumulated because of the complexity of the responses of the plant to water stress and the multiplicity of approaches to the study of these responses. The response of plants will vary depending on other factors such as: (a) the plant species/variety, (b) the intensity and duration of the water stress imposed and (c) many environmental factors such as temperature, light intensity and defoliation managements.

This review will consider aspects of the literature which are relevant to the experiment outlined in the following chapters. It will begin therefore with a discussion of water stress and how it is measured. This will be followed by a more general discussion of the effects of water stress on plant growth. The bulk of this review will comprise a specific consideration of the effects of water stress on pasture production, making special reference where possible to ryegrass dominant pastures, and highlighting areas of agreement in the literature, rather than the many areas of disagreement. Pasture production will be assessed in terms of dry matter yield, and mention will be made of the various components of that yield. This review will conclude with a consideration of the ways in which spring defoliations of pasture might modify the effects of water stress during summer.

The terminology and definitions of Thomas (1980) have been adopted in this thesis.

2.2 Water stress and its measurement

2.2.1 Water stress and water deficit

Water stress (usually implying water deficit stress) has been defined by Levitt (1972) to be any level of water deficit at which an impairment in some plant function has occurred. In other words a state of water stress is said to exist when the deficiency of water (whether in the soil or the plant) is detrimental to the plant.

An important feature of this definition is the distinction between a water deficit and a water stress. This is often not acknowledged by many researchers, who appear to use water stress and water deficit synonomously. The implication of the above definition is that there are some levels of water deficit which do not impair plant function and therefore are not water stresses. There are two examples where plant water deficits can be demonstrated to exist, but which can not be regarded as a water stress.

The first is that maximum rates of leaf growth (indicating optimum plant function) have been observed at small water deficits (-0.15 to -0.25 MPa) even when plants are growing in well watered soils. Boyer and McPherson (1975) consider this "curious" phenomenon as being necessary to maintain a gradient of water potential to supply water for plant growth. This level of water deficit is not stress. Turner and Begg (1981) state that "water deficits occur in the tissues of all transpiring plants as an inevitable consequence of the flow of water along a pathway in which frictional resistances and gravitational potential have to be overcome". In light of the fact that these deficits are a normal part of plant functioning they can not be regarded as a stress.

The second example can be seen in the diurnal cycling of plant water status, where again, water deficits occur but are not necessarily causing a water stress. In the simplest case, a water deficit develops in plants as a consequence of stomata opening in the morning and disappears with the closing of stomata in the evening. The effect of diurnal movements of plant water status on plant function has been examined (Leafe, Jones and Stiles, 1977) where it was found for ryegrass in the field, that diurnal movements down to -1.0 MPa did not affect leaf extension rate (1 mm/hr). It was not until the minimum daily leaf water potential fell below -1.5 MPa that leaf extension rate was reduced (to 0.25 mm/hr). This more severe level of deficit may have resulted in the midday closure of stomata, preventing CO_2 uptake (Zelitch 1969) and thus become a water stress. Similarly, the dramatic yield responses to most irrigation, preventing conditions of high atmospheric demand (cited by Howell, Hiler and van Bavel, 1971), are evidence of stress occurring as a result of the more extreme diurnal movements of plant water status. It is uncertain as to the extent that diurnal movements of water deficit impair plant function however, it is certain that in some circumstances a water deficit (in the above case, as low as -1.0 MPa) does not constitute a water stress. Further experimental work clarifying the point at which the diurnal movements of water status become a stress is necessary.

2.2.2 The measurement of water stress

Water stress research is complicated by the number of methods for measuring water stress. Some authors discuss water stress in the very simplest of terms as either being present (usually severe) or absent. This is misleading and inaccurate since the influence of water stress on plants will vary with the intensity and duration of stress, the rate and pattern with which it develops (Turner and Begg 1978) and the stage of plant growth (Slatyer, 1969). Water stress can be described in qualitative terms such as severe or mild but these are subjective and imprecise, especially when describing extreme environments. This problem of describing water stress was encountered by Gardner and Nieman (1964) when they endeavoured to describe the lower limit of soil water availability to plants i.e. the maximum water stress a plant can survive. They came to the conclusion "that although defining the permanent wilting point as -15 bars may be useful for many practical purposes, it does not represent the absolute lower limit of available water. Indeed, no single limit for all plant processes can be defined in any precise way".

Quantification of water stress is achieved by measuring the water status (deficit) of the soil or plant at which a particular response of the plant is observed. A more severe stress occurring when the measured water deficit is greater. Salter and Goode (1967) concluded that a comparison of the effects of water stress on different plants in different environments can be made by measuring the deficit in terms of plant water potential.

Water potential (ψ) is a measure of the free energy of water (Stocker 1960). All water movements can be thought of as following gradients of decreasing free energy. In the path from the soil to the atmosphere (whether through the plant or not) water will move down on energy gradient, and hence the concept of the soil-plant-atmosphere continuum of Philip (1966).

Water potential can be defined as the partial molal Gibbs free energy of water (or the chemical potential of water) compared to a reference point of pure water, divided by the molal volume of water, at a defined pressure and temperature (usually STP) (Stocker 1960). The dimensions are energy/volume = pressure (Dainty 1976) and is uaually measured in MPa (equivalent to 10 bars, 0.0987 atm, 10^7 ergs/cm^3). Since the reference point of pure water is arbitrarily defined as zero, and water moves down on energy gradient, water potential will generally be negative. It is probably only positive during the process of guttation and is unlikely to exceed 0.1 to 0.2 MPa. Minimum values of plant water potential vary with plant species. Temperate grasses have minimum values of -2.5 to -3.0 MPa whereas some tropical and zone plants have minimum values of -8 to -12 MPa (Ludlow et al. 1983).

Currently the water potential is given as the sum of four major components, as in equation (1) (Rose 1966).

$$\psi = \psi_g + \psi_s + \psi_m + \psi_p \tag{1}$$

where

= total water potential

ψ_g = gravitational potential
This is typically the smallest component of the total water potential. In pasture species gradients in gravitational potential are of the order of 0.01 MPa m^{-1} and are ignored (Turner and Begg 1978)

ψ_s = solute (osmotic) potential
This is the lowering of the water potential due to soluble ions and thus has a concentration dependance (Warren-Wilson, 1967)

ψ_m = matrix potential
This results from forces of attraction of water to the matrix (structural) fraction of the plant cell (Warren-Wilson, 1967)

ψ_p = pressure (turgor) potential
This is a measure of the hydrostatic pressure within a plant cell, giving rise to turgor. Pressure potential is generally positive in plant cells; reductions in potential to values approaching zero will result in a reduction or inhibition of cell growth and division (Weatherly 1970)

Salter and Goode (1967) concluded their extensive review of the crop responses to water at different stages of growth with a list of problems meriting consideration in future research programmes, the first point of which called for "a reliable but simple and rapid field method for measuring plant water potential." Various methods existed for the measurement of plant water potential, however these were neither simple, reliable nor rapid - for example the measurement of water potential in apple leaves by methods involving immersion in sucrose, polyethylene glycol (PEG) or mannitol were complicated by metabolism of these compounds (Goode and Hegarty 1965), and the psychrometric methods described by Boyer (1969) involve complex apparatus and long equilibration times. Almost as if in response to the call of Salter and Goode, Boyer (1967) described the use of a modified pressure chamber (Scholander et al. 1964, 1965a, 1965b) for measuring leaf water potentials. Since that time, many workers e.g. Boyer (1969), DeRoo (1969), Sivakumar and Virmani (1979) have found that the rapidity and ease with which measurements can be made in the field, make the pressure chamber suitable for quick measurements of leaf water potential.

Despite many advantages in measuring water status in the plant to quantify water stress, and thereby taking account of the effects of root density and distribution, soil water release characteristics, transpiration rate and other factors which determine the overall water economy of the plant (Jackson 1974a)the assessment of water stress in the field has largely been confined to the measurement of soil water status. "The preference for soil water measurements has probably arisen from the relative ease with which they can be made" (Jackson 1974a), that is, before the development of the pressure chamber.

Although the measurement of soil water status can be made in terms of soil water potential (MPa), gravimetric (g water/g soil) or volumetric (cm^3 water/cm^3 soil) water content, perhaps the most widely used method to describe soil water status in field water stress studies is the soil water deficit (usually in mm). While each of these methods are related to each other and to plant water status in various ways, the nature of these relationships is specific to individual soil types; a point which complicates comparisons of experimental results.

The soil water deficit is calculated as the depletion of total soil water storage below field capacity, where the total soil water storage is calculated as the integration of volumetric water content over a number of readings from a specified depth. It can therefore be defined as the amount of irrigation water (or rainfall) which must be added to restore the soil to field capacity (-0.001 MPa). As well as its relative ease of measurement the soil water deficit can also be relatively easily predicted from measurements of rainfall and evapotranspiration (e.g. Scotter, Clothier and Turner 1979), and therefore be incorporated into irrigation schedules and soil water balance models. In addition, the effects of modification of the climatic variables rainfall (irrigation) and evapotranspiration on the soil water balance can be predicted. Perhaps the major factors limiting a more widespread application of soil water deficit measurements to water stress research are (a) the variable effects of soil texture and structure (Gradwell 1974), (b) inconsistency in the soil depth which is investigated, and (c) the non-suitability of this type of measurement to glasshouse/growth room pot trials.

2.3 The effects of water stress on plant growth

Hsiao (1973) listed a number of physiological responses to water stress in order of sensitivity to stress. Cell growth was placed at the top of these, being the most sensitive plant process observed (and where cell growth is a fundamental component of plant growth). Hsiao went on to state that "the first change resulting from the onset of water stress is a slowing down of shoot and leaf growth brought about by reduced pressure potential (ψ_p). This is probably followed closely by a reduction in cell wall and protein synthesis in tissue with a high growing potential. As tissue water potential decreases further, cell division and levels of some enzymes, such as nitrate reductase, start to decline. Stomata may begin to close, with a consequent reduction in transpiration and CO_2 assimilation, and abscissic acid probably begins to accumulate. Further increases in the level of stress lead to impairment of major plant processes such as photosynthesis, translocation and ion uptake, resulting in plant senescence and ultimately in plant death."

The extreme expression of a plant's response to water stress is for it to die, and therefore every physiological process in the plant will be affected (whether directly or indirectly) by water stress. Hsiao and Acevedo (1974) considered the problem of the extremely large number of plant responses to water stress recorded in the literature and that there was little use in cataloguing all the metabolic and physiological changes observed under water stress. They concluded that more profit would be obtained by differentiating various processes in terms of their sensitivity to water stress and determining the sequence of events set in motion by the onset of water stress. The early changes would be associated more closely with the primary effects of water stress than later changes, which are frequently the indirect result of the more direct effects. Growth (the combined process of cell expansion and division) is generally considered to be the most sensitive plant process to water stress.

There are various approaches to a consideration of plant growth. Plant growth can be considered in terms of component parts of the plant. In most forage plants (especially vegetative grasses) leaves are a major component of biomass. The effects of water stress on the total plant can be interpreted in terms of the effects of water stress on individual leaves. In a similar way the effects of water stress on a leaf can be interpreted in terms of the effects of water stress on cell growth, where cell growth is the product of cell expansion and cell division.

It is equivocal as to which of the components of cell growth i.e. expansion or division, is the most sensitive to water stress. Cell expansion is generally considered to be the process most sensitive to water stress (Hsiao 1973). In contrast however, other workers have found cell expansion and division were almost equally affected by water stress, with a recalculation of the results of Jones, Leafe and Stiles (1980(b)) showing that a 51% decrease in ryegrass leaf length was accompanied by a 20% decrease on epidermal cell length and a 26% decrease in the number of epidermal cells per leaf. At the opposite extreme, other workers (e.g. Hussain and Aspinal (1970) and Kirkham et al. (1972) give evidence that cell division is more sensitive to water stress than cell elongation.

The component of water potential universally accepted as being the major factor governing cell expansion (cell wall extension) is the force applied to the cell wall i.e. turgor pressure (Cleland 1971). This can be given as equation (2) where growth rate is proportional to the turgor pressure in excess of a critical turgor pressure (Hsiao and Acevedo 1974).

$$G = Eg\ (\Psi_p - \Psi_{p,th}) \tag{2}$$

where

G = growth rate

Eg = gross extensibility of the cell (related to the elastic coefficient and the ability to synthesise cell wall)

Ψ_p = turgor pressure
$\Psi_{p,th}$ = threshhold (critical) turgor

Experimental evidence in support of such a relationship came from Kirkham et al. (1972) where cell growth (estimated as the product of DNA concentration and cell length) showed an approximate linear dependance on turgor pressure. Above a threshold turgor of about 0.3 MPa. Similarly Lawlor (1969) found the rate of leaf extension in ryegrass, relative to controls, was linearly related to turgor pressure above a critical turgor which was about half that of control plants.

In experiments using external pressure (Meyer and Boyer 1972) it was found that elongation is not dependent on the magnitude of the total turgor pressure on cell contents but rather is determined by differences between hydrostatic pressures inside and outside the growing cells.

The relationship between leaf growth and plant water potential has been studied for a range of species; maize (Watts 1974, Hsiao and Acevedo 1974; Boyer and McPherson 1975); soybean (Meyer and Boyer, 1972); sudax (Chu and Kerr, 1977); sunflower (Boyer, 1968) and ryegrass (Leafe et al. 1977, Chu 1979). In general maximum growth rates were observed at the highest (least negative) leaf water potential measured i.e. about -0.2 MPa. The leaf water potential at which growth rates reduced to zero, varied between species but were within the range of -0.4 to -1.0 MPa. This trend conflicts with a lack of a response between leaf water potential and leaf extension rates observed by Leafe et al. (1977) and the entirely opposite response observed by Watts (1974) and Chu (1979) where maximum rates of leaf extension were observed at the maximum leaf water potentials of -0.8 MPa and -0.5 to -0.8 MPa respectively, when the temperatures were optimal for growth.

These observations highlight the complexity of the plant growth response to water stress. It is therefore relevant to note that the three later results were obtained from following the diurnal movements of growth rate and leaf water potential, and also that the results of Leafe et al. (1977) and Watts (1974) were obtained from field experiments, whereas all the other results were from growth room experiments. Turner and Begg (1978) elaborated on the response differences between controlled environment and field grown plants and concluded that much of the data on responses to water stress obtained in controlled environments cannot be applied directly to the field situation, particularly when the stress is imposed with unnatural rapidity as occurs with small soil volumes (Jones, Leafe and Stiles 1980(a)).

The plant responses to water stress have been shown to vary in response to many factors which frequently differ between field and growth room studies, for example with drought hardening and osmotic adjustment (Meyer and Boyer, 1972), with matric or osmotically reduced stress (Sepaskhah and Boersma, 1979), light intensity (Husain and Aspinal, 1970), temperature (Chu, 1979), plant age (Boyer and McPherson, 1975) with compensatory growth (Barlow et al. 1976) and with the pattern of the depletion of soil water (Turner and Begg 1978). These differences which exist emphasise the need for accurate descriptions of water stress studies and the caution which is necessary in comparing results from different water stress experiments (Baker and Jung 1968).

2.4 The effects of water stress on pasture production

The detrimental effects of water stress on pasture production and crop yield in general are universally acknowledged. The effects of water deficit on the vegetative yield of pasture grasses has been reviewed by

Chu (1979) and reductions in the herbage yields of established pastures due to water stress, and responses to irrigation have been observed in many overseas studies (Stiles and Williams (1965), Salter and Goode, (1967), Baker and Jung (1968), Brown and Blaser (1970), Coleman and Lazenby (1975), Leafe et al. (1977),Norris(1982)). This section will however concentrate mainly on the effects of water stress on pasture production for New Zealand soils and environments, where considerable research has been directed in past years.

Rickard (1960) studied the effect of soil moisture and irrigation on both pasture and lucerne production in Canterbury and found that moisture was the major climatic limitation to pasture production during the summer. Similarly, in a wider study incorporating 19 non-irrigated sites throughout N.Z. (Radcliffe 1979), summer and annual rainfall were major determinants of summer, autumn and total yield. Annual dry matter production for lucerne and pasture showed a strong, negative and linear relationship with the number of agricultural drought days per growing season ($R^2 = 0.82$ and 0.83 respectively) (Rickard 1960) where Agricultural drought was defined to exist "when soil moisture in the root zone was at or below the permanent wilting percentage. The condition continues to exist until rain falls in excess of daily evapotranspiration". The permanent wilting percentage was determined to occur (for their Lismore stony silt loam) when the soil water deficit in the top 300 mm reached 51 mm. In another regression the calculated R^2 was 0.34, and it was suggested that the effect of previous seasons (particularly if dry) would influence the pasture production.

Evidence supporting this came from an experiment (Rickard and Fitzgerald 1970) where the R^2 was increased from 0.67 to 0.84 by including days of Agricultural Drought in the preceding season, into the regression. No attempt was made to weight the importance of water stress occurring at different times of a season, although it could be envisaged that stresses occurring earlier in the growing season could have a greater effect on total production.

Baars and Coulter (1974) studied soil moisture and its influence on pasture production in the Waikato. They considered some of the assumptions in Rickard's concept of Agricultural drought were invalid and considered water stress in terms of "deficit days". A day being called a deficit day "when the available soil moisture as calculated (plus any rainfall) insufficient to meet that day's water need" - a point of 75 mm deficit was arbitrarily chosen to be the limit of plant available water. A significant negative correlation was obtained between the number of deficit days and pasture production $R^2=0.83$. Twenty deficit days gave a 21% yield reduction compared to that expected with no deficit days.

Scotter, Clothier and Corker (1979) studied the soil water balance in a fragiaqualf (Tokomaru silt loam) and Scotter, Clothier and Turner (1979), its effect on pasture growth at Palmerston North. They prepared a water balance model for pasture, which took into account the effects of soil water deficits on evapotranspiration and found that it compared well with measured soil water balance over a 3 year period. This model used the weather inputs of pan evaporation and rainfall to calculate mm water deficit. This was used to assess whether growth would occur on a given day (in an all or nothing response) and therefore to predict the total growth over the summer period. The predictions were found to agree closely with measured yields, for both irrigated and non-irrigated pastures.

A comparison of the results of Rickard (1960), Baars and Coulter (1974), and Scotter et al. (1979a,b) is complicated by the fact that each experiment was conducted on a different soil type, in a different environment, using a different concept for evaluating soil water stress and did not record the level of water stress in terms of the plant. To this extent, the comment of Chu (1979) is relevant i.e. "in plant water relations 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". In each model, a level of soil water deficit is chosen for various reasons (-51 mm in the top 300 mm, -75 mm in the top 760 mm, -120 mm in the total profile in the case of the Rickard, Baars and Coulter, and Scotter et al. models respectively). Each model assumes the plant is unaffected below this point and is affected (to varying extents) above this point, although the relationship between soil water deficit and pasture production was not specifically considered. In fact, the yield response to irrigation observed by Rickard and Fitzgerald (1970) for a season with no days of Agricultural Drought is evidence against such an assumption.

Although each of the previous models gives a good estimate of observed yield with predicted yield on an annual basis, little consideration (until recently) had been given to the shorter term responses of plants to water stress. McAneney, Judd and Weeda (1982) presented details of a simple model requiring monthly estimates of maximum weather dependant evapotranspiration (ET) and daily rain to predict the reduction in monthly dryland pasture growth relative to irrigated production. Following up the work of Penman (1962) and Tanner and Ritchie (1974) they assumed that the ratio of actual to potential dry matter production is proportional to the ratio of actual to the maximum weather dependant ET, and that the actual was assumed equal to the potential (pasture production or ET) when the soil water deficit was less than 0.65 times the total available water*

---

* This implies pasture production was reduced before the permanent wilting point was reached, in contrast to the model of Rickard (1960).

(total available water contents for the two soil types used having been determined by Gradwell (1971) as being 87 and 102 mm). The results showed a good fit (r = 0.862) between actual and predicted non-irrigated yield which was not significantly different than the 1:1 line; with the conclusion to their work being, that "given a measurement of potential production, monthly predictions of dryland yields using this model seem adequate to characterise the influence of water stress on pasture trials".

In an examination of the relationship between ET and pasture growth, assumed by McAneney, Judd and Weeda (1982), McAneney and Judd (pers. comm.) found the ratio of non-irrigated to irrigated pasture production was initially constant at 0.83 but decreased linearly as the soil water deficit increased above 38 mm, and extrapolation of the regression line showed the ratio reached zero when the soil water deficit equalled 102 mm. Although this relationship differed from that for ET (with pasture yields being reduced before water consumption and also decreasing at a slower rate) McAneney and Judd (pers. comm.) were cautious about drawing firm conclusions, but considered that the assumption of McAneney, Judd and Weeda (1982) was valid, "as a first approximation for planning purposes and for the analysis of trial results." Clearly however, further experimental data to support this relationship is necessary.

In a different direction of research, Korte and Chu (1983) investigated the effects of water stress on the seasonal pattern of pasture growth and drew conclusions as to how this might be modified by grazing management. They measured ryegrass production during and after a drought, finding that growth rates of non-irrigated plots (where the soil water deficit in the top 30 cm reached 86 mm) were only 30% of that for irrigated plots (where the soil water deficit in the top 30 cm did not exceed

30 mm). Upon release of the stress, they found that the growth rate of previously stressed plots was 56% greater than for irrigated plots, and went on to propose that spring management should be used to prepare a pasture for drought by encouraging a high tiller density, where this will be reflected in a higher density after drought and presumably a faster recovery of the pasture. More research is needed into the mechanisms of the response in terms of the plant water status, and how these might be modified prior, during, and after the stress period.

2.5 The effects of water stress on the components of pasture production.

Any effect of water stress on total yield can be interpreted as an effect derived from the influence of water stress on the component of that yield. In the case of pastures water stress effects on yield can be seen in morphological components such as tiller density and tiller size. The component of tiller size can be divided further into smaller components such as leaf number, leaf size, leaf weight etc., the grass leaf therefore being the smallest morphological component of pasture productivity. In his review, Silsbury (1970) stated that "the study of leaf growth during the vegetative phase is regarded as a step towards understanding the basis for productivity of grass swards", but includes very little discussion on water stress.

Various authors have considered the yield in terms of leaf components. Luxmoore and Millington (1971) considered total leaf area in terms of the components - leaf number per tiller, leaf size and tiller number. Turner and Begg (1981) relate yield to be a function of leaf expansion, leaf senescence, rate of photosynthesis and the distribution of assimilate within the plant. Leaf et al. (1977) found that the reduction in tiller weight during moisture stress is due to a reduction in the rate of leaf expansion, slower rate of leaf appearance and accelerated rate of leaf senescence.

2.5.1 Tiller density and tiller size

Evidence suggests that both the rate and amount of tillering decrease with increasing water stress. Luxmoore and Millington (1971) found that variation in total ryegrass dry weight was related to water stress effects on both tiller number and tiller weight. Variation in tiller number was the major morphological response of perennial ryegrass associated with variation in dry weight and leaf area index. For spaced plants grown in controlled environments the number of tillers per plant was increased from 40 to 60, and mean dry weight per tiller was increased from 56.8 mg to 67.8 mg for plants grown at an average soil water content of 5½% and 12% respectively.

Horst and Nelson (1979) found that summer yield of tall fescue was increased by irrigation due to both increased yield per tiller and increased number of tillers. For plants growing under stressed conditions the mean tiller weight ranged from 40 to 100 mg/tiller with an average density of 1700 tillers/m^2 compared to plants growing under irrigated conditions where the mean tiller weight ranged from 100 to 200 mg/tiller with an average density of 1950 tillers/m^2. It was interesting to note that the subsequent spring yield was lower on the irrigated plots. This was attributed to the possibility that irrigation may have caused a high proportion of tillers that were normally dormant, to break dormancy during summer and begin growth. Consequently a lower proportion of tillers would have overwintered - to continue production in the following season.

Hunt and Brougham (1967) recorded a decline in the tiller density of a sward during the summer and attributed this to the failure of young tillers to establish rather than the mortality of older tillers.

Similarly Korte and Chu (1983) made a detailed study of the tiller dynamics of a perennial ryegrass sward during and after a period of induced water stress. During drought herbage production was reduced initially through a reduction in tiller weight, and subsequently through a reduction in tiller density. By the end of a three month stress period, tiller densities were 11,000 and 4,000 tillers/m^2 in irrigated and stressed plots respectively. The rates of tiller death for tillers marked at the start of the experiment or three weeks later were compared during the period of stress. Tillers present at the start of the experiment died at the same rate in irrigated and stressed plots, however, in stressed plots, young tillers appearing in the first three weeks of the stress period died at a faster rate than the older tillers. In addition they found that the reduction in tiller density was also due to a reduction in the rate at which new tillers appeared. Chu (1979) also found that reductions in tiller numbers resulted from the suspension of tiller production rather than the accelerated death of existing tillers. It was suggested therefore that tillers may survive dessication by remaining dormant.

The detrimental effect of drought on tiller density may, in severe cases, continue into the following season. Rickard and Fitzgerald (1970) related pasture yield to Agricultural drought in one year ($R^2 = 0.67$) and found that the correlation could be improved ($R^2 = 0.84$) by including the number of days of Agricultural drought in the preceeding season. On this basis they proposed that a particularly dry year can affect production in the following season, an effect also observed by Radcliffe (1979). Rickard and Fitzgerald were unable to test their suggestion directly since they were re-analysing data collected almost twenty years earlier, however it is possible that the effect on subsequent years may have resulted from a reduced tiller density continuing into a second year.

2.5.2 Leaf number and leaf length

The components of leaf number and leaf length can both be considered in terms of two processes i.e. the rate of production and the rate of death where (a) changes in leaf length are the result of a difference in the rate of leaf extension, expansion or elongation and the rate of leaf senescence (progressive necrosis from the tip; (b) changes in leaf number are the result of a difference between the rate of leaf appearance and the rate of leaf death. These four processes are differentially affected by water stress, a point not always considered in the literature. Furthermore, the grass leaf comprises a sheath and a lamina. Research into the effects of water stress on grass leaves is almost entirely focused on the lamina, with very little consideration of the effects of water stress on the sheath.

The principle effect of water stress on perennial ryegrass is the reduction of leaf extension (and thus development of leaf area). The effect of this on dry matter yield occurs 2 ways 1) the reduced incorporation of carbon into the plant cell walls; 2) the reduced area for photosynthetic incorporation of CO_2.

Leafe et al. (1977) found that the leaf extension rate (mm/day) was reduced by water stress. The most severe stress (116 mm soil water deficit) reduced leaf extension rate to 25% of the rate in irrigated controls. Considerably smaller stresses still resulted in a decrease of leaf extension rate to 85% of that in irrigated controls. In addition to reducing the rate of leaf extension water stress also resulted in a decrease in final leaf length i.e. from 240 to 205 mm in one case, and from 216 to 143 mm in a more severe case.

Chu (1979) examined the sensitivity of leaf extension to water deficit in two ryegrass cultivars (Nui and Ruanui) under 2 different controlled temperature regimes (27.5/12.5 and 17.5/12.5°C day/night). In general it was found that the leaf extension rate of both cultivars at both temperatures was sensitive to water deficits. Differences in the leaf extension rate between control and stressed plants became apparent once marked differences in the leaf water potential had become apparent. At the higher day temp Nui had a 1.3 to 1.6 times higher leaf extension rate than Ruanui, which was found to continue during the development of water stress.

The rate of leaf appearance is sensitive to water stress. Kumai et al. (cited by Anslow 1966) found that cocksfoot leaves appeared less frequently during a period of low herbage production in midsummer. Changes in the pattern of leaf appearance were closely related to the seasonal growth of plants. Leafe et al. (1977) found that water stress resulted in a decline in the rate of leaf appearance. The leaf appearance interval (reciprocal of leaf appearance rate) was 8.12 days/leaf and 9.76 days/leaf in irrigated and stressed plots respectively. As the stress became more severe leaf appearance intervals of 7.08 and 12.92 days/leaf for irrigated and stressed plots respectively were observed.

Leaf senescence and leaf death are closely related since death is simply the final result of progressive senescence. There is very little literature considering the effects of water stress on either of these processes. This is possibly because the majority of work considers net expansion rather than the two separate processes of actual expansion and senescence. Korte and Chu (1982) stated that the reduction in tiller weight in response to water stress is due to various factors including accelerated leaf senescence, but did not measure this directly. Similarly Leafe et al. (1977) without measuring leaf senescence directly, observed that total leaf area declined during a period of water stress. This could only occur if the rate of leaf senescence and death increased relative to the rate of leaf extension and appearance.

2.6 Modification of the water stress effects on pasture production by spring pasture management.

There are various reports in the literature which investigate the management of pastures during drought, however there is little work specifically using spring managements to modify detrimental effects of summer drought.

An investigation of the interaction between defoliation and moisture in summer (Jantti and Kramer 1956, Jantti and Heinonen 1957) found that severe defoliation of a pasture in summer severely inhibited its regrowth compared to pastures which were less severely defoliated. In relating pasture dry matter production and drought Rickard (1960) found that production records are comparable (with respect to level of drought) only within a particular field experiment, since mowing frequency, topdressing and grazing management all have a marked effect on the measured production. Brougham (1960) stated that differences between seasonal growth patterns produced by the (grazing) treatments were determined by species tolerance to the different intensities of grazing and the modified action of weather factors on growth following changes in herbage cover and in botanical composition. Brougham (1970) considered that the subsequent carryover effects of grazing could be attributed to"interactions between grazing pressure, soil moisture levels as influenced by herbage cover, the proportion of tillers of grass plants in the pasture community with growing points above defoliation height, and the persistence of species in the community."

In the literature there are various factors which have been recorded to be modified by defoliation treatments which could modify the response of ryegrass to periods of water deficit during the summer.

1. Tiller density. Hard frequent defoliations during spring can be used to create higher tiller densities than would lax frequent defoliations (Korte 1981). Since there is a relationship between tiller density and total yields, higher yields might be observed during summer. Korte and Chu (1983) hypothesised that "to prepare a pasture for summer drought, spring management should encourage root growth and a high tiller density." They found that drought had relatively little effect on tillers established before the onset of drought but had a severe effect on tillers emerging during drought. A denser sward in early summer would therefore ensure that more tillers would survive summer drought.

2. The ratio of vegetative to reproductive tillers in the sward; particularly as it relates to the age of vegetative tillers at the onset of drought (Branson 1953). Earlier flowering tillers would be expected to initiate new tillers sooner (i.e. once flowering is completed or prevented) and that new tillers would be more mature and more likely to survive a drought.

3. Soil water content. This has been found to vary with the defoliation treatment. Managements where the herbage cover is maintained have up to 25% higher soil water contents (particularly in the top 7.5 cm) compared to those which are tightly grazed (Brougham 1959, 1960). Since soil water content will decrease with increasing summer moisture stress, soils with a higher water content at the onset of drought would be expected to yield more pasture during summer.

4. The plant carbohydrate reserves would be expected to be reduced with hard and frequent defoliations (Bommer 1966). Recently osmotic adjustments have been observed as an adaptive response to water stress by some species (Turner and Begg 1981, Jones, Turner and Osmond 1981). It has not yet been determined whether ryegrass shows this response, however should it occur, the

lowering of plant carbohydrate status by defoliation would be expected to reduce the extent to which osmotic adjustment could take place.

5. Plant rooting depth has been shown to be influenced by grazing managements where hard frequent grazings well reduce the plant rooting depth (Weinmann 1948). However since drought initially results in a lower availability of water near the soil surface than at greater depths (Gates 1979) deeper rooting plants would be better able to survive. Davidson (1978) and Korte and Chu (1983) point out the conflicting management decisions which must be made between optimising top and root growth. Despite the potential for grazing management to modify the effects of water stress on pasture production it is still uncertain as to what mechanisms might be involved, especially since the relative importance of these mechanisms is likely to vary in different circumstances. It is apparent that the effects of water stress on pasture production can be reduced by hard frequent grazings when considering the increased tiller density and the increased ratio of vegetative tillers in the sward, but this can be offset by the depletion of plant carbohydrate reserves, the decrease in plant rooting depth and the decrease in soil water content. Clearly research into this area is necessary.

CHAPTER III

MATERIALS AND METHODS

The materials and methods are presented in six main sections. These are:

3.1 Experimental site

3.2 Establishment of the experiment

3.3 Experimental pre-treatments and treatments

3.4 Management during the pre-treatment and treatment periods

3.5 Measurements

3.6 Statistical analysis

3.1 Experimental Site

The experiment was conducted from 16 April 1981 to 14 April 1982 on the Pasture and Crop Research and Development Unit of Massey University, Palmerston North, New Zealand, at grid reference NZMS1, N149/099308. This was a relatively exposed, nearly flat site (sloping slightly to the North East), located on the top terrace of the Manawatu River.

The average annual rainfall for Palmerston North (1941-70), measured 2 km from the site, was 1002 mm (N.Z. Official Yearbook 1982).

The previous history of the site was that it had been in permanent pasture for five years prior to the start of the experiment, during which time it was used predominantly for sheep grazing and short term experiments.

The soil type is a Tokomaru silt loam (Cowie, Kear, Orbell 1982). It is classified as an Aeric Fragiaqualf (gleyed yellow-grey earth) (Cowie, 1978; Scotter, Clothier, Corker 1979), and has been characterised in detail by Pollock(1975). It is characteristic of large areas of the flat to rolling hill country at the foot of the western Tararua Ranges. The soil had been mole drained 5-10 years prior to the commencement of the study.

3.2 Establishment of the experiment

Cultivation of the experimental area began on 16 April 1981 when the area was sprayed with glyphosate and then ploughed and harrowed. Lime (3 t/ha) and a 12-10-10 NPK compound fertiliser (500 kg/ha) were incorporated into the soil by rotary cultivation. One week later, Lolium perenne L. "Grasslands Nui" (A3741 84% germination) was sown at a rate of 30 kg/ha (1,575 viable seeds/m^2). Seedlings first emerged two weeks after sowing and two weeks later the density of established seedlings was 1255 ± 130 seedlings/m^2. Eight weeks after sowing (24 June) the pasture was defoliated with 25 sheep for 24 hours. Thereafter, a reel mower (set to 2.5 cms) was used at approximately four week intervals (i.e. 24 July, 17 August and 15 September) until 5 October 1981 when the spring cutting height pretreatments were imposed. Mower clippings were discarded in each case. After each defoliation, urea solution was applied by watering can at rates of 38, 38, 30 and 25 kg N/ha after the first (29 July), second (28 June), third (20 August) and fourth (15 September) defoliations respectively.

3.3 Experimental pretreatments and treatments

3.3.1 Introduction

The plot layout was that for a "combined experiment" (or pooled environments model, see section 3.6.1). There were sixteen "plots", arranged in two groups of eight; the first group being covered by a rain-out shelter and the second group being irrigated. These groups will be referred to from now on as "environments" or treatments. Within each environment the eight plots were subdivided into four pairs of adjacent plots, referred to from now on as "blocks". Within each block defoliation pretreatments were assigned to plots at random using the toss of a coin. The experimental layout and assignment of treatments to plots as illustrated in figure 1.

The pretreatments and treatments were separated in time as well as space. There were two defoliation pretreatments which continued for about three months during spring, beginning on 5 October 1981 and finishing on 28 December 1981. The imposition of the moisture treatments began with the conclusion of the spring defoliations (28 December) and continued for about $3\frac{1}{2}$ months during summer, until 14 April 1982. The timing of operations is illustrated in figure 2.

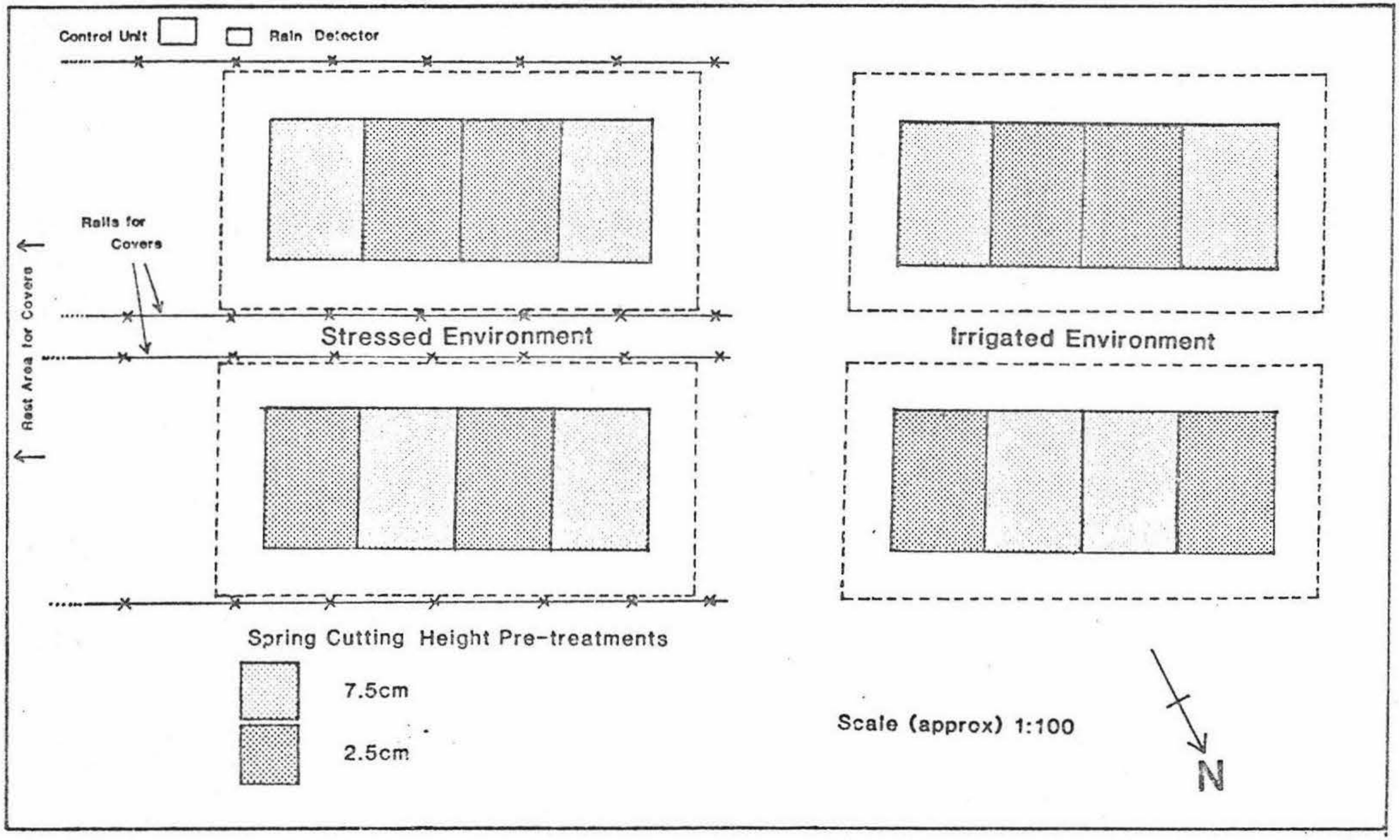

Figure 1. The experimental layout and assignment of treatments to plots.

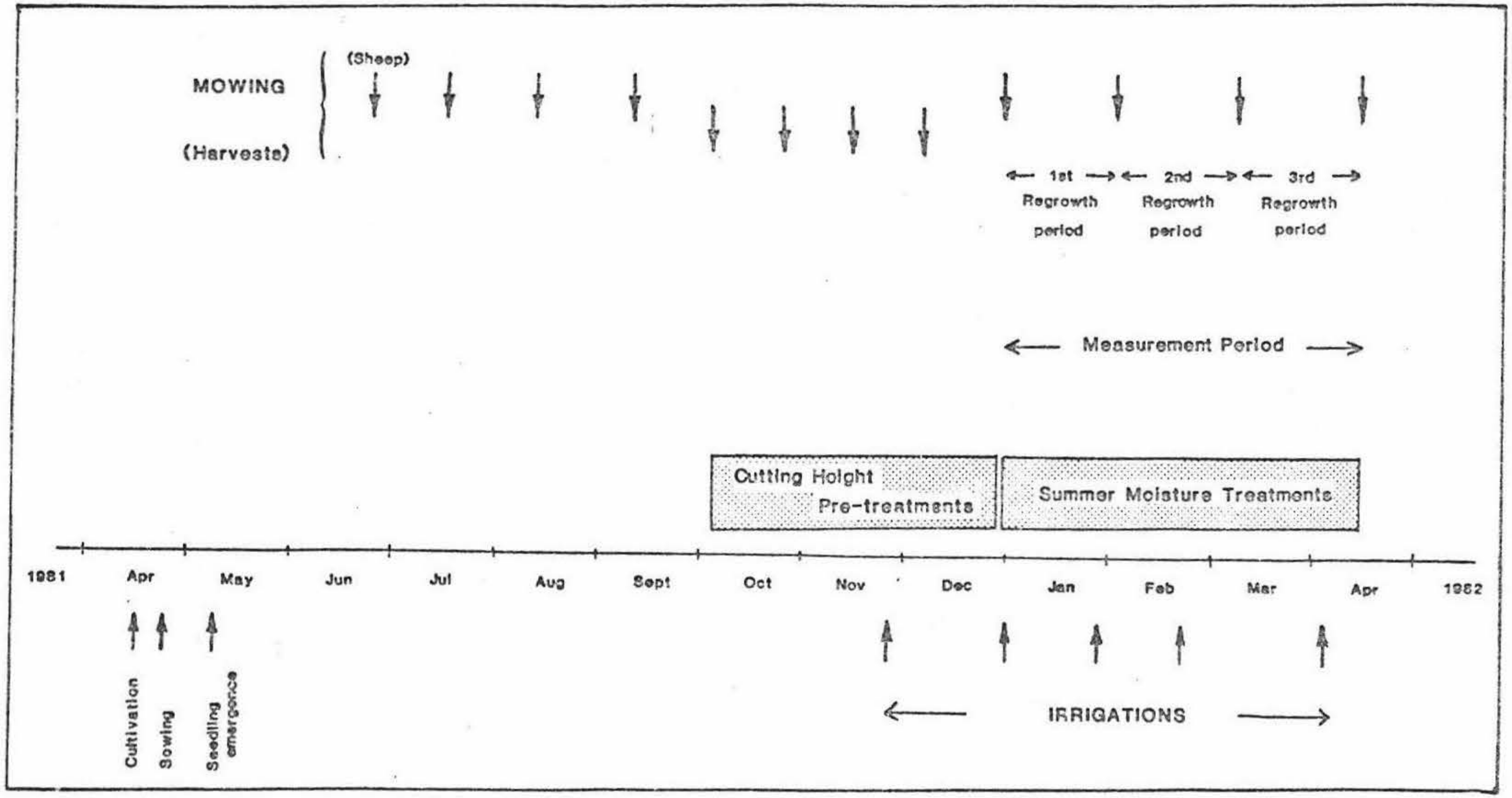

Figure 2. The timing of operations during the experiment.

3.3.2 Spring cutting pretreatments

The spring defoliation pretreatments varied in intensity, with mowing heights of 2.5 cm (using a reel mower) and 7.5 cm (using an Allen oscillating mower) to give hard and lax defoliations respectively. These were first imposed on 5 October 1981 and were repeated three times at three weekly intervals (i.e. on 21 October, 16 November and 14 December). Clippings were discarded in all cases. See Plate 1.

3.3.3 Summer moisture treatments

Summer moisture treatments were imposed from 28 December 1981 until 14 April 1982. The two treatments used in this experiment were:

i) the stressed environment, where plots were covered by an automatic rain out shelter
ii) the irrigated environment, where water stress was minimized by irrigation

i) stressed environment

On 28 December 1981 all plots were irrigated to field capacity to ensure they were at a common and non-limiting soil water content. The stressed plots therefore began with no soil water deficit and became stressed as the water deficit developed during the course of the experiment.

Rainfall was totally prevented from falling on the plots by automatic rainout shelters, which were a particular feature of this experiment. There were two shelters which consisted of 10 m x 5 m aluminium frames, supporting a clear polythene cover. Each frame was mounted on rails and could be driven by manual or automatic control on or off the plots by means of a small electric motor. Automation of the rainout shelter was achieved by means of a mains driven microprocessor and rain sensor which detected a single raindrop, and activated the motors to move the covers over the water stressed plots. Fifteen minutes after the last raindrop was detected the covers moved back off the plots to the rest area. Additional features of the microprocessor controller were an "exercise" function which could be set to automatically operate the covers at any specified time during the day, and an alternative battery source to operate the covers in the event of a power failure (Green 1980). See Plate 2.

In general the electronics of the control unit operated reliably and efficiently, however there were some problems with the covers themselves. The large area of the covers made them particularly vulnerable to wind, which reduced the life of the plastic covers and caused considerable load on the motors. In one instance strong wind blew a cover off its rails allowing about 6 mm of rain onto 4 plots. This was towards the beginning of the dry down phase and did not seriously affect the results of the experiment. In a second instance hail caused some damage to the second cover but did not wet the plots. In a third instance, a mechanical problem in one of the pulleys prevented a cover from sheltering two of the plots. Sufficient rain (> 10 mm) fell on the plots to allow recovery of the plants. Observations on these two plots were excluded from subsequent statistical analyses.

ii) irrigated environment

Plots were irrigated using an oscillating sprinkler, with applications scheduled according to the model of Scotter, Clothier and Turner (1979). This model predicted the total water storage in the top 100 cm on the basis of rainfall and class A pan evaporation, which were obtained from the Massey University Meteorological Station situated about 500 m from the experiment. Plots were irrigated to field capacity whenever the soil water deficit exceeded 60 mm (being half the value at which Scotter, Clothier and Turner (1979) predicted growth of ryegrass was stopped). Irrigation water was added to plots on days 0, 29, 48 and 92 of the measurement (treatment) period.

3.4 Management during the pretreatment and treatment periods

During the spring pretreatment period urea nitrogen was applied by watering can at rates of 25 kg N/ha, 20 kg N/ha and 50 kg N/ha, immediately after mowing on 5 October, 21 November and 14 December respectively. These amounts brought the total application of nitrogen to the plots to 226 kg N/ha, which offset losses of nitrogen in a) removed herbage, and b) by leaching when plots were irrigated in excess of field capacity.

In addition to the added nitrogen, a dressing of 30% potassic superphosphate was made (21 November 1981) towards the end of the spring pretreatments. The fertiliser was bulked with an inert pumice filler and applied by hand at a rate of 238 kg/ha (16.7 kg P/ha). No fertiliser was applied to the plots during the dry down period.

During the summer treatment period all plots were cut to the common height of 2.5 cm.

Argentine stem weevil (Hyperodes bonariensis) control was achieved by spraying the experimental area with Lorsban 40EC at 2-3 l/ha and 1.5 l/ha on 10 February and 19 March respectively. The control of dicotyledonous weeds, particularly Penny Royal (Mentha pulegium) was achieved by spraying 2,4-D ester at 3 l/ha on 19 March.

3.5 Measurements

3.5.1 Soil and plant water status

3.5.1.1 Soil water status

Soil in the top 10 cm was sampled and the gravimetric water content ($\omega \frac{gH_2O}{g\ dry\ soil}$) determined after drying at

105°C for 72-96 hours. The soil bulk density was determined according to the method described by Scotter, Clothier and Corker (1979), and was found to have a mean and standard deviation (for 4 samples) of $1.156 \pm 0.022 \times 10^3$ kg/m^3. This agreed well with the value of $1.12 \pm 0.08 \times 10^3$ kg/m^3 obtained by Scotter, Clothier and Corker (1979), and was used to convert gravimetric water content (ω) to volumetric water content $\left(\theta \ \frac{cm^3 H_2O}{cm^3 \text{ dry soil}}\right)$ using equation (3).

$$\theta = \omega \times \frac{\rho \text{ water}}{\rho \text{ soil}} \qquad (3)$$

The soil water status below 20 cms was measured as the volumetric water content (θ) calculated from counts from a Troxler Neutron Probe comprising an Am-Be 106 mc Neutron Probe (model 1265), a model S.5A shield and standard, and a G-200 Ratemeter modified to give a digital readout (Long, French 1967). Measurements were taken from each plot at approximately 7-10 day intervals. Twenty second counts were taken in duplicate at 10 cm intervals starting at a depth of 20 cm and finishing at a depth of 120 cm. The mean of the two counts was converted to a volumetric water content reading (θ) using equation (4); determined for a Manawatu silt loam (Clothier 1977) but which was suitable for the Tokomaru silt loam soil type used in this experiment.

$$\theta = (0.386 \times \text{count ratio}) - 0.025 \qquad (4)$$

where $\quad \text{count ratio} = \frac{\text{counts in 20 sec in soil}}{\text{counts in 20 sec in shield}}$

The mean of values calculated using this formula was not significantly different from the mean of values of volumetric determinations from the same soil (appendix 1).

The volumetric water contents for each plot, determined from gravimetric sampling and from neutron probe counts were combined and integrated over the top 100 cm (using the Trapezium Rule) to give a total water storage (mm) for that plot for that day. These measurements of total soil water storage were converted to mm of water deficit by subtraction from the total soil water storage at field capacity; where the total soil water storage at field capacity for both environments was determined at the start of the summer period.

3.5.1.2 Plant water status

Plant water status was measured as leaf water potential (ψ_1) (MPa) using a pressure chamber (Scholander *et al.*, 1965, Boyer 1967). The chamber dimensions were 4.0 cm by 27.5 cm and had a maximum capacity of 4.0 MPa. The pressure source was industrial grade dry compressed air, which was humidified by moist blotter at the bottom of the chamber. Rates of increase in pressure were 0.03 to 0.05 MPa/sec and were slowed to 0.01 MPa/sec near the end point. Readings were made on the youngest fully emerged (mature) lamina of a tiller. Laminae (not less than 4.0 cm) were excised within 1 cm from the legule and were transferred to the slotted, screw lid of the pressure chamber for immediate (< 30 sec) measurement.

Leaf water potential measurements were made twice weekly throughout the summer period. Readings were made at dawn (0500-0700 hours), and mid-afternoon (1300-1600 hours) to estimate the maximum and minimum ψ_1 of the diurnal cycle. See Plate 4.

3.5.2 Static sward characteristics

3.5.2.1 Dry matter yield

a) Measurements.

The first measurement of dry matter yield was made before the imposition of any treatments on 15 September 1981 and was used to test the uniformity of the experimental area. No significant differences were detected between any plots (appendix 2). Subsequent to this, dry matter yield determinations were made routinely at approximately 5 week intervals during the summer period. The first harvest was taken on 28 December 1981, which was designated day 0 of the measurement period, while successive harvests were taken on 1 February, 8 March and 14 April being days 32, 70 and 107 of the measurement period, respectively.

Two harvesting methods were used:

i) Mower yields - which was the total herbage harvested from a 3.2 m x 0.5 m strip along the length of the plot, by a reel mower set at a cutting height of 2.5 cm.

ii) Ground level cuts - which were taken using electric shears, harvesting at ground level from within a 625 cm^2 quadrat. This was done before and after mowing for harvests 2, 3 and 4 only.

Samples were weighed (subsampled if necessary) before being dried in ventilated ovens at $80^{o}C$ for 36-72 hours.

b) predictive models

In addition to the destructive measurements, dry matter yields were predicted at each harvest using the three following methods to incorporate various yield components into an equation to return the dry matter yield per plot.

i) where the following components, made before and after mowing, were combined according to equation (5) which accounted for the total herbage mass of the sward.

$$\text{DMY (kg DM/ha)} = \frac{b) \times d) \times e) \times f)}{a) \times c)} \times \frac{10^4 m^2/ha}{10^6 kg/mg} \qquad (5)$$

where a) = fraction of ryegrass in the dry matter yield
b) = ryegrass tiller density ($tillers/m^2$)
c) = fraction of lamina weight to total weight in the ryegrass tiller
d) = average number of lamina per ryegrass tiller
e) = average length of ryegrass lamina (cm)
f) = mass per unit length of ryegrass lamina (mg/cm)

The returned predictions were correlated with the results from ground level cutting. Simple and partial correlations of each component with the dry matter yield from ground level cuts were also determined.

ii) where stepwise multiple regression (using SPSS (Nie et al., 1975)) was used to incorporate the above six components "in order of importance", before and after mowing for each harvest, into equation (6).

The most "important" variable at each step was determined as being that variable which gave the greatest contribution to the regression sum of squares.

$$\text{DMY (ground level cutting)} = \beta_o + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \beta_5 X_5 + \beta_6 X_6 \qquad (6)$$

iii) where multiple regression, again using SPSS (Nie et al., 1975) and also Minitab (Ryan et al. 1981) was used to incorporate the three components d), e) and f) into equation (7), and to return the four β values

$$\text{DMY (ground level cutting)} = \beta_o + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 \qquad (7)$$

This equation was used to predict total herbage mass (or DMY) between the pre-weekly harvests using weekly measurements of the 3 yield components.

3.5.2.2 Components of dry matter yield

Six components of dry matter yield were measured during the course of the experiment. These were:

i) botanical composition (and proportion of ryegrass in the dry matter yield)
ii) tiller density (tillers/m^2)
iii) lamina dry weight as a fraction of total tiller dry weight
iv) lamina number per tiller
v) lamina length (cm/leaf)
vi) mass per unit lamina length (mg/cm)

i) Botanical composition

The botanical composition at each harvest was determined from the dissection of subsamples from the ground level cuts taken before and after mowing. The fractions of dead and green herbage were expressed as a percentage of the total herbage, while the species fractions (ie ryegrass, other grass and other species) were expressed as a percentage of the green herbage.

The percentage of ryegrass in the total herbage was also calculated, to be used in equation 5.

ii) Ryegrass tiller density

Ryegrass tiller density was estimated using the method of Korte (1981) which measured ryegrass tiller density in conjunction with a ryegrass tiller dynamics study. Three (and in some cases four) 83.32 cm^2 PVC rings were fixed using wire clips in permanent positions along the centre line of each plot. Ryegrass tiller density was calculated from a count of the number of new tillers formed and old tillers left alive since the last observation. Observations were made within several days of mowing at approximately 3-5 week intervals, beginning 16 November 1981 (during the spring treatment period) and continuing until the end of the experiment (14 April 1982). No measurement of the tiller density of other grass species was made. See Plate 3.

In addition, the ryegrass tiller density was also estimated by two other techniques, as a comparison with the results of the technique described above.

(a) The first method involved making counts of ryegrass tillers inside 25 randomly placed 22.06 cm^2 rings. This was done for each plot within several days of mowing for each harvest during the summer period. This method was the best approximation to the tiller core method (Mitchell and Glenday 1958) without involving the destructive removal of cores.

(b) The second method was done in conjunction with the ground level cuts made before and after mowing on days 32, 70 and 107. Subsamples from 625 cm^2 quadrats were dissected to give a separate fraction of ryegrass tillers. A count of these was divided by the fraction of the subsample dryweight to total sample dry weight to estimate the total number of ryegrass tillers in the harvested area. Tiller density estimated this way allowed a comparison of densities before and after mowing.

iii) lamina dry weight as a fraction of total tiller dry weight.

The ryegrass lamina fraction was calculated on a weekly basis from a sample of tillers, totalling approximately 100 leaves, which was taken from random positions around each plot. The leaves were stored in plastic bags at 4°C until they could be analysed in the lab. The analyses consisted of separating laminae from pseudo-stem, measuring the total lamina length, oven drying at 80°C before finally being weighed. The following calculation was used:

$$\text{Ryegrass lamina fraction} = \frac{\text{lamina dry weight}}{\text{lamina dry weight + sheath dry weight}}$$

This component was only calculated for the second and third regrowth periods i.e. from day 32 until the end of the experiment.

iv) average number of laminae per ryegrass tiller

This component was calculated from the data collected from marked tillers as described for component v). It only included leaves where all or part of the lamina was present and did not include dead leaves.

v) average length of ryegrass lamina

The average length of ryegrass lamina was determined from measurements of laminae from marked tillers in the field (Hunt pers. comm.). Twenty tillers were marked with split plastic rings at 5 cm intervals along a transect across each plot. Twice each week measurements of the green and total (green and dead) lamina length for the parent and any daughter tillers were made. The presence of stem weevil or slug damage, and the identification of the leaf axils in which tillers had appeared were also recorded.

Recordings were made during the three regrowth periods, beginning within 2 days of mowing and continuing until the markers were removed just prior to mowing for the following harvest. A new set of tillers was marked at each period.

Analyses of the data obtained from this technique was simplified using a computer programme to obtain the necessary data summaries. This stored the summaries in an easily read tabular format, as well as in a form suitable for analysis with commonly used statistical packages. Tillers where death was attributable to infection with stem weevils were not included in the analysis.

In addition to average lamina length this technique also allowed estimates of the following components and lamina dynamics to be made:

i) leaf extension rate and lamina senescence rate (die-back from tip)
ii) average number of laminae per ryegrass tiller
iii) leaf appearance and death rates

An additional, but less frequent, estimate of lamina length was also determined from the lamina samples collected for the determination of component iii) above. Average lamina length was calculated by dividing the total length measured by the number of laminae. The laminae included in this sample were only those which were green for more than 75% of their length, and the necrotic portion frequently found at the ends of leaves was included in the measurement.

vi) mass per unit length of ryegrass lamina

This component was calculated from the same sample used in the calculation of component i) above. The total lamina dry weight was divided by the total lamina length to give the mass per unit length of ryegrass lamina in units of mg/cm.

3.5.3 Dynamic sward characteristics

Dynamic sward characteristics (i.e. rates of change) were calculated as the difference between sward characteristics expressed as a fraction of the time interval over which the difference was observed.

3.5.3.1 Pasture growth rates

Pasture growth rates were calculated from the predicted dry matter yields, and were therefore calculated on a weekly basis within each regrowth period.

3.5.3.2 Dynamics of the components of yield

The dynamics of the following components were studied:

i) ryegrass tiller density
ii) average number of laminae per ryegrass tiller
iii) average length of ryegrass laminae

i) Ryegrass tiller density

Changes in ryegrass tiller density were studied in greater detail as being the result of two opposing processes:

a) the rate at which new tillers appeared (TAR)
b) the rate at which existing tillers died (TDR)

The relative sizes of these two processes determined the changes in ryegrass tiller density.

Tiller dynamics were measured using the method of Korte (1981), where all the ryegrass tillers in a fixed 83.32 cm^2 ring were marked with coloured, split plastic rings. At each observation the new ryegrass tillers which had appeared were marked with a new colour and the markers from old dead tillers were removed. In addition to allowing the calculation of tiller appearance and tiller death rates, this technique also allowed the determination of the age structure of the remaining live tillers and the age of tillers which had died. See Plate 3.

ii) Average number of laminae per ryegrass tiller

This dynamic component is also considered to be the result of two processes -

1. the rate of leaf appearance (leaves/100 tillers/day) (LAR)
2. the rate of leaf death (leaves/100 tillers/day) (LDR)

These were both determined from the marked tillers described for component ii) b.

LAR was determined from the total number of new leaves on twenty marked tillers and their daughters, which were not present at the last observation, divided by the number of days since the last observation and the number of tillers.

LDR was determined as the number of leaves which were still alive at the last observation but not the current observation, divided by the number of days since the last observation and the number of tillers. The difference between leaf death and leaf senescence was important since leaf senescence was the progressive chlorosis or necrosis of the lamina (typically from the tip) and death not occurring with the entire lamina was chlorotic or necrotic.

iii) The change in average length of ryegrass laminae.

The average length of ryegrass laminae were also the result of the two opposing processes of leaf extension and leaf senescence. The change in average lamina length is therefore the result of a difference in the relative rates of these two processes. In general these processes occur in separate leaves i.e. leaf extension occurring in younger immature laminae with leaf senescence occurring in older mature leaves, however some examples were observed with both processes occurring in a single leaf.

The green and total (green and dead) lamina lengths were recorded on every leaf for twenty marked tillers per plot (as well as on daughter tillers) twice each week. From this data the leaf extension rate was calculated (in units of mm/leaf/day) as the total increase in green length since the last observation (for all the measured leaves in the sward), divided by the number of green leaves which were measured and the number of days since the last observation. Leaf senescence rate was calculated as the total increase in necrotic and chlorotic length divided by the total number of leaves and the number of days since the last observation. These values are averaged across all leaves and are therefore less than the actual rates of extension and senescence individual lamina.

3.6. Statistical analyses

In all cases, unless otherwise stated, significance and non significance refers to the 5% level. The symbols used throughout this thesis are NS = not significant $P>0.05$; * = significant $P\leqslant0.05$; ** = significant $P\leqslant0.01$; *** = significant $P\leqslant0.001$.

3.6.1 Analysis of variance

The pooled "environments" model (Le Clerg, Leonard and Clark 1962, Gordon *et al.* 1972, Gordon 1979) was used for ANOVA where pretreatments were arranged in a randomised block design within the two environments to which the moisture regimes were assigned. This model allowed the separate analysis of pretreatment effects, treatment effects and the pretreatment x treatment interaction. The subprogramme MANOVA in SPSS (Nie *et al.* 1975) was used, where pretreatments ("treatments") were crossed with blocks, within treatments ("environments"). This necessitated the manual calculation of the complex

F statistic (F') and the associated degrees of freedom (f' numerator and f' denominator) for the treatment ("environment") effect as follows (Le Clerg, Leonard and Clark 1962).

$$F' = \frac{MS_E + MS\ error}{MS_{B(E)} + MS_I}$$

$$f'\ numerator = \frac{(MS_E + MS\ error)^2}{\frac{MS_E^2}{f_E} + \frac{MS\ error^2}{f\ error}}$$

$$f'\ denominator = \frac{(MS_{B(E)} + MS_I)^2}{\frac{MS_{B(E)}^2}{f_{B(E)}} + \frac{MS_I^2}{f_I}}$$

where: MS = mean square and f = degrees of freedom for the following sources of variation:

environments (E)
blocks within environments (B(E))
pretreatment x environment interaction (I)
residual error (error)

F statistics for the pretreatment effect and for the pretreatment x environment interaction were calculated as the relevant mean square divided by the mean square for the preatreatment x environment interaction mean square and residual error mean square respectively. The degrees of freedom were those appropriate to the particular mean squares used.

3.6.2 T-tests

When the analysis of the pretreatment x treatment interaction was not required pretreatment and treatment effects were compared statistically by simple T-test. Pretreatments and treatments were pooled to test the treatment and pretreatment effects respectively, the replication therefore being increased from 4 to 8. In most cases there were unequal variances and the effective degrees of freedom were calculated according to the following equation (Steele and Torrie 1980).

$$\text{effective df} = \frac{(s_1^2/n_1 + s_2^2/n_2)^2}{[s_1^2/n_1)^2/n_1-1]+[s_2^2/n_2)^2/n_2-1]}$$

3.6.3 Multiple regression

i) Linear multiple regression (using MINITAB (Ryan, Joiner and Ryan (1981) was used to regress several independant X variates with a dependant Y variate. T-tests were used to test the significance of the returned β values. Stepwise multiple regression (using SPSS (Nie *et al.* 1975)) was used to obtain incremental R^2 values and standardised β values

ii) Multiple regression with dummy variables was used to fit two simple regression equations to a set of data in one operation, and returning a single R^2 value (Draper and Smith 1981). In both cases where this procedure was used the R^2 obtained was greater than if a single, simple regression equation had been used.

Plate 1. The cutting height pretreatments. Aluminium tins at the centre of each plot cover neutron probe access tubes.

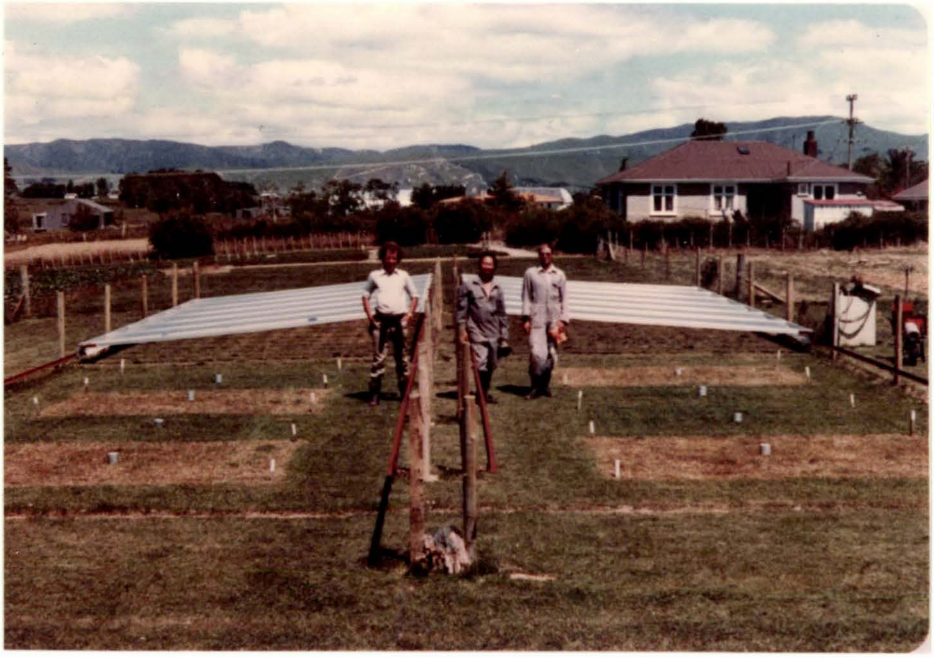

Plate 2. The eight plots of the stressed environment at the end of the pretreatment period and the beginning of the treatment period, immediately after the uniform mowing across all plots. The Rain-Out-Shelters are in the resting position with the control box at the extreme right.
From left: the author, Dr A.C.P. Chu, Dr C.J. Korte

Plate 3. The ryegrass tiller marking technique. All ryegrass tillers within the 83.32 cm^2 ring were marked with coloured split plastic rings. At successive intervals during the experiment new tillers were marked with a different colour and rings from dead tillers were removed.

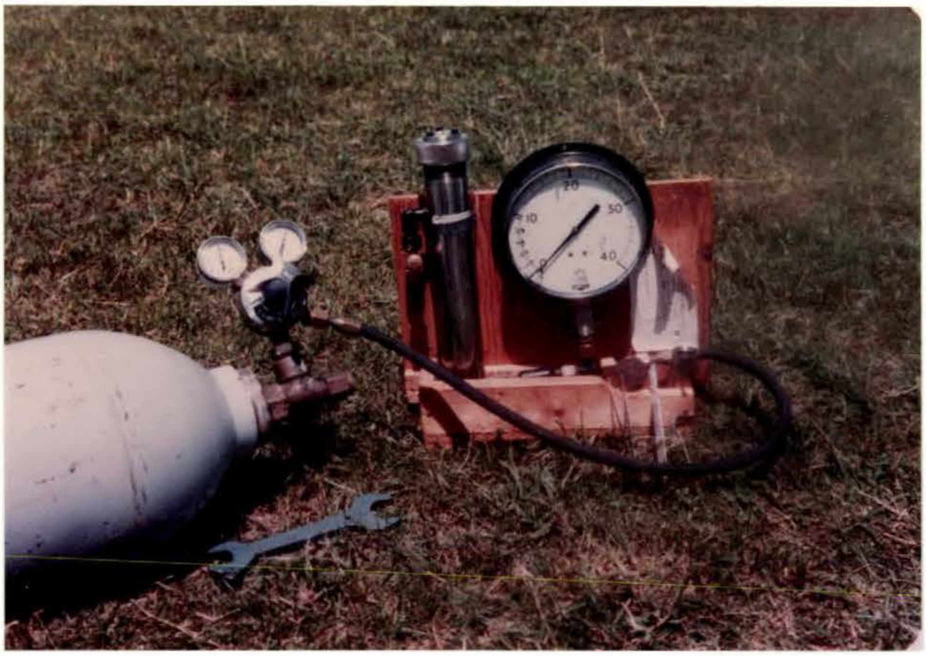

Plate 4. The pressure chamber apparatus.

Plate 5. The stressed sward at the conclusion of the experiment (14.4.82) being day 107 of the measurement period.

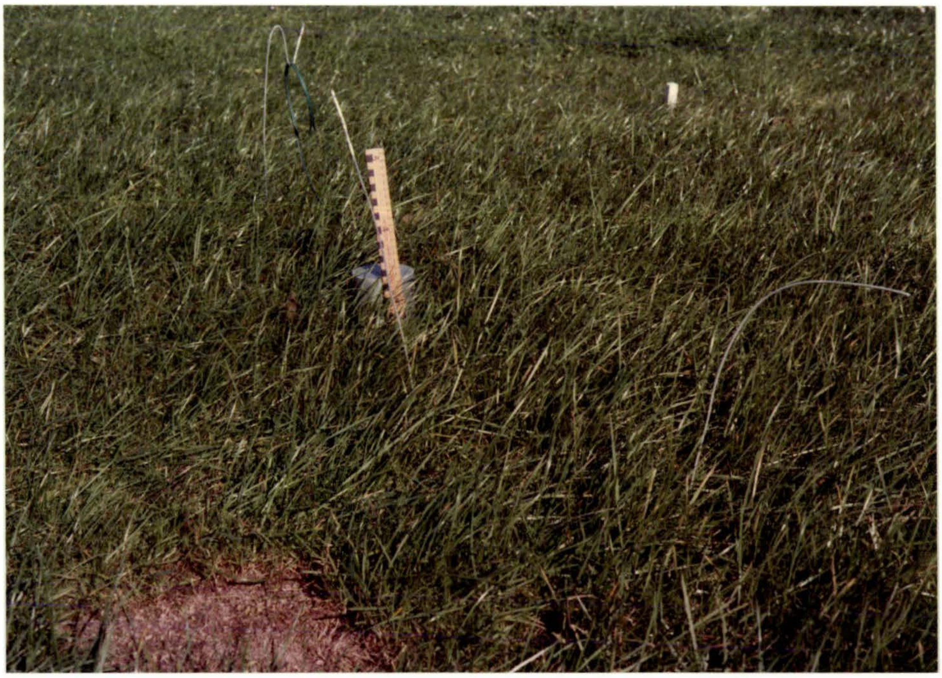

Plate 6. The irrigated sward at the conclusion of the experiment. Bare patches are the areas from where ground level samples had been taken; wires show the location of 83.32 cm^2 rings illustrated in Plate 3; and aluminium tins at the centre of each plot cover neutron access tubes.

CHAPTER IV

RESULTS

The results are presented in four main sections. These are:

4.1 Water status measurements
4.2 Static and Dynamic sward characteristics
4.3 The prediction of dry matter yield from its components
4.4 The relationships between dynamic sward characteristics and water status measurements

4.1 Water status measurements

4.1.1 Soil water status

The results of soil water deficit (mm) for the duration of the measurement period are given in figure 3. Both stressed and irrigated plots were irrigated in excess of field capacity on day 0, and the soil water content on day 2 (mean for all plots = 428 mm) was designated as being 0 mm deficit. The differences between hard and lax defoliation pretreatments were not significant and so the results presented only compare differences between stressed and irrigated treatments.

The maximum deficit on irrigated plots was 76 mm, compared to 182 mm on stressed plots. The difference between the water deficit of stressed and irrigated plots was first detected as being significant on day 16 (after 21 mm of rain on day 10).

Rainfall, class A pan evaporation, and potential and actual evapotranspiration (PET and AET) (calculated according to Scotter, Clothier and Turner (1979))are given in appendix 3. In general AET equalled PET except when the soil water deficit exceeded 107 mm, in which case AET was less than PET.

Figure 3 also includes the soil water deficit predictions calculated using the model of Scotter, Clothier and Turner (1979). In general the predicted deficits followed the same pattern as measured deficits, however there were significant differences between predicted and measured values in many cases. The relationship between predicted and measured deficits was investigated, using multiple regression with dummy variables to obtain the following 2 equations (8a and 8b).

$$y = -83.17 + 1.73\,x \qquad (x > 107 \text{ mm}) \qquad (8a)$$

$$y = 1.03 + 0.758\,x \qquad (x \leq 107 \text{ mm}) \qquad (8b)$$

where: y = predicted soil water deficit
x = measured soil water deficit

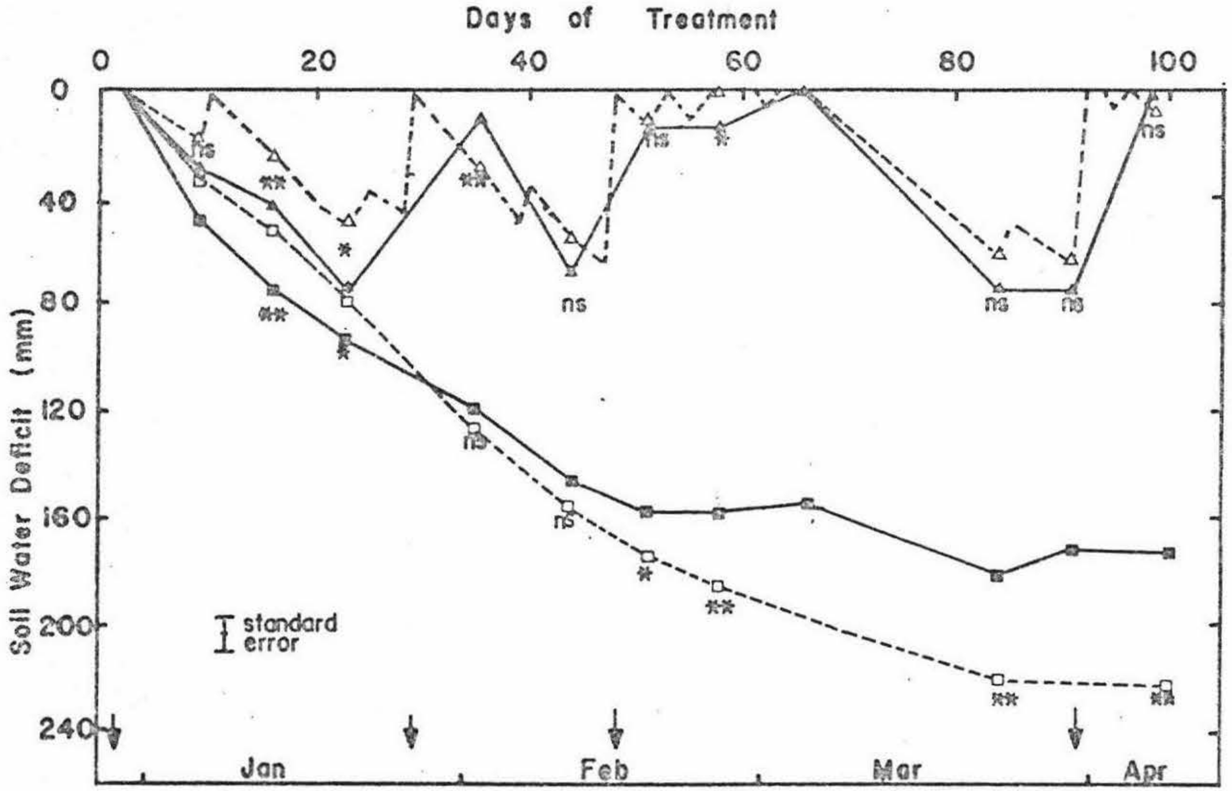

Figure 3. The movements of soil water deficit (SWD) during the measurement period for predicted (△----△) and measured (▲—▲) SWD on irrigated plots and predicted (□---□) and measured (■—■) SWD on water stressed plots. Arrows indicate the times of irrigation.

The slope for the first equation (i.e. 1.73) was significantly greater than for the second equation (i.e. 0.758). The multiple regression technique increased the coefficient of determination (R^2) from 95.1% (for simple linear regression) to 98.6%.

The profiles of volumetric water content (θ) for the top 100 cm of soil are illustrated in figures 4a and b for stressed and irrigated plots respectively. Also shown for comparison in figure 4a are the profiles at soil water potentials of -1.5 and -0.1 MPa determined by Scotter, Clothier and Turner (1979) for the same soil type. In addition to the pattern of soil water depletion (fig 4a) and recovery after irrigation (fig 4b) both figures showed a difference in the volumetric water content at 100 cm between wet and dry soils. This is evidence that water was lost from the profile below 100 cm. On the basis of Scotter, Clothier and Turner (1979) who observed water was lost from up to 1.7 m depth, it was calculated for this study that up to 25 mm of water may have been removed from below 100 cm, and therefore been unaccounted for in the measurements of soil water deficit.

The difference between water profiles on days 0, 35 and 51 in fig 4b show that the irrigations on days 29 and 48 did not completely return the profiles to field capacity.

4.1.2 Plant water status

Figure 5 shows the changes in maximum leaf water potential (ψ_1) (measured at dawn 0500-0700 hours) during the measurement period. No differences were detected between ψ_1 of plants from the two defoliation pretreatments, therefore only the comparison between stressed and irrigated environments is presented. There were no significant differences between moisture regimes until after day 31 of the measurement period; when, the ψ_1 of the irrigated plots remained at levels of -0.1 to

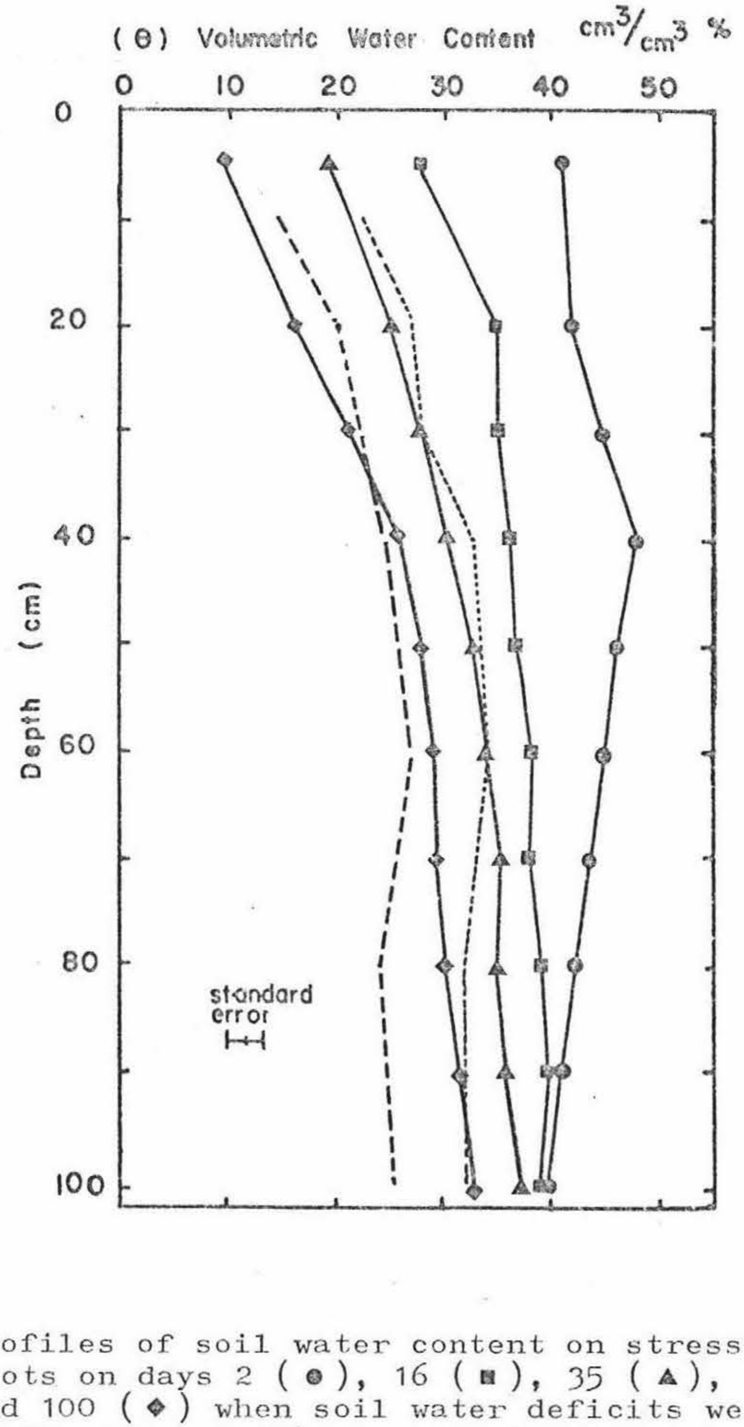

Figure 4a. Profiles of soil water content on stressed plots on days 2 (●), 16 (■), 35 (▲), and 100 (◆) when soil water deficits were 0, 73, 119 and 174 mm respectively. The profiles at -1.5 MPa (----) and at -0.1 MPa (----------) from Scotter, Clothier and Corker (1979) are also presented.

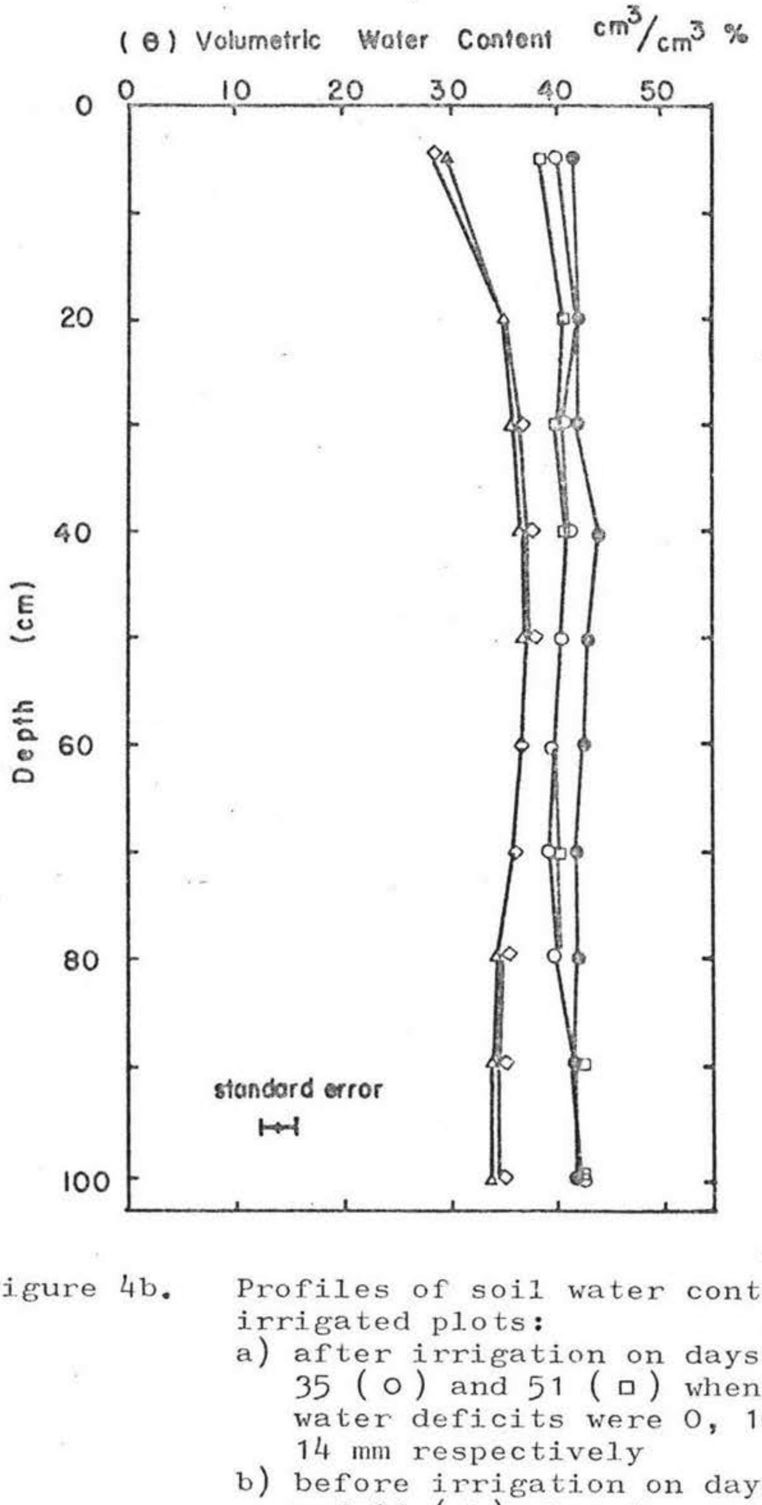

Figure 4b. Profiles of soil water content on irrigated plots:
a) after irrigation on days 0 (●), 35 (○) and 51 (□) when the soil water deficits were 0, 10 and 14 mm respectively
b) before irrigation on days 23 (△) and 91 (◇) when the soil water deficits were 76 and 75 mm respectively.

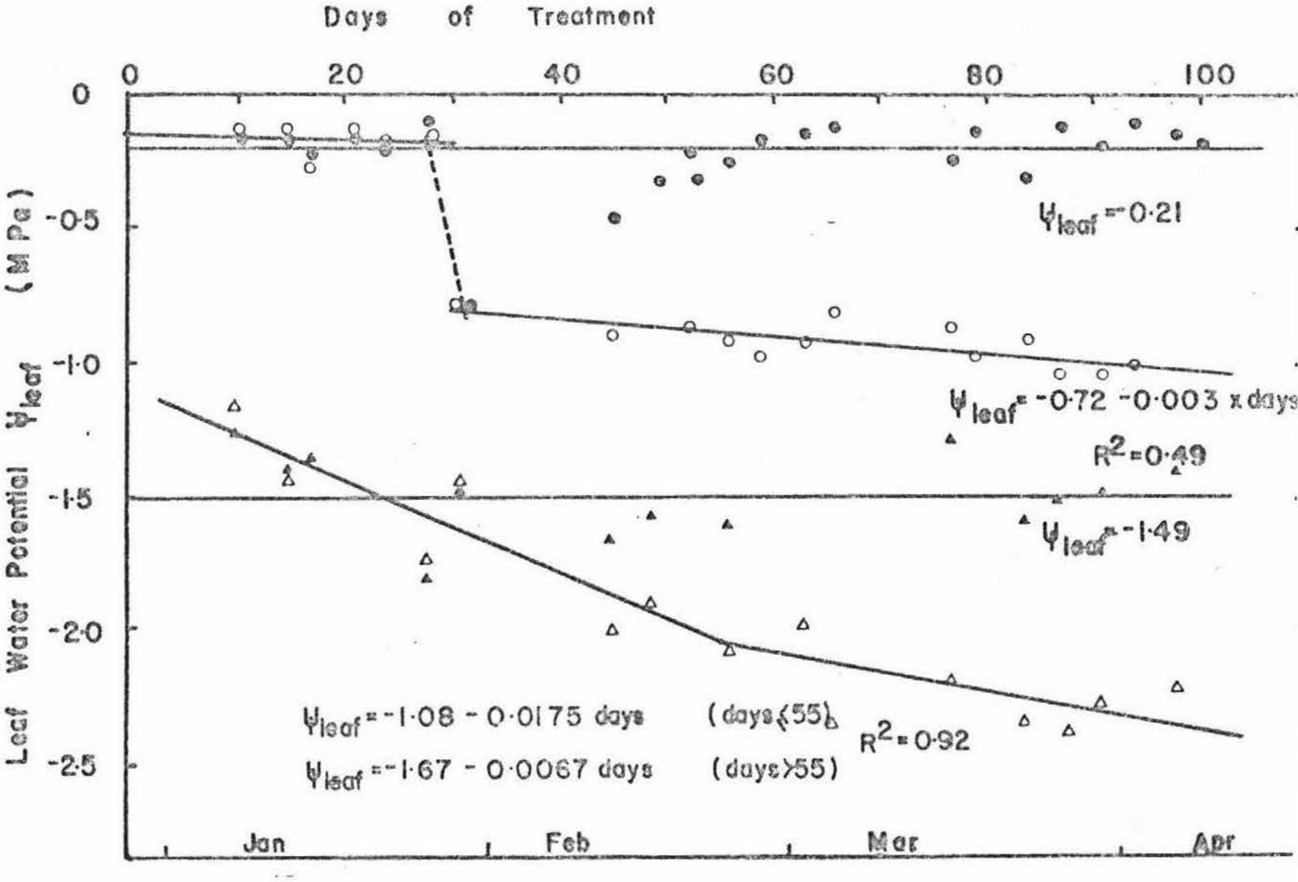

Figure 5. The pattern of change of leaf water potential (ψ_1) during the measurement period for:

a) dawn readings from irrigated plots (●) and stressed plots (○)

b) afternoon readings from irrigated plots (▲) and stressed plots (△)

-0.3 MPa whereas those of the stressed plots dropped to -0.78 MPa and thereafter progressively declined to levels of -1.0 MPa.

Figure 5 also shows the changes in minimum ψ_1 (measured at mid-afternoon (1300-1700 hours)). This pattern of change in ψ_1 during the experiment was different to that for dawn values, since the 0.68 MPa drop in ψ_1 between days 28 and 31 did not occur. In this case the ψ_1 for irrigated plants was relatively constant, fluctuating around a value of -1.5 MPa. For stressed plants, ψ_1 decreased from -1.4 MPa to -2.4 MPa as the water deficit increased and multiple regression with dummy variables was used to fit 2 regression lines to show the pattern of this decrease. (This technique increased the coefficient of determination (R^2) from 0.86, for simple linear regression, to 0.92). The rate of decrease of ψ_1 on stressed plots was initially quite high (0.0175 MPa/day) but slowed to 0.0067 MPa/day during the second half of the measurement period. This rate of decrease of mid-afternoon ψ_1 in this second half of the measurement period was not significantly different than the rate of decrease in dawn ψ_1 (0.0030 MPa/day) over the same period.

The ψ_1 of leaves which were wet with surface moisture (eg dew, rain or irrigation) were significantly greater than would have been expected if the leaves had been "dry"; where dawn readings from stressed plots after day 31 were up to 0.6 MPa greater and mid-afternoon readings from stressed or irrigated plots were up to 1.5 MPa greater. This effect was observed to be temporary, in general lasting only as long as the leaves remained wet. These measurements from wet leaves were not included in figure 5.

4.1.3 The relationship between leaf water potential and soil water deficit.

The relationship between leaf water potential (ψ_1)

and soil water deficit is presented in figure 6. Four regression lines have been fitted to the data and represent the two times of measurement of leaf water potential (ie dawn and mid-afternoon) for the two moisture treatments; with the exception that dawn readings from stressed plots before the soil water deficit exceed 105 mm have been included in the regression of dawn readings from irrigated plots.

For the irrigated plots (and stressed plots at low levels of soil water deficit) leaf water potential was uncorrelated with the soil water deficit, with correlation coefficients being $R^2 = 0.001$ and $R^2 = 0.06$ for dawn and mid-afternoon data respectively.

For the stressed plots, figure 6 shows the 0.68 MPa drop in dawn leaf water potential between days 28-31 to be occurring between 105 and 110 mm deficit. For mid-afternoon data and dawn data in excess of 105 mm deficit, leaf water potential was significantly related to soil water deficit, with the slopes -0.088 and -0.0299 MPa/10 mm deficit respectively being significantly lower than 0. The mid-afternoon data was found to be more strongly correlated with soil water deficit than dawn data, with R^2 values being 0.91 and 0.40 respectively.

4.2 Static and dynamic sward characteristics

4.2.1 Dry matter yield

Results of total herbage mass, measured by cutting to ground level before mowing for harvests 2, 3 and 4, are given in Table 1a. For the cutting height pretreatment at each of the three harvests, the low cut plots had yields greater than for the high cut treatments, however this effect was only significant at harvest 2.

Similarly, the irrigated treatments had yields greater than for the stressed treatments in harvests 3

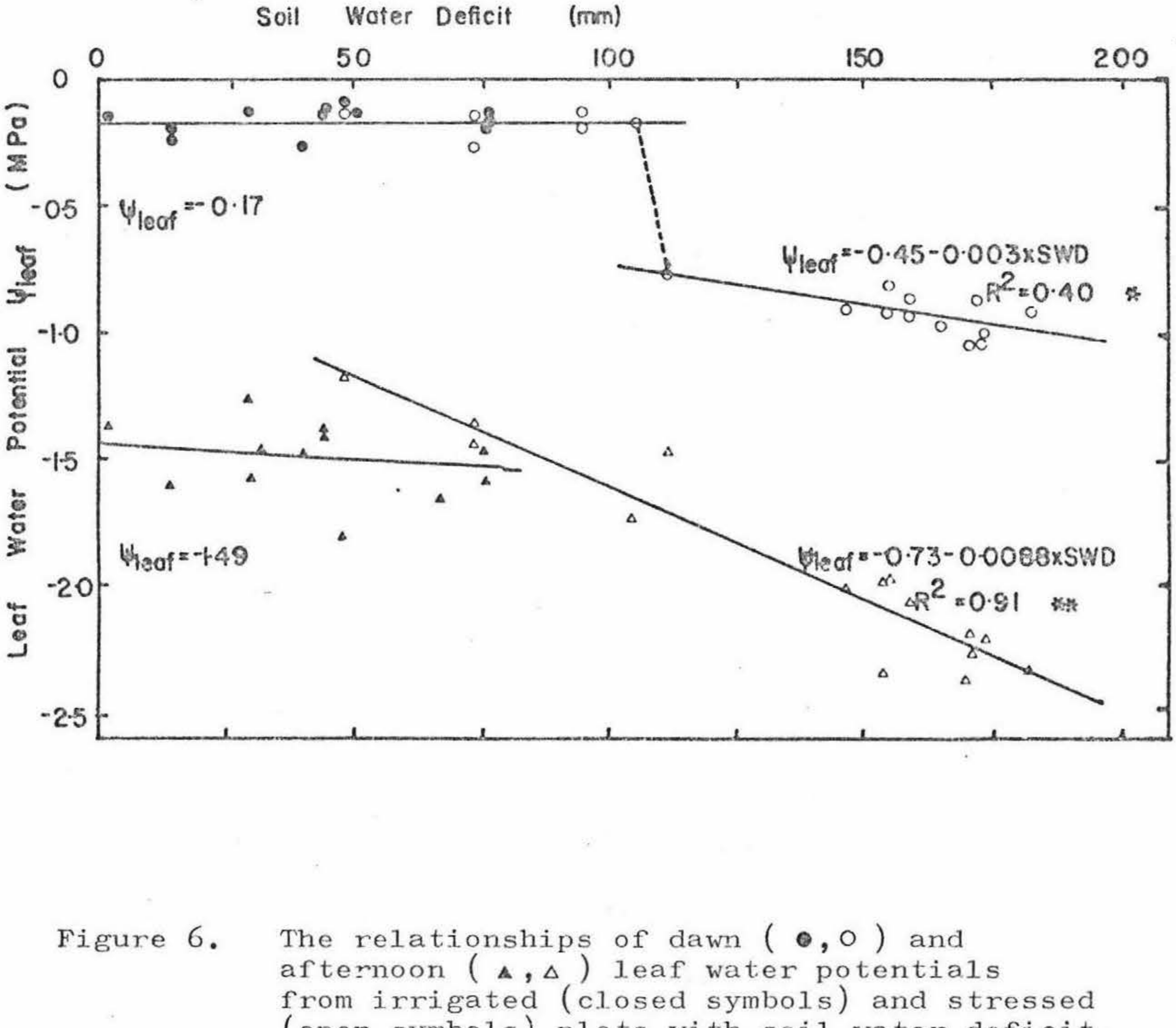

Figure 6. The relationships of dawn (●, ○) and afternoon (▲, △) leaf water potentials from irrigated (closed symbols) and stressed (open symbols) plots with soil water deficit.

and 4, but the difference failed to reach significance. There were no significant interactions.

Data for the residual herbage cover remaining after mowing, also measured by ground level cutting, are given in Table 1b. Initially, at harvest 2, for the cutting height pretreatments, the low cut plots had a significantly greater yield than the high cut plots. This effect was also present at the final harvest, where low cut plots had residual yields 40% greater than high cut plots. Moisture treatment and interaction effects were not significant throughout the measurement period.

The dry matter yield of herbage removed by mowing (mass of clippings retained in the catcher) is presented in Table 2. At harvest 1, under the cutting height pretreatments yields were greater for the high cut pretreatment, reflecting the change in cutting height, however differences for subsequent harvests were all non-significant. This result contrasts with that for the moisture treatments which showed no significant differences at harvests 1 and 2, and significant differences ($P<0.01$) at harvests 3 and 4. At the end of the experiment the mower yields on stressed plots were only 8% of those on irrigated plots. The interaction between moisture treatments and cutting height pretreatments was found to be non-significant at all harvests.

One deficiency of this mower yield data was that at each harvest a significant Bartletts X^2 statistic was obtained , invalidating the assumption of homogeneity of variance made in Analysis of Variance (Eisenhart 1947). Transforming data by $\sqrt{x}$ was found to validate the assumption in most cases, but did not alter the levels of significance.

Mower yields were poorly correlated ($R^2 = 0.31$) with the dry matter yield of herbage removed by mowing, calculated as the difference between ground level cutting before (Table 1a) and after (Table 1b) mowing.

TABLE 1a. Total herbage mass before mowing (kg DM/ha) - measured by ground level cutting.

Treatment	Harvest	2	3	4
	Day of experiment	32	70	107
Cutting Height	High	2857	1789	1785
	Low	3674	3388	2013
		*	NS	NS

Moisture Regime	Irrigated	3267	2994	2083
	Stressed	3264	2183	1715
		NS	NS	NS

Interaction	NS	NS	NS

Coefficients of variation ranged from 7% to 34%

TABLE 1b. Residual herbage mass after mowing (kg DM/ha) measured by ground level cutting

	Harvest	2	3	4
Treatment	Day of experiment	32	70	107
Cutting Height	High	2050	1382	1256
	Low	2795	1667	1761
		*	NS	*

Moisture Regime	Irrigated	2438	1341	1484
	Stressed	2406	1709	1533
		NS	NS	NS

Interaction	NS	NS	NS

TABLE 2. Mower yields (kg DM/ha) (clippings retained in the catcher, mowing to 2.5 cm)

Treatment	Harvest Day of expt.	1 0	2 32	3 70	4 107
Cutting Height	High	3590	1056	567	264
	Low	831	1247	608	240
		*	NS	NS	NS

Moisture Regime	Irrigated	2173	1263	1067	467
	Stressed	2248	1040	109	37
		NS	NS	**	**

Interaction		NS	NS	NS	NS

Coefficients of variation range from 6% - 67%

4.2.2 Components of dry matter yield

Results for the following components of dry matter yield are presented in this section.

i) botanical composition
ii) tiller density (tillers/m^2)
iii) lamina dry weight as a fraction of total tiller dry weight
iv) lamina number per tiller
v) lamina length (cm/lamina)
vi) mass per unit lamina length (mg/cm)

In addition, the dynamics i.e. rates of appearance and death for the components of tiller density, leaf number per tiller and lamina length are also presented.

i) Botanical Composition

Botanical composition percentages for the comparison between the cutting height pretreatments are given in Table 3a and for the comparison between the moisture regimes are given in Table 3b. In both tables the fractions of green and dead herbage are given as a percentage of the total dry matter. The green herbage fraction was further dissected into fractions of ryegrass, other grass and other species, which were expressed as a percentage of the green material. The component of other grass was almost entirely _Poa_ spp. and the component of other species was a mixture comprising: broad leaved dock (_Rumex_ _obtusifolius_ L.), penny royal (_Mentha_ _pulegium_ L.) catsear (_Hypochoeris_ _radicata_ L.) and dandelion (_Taraxacum_ _officinale_ Weber). White clover (_Trifolium repens_ L.) not having been sown with the ryegrass was a rare component of the sward.

The effect of low (compared to high) cutting at the beginning of the measurement period was to decrease

Table 3a. Botanical composition before mowing - for the cutting height pretreatments.

Figures in parenthesis are the botanical composition after mowing, where they differ significantly from the value before mowing. Botanical compositions after mowing for harvest 1 were not measured.

Harvest	pre-treat-ment	% of total dry matter		% of green herbage		
		dead herbage	green herbage	Ryegrass	Other grasses	Other Species
1	Hi	31	69	45	53	2
	Lo	28	72	27	65	8
		NS	NS	**	*	**
2	Hi	23(47)	77(53)	67(37)	30(54)	3(9)
	Lo	25(41)	75(59)	31(20)	50(61)	19
		NS NS	NS NS	*** **	*** NS	***
3	Hi	53	47	61(37)	25	14
	Lo	50	50	15	33	53
		NS	NS	***	NS	***
4	Hi	60	40	59	31	10
	Lo	54	46	40	34	26
		NS	NS	*	NS	NS

Table 3b. Botanical composition before mowing - for the moisture treatments.

Figures in parenthesis are the botanical compositions after mowing where they differ significantly from the values before mowing. Botanical compositions after mowing for harvest 1 were not measured.

Harvest	Treatment	% of total dry matter		% of green herbage		
		dead herbage	green herbage	Ryegrass	Other grasses	Other Species
1	Stressed	28	72	38	57	5
	Irrig.	31	69	34	61	5
		NS	NS	NS	NS	NS
2	Stressed	23(50)	77(50)	50(29)	40	10
	Irrig.	25(38)	75(62)	48(27)	41(62)	11
		NS **	NS **	NS NS	NS	NS
3	Stressed	71	29	41	23	36
	Irrig.	32	68	35(17)	34	31
		***	***	NS	*	NS
4	Stressed	77	23	51	21	28
	Irrig.	37(49)	63(51)	48(26)	44	8
		***	***	NS	**	*

the percentage of ryegrass, increase the percentage of other grass and other species and to make no difference to the levels of dead material. At the end of the experiment the only significant difference between cutting height pretreatments was for low cut plots to still have a lower ryegrass percentage.

There were no differences in botanical composition between the moisture regimes at the beginning of the experiment. In contrast however, the water stress effects were the greatest at the end of the experiment (harvest 4), when the fraction of green herbage was reduced from 63% to 23% of the total dry matter.

Significant differences in botanical composition before and after mowing occurred for all of the components measured, where an increase in the dead herbage fraction with mowing was accompanied by a decrease in the green herbage fraction, and a decrease in the ryegrass fraction was accompanied by increases in both other grass and other species. There was an interaction of mowing with water stress, where for harvests 3 and 4 (when the water deficit was relatively severe) differences in botanical composition before and after mowing only occurred on irrigated plots (Table 3b).

ii) Ryegrass tiller density

The differences in tiller density between the cutting height pretreatments are shown in fig. 7a and between the moisture regimes are shown in fig. 7b .

The tiller densities on high and low cut plots were almost identical at the beginning of the measurement period, however by the beginning of the second regrowth period (day 37) the maximum difference between pretreatments was obtained, with the tiller density of low cut plots being only 57% of that on high cut plots.

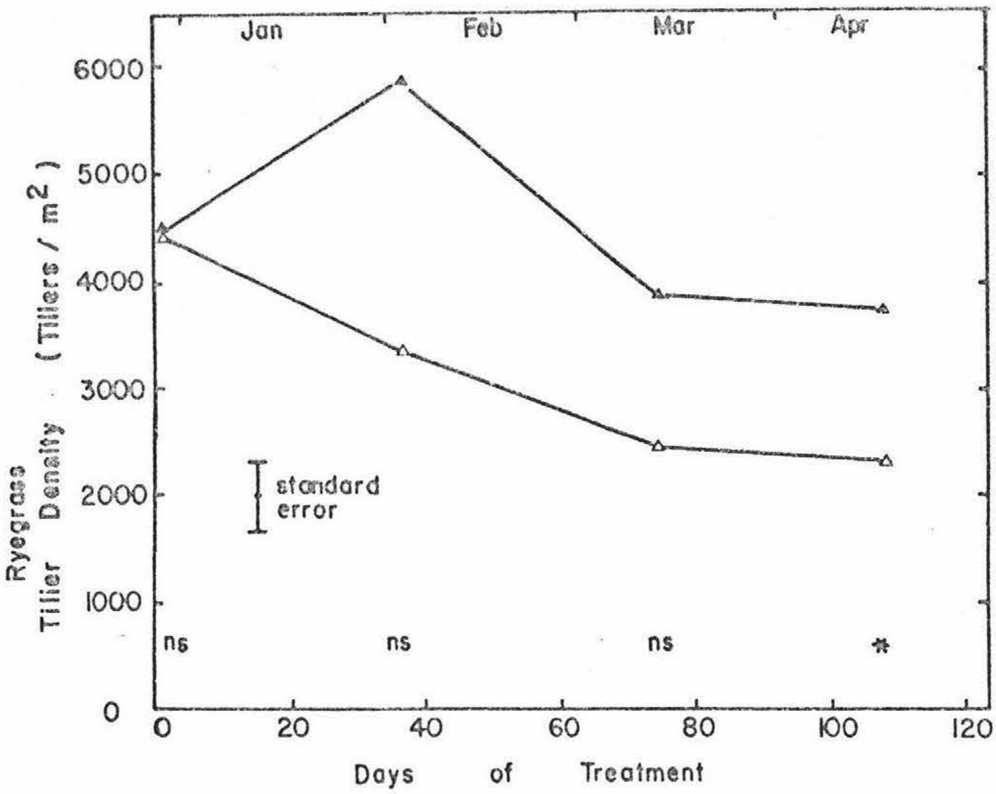

Figure 7a. Tiller densities during the measurement period, for high cut (▲) and low cut (△) pretreatments.

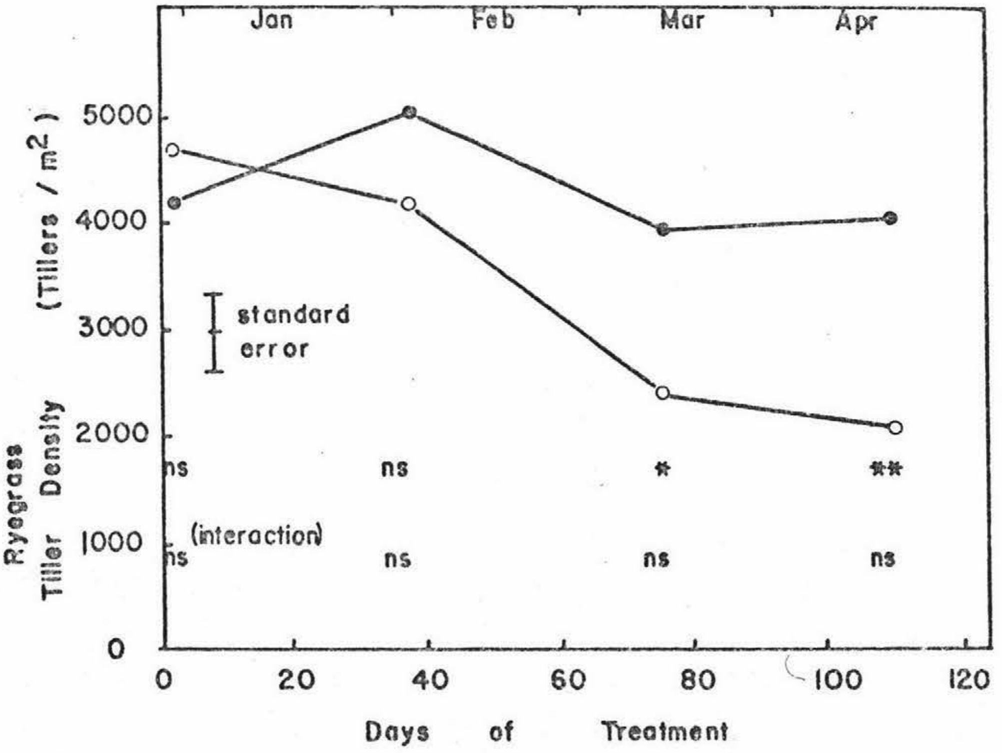

Figure 7b. Tiller densities during the measurement period for irrigated (●) and stressed (○) treatments.

At the end of the measurement period the difference between pretreatments was still present, but smaller, with the tiller density of low cut plots being 63% of that on high cut plots.

The differences in tiller density between irrigated and stressed plots were non-significant at the beginning of the measurement period but became progressively greater, so that by the end of the measurement period significance ($P<0.01$) was attained, with the tiller density of stressed plots being about half that of irrigated plots.

The number of tillers removed by mowing was calculated as the difference in tiller density (measured by ground level cutting) before and after mowing. On average mowing reduced the tiller density by 581 tillers/m^2.

No statistically significant interactions between cutting height and moisture regime on tiller density were detected.

The measurements of tiller density (presented in figures 7a and b) were well correlated with other measurements of tiller density which were also made.

The coefficients of determination (R^2) with counts inside 25 randomly placed rings and counts from ground level cuts before and after mowing were 0.73, 0.82 and 0.77 respectively.

The changes in tiller density (Fig 7a and b) (net tiller appearance/death) are the result of differences in the absolute tiller appearance and death rates (tillers/m^2/day) the data for which are presented in table 4 and 5 . Proportional tiller appearance and death rates (tillers/1000 tillers/day) are given in tables 6 and 7, and show the physiological activity of tillers with respect to tillering.

By and large the variation of values was high and discriminating power of the statistical analyses was low resulting in few significant differences and interactions being declared, despite the fact that differences were as high as 400%.

(a) Absolute tiller appearance rates (table 4)

The absolute tiller appearance rates of high cut plots were greater than for low cut plots throughout the entire measurement period by 452%, 264% and 168% for the 1st, 2nd and 3rd regrowth periods respectively. Similarly, absolute tiller appearance rates on irrigated plots were greater than for stressed plots by 149%, 440% and 158% for the same periods.

In all cases the rates of tiller appearance decreased from the first to the second regrowth period and increased from the second to the third regrowth period, with the average rate of tiller appearance for the second and third regrowth periods being 29% and 42% of the rate in the first regrowth period.

(b) Absolute tiller death rates (Table 5)

The absolute tiller death rates for both the cutting height pretreatments and moisture treatments did not show as consistent trends during the measurement period as did absolute tiller appearance rate. During the first regrowth period the tiller death rates on low cut and stressed plots were 158% and 174% of the rate on high cut and irrigated plots, whereas during the second regrowth period the situation was completely reversed with death rates on low cut and stressed plots being 41% and 97% of the rate on high cut and irrigated plots. In the third regrowth period tiller death rates were higher on high cut and stressed plots.

The absolute tiller death rate was uncorrelated with absolute tiller appearance rate ($R^2 = 0.03$) in the same regrowth period but was highly correlated ($R^2 = 0.71$) with the absolute tiller appearance rate in the previous regrowth period, consequently the highest mean absolute tiller death rate occurred for the second regrowth period, following the highest mean absolute tiller appearance rate occurring in the first regrowth period, and the lowest mean absolute tiller death rate occurred for the third regrowth period, following the lowest mean absolute tiller appearance rate occurring in the second regrowth period.

(c) Proportional tiller appearance rates. (Table 6).

The difference in proportional tiller appearance rates between the high and low cutting treatments were the greatest during the first regrowth period with high cut plots having rates 254% greater than low cut plots and subsequently were smaller with rates on high cut plots being 175% and 98% of low cut plots for the second and third regrowth periods respectively. Similarly, the proportional tiller appearance rates on irrigated plots were 126%, 272% and 110% of those on stressed plots for the 3 regrowth periods. In both instances these differences were smaller than for the absolute tiller appearance rates since effects resulting from differences in tiller density had been removed.

The proportional tiller appearance rate showed a similar pattern of change between regrowth periods as did absolute tiller appearance rate, with the average proportional tiller appearance beginning from 7.8 tillers/1000 tillers/day, falling to 3.32 tillers/1000 tillers/day and then increasing to 5.6 tillers/1000 tillers/day.

(d) Proportional tiller death rate. (Table 7).

During the measurement period proportional tiller death rates (tillers/1000 tillers/day) from low cut plots were on average 54% greater than for high cut plots. The only exception to this trend occurred during the second regrowth period when the proportional tiller death rate from high cut plots exceeded that for low cut plots, following a rapid rate of (proportional and absolute) tiller appearance on high cut plots during the first regrowth period.

The difference between the proportional tiller death rates on stressed and irrigated plots increased during the measurement period with rates on stressed plots being 108%, 73% and 490% greater than on irrigated plots for the 1st, 2nd and 3rd regrowth periods.

The average proportional tiller death rate during the first regrowth period increased from 9.3 tillers/1000 tillers/day to 13.8 tillers/1000 tillers/day for both the second and third regrowth periods.

Unlike the correlated between absolute tiller appearance and death rates, the proportional tiller death rates were poorly correlated with proportional tiller appearance rates from either the same or the previous regrowth period (R^2 = 0.26 and 0.05 respectively) since the common factor of population size had been removed in the calculation of proportional tiller dynamics.

Table 4. Absolute tiller appearance rates (tillers/m^2/day) for the three regrowth periods during the measurement period.

		Regrowth period		
		1	2	3
Cutting Height	High	67.8	17.7	21.9
	Low	15.0	6.7	13.0
		NS	NS	NS

Moisture Regime	Stressed	33.2	4.5	13.5
	Irrigated	49.6	20.0	21.4
		NS	NS	NS

Interaction	Significance	NS	NS	NS

Table 5. Absolute tiller death rates (tillers/m^2/day) for the three regrowth periods during the measurement period.

		Regrowth period		
		1	2	3
Cutting height	High	28.5	59.6	27.3
	Low	45.1	24.4	23.9
		NS	NS	NS

Moisture regime	Stressed	46.7	41.4	34.2
	Irrigated	26.8	42.6	17.0
		NS	NS	NS

Interaction	Significance	NS	NS	*

Table 6. Proportional tiller appearance rates (tillers/1000 tillers/day) for the three regrowth periods during the measurement period.

		Regrowth period		
		1	2	3
Cutting height	High	11.2	4.2	6.1
	Low	4.4	2.4	6.2
		*	NS	NS

Moisture regime	Stressed	6.9	1.8	4.8
	Irrigated	8.7	4.9	5.3
		**	NS	NS

Interaction	Significance	NS	NS	NS

Table 7. Proportional tiller death rate (tillers/1000 tillers/day) for the three regrowth periods during the measurement period.

		Regrowth period		
		1	2	3
Cutting height	High	5.0	15.8	8.3
	Low	13.7	11.8	19.3
		NS	NS	NS
Moisture regime	Stressed	12.6	17.5	23.6
	Irrigated	6.05	10.1	4.0
		NS	NS	NS
Interaction	Significance	NS	NS	NS

iii) Lamina dry weight as a fraction of total tiller dry weight

The percentage of lamina weight to the total tiller weight is presented in figure 8a and 8b for cutting height pretreatment and moisture treatments respectively.

The only significant difference obtained between the two cutting height pretreatments was at the end of the first regrowth period, just before the plots were mown. Other differences may have occurred in this first period when the greatest cutting height effects would have been expected, however measurements were not taken during this period.

Significant differences between irrigated and stressed plots were observed on days 50, 57, 70 and 92 when values from irrigated plots exceeded those for stressed plots. In only one case (on day 78) which was soon after mowing for the third harvest, did the percentage of lamina weight to total tiller weight on stressed plots exceed that from irrigated plots. The response of the percentage of lamina weight in the tiller to water stress was inconsistent, since in the third regrowth period when the water deficit was the greatest the differences between stressed and irrigated plots were generally not significant.

iv) Lamina number per tiller

Figures 9a and 9b show the average lamina number per tiller for cutting height pretreatments and moisture treatments respectively. Changes in the number of laminae per tiller resulted from a difference in the

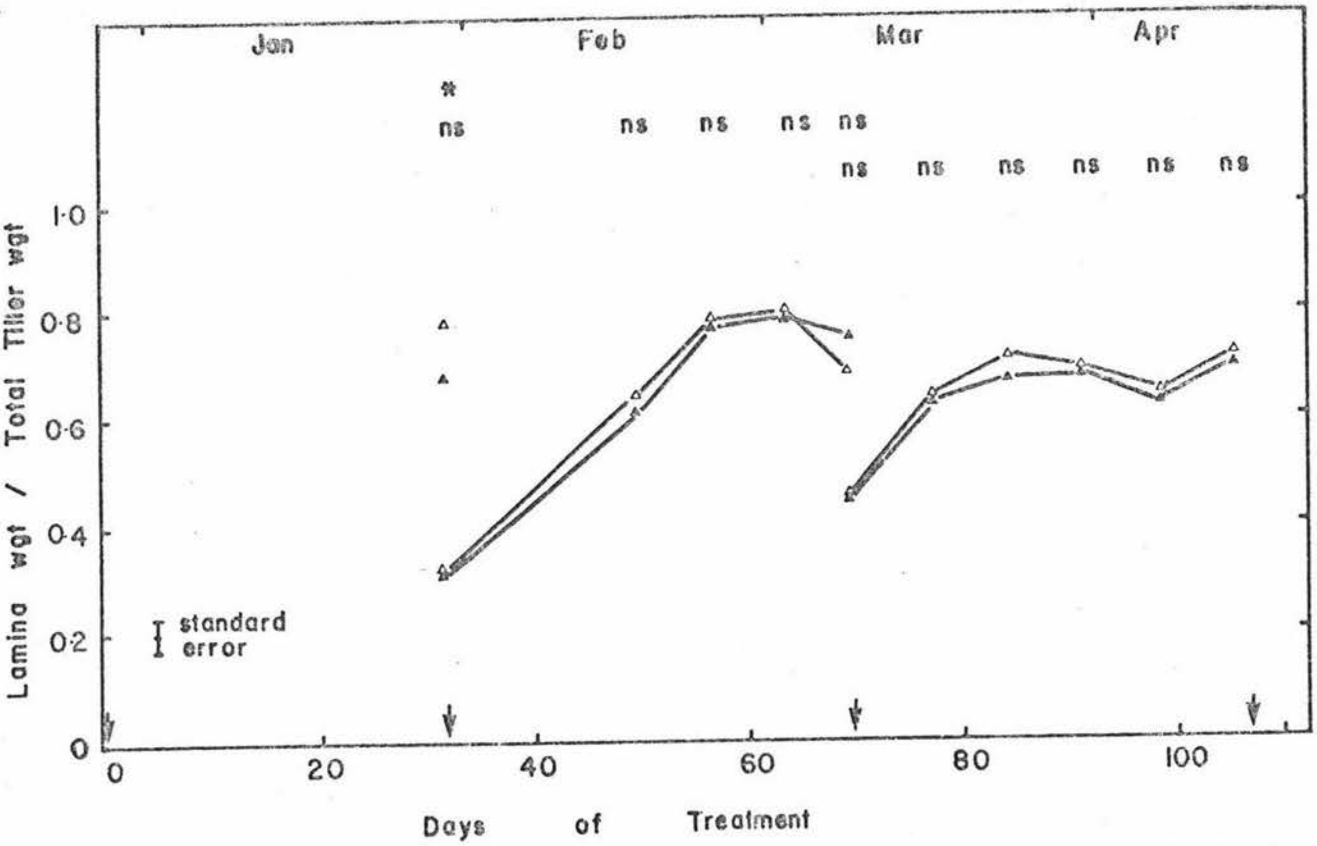

Figure 8a. The fraction of lamina dry weight to total tiller dry weight during the measurement period for high cut (▲) and low cut (△) pretreatments. Arrows indicate the time of harvests.

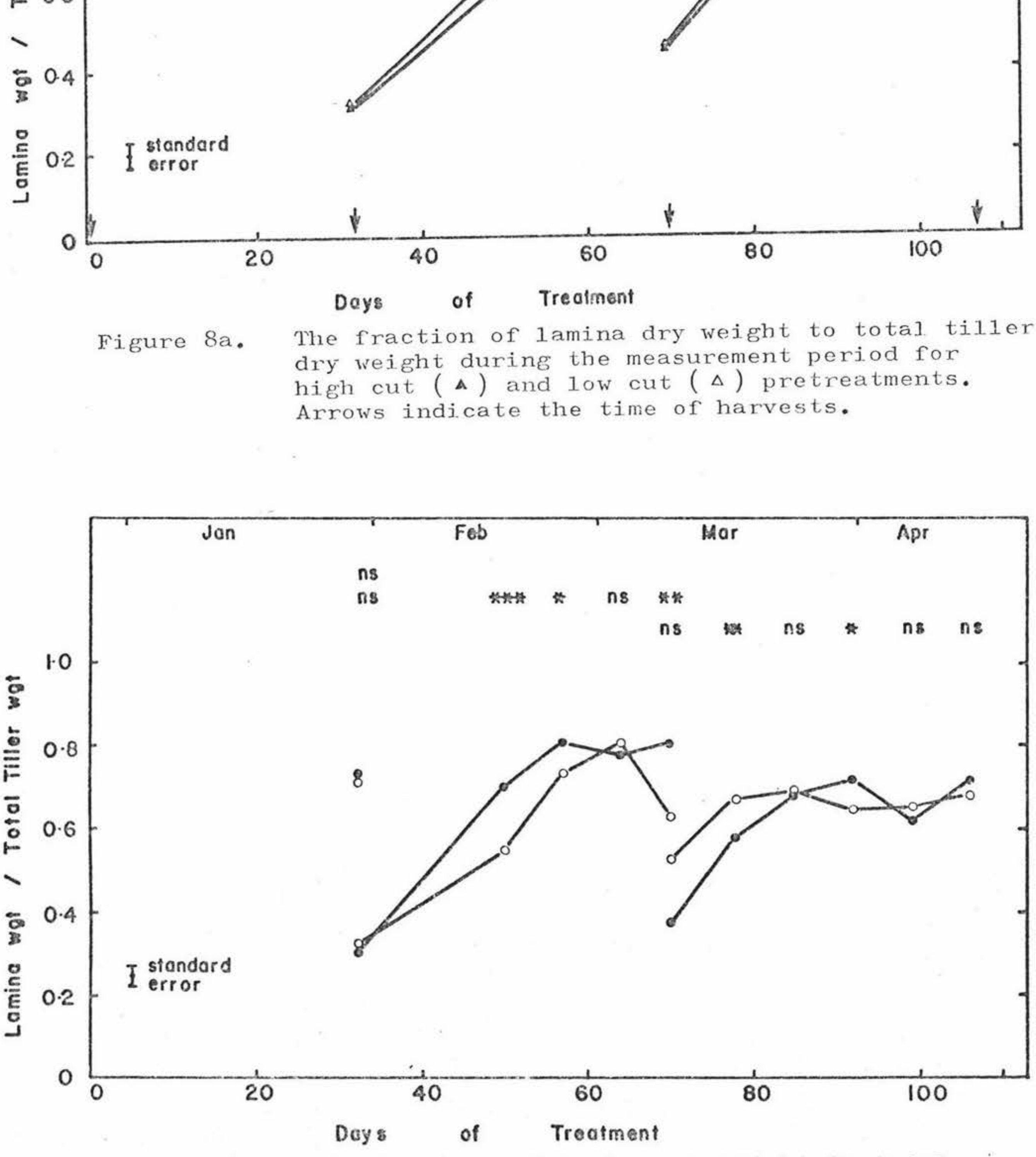

Figure 8b. The fraction of lamina dry weight to total tiller dry weight during the measurement period for irrigated (●) and stressed (○) treatments.

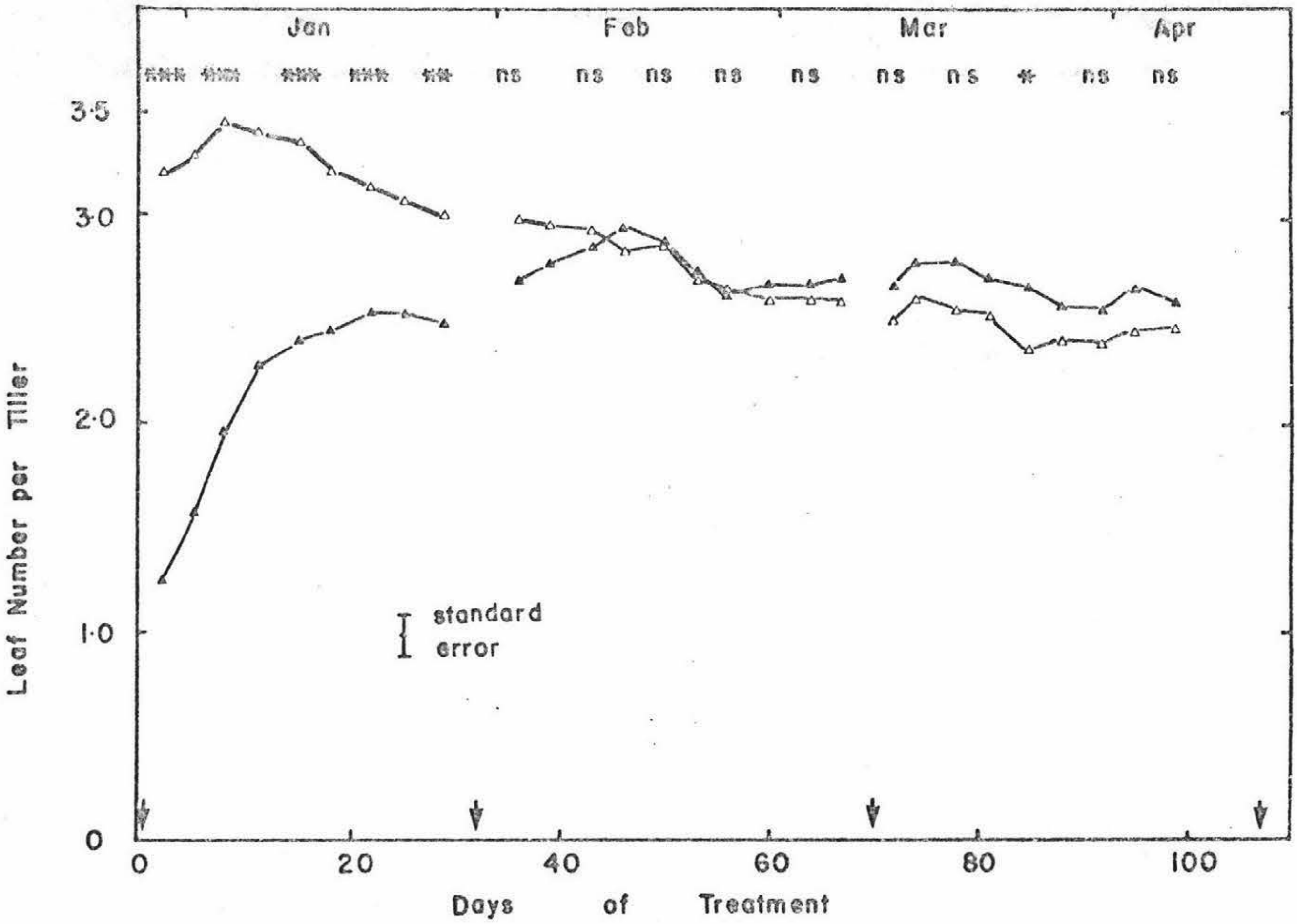

Figure 9a. Number of laminae per tiller during the measurement period for high cut (▲) and low cut (△) pretreatments.

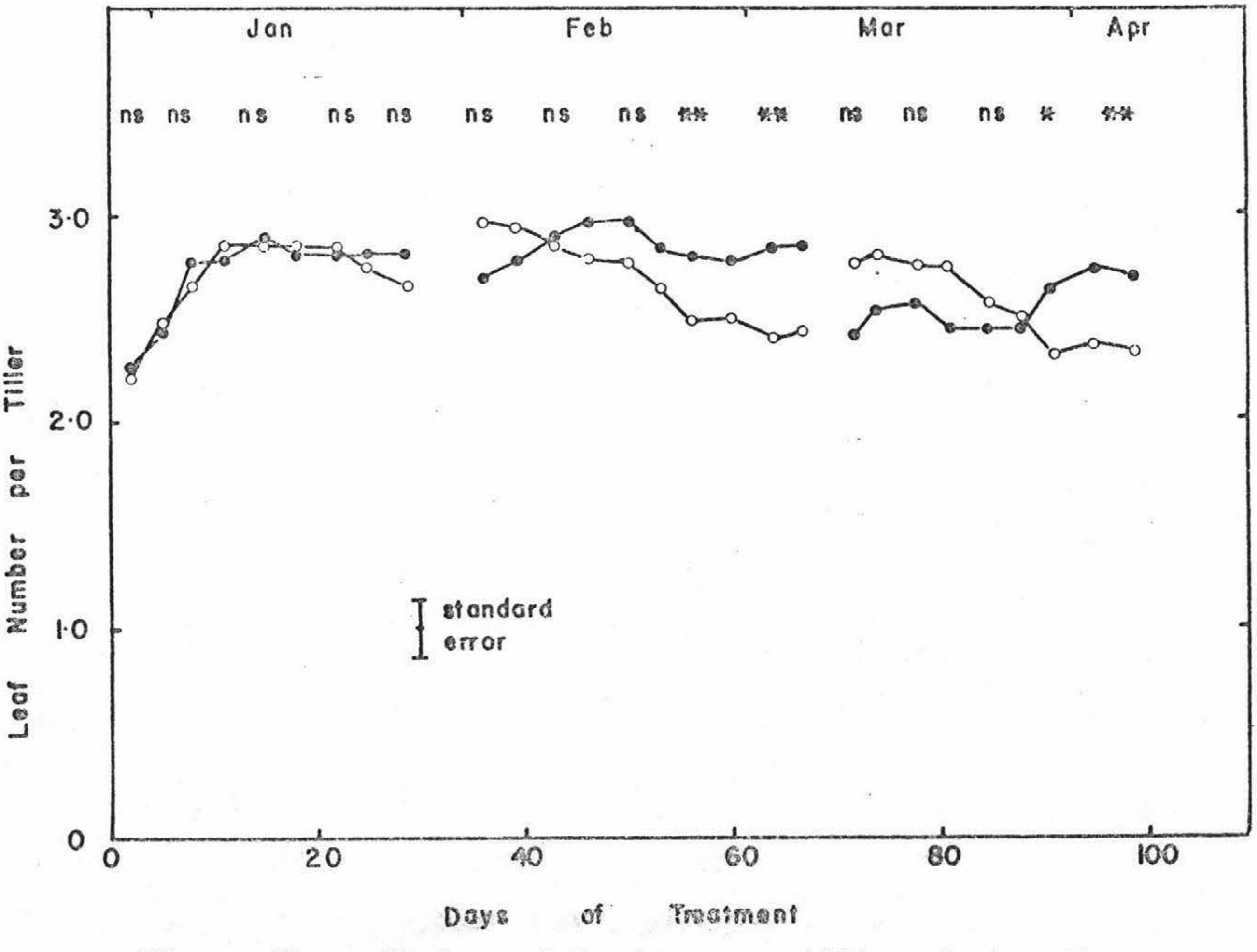

Figure 9b. Number of laminae per tiller during the measurement period for irrigated (●) and stressed (○) treatments.

relative rates of leaf appearance and death, the data for which are presented in figures 10 and 11 respectively (figures 10a and 11a showing the cutting height pretreatment effects and figures, 10b and 11b showing the moisture treatment effects).

There were no significant effects of the pretreatments on leaf number per tiller during the measurement period, except during the first 29 days and on day 85, when the number on previously low cut plots was greater than for previously high cut plots. The greatest difference between high and low cut plots occurred on day 2, when low cut plots had almost 3 times as many lamina as high cut plots.

Differences between irrigated and stressed plots did not occur until after the first regrowth period. The trends for the second and third regrowth periods were similar, where, initially counts on irrigated plots were lower than for stressed plots, but increased relative to stressed plots so that by the end of the two regrowth periods irrigated plots had 16% more laminae per tiller.

(a) Leaf appearance rates (leaves/100 tillers/day) (LAR)

Figure 10a shows the leaf appearance rates per tiller (LAR) for the two cutting height pretreatments. In general there were no differences between high and low cutting heights except in the two periods i) between days 43 and 46 and ii) between days 78 and 81 when significantly more leaves per tiller appeared on high cut than low cut plots.

Figure 10b shows the leaf appearance rates for the two moisture regimes. Statistically significant differences between stressed and irrigated treatments occurred in the second and third regrowth periods when leaf appearance rates on irrigated plots were on average 2.4 times greater than on stressed plots.

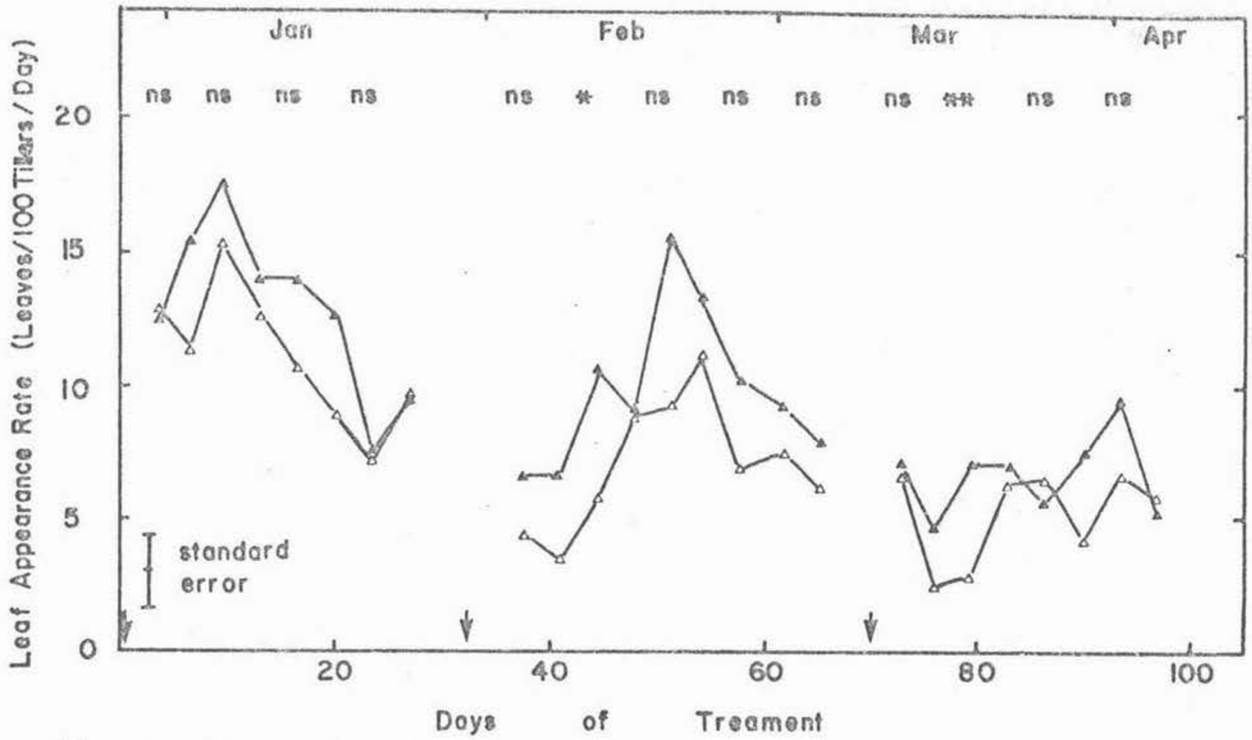

Figure 10a. Leaf appearance rates during the measurement period for high cut (▲) and low cut (△) pretreatments.
Arrows indicate the time of harvests.

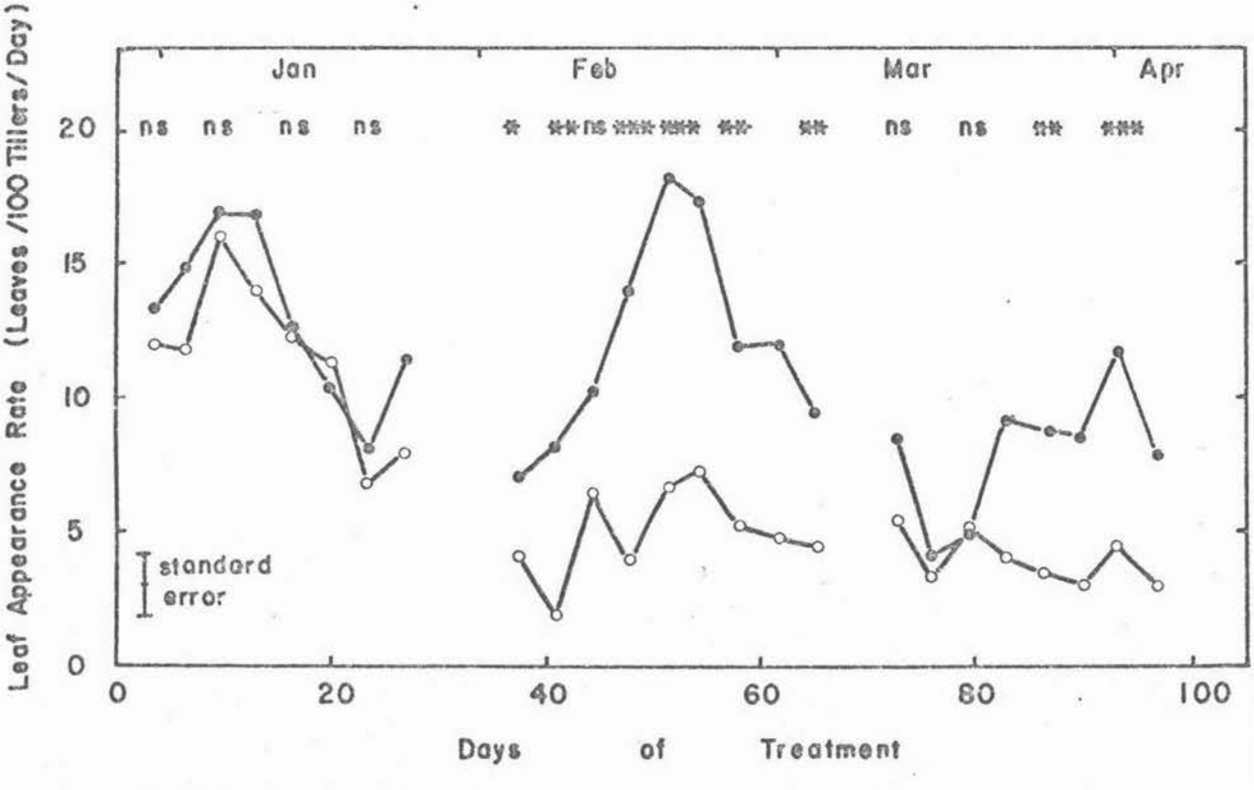

Figure 10b. Leaf appearance rates during the measurement period for irrigated (●) and stressed (○) treatments.

(b) Leaf death rate

In general there were few differences in the death rates (LDR) of leaves between either of the imposed pretreatments (fig 11a) or treatments (fig 11b). The only differences observed, were between high and low cutting within the first 38 days of the measurement period, when low cut pretreatments had higher rates of leaf death than high cut pretreatments.

Despite the fact that no differences were found between moisture regimes, the relative size of the leaf death rate compared to the appearance rate was quite different between stressed and irrigated plots. On average for the first, second and third regrowth periods, the rates of leaf death on irrigated plots were 38%, 57% and 61% of the rates of leaf appearance, which compares to 44%, 102% and 112% for the same periods in stressed plots.

A sharp increase in the rate of leaf death on day 83 coincided with the spraying of plots with 2,4-D on day 81.

v) lamina length

The results of lamina length presented in fig 12a and b show the mean length of green lamina (i.e. not including the necrotic leaf tip) on marked tillers in the field, for the cutting height pretreatments and moisture treatments respectively. The dynamics of lamina length i.e. leaf extension rates and leaf senescence rates are presented in figures 13 and 14 respectively (figures 13a and 14a showing the cutting height pretreatment effects and figures 13b and 14b showing the moisture treatment effects).

The only significant differences between the high

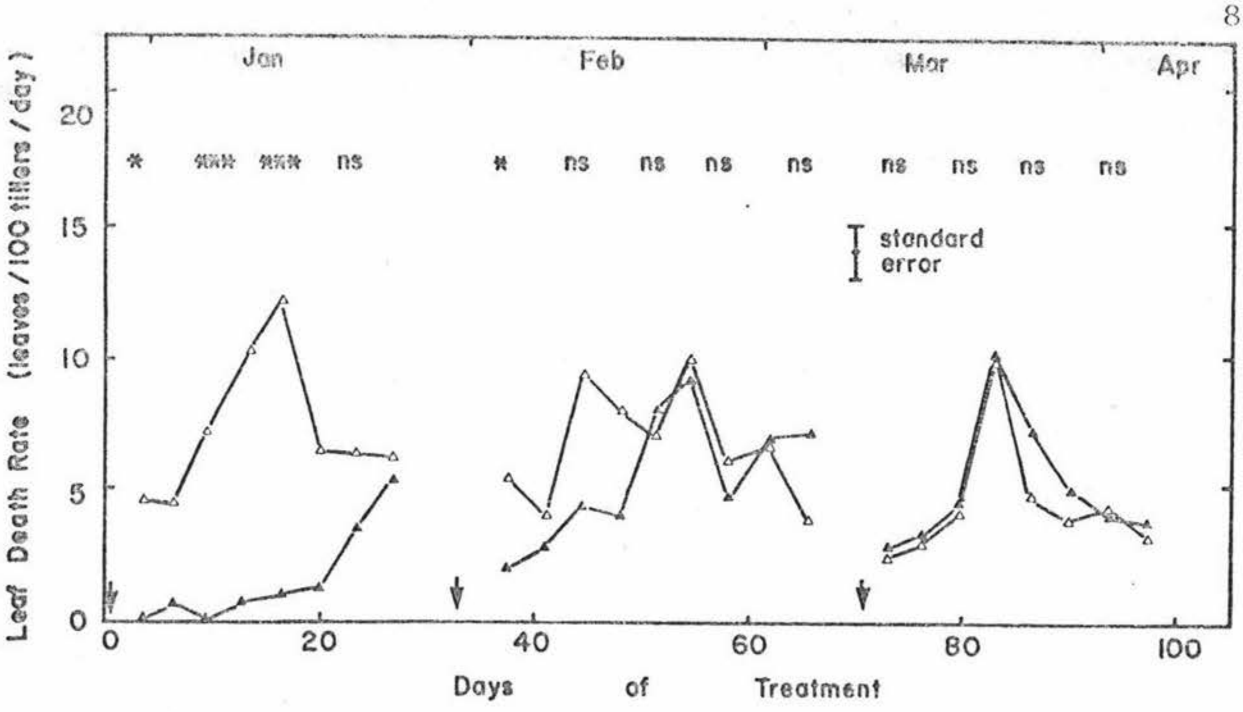

Figure 11a. Leaf death rates during the measurement period for high cut (▲) and low cut (△) pretreatments. Arrows indicate the time of harvests.

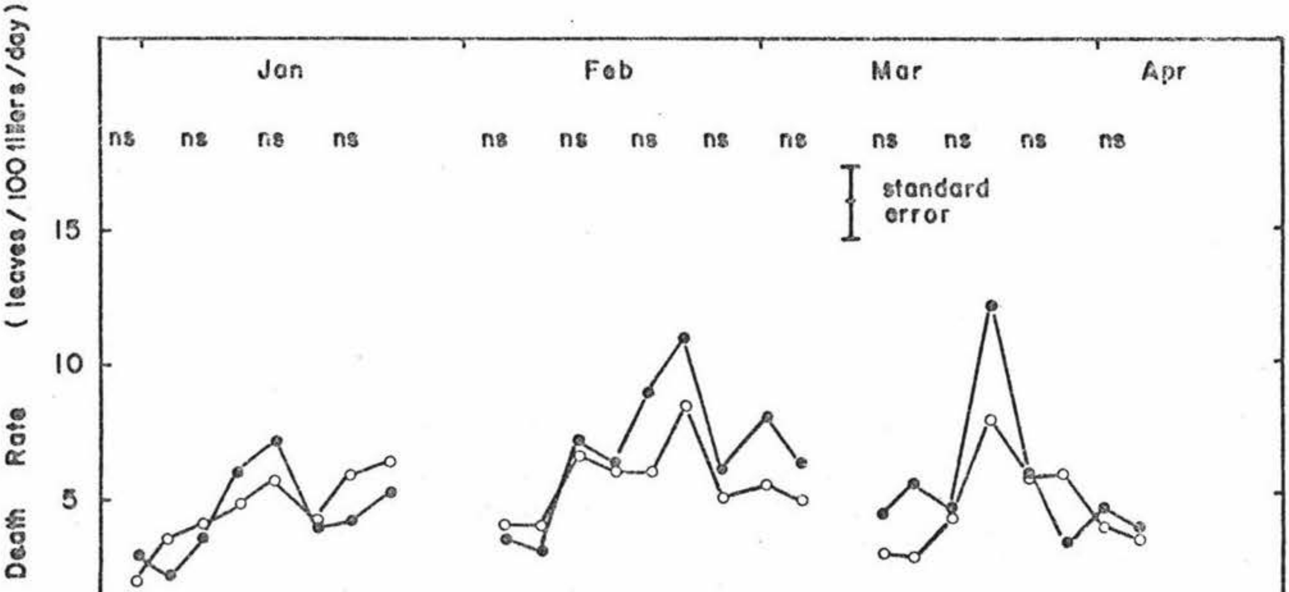

Figure 11b. Leaf death rates during the measurement period for irrigated (●) and stressed (○) treatments.

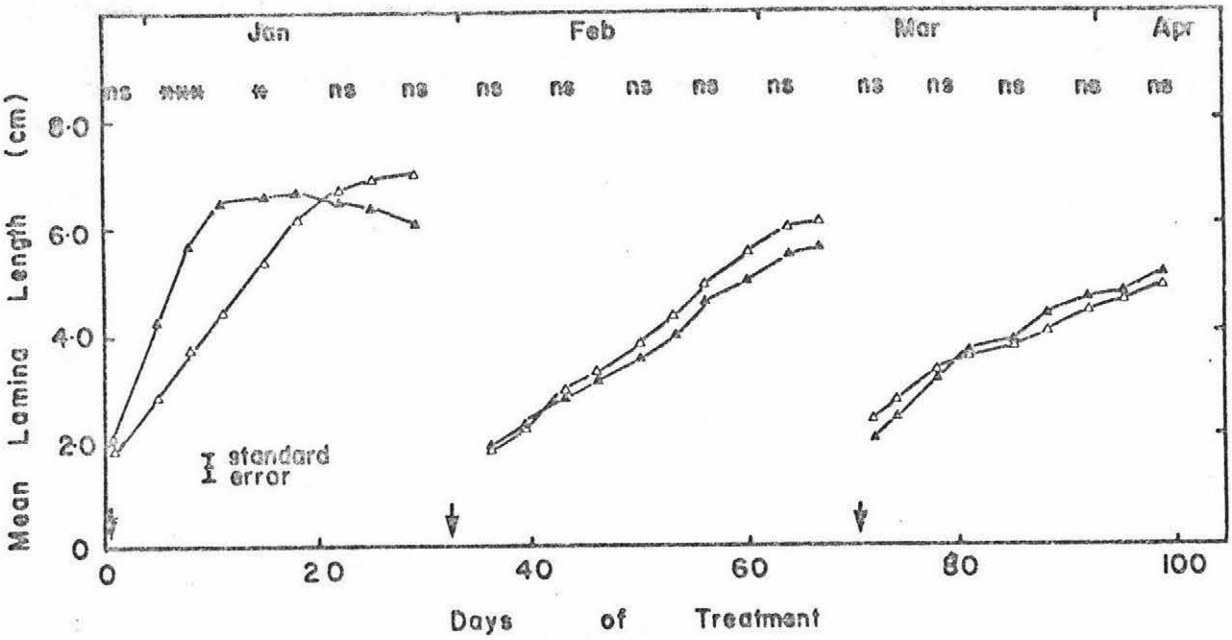

Figure 12a. Mean lamina lengths (cm) during the measurement period for high cut (▲) and low cut (△) pretreatments.
Arrows indicate the time of harvests.

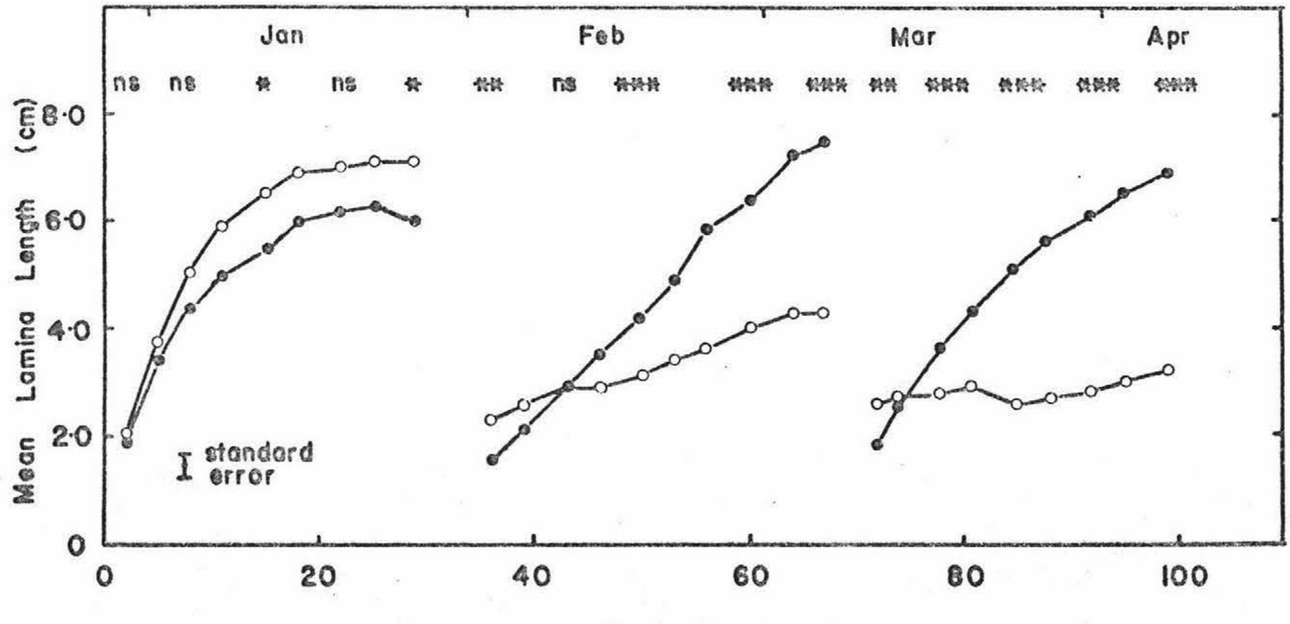

Figure 12b. Mean lamina lengths (cm) during the measurement period for irrigated (●) and stressed (○) treatments.

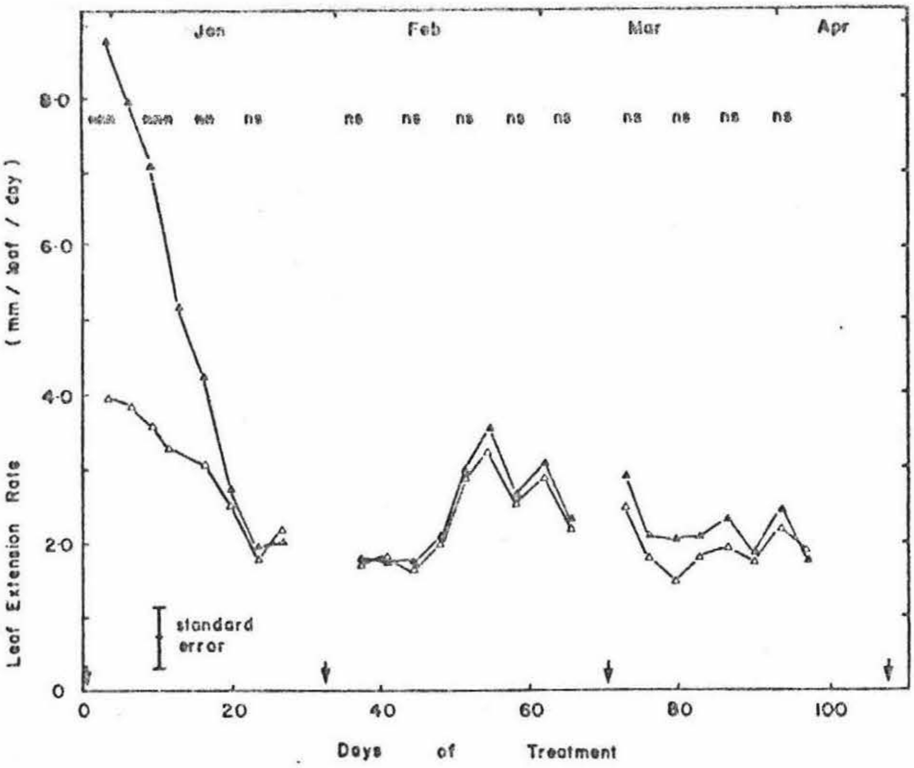

Figure 13a. Leaf extension rates during the measurement period for high cut (▲) and low cut (△) pretreatments.
Arrows indicate the time of harvests.

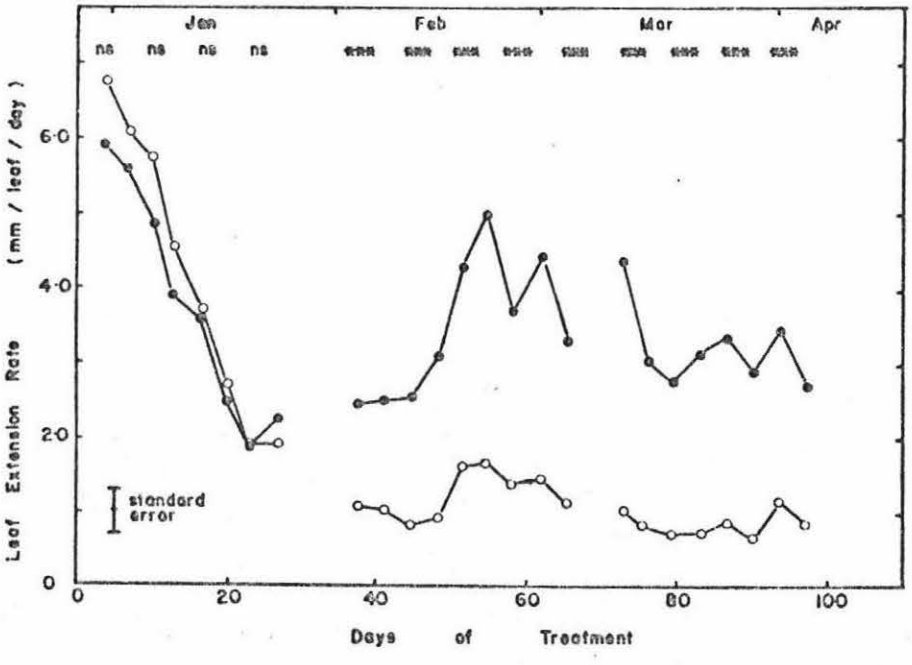

Figure 13b. Leaf extension rates during the measurement period for irrigated (●) and stressed (o) treatments.

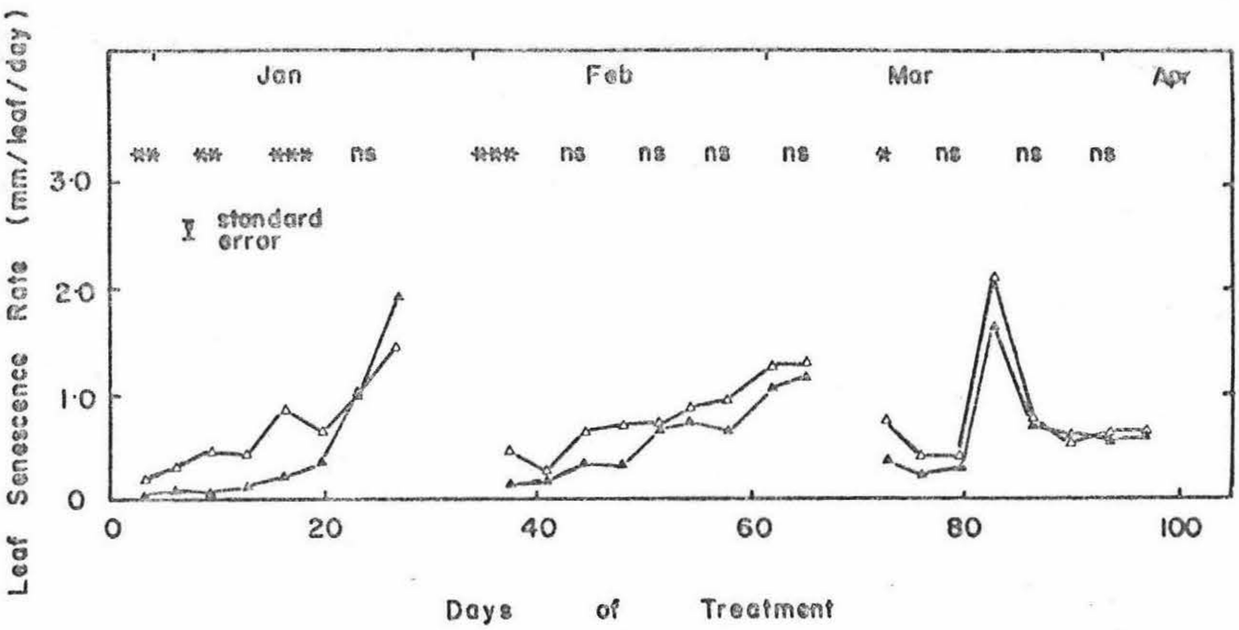

Figure 14a. Leaf senescence rates (die back from the tip) during the measurement period for high cut (▲) and low cut (△) pretreatments. Arrows indicate the time of harvests.

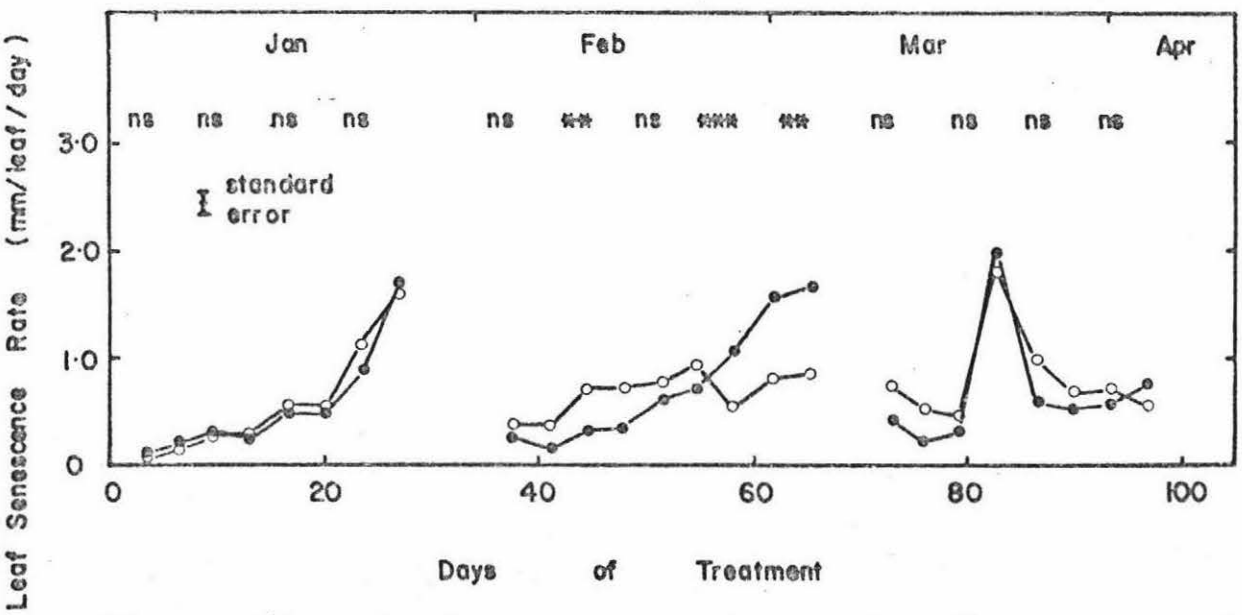

Figure 14b. Leaf senescence rates during the measurement period for irrigated (●) and irrigated (○) treatments.

and low cut plots (fig 12a) occurred between days 5 and 15 during the first regrowth period, where laminae from the high cut plots were longer than for the low cut plots.

In the comparison between stressed and irrigated plots (figure 12b) for the first regrowth period, lamina lengths from both moisture regimes were initially similar, but between days 15 and 29 laminae from stressed plots were 18% longer. The second and third regrowth periods showed a different response, with laminae from stressed plots being initially longer but were elongating more slowly, so that by day 50 in the second regrowth period and day 85 in the third regrowth period laminae from irrigated plots had become longer. By the end of the experiment laminae from stressed plots were only half the length of laminae from irrigated plots.

Lamina lengths were well correlated with results from a second method involving the measurement of a sample of leaves in the lab; the regression equation being:

$$y = 1.33\ X - 0.450 \qquad R^2 = 0.92\ ***$$

where y = total lamina length (lab)
x = green lamina length (field)

1.33 is significantly greater than 1 ($P<.001$)
-0.45 is not significantly different than zero

When total lamina length measured in the lab (y above) was regressed against total lamina length measured on marked tillers in the field (i.e. x above with the length of necrotic leaf tips also included) the strength of the correlation was not increased and the slope of the regression (1.28) was still significantly greater than 1 and not significantly less than 1.33. On average, the length of necrotic leaf tips was 2.5 mm for irrigated plots and 4.2 mm for stressed plots.

(a) Leaf extension rates (mm/leaf/day)

Leaf extension rates (LER) calculated from figures 12a and 12b as an average for all the live leaves in the sward are presented in figures 13a and 13b.

The only significant differences in leaf extension rates between high and low cutting occurred between days 2 and 18, when high cut plots had approximately twice the rate of leaf extension (figure 13a). During this time, high cut plots had significantly fewer leaves per tiller than low cut plots (figure 9a) and consequently a higher proportion of the leaves were elongating.

Significant differences between stressed and irrigated plots were observed during the entire second and third regrowth periods (fig 13b), during which times the rate of leaf extension on stressed plots averaged 38% and 28% of the rate on irrigated plots, compared to 109% for the first regrowth period.

(b) Leaf senescence rates (mm/leaf/day)

Leaf senescence rates (LSR) (i.e. rates of dieback from the leaf tip) calculated as an average of all leaves in the sward are presented in figures 14a and 14b. In general rates of leaf senescence were less than 1 mm/leaf/day and were also less than rates of leaf extension. On average for the first, second and third regrowth periods, the rates of leaf senescence on irrigated plots were 17.5%, 23.4% and 13.5% of the rates of leaf extension, which compares to 21%, 55% and 74% for the same periods in stressed plots.

There were significant differences in the rates of leaf senescence between high and low cutting pretreatments and between stressed and irrigated treatments, however they were very small compared to differences in leaf extension rates.

A sharp increase in leaf senescence on day 83 coincided with the spraying of plots with 2,4-D on day 81.

(vi) Lamina mass per unit length

Results of lamina mass per unit length (mg/cm) are presented, in figure 15a for the cutting height pretreatments and in figure 15b for the moisture treatments.

In general values from the low cut pretreatments were 9% heavier than those from the high cut pretreatments, however these differences were only significant on days 1, 8 and 85. In the case of the moisture treatments, although the values for stressed plots began to increase relative to irrigated plots on day 22, they did not become significantly greater until day 43. On average, values from stressed plots were about 20% greater than irrigated plots for the remainder of the experiment.

4.3 The prediction of dry matter yield from its components

The simple and partial correlations of the six yield components with dry matter yield (DMY) are given in table 8. Lamina length was the component most strongly correlated with DMY, however in general, individual components were poorly correlated with DMY.

When the six components were multiplied according to equation (5) (section 3.5.2.1b) their combined correlation with DMY was increased to $r = 0.730$ ($R^2 = 53.3\%$). This prediction of DMY was a poor estimate of measured DMY since for the regression of measured values (y) with predictions (x) the intercept (1122) was significantly greater than 0 and the slope (0.459) was significantly less than 1. When this regression was repeated for specific harvests or treatments, coefficients of determination were (in general) greater, and in cases

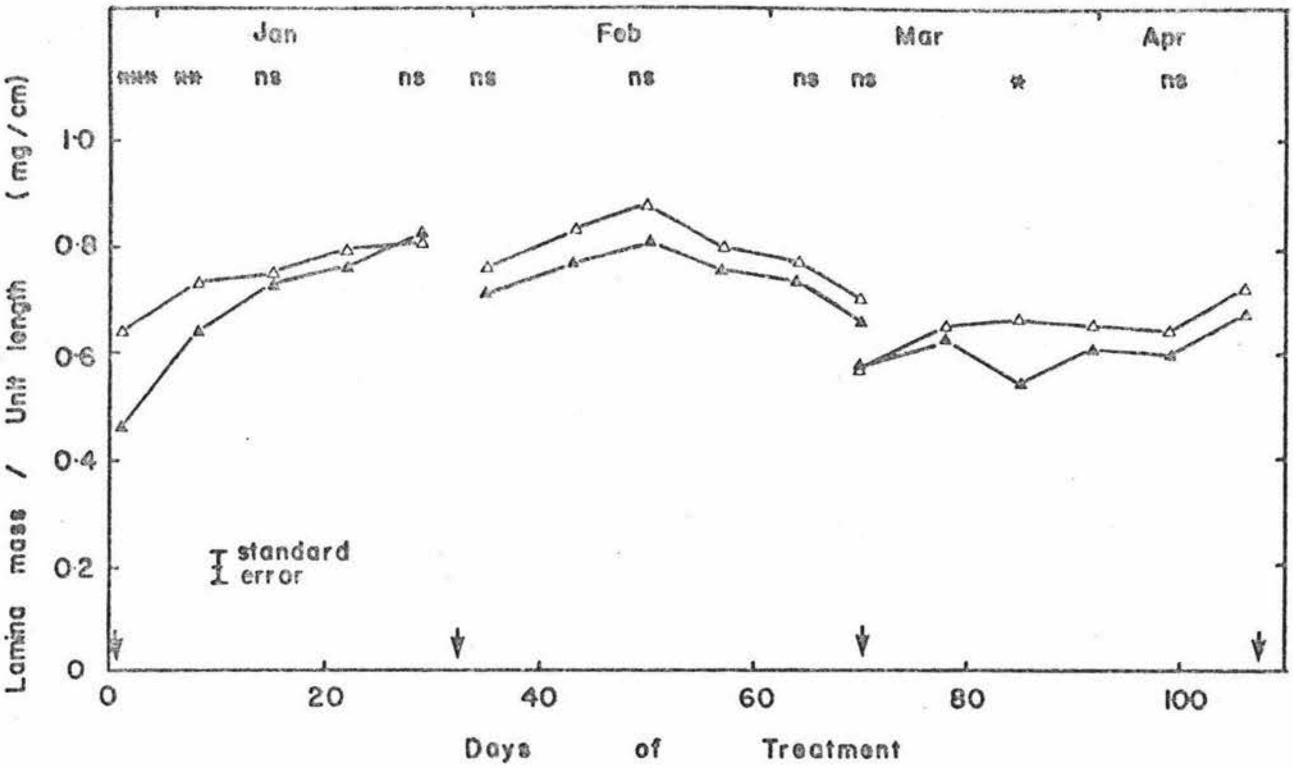

Figure 15a. Lamina mass per unit length (mg/cm) during the measurement period for high cut (▲) and low cut (△) pretreatments. Arrows indicate the time of harvests.

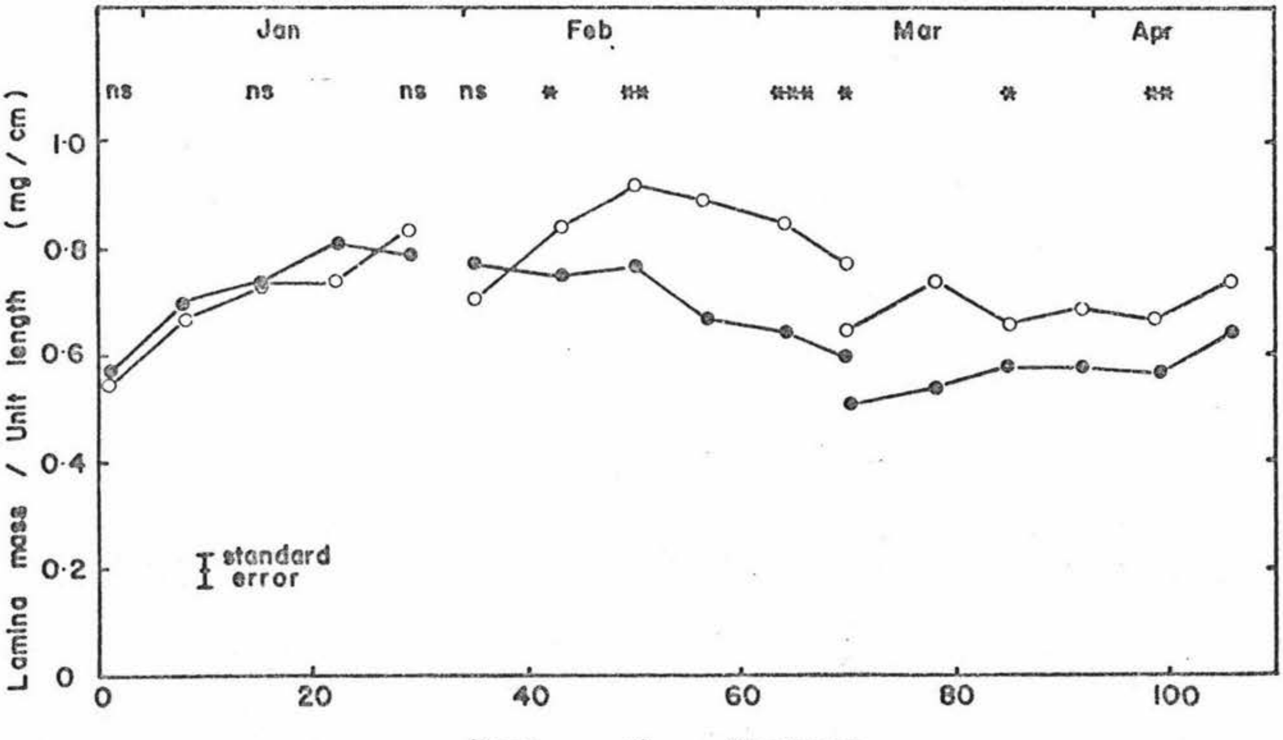

Figure 15b. Lamina mass per unit length (mg/cm) during the measurement period for irrigated (●) and stressed (○) treatments.

Table 8. Simple and partial correlations of the yield components with dry matter yield measured by ground level cutting

Yield component	Simple Correlation	Partial Correlation
fraction of ryegrass in DMY	-.027 NS	0.448**
tiller density	0.260 **	0.302**
fraction of lamina in tiller	-0.120 NS	0.280**
leaf no. per tiller	0.262 **	0.287**
lamina length	0.583**	0.629**
lamina mass per unit length	0.374**	0.308**

with a high herbage mass e.g. before mowing or with irrigation, regression slopes were nearer (but still significantly less than) 1 and intercepts were in some cases nearer (but still significantly greater than) 0.

When the six components were included into a six factor regression equation (equation (6)) using stepwise multiple regression the coefficient of determination (R^2) was increased to 62.3%, and again, when repeated for specific harvests or treatments the R^2 was either similar or greater. The regression constant (βo) was not significantly different than 0 in all cases tested. Lamina length was almost always the most important component determining DMY (the exception being when the grass was short, as occurred after mowing) and lamina number per tiller was generally the least important component determining DMY.

When the 3 components leaf mass per unit length (x_1), lamina length (cm) (x_2) and leaf number per tiller (x_3) were included into a 3 factor multiple regression equation the coefficient of determination (R^2) was reduced to 40.8%. Although this varied for specific harvests or treatments, the overall equation (equation (9)) was used to predict herbage mass on a weekly basis from component measurements for all treatments and pretreatments throughout the measurement period.

$$\text{DMY (kg DM/ha)} = 1124\, x_1 + 158\, x_2 + 321\, x_3 - 222 \quad (9)$$

where $x_1 - x_3$ are defined above.

The weekly predictions of DMY are presented in fig 16a and 16b for the cutting height pretreatments and moisture regimes respectively.

The pattern of herbage accumulation under low and high cutting pretreatments (fig 16a) were similar, although in the first regrowth period the high cut pretreatments had more accumulated herbage (i.e. 1756 kg DM/ha c.f. 1276 kg DM/ha). There were significant

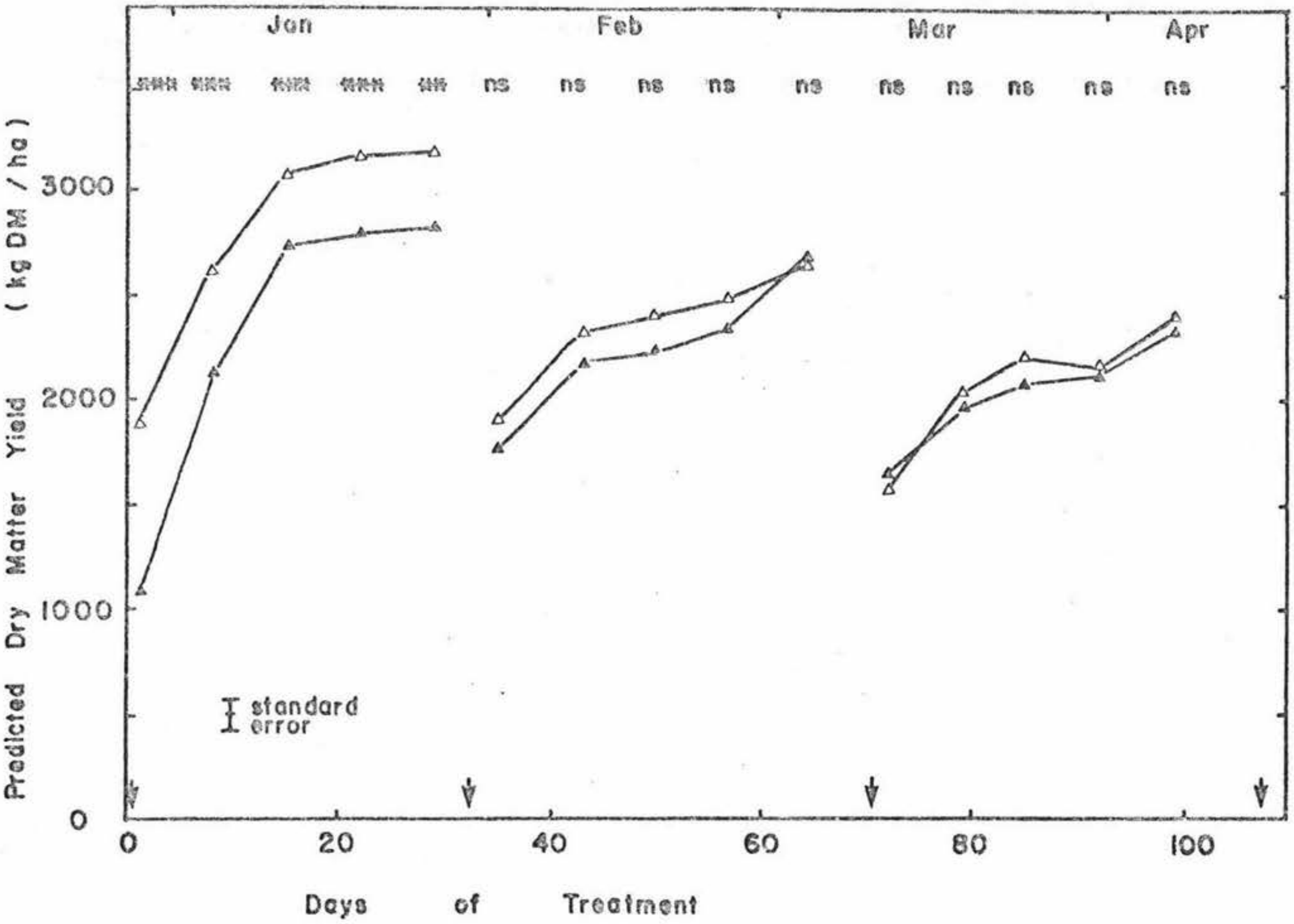

Figure 16a. Predicted dry matter yield during the measurement period for high cut (▲) and low cut (△) pretreatments.

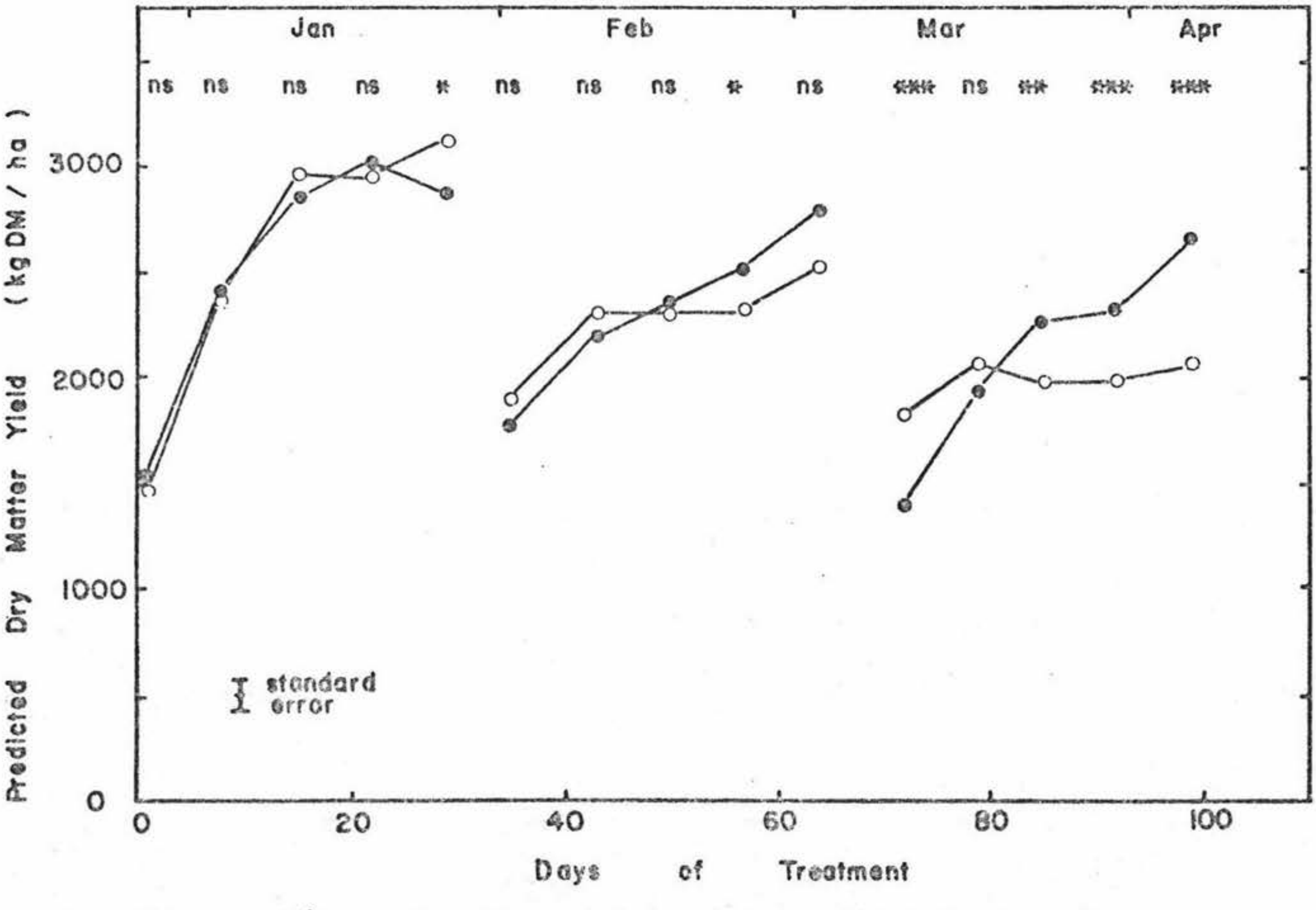

Figure 16b. Predicted dry matter yield during the measurement period for irrigated (●) and stressed (○) treatments.

differences in the total herbage cover between the two pretreatments, where, at the beginning of the measurement period (day 1) low cut pretreatments had 76% more dry matter than high cut pretreatments. This advantage was reduced to 7.5% by day 35 and was not significant.

The patterns of herbage accumulation under the two moisture regimes (fig 16b) were also similar in the first regrowth period, but were different in the second and third regrowth periods. In both the second and third periods, total herbage cover was initially greater in stressed plots, however by the end of these periods the total herbage cover was greater in irrigated plots. The net herbage accumulation (total growth) under irrigation in the first, second and third regrowth periods (calculated as the increase in total herbage mass from the start to the end of the period) was 1371, 1014 and 1250 kg DM/ha respectively, which compares to 1663, 610 and 225 kg DM/ha grown on stressed plots. These data for each harvest were moderately well correlated with mower yields at each harvest ($R^2 = 65.5\%$) and the regression of mower yield (y) with total growth (x) had a slope (0.813) and intercept (-168) which were not significantly different than 1 and 0 respectively.

Pasture growth (kg DM/ha/day) rates calculated from the slopes in figures 16a and 16b are given in tables 9a and 9b respectively.

The growth rate of high cut plots was significantly greater than low cut plots on days 1-8 and 8-15, and the growth rate of irrigated plots was significantly greater than stressed plots on days 72-79, 79-85 and 92-99. In general, coefficients of variation for these data were large and ranged from 18% - 770%.

Table 9a. Pasture growth rates (kg DM/ha/day) during the measurement period for the cutting height pretreatments.

	Days of measurement period											
Cutting height pretreatment	1-8	8-15	15-22	22-29	35-43	43-50	50-57	57-64	72-79	79-85	85-92	92-99
High (7.5 cms)	163	94	13	8	48	12	7	29	47	4	6	24
Low (2.5 cms)	106	52	20	-14	47	12	-5	16	63	17	-6	32
Significance	***	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

Table 9b. Pasture growth rates (kg DM/ha/day) during the measurement period for the moisture treatments.

Moisture regime	Days of measurement period											
	1-8	8-15	15-22	22-29	35-43	43-50	50-57	57-64	72-79	79-85	85-92	92-99
Stressed	135	84	12	9	48	3	-5	12	37	-24	-5	6
Irrigated	134	63	22	-15	47	21	7	32	73	45	4	50
Significance	NS	NS	NS	NS	NS	NS	NS	NS	*	***	NS	**

4.4 The relationship between dynamic sward characteristics and water status measurements

Figure 17 shows the relationship between the ratio of irrigated leaf extension rate : stressed LER and soil water deficit, and figure 18 shows the relationship between the ratio of irrigated leaf appearance rate (LAR): stressed LAR and soil water deficit. Both these figures show similar trends, where the ratio is uncorrelated with the soil water deficit until the soil water deficit exceeds 100 mm. In both figures the ratio first deviates from the (approx.) 1.0 line at 104 mm deficit, after which point there is an approximately linear increase in the ratio until the end of the experiment when the maximum soil water deficit was 180 mm.

Figures 19 and 20 show the relationship of leaf extension rate (LER) and leaf appearance rate (LAR) respectively with dawn leaf water potential (for which the curves have been fitted by eye). The leaf extension rates were calculated as the total leaf extension for all the live leaves in the sward and so this relationship (fig 19) shows the relationship averaged over many leaves and a range of environmental conditions (particularly temperature). High rates of leaf extension are dependent on a high dawn leaf water potential, and rapidly fall to a minimum value of 1 mm/leaf/day as dawn leaf water potential is lowered to -0.7 to -0.8 MPa.

Leaf appearance rate showed a similar relationship with dawn leaf water potential (fig 20) as did leaf extension rate, however, was more sensitive initially to a decreasing dawn leaf water potential, with leaf appearance rate declining more rapidly and reaching a minimum at a higher water potential of -0.5 MPa, than did leaf extension rate.

The leaf appearance rate slowed to a minimum of approximately 4.5 leaves/100 tillers/day as dawn leaf water potential was lowered, which was 31% of the maximum rates of leaf appearance observed at high leaf water potentials. This compares to minimum rates of leaf extension of 1 mm/leaf/day which were 15% of the maximum rates of leaf extension observed at high leaf water potentials.

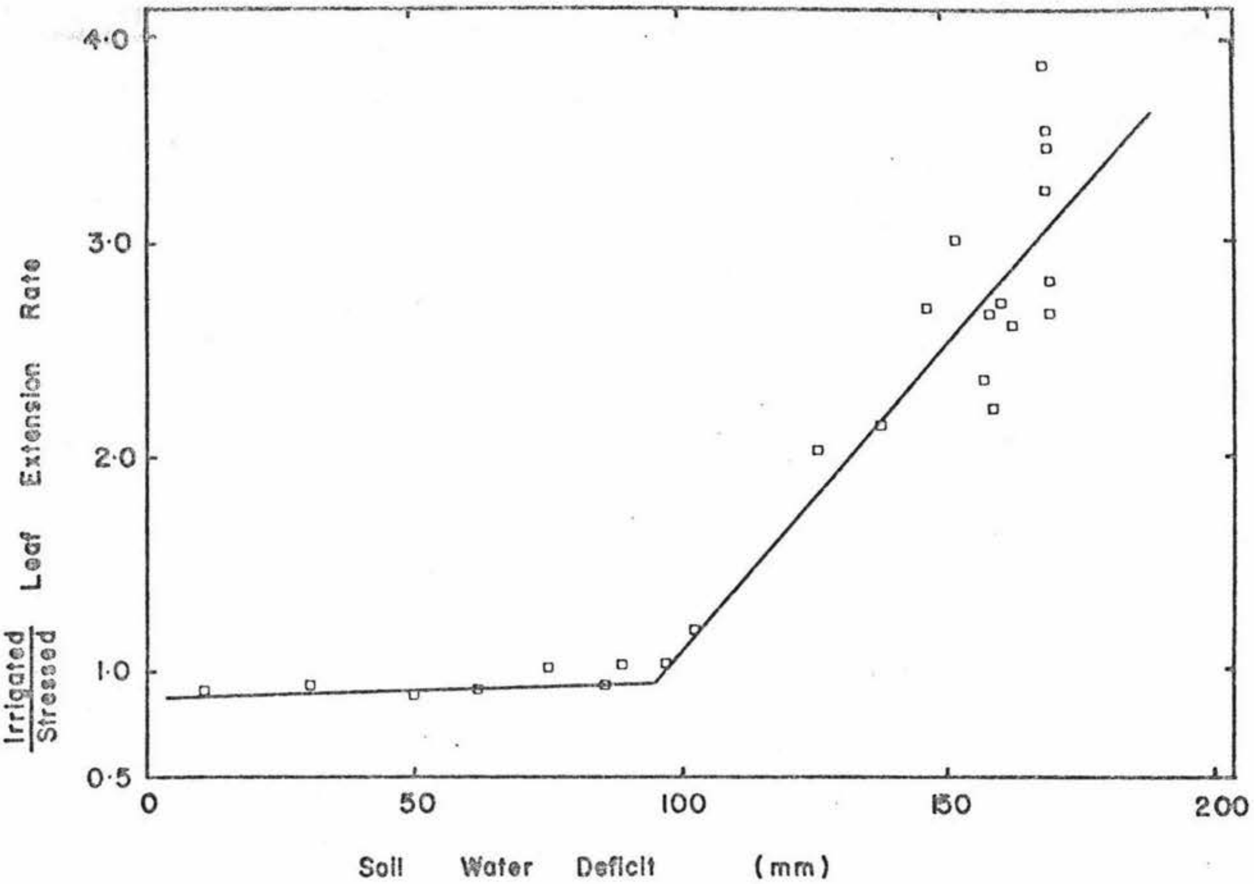

Figure 17. The relationship between the ratio of irrigated-stressed leaf extension rate and soil water deficit.

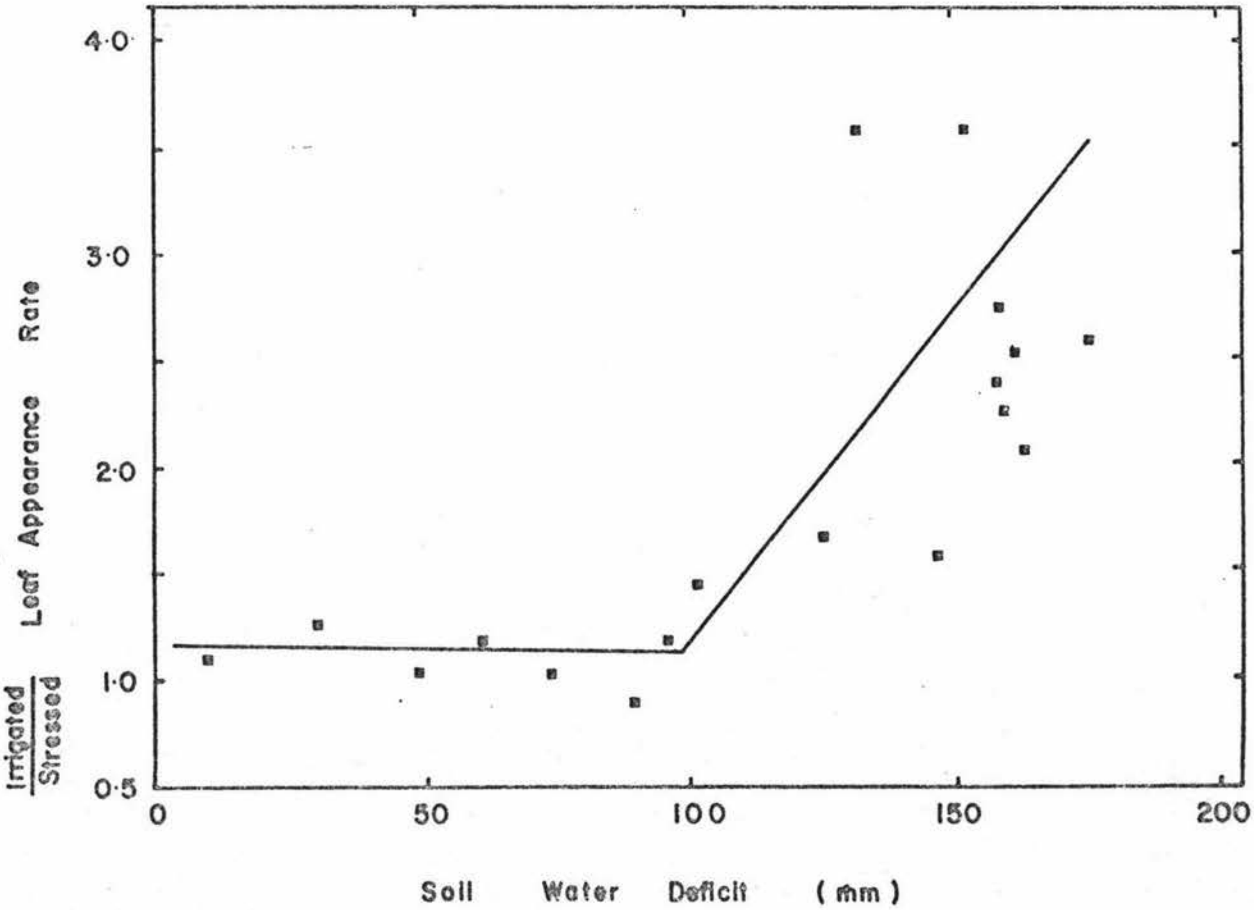

Figure 18. The relationship between the ratio of irrigated-stressed leaf appearance rate and soil water deficit.

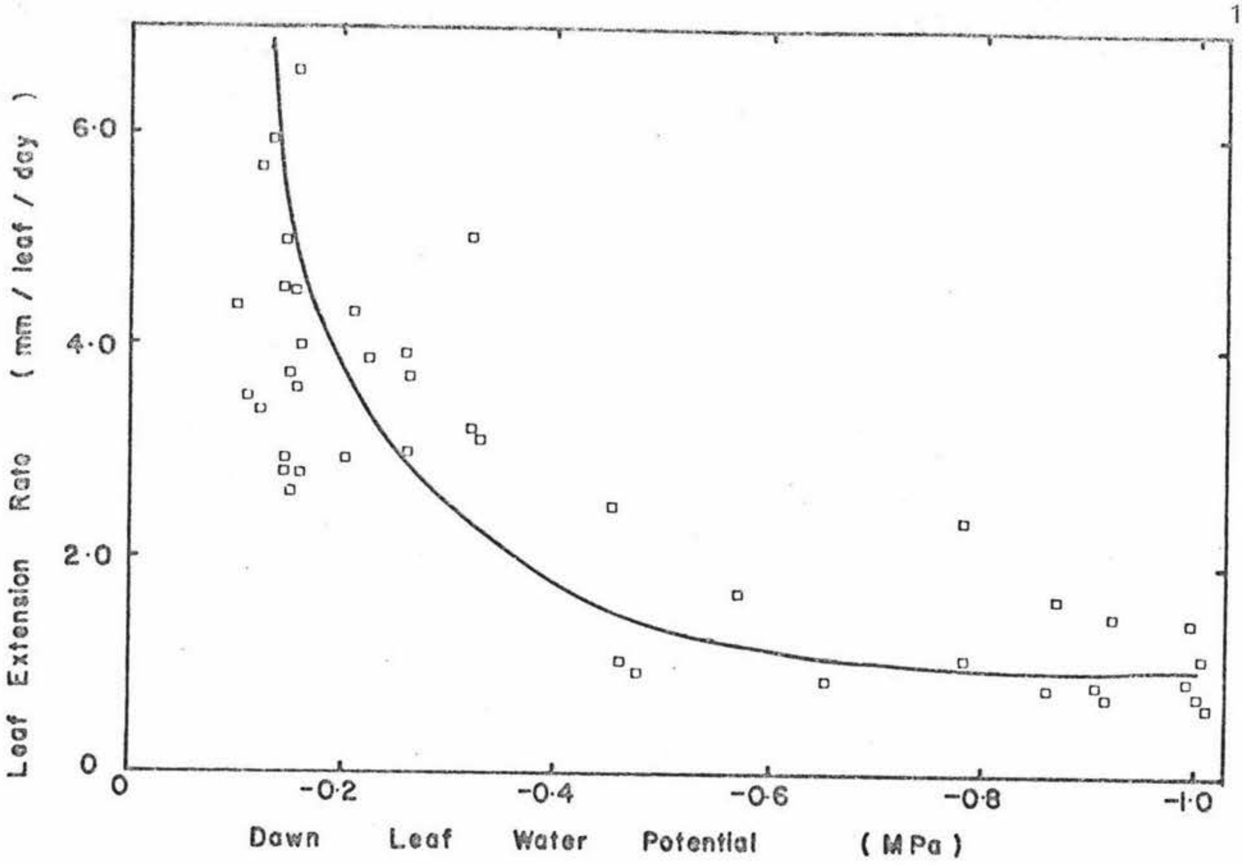

Figure 19. The relationship between leaf extension rate and dawn leaf water potential.

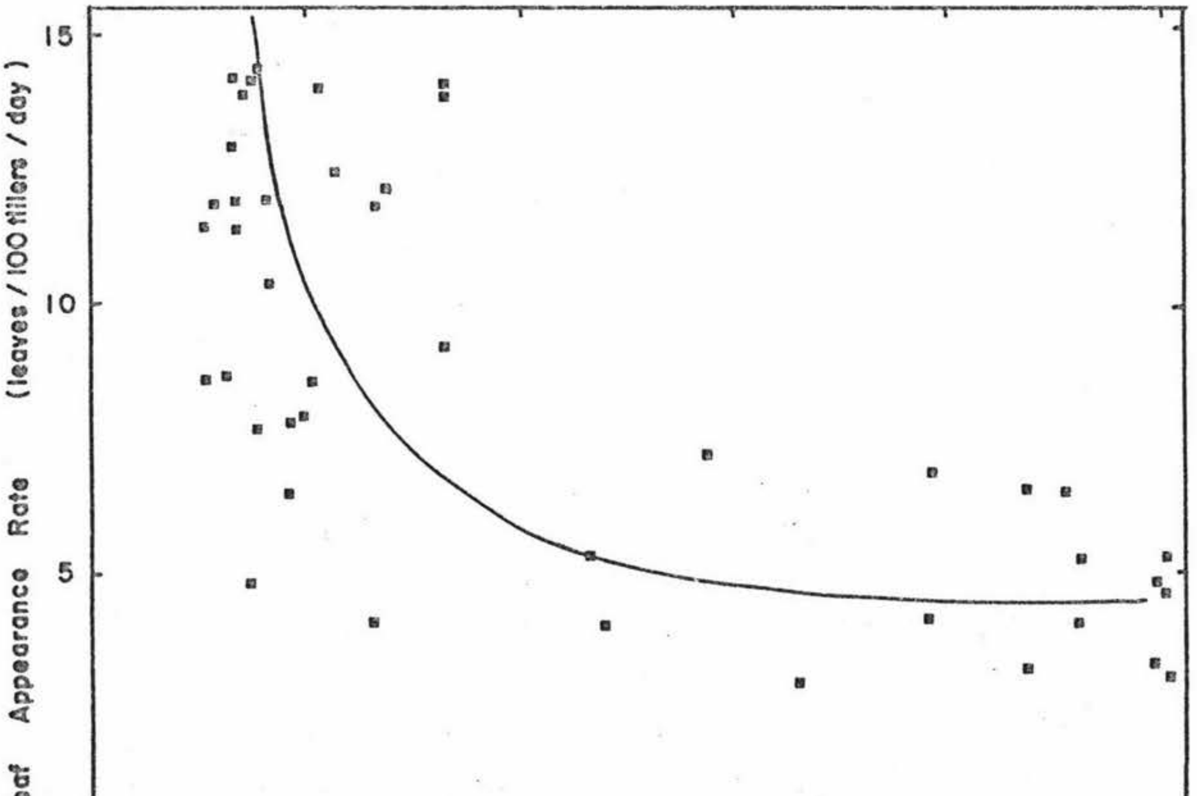

Figure 20. The relationship between leaf appearance rate and dawn leaf water potential.

CHAPTER V

DISCUSSION AND CONCLUSIONS

The discussion and conclusions are presented in the following sections:

5.1 The cutting height pretreatment effect

5.2 The interaction of spring management and summer moisture stress

5.3 The moisture regime effect

- 5.3.1 soil water status
- 5.3.2 plant water status
- 5.3.3 the relationship between plant and soil water status
- 5.3.4 the response of dry matter yield and its components to water stress

5.4 Conclusions

5.1 The cutting height pretreatment effect

The first objective of this experiment was to use two spring defoliation pretreatments to establish different swards, prior to the summer drying down phase. The main differences established between swards were botanical composition and the distribution of dry matter between levels within the canopy (sward structure). Effects of rooting depth on soil moisture extraction patterns were not detected. Differences in all other parameters (particularly specific leaf length, leaf number per tiller and tiller density) could be interpreted in terms of either the botanical composition or sward structure. The effects of the pretreatments on all the measured parameters were greatest at the beginning of the summer dry down phase and declined thereafter. The only difference at the end of the experiment which could be attributed to the cutting height pretreatments was that the ryegrass tiller density of laxly cut plots was greater than for hard cut plots.

Throughout the measurement period plant and soil water status were not significantly influenced by the cutting height pretreatments. This is in contrast with Brougham (1959) who found that lax grazing increased the soil water content in the top 30 cm, and with Evans (1976) who found the reverse effect, where the continued growth of a ryegrass white clover sward under lax defoliation depleted soil water in the top 10 cm to a level below that for land defoliations. The absence of a response in this study can be attributed to the irrigation of plots to field capacity at the beginning of the measurement period, which would have obscured any differences in soil water content which may have existed.

At the beginning of the dry down period, differences in botanical composition were apparent under the different cutting height pretreatments. Laxly cut plots had a higher percentage of ryegrass (31% cv. 19%)

which was encouraged at the expense of Poa and other weed species (table 3a). A similar result was reported by Appadurai and Holmes (1964) who observed that perennial ryegrass-white clover swards cut to 2.5 cm had a higher percentage of other grass species (especially Poa) than when cut to 7 cm. In the case of this experiment under hard cutting it is likely that the newly established ryegrass tillers were insufficiently dense to compete with other grass and weed species. Percentages of dead material were similar for both pretreatments.

The effect of hard cutting was to encourage more prostrate plants than for lax cutting, with more herbage in the base of the sward, similar to the effect found by Jackson (1974(b)), where close cutting (3 cm cf 12 cm) in ryegrass (var S23) swards :

a. reduced the height of insertion of the lowest green leaf blade
b. reduced the mean level of the apex above ground, and
c. reduced the number of subsidiary (aerial) tillers arising above ground

Consequently, when all plots were cut to a common height of 2.5 cm there was considerably more green material remaining on the previously hard cut plots (plate 2). There were about three times as many leaves per tiller on hard cut plots, again in agreement with Jackson (1974(b)), although the average leaf lengths for both pretreatments were similar. The mass per unit length of lamina on the lax cut plots was only 70% of that on hard cut plots (fig 15a) which may be due to leaves in the base of the sward being etiolated. Furthermore it was found that, at day 1, leaves from the lax cut plots were only 80% of the width of leaves from the hard cut plots (1.31 mm cv 1.62 mm). Since not all of the reduction in lamina mass per unit length could be explained by a reduction in leaf width, leaves from the lax cut plots were also likely to be thinner and less dense. Silsbury (1970) summarized the effects of low light intensity as causing leaves to be longer, narrower and thinner, possibly as a result of the reduced photo-oxidation of auxin.

Instead of the increased ryegrass tiller density expected with closer mowing during the pretreatment period (Langer 1963, Appadurai and Holmes 1964), the ryegrass tiller densities under both cutting heights at the start of the dry down period (day 0) were quite similar. However, the greater ryegrass percentage under the high (lax) cut pretreatment suggested that these tillers were larger in size and more may have been reproductive. Furthermore, with the imposition of the common cutting height of 2.5 cm on the different sward structures at this time, a number of factors such as:

a. the increased penetration of light to the base of the laxly cut sward (Langer 1963)
b. the release of apical dominance by the removal of reproductive tillers (Jewiss 1972)
c. the relative lack of competition between other species and ryegrass in the residual herbage of lax plots,

contributed to a markedly different response by tillers from the two cutting height pretreatments. Under the high (lax) cut pretreatment in the first regrowth period (day 1-35) the rate of tiller appearance (67.8 tillers/m^2/day) was four times greater, and the rate of tiller death (28.5 tillers/m^2/day) was about half that for low (hard) cut pretreatments (tables 4 and 5). By day 37 tiller densities on previously lax cut plots were 75% greater than those of the previously hard cut plots (ie 5900 tillers/m^2 and 3400 tillers/m^2 respectively). This difference was still apparent, although slightly reduced (50%) at the end of the experiment (day 109), and confirms the suggestion by Korte and Chu (1983) that higher tiller densities at the beginning of a drought could result in a denser sward after drought.

5.2 The interaction of spring management and summer water stress

This study did not show any significant spring management-summer water stress interactions on Dry Matter yield or tiller density. That is, the response of the swards to water stress was either a) not influenced by spring grazing management, or b) where a response was observed it was the same as that observed in irrigated plots. The reason for this is likely to be that the maximum effect of different spring cutting heights was observed at the beginning or early phase of the measurement period and did not overlap with the maximum levels of water deficit occurring at the end of the experiment. This is further reinforced by the result of Jantti and Heinonen (1957) who found that "complete defoliation while the soil moisture was at or near PWP ...arrested growth almost completely, but the growth rate of plants with assimilating parts left was 70-90% of the corresponding rate on moist soil."

A further reason for the lack of any significant interactions may be that the cutting height treatments were not sufficiently different. Jantti and Heinonen (1957), working with Festuca pratensis and Dactylis glomerata swards, concluded that there was no interaction of soil moisture and defoliation in both 4 and 12 cm cutting height treatments, and that it was only after close mowing (< 1 cm) that regrowth declined steeply with decreasing soil moisture.

It could be concluded therefore, that spring managements to increase tiller density will result in a greater tiller density at the end of the drought but will not give any advantage in terms of dry matter yield during moisture stress. Any benefit which might result from a management system to prepare a sward for drought is unlikely to be in summer production, but may be in the potential for faster recovery after the drought.

5.3 The moisture regime effect

Withholding water from pastures will result in a reduction of the soil and plant water status. Both of these parameters were measured in this experiment. It was found that the soil water status of stressed plots (protected by an automatic rain out shelter) decreased to levels typical for a Tokomaru silt loam in an "average" Manawatu summer (Scotter, Clothier and Turner 1979) and plant water status decreased to a level similar to that of ryegrass at a moderate level of water stress (Korte and Chu 1983).

5.3.1 Soil water status

Reduced soil water status has been found to be a major factor limiting pasture production in many areas of New Zealand e.g. Canterbury (Rickard and Fitzgerald 1970), Manawatu (Scotter, Clothier and Turner 1979), Waikato (Baars and Coulter 1974). However in each of these cases, soil water status was expressed using a different approach. Rickard and Fitzgerald (1970) expressed soil water status in terms of Agricultural drought, Baars and Coulter (1974) expressed soil water status in terms of (soil water) deficit days and Scotter, Clothier and Turner (1979) expressed soil water status in terms of mm deficit.

The approach of Scotter, Clothier and Turner (1979) was used in this study to describe soil water status. It had the advantages that:

1. it related to the identical soil type
2. it overcame any problems of trying to determine the permanent wilting point, necessary for the other two methods

3. measured soil water deficits had been related to a simple water balance model using rainfall and evapotranspiration

In stressed plots the measured soil water status began at field capacity (deficit = 0 mm) and decreased to a maximum soil water deficit of 182 mm (fig 3). This compared with the maximum predicted soil water deficit of 238 mm. This discrepancy was larger than that obtained by Scotter, Clothier and Turner (1979) who found that the predicted and measured data sets were in quite close agreement, however in some cases their measured profiles were as much as 38 mm wetter than the computed values. For this study the relationship between predicted and measured values (incorporating data from both stressed and irrigated treatments) was best explained by two regression lines for a) measured deficits $\leqslant$ 107 mm and b) measured deficits > 107 mm.

For the first equation ($y = 1.03 + 0.758\ x$, $x \leqslant 107$ mm), predicted deficits (y) were significantly smaller than measured deficits (x). In this range of soil water deficit actual evapotranspiration (AET) was calculated as being 0.75 x class A pan evaporation (Scotter, Clothier and Turner 1979), a procedure which apparently underestimated evapotranspiration, and could have justified the use of a larger multiplier. The value 0.86 was found to increase the slope of the regression of predicted and measured soil water deficit so that it was not significantly different than 1. Similarly, Scotter, Clothier and Turner (1979) found 0.82 was a better factor relating AET to class A pan evaporation, for pans located in more sheltered sites. In the case of this study the evaporation pan was in the lee of a shelter belt, which was less exposed than the experimental site.

For the second equation ($y = -83.17 + 1.73\ x$, $x > 107$ mm), predicted deficits (y) in general significantly overestimated the measured deficits. While part of the discrepancy was likely attributed to the failure in measuring water loss below 100 cm depth (estimated to be about 25 mm), the measured deficits (x) thus underestimating actual soil water deficit, it is also likely that the linear equation to calculate soil controlled evapotranspiration (from Scotter, Clothier and Turner 1979) overestimated the evapotranspiration which was actually occurring. The equation of Scotter, Clothier and Turner (1979) was determined in the summer of 1977-78, which was one of the driest on record, and higher levels of vapour pressure deficit may have overestimated evapotranspiration for the same level of soil water deficit as in this experiment (summer 1981-82).

Typical maximum water deficits in a Tokomaru silt loam have been measured to be 170 mm and 160 mm for the summers of 1975-76 and 1976-77 respectively (Scotter, Clothier and Turner 1979). The summer of 1977-78 was one of the driest on record and had a deficit of 230 mm, while the largest deficit recorded on this soil type was 240 mm (Jackson cited by Scotter, Clothier and Turner 1979). The level of soil water deficit measured in this experiment was therefore, almost identical to the average summer deficit from 1975-78. It did however differ from the natural situation in two ways:

1. due to the total exclusion of rain by the rain-out shelter, the water deficit developed from field capacity to 182 mm in only 100 days, compared to 4-6 months as would normally occur,
2. the deficit resulted from a continuous drying down phase which differed from a normal situation where cycles of rewetting from sporadic rainfall would be expected during the period.

Both these factors may have had an effect on plant growth since a prolonged exposure to water stress (Turner and Begg, 1974; Jones, Leafe and Stiles 1980(a)) and cycles of wetting and drying (Brown 1974, McCree 1974) can modify the plant response to water stress. However in the case of this experiment, these effects were expected to have been small compared to the more extreme treatments used in the cited studies.

In the irrigated plots the measured water deficit fluctuated between field capacity and 76 mm (fig. 3). Initially it was envisaged that the maximum soil water deficit should not exceed 60 mm. However, delays in calculating soil water and applying irrigation water resulted in the predicted soil water deficit temporarily reaching 66 mm on day 91 of the measurement period. Furthermore, the discrepancy between predicted and measured soil water status, discussed earlier, resulted in the maximum deficit measured on the irrigated plots being 76 mm. This was greater than deficits which have been used by other researchers. Leafe, Jones and Stiles (1977) found water deficits of 40-60 mm reduced dry matter production and leaf area expansion. In their case water deficits on irrigated plots were kept below 10 mm. Korte and Chu (1983) scheduled irrigation so that soil water deficit did not exceed 45 mm. However, in the case of this experiment, it was unlikely that plant growth under the irrigated treatment would have been affected since the water potential of plants from stressed plots was not affected until the soil water deficit exceeded 104-111 mm.

Mean soil water deficits on irrigated plots for the first second and third regrowth periods were 37 mm, 21 mm and 51 mm respectively. This compared with values of 75 mm, 152 mm and 174 mm for the same regrowth periods in the stressed treatments. The comparison in this experiment was therefore one of a relatively low and a relatively high level of soil water deficit continued over 100 days.

5.3.2 Plant water status

While soil water status is often used as an indicator of plant stress, a more mechanistic indicator of stress is the bulk leaf water potential (Leafe, Jones and Stiles 1977). Measurements of leaf water potential were made at dawn and mid-afternoon to show the upper and lower extremes of the diurnal cycle.

For irrigated plots, dawn leaf water potentials were -0.1 to -0.3 MPa and decreased to values of about -1.6 MPa by mid afternoon. For stressed plots, the leaf water potentials at the beginning of the measurement period were similar to those on irrigated plots, but by the end of the experiment predawn and mid afternoon leaf water potentials were -1.0 MPa and -2.4 MPa respectively (fig. 5). These values were similar to those obtained by Leafe, Jones and Stiles (1977) who found minimum leaf water potentials in irrigated plots of -0.8 and -1.0 MPa and in stressed plots -1.6 to -3.0 MPa; and mid-afternoon leaf water potentials were identical to the values reported by Korte and Chu (1983).

In both maximum (dawn) and minimum (mid-afternoon) leaf water potential data (figure 5) there were no significant differences between stressed and irrigated plots for the first 31 days of the measurement period. During this time the soil water content was sufficiently high for irrigated and stressed plant to recover full turgidity at night. Day 31 had particularly low dawn leaf water potentials (-0.773 MPa and -0.783 MPa for stressed and irrigated plots respectively) which could be attributed to a much higher atmospheric demand for water during that night. The relative humidity was 63% (vapour pressure deficit = 718 Pa), the previous day's sunshine hours were 11.2, the wind run was 658 km and the raised pan evaporation was 7.6 mm; compared to January 1982 averages of 73% (vapour pressure deficit = 528 Pa), 6.1 hours, 544 km and 5.6 mm respectively (data from the Pasture and Crop Research and Development Unit climate station). The stressed plants were unable to recover from this stress, whereas the irrigated plants were able to recover to the normal pre-dawn levels. Beyond day 31 the soil water content in stressed plots was insufficient to allow the plants to recover.

The presence of dew on the surface of leaves has been found to be a major factor which prevented the lowering of leaf water potential in paspalum (Kerr and Beardsell 1975) and wheat (Dougherty 1973). Similarly in this experiment, wet conditions such as occur during rain, irrigation or heavy dew allowed a partial recovery of plant water status to such an extent that leaf water potential was significantly higher than would have been expected had the day been one of "average" atmospheric demand for water.
Examples which support this point are:

1. After day 31, surface moisture on leaves from plants in the stressed plots, resulting from occasional dew or misty rain, allowed a partial (but temporary) recovery of leaf water potential by as much as -0.5 MPa for that day.
2. Plants being irrigated had a high leaf water potential, however within 45 minutes of the irrigation being turned off, this decreased rapidly to a level which would have been expected for unirrigated plants with a similar soil water content (appendix 4).
3. The failure of the automatic rainout shelter on day 56 allowed about 10 mm of rain onto two plots. This resulted in a virtually immediate (within 1 day) recovery of dawn leaf water potential to a level similar to that for irrigated plants (-0.12 MPa).

Leaf water potentials were the most sensitive indicator which showed that this water had allowed the plants to recover.

The lowering of leaf water potential by small amounts of surface water would appear to be the physiological basis behind the observation of Mitchell (comment in response to the paper of Jantii and Kramer 1956) that "dew may have a much larger effect on the regrowth of a pasture than would be expected from the quantity of water in a dew fall. Also, recovery after grazing or defoliation may be stimulated under dryish conditions by a series of very light waterings, as an alternative to a heavy application of water to thoroughly wet the soil, as in normal irrigation practise". Similarly, Kerr and Beardsell (1975) state that "although dew and fog contribute very small amounts of water to the crop water budget, they may be significant for the growth and survival of plants", by reducing transpiration. The prospect of high frequency irrigation with low volumes, or of mist irrigation to increase plant productivity by preventing a lowering of leaf water potential has been considered for pastures (Jackson 1974(a); McAneney and Judd pers.comm.) and demonstrated for some vegetable crops (Howell, Hiler, van Bavel 1971; Rawlins 1973; Rawlins and Raats 1975) but under New Zealand conditions is unlikely to be practical or economical for grassland farmers.

It was found that the standard error of the mean dawn leaf water potential of stressed plots increased towards the end of the experiment. This effect was most likely attributed to the large variation in the physiological status of the youngest mature leaves of these plots, since some leaves were unable to recover at night and had a leaf water potential only several bars higher than the mid-afternoon value. These leaves were noticeably less green than other leaves, were shorter and generally less healthy in appearance. It was likely that these leaves were water stressed to the point where they had lost stomatal control and would soon die. The remaining leaves were able to partially regain turgidity during the night, but still had a leaf water potential significantly lower than that of the irrigated controls.

The position of leaves in the canopy has been shown to influence the measured leaf water potential, particularly the mid-afternoon leaf water potential (Chu and Kerr, 1977). In this experiment it was found that leaves sampled from the top of the canopy had a leaf water potential 0.1 to 0.2 MPa lower than leaves from the middle of the canopy. This observation can be attributed to the fact that the middle of the canopy has a higher humidity and lower windspeed than the top of the canopy (Chu and Kerr 1977).

In addition to the dawn measurements of leaf water potential, observations were also made as to the presence or absence of guttation droplets at the tips of laminae (Kerr and Beardsell 1975). Guttation droplets were only observed on mornings when dew was also observed. In almost all cases this was also when measured leaf water potential was greater than -0.2 MPa. Guttation was not observed in the stressed plots after day 31 of the experiment, except in the case of the two plots which had accidentally received rain. Guttation may therefore be a useful observational indicator of plant water status.

5.3.3 The relationship between plant and soil water status

The relationship between soil water deficit and leaf water potential (figure 6) was different for maximum (dawn) and minimum (mid afternoon) leaf water potentials. This was expected since soil water content was relatively constant compared to the diurnal cycling of leaf water potential.

The maximum (dawn) leaf water potential was found to be uncorrelated with soil water deficits in both stressed and unstressed plants until the deficit reached 104 mm. As the soil water deficit increased beyond this level to 111 mm deficit, the leaf water potential dropped relatively quickly to a level of about -0.8 MPa, and subsequently, more gradually to -1.0 MPa as the level of soil water deficit increased to 180 mm. At water deficits beyond 111 mm there was insufficient soil water to allow stressed plants to recover leaf water potential to the levels of irrigated plants at night.

The importance of this critical water deficit in terms of the plant water balance was further reinforced by the result (using the model of Scotter, Clothier and Turner, 1979) that at a deficit of 107 mm actual evapotranspiration became soil water limited, and was less than the potential evapotranspiration expected if the soil had been wet. It was likely that these two observations were related by the common mechanism of restricted uptake of water from the soil (whether by root shrinkage or an otherwise impaired water uptake system) thus resulting in both restricted transpiration and an impaired plant water balance. The modification of stomatal control by a hydropassive feedback mechanism (Raschke 1975) was unlikely to be involved since if stomatal closure had decreased transpiration it would have also increased the plant water status. In support of this hypothesis Johns (1978) found that for four temperate pasture species, a reduced plant water use under water stress conditions was not the result of stomatal closure, but rather was the result of soil moisture uptake failing to keep up with transpirational losses.

Although soil water potentials (ψ soil) were not measured in this experiment, a comparison with the results of Scotter, Clothier and Corker (1979) (interpolating to estimate the profile at a deficit of 104-111 mm (figure 4a')) showed that for this range of soil water deficit, in the top 60 cm, ψ soil was approximately equal to -0.1 MPa, and at no part of the profile had reached the permanent wilting point (-1.5 MPa).

The minimum (mid-afternoon) leaf water potential was also found to be uncorrelated with soil water deficit in the range of deficits occurring on the irrigated plots ($R^2 = 0.06$). In the stressed plots, the minimum leaf water potential was linearly related to soil water deficit ($R^2 = 0.86$). As the level of water deficit increased from 49 to 180 mm the minimum leaf water potential decreased from -1.2 MPa to -2.3 MPa. Variation around these relationships can be attributed largely to differences in climate (atmospheric demand) on the day of measurement.

The significance of this relationship between water deficit and leaf water potential will be discussed with respect to plant growth in a later section (5.3.4.4), however some implications with respect to drought and irrigation research are immediately apparent. Firstly, it is clear that the effect of increasing the soil water deficit on leaf water potential is not linear. Any study of water stress or drought must therefore involve a consideration of plant water status as well as soil water status if progress in understanding the plant responses to drought is to be made. Jackson (1974(a)) considered that, "whereas in the past soil water deficit has largely been used to measure water stress in field crops, it would seem more logical to measure water stress in the plant, thereby taking account of the effects of root density and distribution, soil water release characteristics, transpiration rate and other factors which determine the overall water economy of the plant".

Secondly, it is important when scheduling irrigation on the basis of soil water status to fully understand the critical soil water deficits at which physiological responses in the plant are initiated. In the case of this experiment for ryegrass growing in a Tokomaru silt loam soil type, the "invisible" lowering of leaf water potential occurred earlier (104 mm) than did the first visual symptoms of water stress observed by Scotter, Clothier and Corker (1979) at 125 mm. This difference could result in a 7 day delay in the timing of irrigation.

5.3.4 The response of dry matter yield and its components to water stress.

5.3.4.1 Introduction

A change in total yield from a sward occurring in response to a water deficit could result from the individual response of any components of that yield. In this study, dry matter yield and the rate at which it accumulated, were reduced by water stress. The mass per unit length of ryegrass lamina increased in response to the water stress (figure 15b) however this was insufficient to compensate for the relatively greater decreases in tiller density, leaf length, number of leaves per tiller and the percentage of ryegrass in the sward (figures 7b, 9b and 12b, table 3b). The leaf to sheath ratio was not affected significantly by the water stress (figure 8b).

5.3.4.2 Dry matter yield

Mower yields taken during the measurement period showed clearly that herbage accumulation was reduced by water stress with the harvested yield of stressed plots being only 8% of the yield of irrigated plots at the end of the experiment.

The difference between stressed and irrigated plots was less clear for the ground level cuts, however, since statistically significant differences were not detected between the two moisture regimes as a consequence of high sample variability (cv's as high as 93%) and the nature of the experimental design. This was in spite of large differences between some results. The results were analysed by Analysis of Variance methods using the Pooled Environments Model (LeClerg, Leonard and Clark 1962) which was appropriate to the experimental design used (Gordon pers. comm.). However, in this experiment, because of the nature of the complex F statistic and the number of treatments and environments, there was sometimes only one degree of freedom for the numerator and denominator used in the test, giving a low discriminating power. Furthermore, water damage to one plot resulted in the rejection of the fourth replicate from harvests 3 and 4 with the consequent loss of a degree of freedom and discriminating power.

The response of yield to water stress was most clearly demonstrated by the dry matter yield data predicted using multiple regression. The weekly predictions show the time course of this response (figures 16a and b) which was not apparent from the harvests taken every fifth week.

At the beginning of the measurement period when both the stressed and irrigated plots were at similar levels of water deficit, levels of dry matter and botanical composition were very similar. However, at the end of the first growth period (day 35) dry matter yields (from the predictions and also the mower yields) were slightly higher on the stressed plots. This was the result of higher growth rates in the stressed plots (table 9b) which may have resulted from:

a) warmer temperatures of the drier environment, or more likely,
b) the accumulation of dead material in the sward, where decay rates of the dead material would be expected to be slower in the drier environments.

Evidence in favour of this later supposition is:

1. the negative growth rate between day 22 and 29 in irrigated plots compared to an increase in dry

matter in stressed plots (table 9b).

2. the accumulation of dead material in the base of the sward of stressed plots at day 35 (dead matter percentages being 50% and 38% for the residual dry matter of stressed and irrigated plots respectively (table 3b)).

As the water deficit increased during the second and third regrowth periods, the pattern of change of dry matter yield became quite different. Initially the trend in both these growth periods was for the dry matter yield of stressed plots to be greater than for irrigated plots. This was attributed to the repeated mowing of stressed plots encouraging the sward to become prostrate, and for herbage to accumulate below the mowing height. Subsequently however, as the growth rate for irrigated plots was greater than stressed plots, the total herbage cover on irrigated plots at the end of both these periods was greater (figure 16b). As was discussed earlier in the literature review (chapter 2.4), this depression of growth rate is perhaps the most universally accepted effect of water stress on pasture.

5.3.4.3 Components of dry matter yield

The tiller can be considered to be the basic unit of a community (Langer 1977). Therefore, the total yield of the grass component of a pasture can be expressed as the product of the density of these tillers and their average size (Nelson and Zarrough 1981). This experiment showed that water stress reduced tiller density by preventing tiller appearance and increasing tiller death rates. Similarly, it was also found that water stress reduced the size of each tiller as a result of there being fewer and smaller leaves. This was similar to Jones, Leafe and Stiles (1980 (a)) who found that a 20% reduction in dry matter production due to water stress, was the result of both a decline in tiller numbers and reduced production and expansion of leaves.

5.3.4.3.1 Tiller density

Throughout the experiment ryegrass tiller densities were within the range of 1000-6000 tillers/m^2. This was very low compared to the densities observed in:

a. sheep grazed swards 30,000 tillers/m^2 (Jones, Collett and Brown 1982) and 24,000-64,000 tillers/m^2 (Bircham, 1981), and,

b. mown swards measured under similar climatic conditions 12,000-14,000 tillers/m^2 (Korte 1981) and 17,000 tillers/m^2 (Korte and Chu 1983) but similar to densities not exceeding 3,000 tillers/m^2 reported by Brougham (1959). Reasons for the lower ryegrass tiller densities obtained in this study might be:

1. the sward was relatively newly established
2. the sward had not been grazed regularly, especially by sheep
3. Ryegrass averaged only 25% of the sward
4. the nitrogen fertilizer level was low compared to the amounts lost in removed herbage and by leaching during irrigation in excess of field capacity.

Changes in tiller density under the two moisture regimes were measured using three different techniques:

a. counts inside 25 randomly placed 22.06cm^2 rings per plot

b. counts inside 3 fixed 83.32 cm^2 rings per plot

c. counts inside 1 randomly placed 625 cm^2 quadrat cut to ground level

Although there were differences in the magnitude of the values determined, and the relative magnitude of tiller appearance and death rates implied by each method, the general trends were similar. As the level of soil water deficit increased during the measurement period, the difference between the tiller densities of stressed and irrigated plots became progressively greater, so that by the end of the experiment the tiller density of stressed plots was about half that of irrigated plots (figure 7b).

The technique using three fixed 83.32 cm^2 rings per plot also allowed the determination of the rates of tiller appearance and tiller death. Absolute tiller appearance and death expressed on an area basis were confounded with different tiller densities (Langer 1963). This was not so when tiller appearance and death was expressed on a per tiller basis as proportional tiller appearance or death rate (Thomas 1980). Thus the high absolute tiller death rate for the high cutting pretreatment between day 37 and 75 (i.e. 59.6 cf 24.4 tillers/m^2/day) was a reflection of a greater tiller density rather than a physiological difference between tillers. The proportional tiller death rates were quite similar (15.8 cf 11.8 tillers/1000 tillers/day).

The gradual decline in tiller density on the water stressed plots throughout the experiment resulted from a considerably greater death rate than appearance rate. This decline is a common result observed by other workers e.g. Hunt and Brougham (1967), Norris and Thomas (1982). Under irrigation tiller density was relatively constant since the rates of tiller appearance and death were approximately equal. On average 0.7% of the tiller population of irrigated plots was renewed each day.

The difference in tiller density between stressed and irrigated plots at the end of the experiment was attributable to both a lower rate of tiller appearance and a higher rate of tiller death in stressed than in irrigated plots. This was similar to Norris (1982) who, working with ryegrass and other pasture species, found that in general irrigated plants had significantly faster rates (0.037 tillers/tiller/day) than covered plants (0.010 tillers/tiller/day); but contrasted with the result of Korte and Chu (1983) who found that "the reduction in tiller density was mainly due to cessation of tillering under moisture stress rather than a faster rate of tiller death. This difference may be because the maximum soil water deficit of 86 mm obtained by Korte and Chu (1983) was considerably less severe than the maximum deficit of 180 mm obtained in this study.

5.3.4.3.2 Tiller size

Although tiller size was not measured directly in this experiment the results implied an effect of water stress on tiller size by reducing both the number and area of laminae. Two further components of tiller size were not reduced by water stress. These were a) the leaf:sheath ratio which was not altered by water stress and b) the mass per unit length of leaf which was increased by water stress.

The response patterns of lamina length (fig 12b), lamina number per tiller (fig 9b) and mass per unit length of lamina (fig 8b) were similar in that there were no significant differences between stressed and irrigated plots in the first regrowth period when the soil water deficit in stressed plots was between 0 and 117 mm. At the beginning of both the second and the third regrowth periods leaf length and leaf number per tiller in irrigated plots were less than in stressed plots, however at the end of both these periods the situation was reversed, where leaf length and leaf number per tiller in irrigated plots were greater than in stressed plots. This trend is similar to that observed for dry matter yield (fig 16b) and can be attributed to the effect of stress on sward structure - encouraging plants to be more prostrate and not as severely defoliated by mowing. It is evident therefore, that the effects of water stress on these parameters were not so apparent in the absolute values per se, but rather in their rates of change.

Absolute rates of leaf extension, leaf senescence, leaf appearance and leaf death showed no differences between moisture regimes at deficits between 0 and 117 mm, however as the deficit increased, consistently significant differences between moisture regimes became apparent only for leaf extension rates and leaf appearance rates (figures 13b and 10b). It is significant that these differences were not observed until the soil water deficit had exceeded 117 mm because it was immediately before this point (i.e. at 104 mm) that predawn leaf water potential had shown a sudden drop from -0.2 MPa to -0.8 MPa; implying a close dependance of both leaf extension and leaf appearance on a high (> -0.3 MPa) leaf water potential. This relationship will be discussed in more detail in a later section (5.3.4.4).

A discussion of rates of leaf appearance does not include a consideration of the rate of production of leaf initials on the tiller apex, nor the growth of leaves before their emergence from the enclosing sheath (Anslow 1966). In view of the generality that cell expansion is more sensitive than cell division to water stress (Hsiao 1973) it is plausible that the reduced rate of leaf appearance is attributable to the restricted cell expansion of leaf initials rather than the inhibited formation of leaf initials. This is an important distinction since the accumulation of leaf primordia at the tiller apex gives potential for compensatory growth upon relief from the water stress. The compensatory growth observed by Chu (1979) and Korte and Chu (1983) was attributed to the rapid expansion of dormant tillers, but could have also been attributed to the rapid expansion of dormant leaf primordia.

One final observation was a sharp increase in leaf senescence and death rates on day 83 for both stressed and irrigated treatments (figures 14b and 11b), as a result of spraying the plots with 2,4-D on day 81 to control dicotyledonous weeds. No effect on leaf extension rates and leaf appearance rates were observed.

Good control of the weeds was obtained with percentages of green herbage between harvests 3 and 4 falling from 36% and 31% to 28% and 8% for stressed and irrigated plots respectively (table 3b).

5.3.4.3.3 Leaf morphology

Morphological responses of leaves to water stress have been observed by many researchers (Stocker 1960; Woolley 1973; Fellows and Boyer 1978). In this experiment, water stress initially had no effect on leaf morphology until the soil water deficit exceeded 142 mm (day 43). After this point, a change in leaf morphology was evidenced by the fact that the mass per unit lamina length for irrigated plants was significantly less than for stressed plants (0.64 mg/cm cf 0.79 mg/cm). These were about half the values recalculated from the data given by Leafe, Jones and Stiles (1977) for perennial ryegrass leaves which in their case were about twice as wide. In addition it was also observed that the effect of water stress was to reduce average leaf width, leaf area index and specific leaf area (appendix 7). From this it could be deduced that water stressed leaves were also thicker and denser. These observations are in agreement with Leafe, Jones and Stiles (1977) and Jones, Leafe and Stiles (1980(b)). Both these studies went on to show that water stressed perennial ryegrass leaves had a higher density of stomata which were smaller and placed at the bottom of deeper epidermal ridges, smaller but denser epidermal cells and a higher concentration of chlorophyll.

5.3.4.4 The relationship of leaf extension and leaf appearance with leaf water potential

Many authors have stressed the relationship between leaf extension rate and leaf water potential (Boyer 1968; Acevedo, Hsiao and Henderson 1971; Hsiao and Acevedo 1974; Chu and McPherson 1977), however few authors have described the relationship between leaf appearance rate and leaf water potential. Only Leafe, Jones and Stiles (1977) measured leaf appearance rates and leaf water potential and found, as in this study, that water stresses which lowered leaf water potential also reduced the rate of leaf appearance.

i. Leaf extension.

In this experiment measurements of leaf extension were made on immature elongating leaves, whereas measurements of leaf water potential were most easily made on mature elongated leaves.

In view of the different positions of these leaves in the canopy and their physiological differences with respect to elongation, it was decided to investigate the relationship between the leaf water potentials of these two leaf classes. The results of this comparison (appendix 5) showed that differences between mature and immature leaves were non-significant. It was concluded therefore, that the leaf water potential measurements made on the youngest fully mature leaves were valid as estimates of the leaf water potential of the next youngest emerging leaf. This has generally been assumed by other workers (Jackson 1974, Leafe, Jones and Stiles 1977).

The relationship between leaf extension rate and dawn leaf water potential determined in this experiment (fig 19) showed a similar decline in extension rate with decline in leaf water potential to that obtained by other workers (Boyer 1968, Hsiao and Acevedo 1974, Boyer and McPherson 1975, Chu and McPherson 1977) except that leaf extension rate levelled out at 1 mm/day rather than completely stopping as in the above cases. This result was also obtained by Jones, Leafe and Stiles (1980a) and was attributed to the slower development of water stress in the field allowing time for plants to adjust physiologically, rather than the more rapid development of water stress in the cited studies. The relationship determined in this experiment must be interpreted with caution since it represents all leaves in the sward, rather than the relationships for individual leaves cited by the authors mentioned above. The leaf extension rate (mm/leaf/day) was calculated as the total increase in green length of a sample of all the leaves in a pasture, divided by the number of leaves sampled and the number of days over which growth occurred (2-4). The extension rates would be expected to be greater in many cases for individual, extending leaves and on some specific days, times of the day and at day or night, therefore implying many different LER vs Ψ_1 relationships (Chu 1979).

Boyer (1970) found that growth of corn, soybean and sunflower was so sensitive to a decrease in leaf water potential that leaf extension only occurred at night. On this basis, the leaf extensions measured in this study might be interpreted to be occurring only at night when plant water status was the most favourable for growth, however this hypothesis can be discounted since between days 49 and 53 in this study it was found that average rates of leaf extension during the day in stressed and irrigated plots were 0.218 and 0.491 mm/leaf/hour respectively and during the night were slightly slower at 0.198 and 0.408 mm/leaf/hour respectively (appendix 6). Chu and Kerr (1977) observed a similar response in sudax and found that maximum rates of leaf extension coincided with maximum air temperatures rather than maximum leaf water potential.

ii. Leaf appearance

The rate of leaf appearance showed a similar decline with decreasing dawn leaf water potential to that observed for leaf extension, except that leaf appearance was more sensitive, reaching its minimum (of 4 mm/100 tillers/day) earlier than leaf extension. This result could be interpreted in terms of the effect of a lowered leaf water potential on leaf initiation (Husain and

Aspinal 1970) or pre-appearance growth of primordia (Hsiao 1973) and only a detailed study of the tiller apex could answer this question. Furthermore, in view of the observation of Husain and Aspinal (1970) that the water potential of the apex in barley was unaffected when leaf relative turgidity had fallen as low as 75% (approximately -1.0 MPa to -1.5 MPa (Lawlor 1969)) suggests that further work investigating the mechanism of the observed relationship between leaf appearance and leaf water potential is necessary.

5.4 Conclusions

In consideration of the objectives of this thesis (presented in chapter 1) i.e.

1. measuring the response of perennial ryegrass to an imposed drought (compared to irrigation) and relating this to measurements of soil and plant water status under field conditions, and,
2. studying the effect of spring cutting managements on the patterns of tiller and leaf growth in a sward of perennial ryegrass during summer under two contrasting moisture regimes;

The conclusions of this thesis are therefore:

i) that the growth of the components of pasture production was reduced when the soil water deficit exceeded a critical point of 104-111 mm, which could be predicted, for the Tokomaru silt loam soil type, according to the soil water balance of Scotter, Clothier and Turner (1979). At this point the Ψsoil was approximately equal to -0.1 MPa and had not reached the permanent wilting point (PWP) -1.5 MPa. This point was characterised by a sharp 0.6 MPa decrease in dawn Ψ leaf which contrasted with the more gradual decline in mid-afternoon Ψleaf.
Such a change in Ψleaf (particularly at dawn)

was found to be a very sensitive indicator showing that this change in water status had occurred. At deficits exceeding this critical point reductions in pasture yield were attributed to:

1. a reduction in the rate of tiller appearance
2. an increase in the rate of tiller death, and
3. a reduction in the rate of leaf production, with no significant effect observed on the rate of leaf senescence and death, and,

ii) that spring managements to increase tiller density will result in a greater tiller density at the end of drought but will not give any advantage in terms of dry matter yield during moisture stress. Any benefit which might result from a management system to prepare a sward for drought is unlikely to be in summer production but may be in the potential for faster recovery after drought.

Appendix 1. A comparison of volumetric water content (θ) calculated from a) neutron probe data and b) direct soil sampling

In order to test the calculation of volumetric water content (θ) from neutron probe data according to equation 4, soil samples were taken at various depths from beside a surplus neutron probe access tube immediately after neutron probe counts had been taken. The results presented in the table below showed no significant difference between the two methods used to calculate θ, which validates the use of the neutron probe method using equation 4.

Depth (cm)	Gravimetric water content (ω)	Bulk density ($\times 10^3 kg/m^3$)	Direct measurement of θ	θ calculated from neutron probe data
20	21.77	1.35	29.39	29.46
30	21.39	1.46	31.23	31.12
40	19.57	1.57	30.73	31.92
50	18.70	1.60	29.92	31.73
60	18.76	1.61	30.20	31.13
70	18.16	1.62	29.42	31.41
		$\bar{x} \pm$ se	30.15 ± .298	31.13 ± 0.358

$$t_{10} = \frac{31.13 - 30.15}{\sqrt{0.298^2 + 0.358^2}} = 0.4753 \quad \text{NS}$$

Appendix 2. Uniformity test of dry matter yield (15.9.81)

kg DM/ha

	west plot	east plot
	2930	3378
	2768	3133
	3162	2649
	3004	2969
	2280	3578
	2924	2799
	3206	2866
	2977	3168
$\bar{x}$ =	2906.375	3067.50

Analysis of Variance

Source	Degrees of freedom	SS	MS	F
between plots	1	103,844.9	103,844.9	1.1622 NS
within plots	14	1,250,950.0	89,353.57	
Total	15	1,354,794.9		

Appendix 3. Rainfall and Class A pan evaporation from the Massey University Meteorological Station, and potential evapotranspiration (PET) and actual evapotranspiration (AET) for the water stressed plots during the measurement period.

Date	Day of measurement period	Rainfall and (irrigation) (mm)	Class A pan evapotranspiration (mm)	PET (mm)	AET (mm)
28.12.81	0		11.6		
	1		6.8		
	2	0.1	7.2	5.4	5.4
	3	43.3	1.3	0.9	0.9
1.1.82	4	0.1	4.6	3.4	3.4
	5	0.1	4.5	3.3	3.3
	6	2.7	6.9	5.1	5.1
	7		6.0	4.5	4.5
	8		7.7	5.7	5.7
	9	4.0	5.0	3.7	3.7
	10	21.3	5.6	4.2	4.2
	11		7.9	5.9	5.9
	12		5.3	3.9	3.9
	13		3.4	2.5	2.5
	14		5.0	3.7	3.7
	15		6.3	4.7	4.7
	16		0.0	0.0	0.0
	17		5.9	4.4	4.4
	18		6.0	4.5	4.5
	19		5.4	4.0	4.0
	20		7.2	5.4	5.4
	21		3.0	2.2	2.2
	22		5.3	3.9	3.9
	23		5.2	3.9	3.9
	24		7.3	5.4	5.4
	25	22.8	3.9	2.9	2.9
	26	0.6	7.3	5.4	4.8
	27	3.0	5.3	3.9	3.9
	28		5.2	3.9	3.9
	29	3.3 (75)	4.6	3.4	3.4
	30	3.9	3.7	2.7	2.7
	31		7.6	5.7	4.3
	32		7.5	5.6	4.1
	33		8.0	6.0	4.0
	34		6.1	4.5	3.9
1.2.82	35		7.7	5.7	3.8
	36		8.7	6.5	3.6
	37		5.0	3.7	3.5
	38		7.7	5.7	3.4
	39	1.1	8.2	6.1	3.3
	40	14.0	4.0	3.0	3.0
	41		5.3	3.9	3.1

Appendix 3 (Cont.)

Date	Day of measurement period	Rainfall (and irrigation) (mm)	Class A pan evapotranspiration (mm)	PET (mm)	AET (mm)
	42		6.9	5.1	3.0
	43		7.9	5.9	2.9
	44		6.0	4.5	2.9
	45		9.5	7.1	2.8
	46		10.0	7.5	2.7
	47		7.5	5.6	2.6
	48	(80)	5.8	4.3	2.5
	49		5.9	4.4	2.4
	50		7.3	5.4	2.4
	51		4.0	3.0	2.3
	52	4.5	0.1	0.0	0.0
	53	9.0	1.4	1.0	1.0
	54		7.5	5.6	2.2
	55		6.8	5.0	2.1
	56	8.6	7.9	5.9	2.1
	57	12.2	4.7	3.5	2.0
	58	5.0	3.5	2.6	1.9
	59	17.8	0.6	0.4	0.4
	60	2.5	1.6	1.1	1.1
	61		6.1	4.5	1.8
	62		4.6	3.4	1.8
1.3.83	63	7.6	1.3	0.9	0.9
	64	9.7	6.7	5.0	1.7
	65	41.7	1.6	1.1	1.1
	66		2.0	1.5	1.5
	67		6.0	4.5	1.6
	68		2.8	2.1	1.5
	69		2.8	2.1	1.5
	70	0.2	4.2	3.1	1.4
	71		3.1	2.3	1.4
	72		4.7	3.5	1.3
	73		6.3	4.7	1.3
	74		5.7	4.2	1.2
	75		6.4	4.7	1.2
	76		5.2	3.9	1.2
	77		9.1	6.8	1.1
	78		4.0	3.0	1.1
	79		3.6	2.7	1.1
	80		3.2	2.3	1.0
	81		4.1	3.0	1.0
	82		5.3	3.9	1.0
	83		3.6	2.7	0.9
	84		3.7	2.7	0.9
	85	15.7	2.2	1.6	0.9
	86		4.0	3.0	0.8
	87	0.3	2.6	1.9	0.8
	88		4.6	3.4	0.8
	89		4.5	3.7	0.8

Appendix 3 (Cont.)

Date	Day of measurement period	Rainfall (and irrigation) (mm)	Class A pan evapotranspiration (mm)	PET (mm)	AET (mm)
	90		2.9	2.1	0.7
	91		2.8	2.1	0.7
	92	5.1(75)	4.0	3.0	0.7
	93	5.6	0.7	0.5	0.5
1.4.83	94	0.3	1.6	1.1	0.7
	95	0.2(75)	1.6	1.1	0.6
	96	1.0	3.4	2.5	0.6
	97	1.7	2.9	2.1	0.6
	98		2.6	1.9	0.6
	99	0.9	3.4	2.5	0.5
	100		3.5	2.6	0.5
	101	0.9	2.9	2.1	0.5
	102	2.1	4.5	3.3	0.5
	103	0.9	2.9	2.1	0.5
	104		1.6	1.1	0.4
	105		2.0	1.5	0.4
	106		3.4	2.5	0.4
	107		4.4	3.3	0.4

Appendix 4. The lowering of leaf water potential (ψ_1) following the completion of irrigation.

Minutes since irrigation stopped	ψ_1 (MPa)
10	-0.98
13	-1.32
16	-1.48
37	-1.88
40	-1.66
44	-1.90

Appendix 5. Comparison of leaf water potential (ψ_1) measurements from mature and immature laminae of the same tiller

day-time	treatment	ψ_1 of mature laminae	ψ_1 of immature laminae
52 dawn	irrigated	-0.26 (4)	-0.31 (4)
	stressed	-0.81 (2)	-0.83 (2)
53 dawn	irrigated	-0.35 (6)	-0.29 (6)
77 afternoon	irrigated	-1.24 (3)	-1.36 (5)
	stressed	-1.94 (5)	-2.14 (5)
98 afternoon	irrigated	-1.31 (3)	-1.26 (4)
	irrigated	-1.44 (3)	-1.45 (3)
	stressed	-2.15 (3)	-1.52 (4)
	stressed	-2.29 (3)	-1.68 (3)
x ± se		-1.31 ± 0.25	-1.20 ± 0.21

figures in parenthesis are the number of values meaned to give the reading

paired t-test

$$t = \frac{\bar{D}}{S_{\bar{D}}} = \frac{0.106}{0.101} = 1.051 \text{ ns for 8 d.f.}$$

where D = difference

Appendix 6. Determination of night and day leaf extension rates between days 49 and 53.

Ten elongating leaves, marked on separate tillers in each of four plots from the two water treatments, were measured at early morning and late evening for four days between days 49 and 53. The rates of leaf extension (mm/leaf/hour) for the day and night were calculated as the net change in length divided by the period of growth, and are presented in the following table.

Treatment	Plot	LEAF EXTENSION RATE (mm/leaf/hour)							
		day				night			
irrigated	1	0.565	0.536	0.546	0.580	0.535	0.523	0.516	0.527
	2	0.52	0.51	0.54	0.54	0.48	0.33	0.42	0.42
	3	0.481	0.529	0.413	0.431	0.334	0.367	0.399	0.311
	4	0.417	0.433	0.370	0.451	0.343	0.338	0.308	0.384
$\bar{x}$ ± se		0.491 ± 0.016				0.408 ± 0.021			
stressed	1	0.42	0.35	0.33	0.39	0.24	0.22	0.27	0.27
	2	0.110	0.123	0.138	0.211	0.152	0.128	0.238	0.178
	3	0.140	0.126	0.183	0.212	0.185	0.115	0.222	0.241
	4	0.171	0.148	0.197	0.241	0.087	0.183	0.254	0.179
$\bar{x}$ ± se		0.218 ± 0.025				0.198 ± 0.014			

Appendix 7. Leaf morphology

day of measurement period	mean leaf width (mm)		specific leaf area (cm^2/g)		leaf area index	
	stressed	irrigated	stressed	irrigated	stressed	irrigated
1	1.4	1.5	262	278	-	-
8	1.6	1.4	236	200	-	-
15	1.4	1.4	188	183	-	-
22	1.4	1.5	187	187	-	-
29	1.4	1.4	163	183	-	-
35	1.0	1.5	139	198	-	-
43	1.0	1.1	118	147	-	-
50	1.0	1.2	112	162	1.54	2.85
57	1.0	1.3	115	199	2.07	4.02
64	1.0	1.2	105	191	2.28	4.17
70	0.5	1.1	86	204	0.90	1.18
78	0.9	1.2	116	212	1.72	2.42
85	0.8	1.3	115	219	1.67	3.35
92	0.8	1.1	121	183	1.62	2.98
99	0.7	1.1	110	198	1.47	3.18
107	0.5	1.0	70	143	0.49	1.27

REFERENCES

Acevedo, E.; Hsiao, T.C. and Henderson, D.W. (1971). Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiol. 48: 631-636.

Anslow, R.C. (1966). The rate of appearance of leaves on tillers of the graminae. Herbage Abstracts 36: (3) 149-155.

Appadurai, R.R. and Holmes, W. (1964). The influence of stage of growth, closeness of defoliation, and moisture on the growth and productivity of a ryegrass-white clover sward I. Effect on herbage yields. J. Agric. Sci. 62: 327-332.

Baars, J.A. and Coulter, J.D. (1974). Soil moisture and its influence on pasture production in the Waikato. Proc. N.Z. Grassl. Assoc. 35: 197-203.

Baker, B.S. and Jung, G.A. (1968). Effect of environmental conditions on the growth of four perennial grasses II. Response to fertility, water and temperature. Agron. J. 60: 158-162.

Barlow, E.W.R.; Boersma, L. and Young, J.L. (1976). Root temperature and soil water potential effects on the growth and soluble carbohydrates of corn seedlings. Crop Science 16: 59-62.

Bircham, J.S. (1981). The effects of a change in herbage mass on herbage growth, senescence and net production rates in a continuously stocked mixed species sward. Occasional symposium number 13, British Grassl. Soc. pg 85-87.

Bommer, D.F.R. (1966). The influence of cutting frequency and nitrogen level on the carbohydrate reserves of three grass species. Proc. of the X Int. Grassl. Cong., Helsinki. 156-160.

Boyer, J.S. (1967). Leaf water potentials measured with a pressure chamber. Plant Physiol. 42: 133-137.

Boyer, J.S. (1968). Relationship of water potential to growth of leaves. Plant Physiol. 43: 1056-1062.

Boyer, J.S. (1969). Measurement of the water status of plants. Ann. Rev. Plant Physiol. 20: 351-364.

Boyer, J.S. (1970). Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. Plant Physiol. 46: 233-235.

Boyer, J.S. and McPherson, H.G. (1975). The physiology of water deficits in cereal crops. Adv. in Agron. 27: 1-23.

Branson, F.A. (1953). Two new factors affecting resistance of grasses to grazing. J. Range Management 6: 165-171.

Brougham, R.W. (1959). The effects of frequency and intensity of grazing on the productivity of a pasture of short-rotation ryegrass and red and white clover. N.Z. J. Ag. Res. 2: 1232-1248.

Brougham, R.W. (1960). The effects of frequent hard grazings at different times of the year on the productivity and species yields of a grass-clover pasture. N.Z. J. Agric. Res. 3: 125-136.

Brougham, R.W. (1970). Frequency and intensity of grazing and their effects on pasture production. Proc. N.Z. Grassl. Assoc. 32: 137-144.

Brown, K.W. (1974). Calculations of evapotranspiration from crop surface temperature. Agric. Meteorol. 14: 199-209.

Brown, R.H. and Blaser, R.E. (1970). Soil moisture and temperature effects on growth and soluble carbohydrates of Orchard grass (Dactylis glomerata). Crop Sci. 10(3): 213-216.

Chu, A.C.P. (1979). Aspects of water deficit and vegetative growth in selected pasture and forage grasses. Ph.D thesis, Massey University.

Chu, A.C.P. and Kerr, J.P. (1977). Leaf water potential and leaf extension in a sudan crop. N.Z. J. Agric. Res. 20: 467.

Chu, A.C.P. and McPherson, H.G. (1977). Sensitivity to desiccation of leaf extension in prairie grass. Aust. J. Plant Physiol. 4: 381-387.

Cleland, R. (1971). Cell wall extension. Ann. Rev. Pl. Physiol. 22: 197-222.

Clothier, B.E. (1977). Aspects of the water balance of an oats crop grown on a layered soil. Ph.D Thesis, Massey University.

Colman, R.L. and Lazenby, A. (1975). Effect of moisture on growth and nitrogen response by Lolium perenne. Plant and Soil 42: 1-13.

Cowie, J.D. (1978). "Soils and Agriculture of Kairanga County, North Island, New Zealand". Soil Bureau Bull. No. 33 (DSIR: Wellington).

Cowie, J.D., Kear, B.S. and Orbell, G.E. (1972). Soil Map of Kairanga County, North Island, New Zealand. Scale 1:63 360. New Zealand Soil Bureau Map 102.

Dainty, J. (1976). Water relations of plant cells. in Encl. of Plant Phys. New Senes Vol 2 eds. Luttge and Pitman pg 12-35.

Davidson, R.L. (1978). Root systems - the forgotten component of pastures in "Plant relations in pastures" pg 86-94, J.R. Wilson. CSIRO publ. CSIRO Australia. 425 p.

De Roo, H.C. (1969). Leaf water potentials of sorghum and corn estimated with the pressure bomb. Agron. J. 61: 969-970.

Draper, N.R. and Smith, H. (1981). "Applied Regression Analysis, Second edition". Wiley-Interscience 709 p.

Dougherty, C.T. (1973). Observations on dew and the water relations of wheat. N.Z. J. Ag. Res. 16: 493-496.

Eisenhart, C. (1947). The assumptions underlying the analysis of variance. Biometrics 3: 1-21.

Evans, P.S. (1976). Root distribution and water withdrawal patterns of some crops and pasture species. Proc. of Soil and Plant Water Symp. Palmerston North 25-27 May 1976: 186-190.

Fellows, R.J. and Boyer, J.S. (1978). Altered ultrastructure of cells of sunflower leaves having low water potentials. Protoplasma 93: 381-395.

Gardner, W.R. and Nieman, R.H. (1964). Lower limit of water availability to plants. Science 143: 1460-1462.

Gates, K. (1979). Effects of water supply on partitioning of dry matter between roots and shoots in *Lolium perenne* L. Journal of Appl. Ecol. 16: 863-877.

Goode, J.E. and Hegarty, T.W. (1965). Measurement of water potential of leaves by methods involving immersion in sucrose solutions. Nature 206: 109-110.

Gordon, I.L. (1979). Standard errors of heritabilities based on perennial observations, with application to Yorkshire Fog Grass. Euphytica 28: 81-88.

Gordon, I.L.; Byth, D.E. and Balaam, L.N. (1972). Variance of heritability ratios estimated from phenotypic variance components. Biometrics 28: 401-415.

Gradwell, M.W. (1971). The available-water capacities of North Auckland soils. N.Z. J. Ag. Res. 14: 253-287.

Gradwell, M.W. (1974). The available-water capacities of some southern and central zonal soils of New Zealand. N.Z. J. Ag. Res. 17: 465-478.

Green, A. (1980). "Rainout shelter Manual". unpublished. Plant Physiology Division, DSIR, Palmerston North, New Zealand.

Horst, G.L. and Nelson, C.J. (1979). Compensatory growth of tall fescue following drought. Agron. Journal 71: 559-563.

Howell, T.A.; Hiler, E.A. and van Bavel, C.H.M. (1971). Crop response to mist irrigation. Trans. of the Am. Soc. Ag. Eng. 14: 906-910.

Hsiao, T.C. (1973). Plant responses to water stress. Ann. Rev. Pl. Phys. 24: 519-570.

Hsiao, T.C. and Acevedo, E. (1974). Plant responses to water deficits, water use efficiency and drought resistance. Agric. Meteorol. 14: 59-84.

Hunt, L.A. and Brougham, R.W. (1967). Some changes in the structure of a perennial ryegrass sward frequently but leniently defoliated during the summer. N.Z. J. Agric. Res. 10: 397-404.

Husain, I. and Aspinal, D. (1970). Water stress and apical morphogenesis in barley. Anal. Bot. 34: 393-407.

Jackson, D.K. (1974(a)). The course and magnitude of water stress in Lolium perenne and Dactylis glomerata. J. Agric. Sci., Camb. 82: 19-27.

Jackson, D.K. (1974(b)). Some aspects of production and persistency in relation to height of defoliation of Lolium perenne (var. S.23). 12th Int. Grassl. Cong. 3). Pasture utilization: 202-214.

Jantti, A. and Kramer, P.J. (1956). Regrowth of pastures in relation to soil moisture and defoliation. Proc. 7th Int. Grassl. Cong. pg 33-44.

Jantti, A. and Heinonen, R. (1957). Effect of defoliation and soil moisture on grassland regrowth. J. Brit. Grassl. Soc. 12: 56-61.

Jewiss, O.R. (1972). Tillering in grasses - its significance and control. J. Br. Grassl. Soc. 27: 65-82.

Johns, G.G. (1978). Transpirational, leaf area, stomatal and photosynthetic responses to gradually induced water stress in four temperate herbage species. Aust. J. Plant Physiol. 5: 113-125.

Jones, M.B.; Collet, B. and Brown, S. (1982). Sward growth under cutting and continuous stocking managements - sward canopy structure, tiller density and leaf turnover. Grass and Forage Sci. 37(1): 67-73.

Jones, M.B.; Leafe, E.L. and Stiles, W. (1980(a)). Water stress in field-grown perennial ryegrass. I. Its effect on growth, canopy photosynthesis and transpiration. Ann. Appl. Biol. 96: 87-101.

Jones, M.B.; Leafe, E.L. and Stiles, W. (1980(b)). Water stress in field-grown perennial ryegrass. II. Its effect on leaf water status, stomatal resistance and leaf morphology. Ann. Appl. Biol. 96: 103-110.

Jones, M.M.; Turner, N.C. and Osmond, C.B. (1981). Mechanisms of drought resistance. in "Physiology and Biochemistry of Drought Resistance". pg 15-37. eds. Paleg, L.G. and Aspinal, D. Publ. Academic Press. 485 p.

Kerr, J.P. and Beardsell, M.F. (1975). Effect of dew on leaf water potentials and crop resistances in a paspalum pasture. Agron. J. 67: 596-599.

Kirkham, M.B.; Gardner, W.R. and Gerloff, G.C. (1972). Regulation of cell division and cell enlargement by turgor pressure. Pl. Physiol. 49: 961-962.

Kleindorst, A. and Brouwer, R. (1970). The effect of temperature of the root medium and of the growing point of the shoot on growth, water content and sugar content of maize leaves. Neth. J. Agric. Sci. 18: 140-148.

Korte, C.J. (1981). Studies of late spring grazing management in perennial ryegrass dominant pasture. Ph.D thesis. Massey University.

Korte, C.J. and Chu, A.C.P. (1983). Some effects of drought on perennial ryegrass swards. Proc. N.Z. Grassl. Assoc. 44: 211-216.

Langer, R.H.M. (1963). Tillering in herbage grasses. Herbage Abstracts 33: 141-148.

Langer, R.H.M. (1977). "Pastures and pasture plants". Reed, Wellington. 430 p.

Lawlor, D.W. (1969). Plant growth in polyethylene glycol solutions in relation to the osmotic potential of the root medium and the leaf water balance. J. Exp. Bot. 20: 895-911.

Leafe, E.L.; Jones, M.M. and Stiles, W. (1977). The physiological effects of water stress on perennial ryegrass in the field. Proc. XIII Int. Grassl. Congr. Leipzig pg 253-260.

Le Clerg, E.L.; Leonard, W.H. and Clark, A.G. (1962). "Field Plot Technique" second edition Burgess Publishing Co. 286 p.

Levitt, J. (1972). Responses of plants to environmental stresses. publ. Academic Press, New York. 697 p.

Ludlow, M.M.; Chu, A.C.P.; Clements, R.J. and Kerslake, R.G. (1983). Adaptation of species of <u>Centrosema</u> to water stress. Aust. J. Plant Physiol. (in press).

Luxmoore, R.J. and Millington, R.S. (1971). 'Growth of perennial ryegrass (<u>Lolium</u> <u>perenne</u> L.) in relation to water, nitrogen and light intensity I) effects on leaf growth and dry weight. Plant and Soil <u>34</u>: 269-281.

Meyer, R.F. and Boyer, J.S. (1972). Sensitivity of cell division and cell elongation to low water potentials in soybean hypocotyls. Planta (Berl.) <u>108</u>: 77-87.

McAneney, K.J.; Judd, M.J. and Weeda, W.C. (1982). Loss in monthly pasture production resulting from dryland conditions in the Waikato. N.Z. J. Ag. Res. <u>25</u>: 151-156.

McCree, K.J. (1974). Changes in the stomatal response characteristics of grain sorghum produced by water stress during growth. Crop Sci. <u>14</u>: 273-278.

Mitchell, K.J. and Glenday, A.C. (1958). The tiller population of pastures. N.Z. J. Ag. Res. <u>1</u>: 305-318.

Nelson, C.J. and Zarrough, K.M. (1981). Tiller density and tiller weight as yield determinants of vegetative swards. Occasional Symposium Number 13, British Grassland Society. pg 25-29.

New Zealand Official Year Book (1982): 1032 p. Government Printer, Wellington.

Nie, N.H.; Hull, C.H.; Jenkins, J.G.; Steinbrenner, K. and Bert, D.M. (1975). "SPSS: Statistical package for the social sciences", second edition. New York, McGraw-Hill. 675 p.

Norris, I.B. (1982). Soil moisture and growth of contrasting varieties of <u>Lolium</u>, <u>Dactylis</u> and <u>Festuca</u> species. Grass and Forage Science <u>37</u>: 273-283.

Norris, I.B. and Thomas, H. (1982). Recovery of ryegrass species from drought. J. Agric. Sci., Camb. 98: 623-628.

Penman, H.L. (1962). Woburn irrigation, 1951-59 II. Results for grass. J. Agric. Sci. 58: 349-364.

Philip, J.R. (1966). Plant water relations: Some physical aspects. Ann. Rev. Pl. Phys. 17: 245-268.

Pollock, J.A. (1975). A comparative study of certain New Zealand and German soils formed from loess. Ph.D Thesis. Fredrich-Wilhelms-Universitat, Bonn.

Radcliffe, J. (1979). Variations in grassland production. Symposium on the value of meteorology in economic planning. 9-10 October 1979. pg 79-97. N.Z. Met. Service.

Raschke, K. (1975). Stomatal action. Ann. Rev. Pl. Physiol. 26: 309-340.

Rawlins, S.L. (1973). Principles of managing high frequency irrigation. Proc. Soil Sci. Soc. of America 37: 626-629.

Rawlins, S.L. and Raats, P.A.C. (1975). Prospects for high frequency irrigation. Science 188: 604-610.

Rickard, D.S. (1960). The occurrence of agricultural drought at Ashburton, New Zealand. N.Z. J. Agric. Res. 3: 431-441.

Rickard, D.S. and Fitzgerald, P.D. (1970). The effect of soil moisture and irrigation on pasture production in Canterbury, New Zealand. Proc. XI Int. Grassl. Cong. pg 487-492.

Ritchie, J.T. (1974). Atmospheric and soil water influences on the plant water balance. Agric. Meteorol. 14: 183-198.

Rose, C.W. (1966). "Agricultural Physics" publ. Pergamon Press Ltd. 226 p.

Ryan, T.A.; Joiner, B.L. and Ryan, B.F. (1981). "Minitab Reference Manual". Penn. State Univ.

Salinger, M.J. (1979). Agricultural implications of climate change in New Zealand. Symposium on the value of meteorology in economic planning. 9-10 October 1979. pg 63-78. N.Z. Met. Service.

Salter, P.J. and Goode, J.E. (1967). "Crop responses to water at different stages of growth." Commonw. Agr. Bur., Farnham Royal. 246 p.

Scholander, P.F.; Hammel, H.T.; Hemmingsen, E.A. and Bradstreet, E.D. (1964). Hydrostatic pressure and osmotic potential in leaves of mangroves and some other plants. Proc. Natl. Acad. Sci. USA 52: 119-125.

Scholander, P.F.; Hammel, H.T.; Bradstreet, E.D. and Hemmingsen, E.A. (1965a). Sap pressure in vascular plants, negative hydrostatic pressure can be measured in plants. Science 148: 339-346.

Scholander, P.F.; Hammel, H.T.; Bradstreet, E.D. and Hemmingsen, E.A. (1965b). Sap pressure in vascular plants (letter to the editor). Science 149: 920-922.

Scotter, D.R.; Clothier, B.E. and Corker, R.B. (1979). Soil water in a fragiaqualf. Aust. J. Soil Res. 17: 443-453.

Scotter, D.R.; Clothier, B.E. and Turner, M.A. (1979). The soil water balance in a fragiaqualf and its effect on pasture growth in Central New Zealand. Aust. J. Soil Res. 17: 455-465.

Sepaskhah, A.R. and Boersma, L. (1979). Shoot and root growth of wheat seedlings exposed to several levels of matric potential and NaCl-induced osmotic potential of soil water. Agron. J. 71: 746-752.

Silsbury, J.H. (1970). Leaf growth in pasture grasses. Trop. Grassl. 4(1): 17-36.

Sivakumar, M.V.K. and Virmani, S.M. (1979). Measuring leaf water potential in chickpea with a pressure chamber. Exp. Agric. 15: 377-383.

Slatyer, R.O. (1969). Physiological significance of internal water relations to crop yield. in "Physiological Aspects of Crop Yield" pg 53-83. Eds. J.D. Easton, F.A. Haskins, C.Y. Sullivans, C.M.M. van Bavel (Am. Soc. of Agron., Madison, Wis. 1969).

Stiles, W. and Williams, T.E. (1965). The response of a ryegrass/white clover sward to various irrigation regimes. J. Agric. Sci. (Camb.) 65: 351-364.

Steele, R.G.D. and Torrie, J.H. (1980). "Principles and Procedures of Statistics - a Biometrical Approach" second edition. publ. McGraw-Hill, Kogakusha. 633 p.

Stocker, O. (1960). Physiological and morphological changes in plants due to water deficiency. in "Plant-water relationships in arid and semi-arid conditions XV Reviews of Research" UNESCO pg 63-104.

Tanner, C.B. and Ritchie, J.T. (1974). Evapotranspiration empiricisms and modelling. Am. Soc. of Agron. Abstr. p 15.

Thomas, H. (1980). Terminology and definitions in studies of grassland plants. Grass and Forage Sci. 35: 13-23.

Turner, N.C. and Begg, J.E. (1974). Adaptation to water stress in crops of sorghum and sunflower - physiological mechanisms. Annual Report, Division of Plant Industry, CSIRO. pg 102.

Turner, N.C. and Begg, J.E. (1978). Responses of pasture plants to water deficits in "Plant Relations in Pastures" pg 50-66. ed Wilson, J.R. publ. CSIRO. 425 p.

Turner, N.C. and Begg, J.E. (1981). Plant-water relations and adaptation to stress. Plant and Soil 58: 97-131.

Warren-Wilson, J. (1967). The components of leaf water potential I. Osmotic and Matric potentials. Aust. J. Biol. Sci. 20: 329-347.

Watts, W.R. (1974). Leaf extension in Zea mays III. Measurement of leaf extension in response to temperature and leaf water potential. J. Exp. Bot. 25: 1085-1096.

Weatherly, P.E. (1970). Some aspects of water relations. Adv. in Bot. Res. 3: 171-206.

Weinmann, H. (1948). Underground development and reserves of grasses - A review. J. Br. Grassl. Soc. 3: 115-140.

Woolley, J.T. (1973). Change of leaf dimensions and air volume with change in water content. Pl. Physiol. 41: 815-816.

Zelitch, I. (1969). Stomatal control. Ann. Rev. Pl. Phys. 20: 329-350.