THE EFFECTS OF DROUGHT ON THE GROWTH AND WATER BALANCE OF *LOLIUM PERENNE* AND *DACTYLIS GLOMERATA*

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1971

A Thesis presented for the Diploma of
Membership of Imperial College

ABSTRACT

Simulated swards of Dactylis glomerata and Lolium perenne were grown in containers of sufficient depth to permit largely unrestricted root development.

Flowering and non-flowering plants, subjected to cut and uncut treatments, were allowed to dry the profile and were compared with watered controls. The effects of a drying cycle on the growth, water balance and nutrient uptake were measured.

The rate of dry weight increase was reduced by drought from an early stage. The cause appeared to be reduced leaf expansion rather than a decline in net assimilation rate. Root weight was particularly affected due to suppressed elongation of new adventitious roots. There was some compensatory growth at depth. Defoliation severely retarded root growth.

Leaf water potential fell during the day in treatments and controls to levels which would be expected to affect growth processes.

Defoliation reduced water stress and stomatal closure but not drought susceptibility.

There was little relationship between leaf water potential and stomatal diffusion.

Dactylis initiated water economy measures at a lower soil water deficit than Lolium, possibly because of a less vigorously extending root system. It was more sensitive to increasing deficit in terms of leaf water potential, relative turgidity and stomatal diffusion rate and so did not manifest the early abrupt exhaustion of water supplies typical of Lolium.

Root density was adequate to allow current water requirements to be met from a small volume of wet soil. The effect of drying of a horizon was to shift the main uptake zone downwards, with no corresponding fall in leaf water potential.

Calculated mean soil water potential was most closely related to soil water potential in the few zones of maximum uptake.

Resistance to the movement of water from the soil to the roots was $10^2 - 10^4$ times smaller than resistance to movement through the plant i.e. a major source of water stress lay within the plant itself.

No evidence was found that droughted swards ceased growth due to N shortage. Reduced P uptake was detected.

ACKNOWLEDGEMENTS

My thanks are due to Professor A.J. Rutter for his constant help and advice during the course of this work which was carried out with the support of a Scholarship from the Ministry of Agriculture, Fisheries and Food. Dr. P. C. Robins kindly loaned the diffusion porometer and the pressure apparatus was based on his design.

I also thank my Wife, Nonie, who has freely given her help with both the technical work and typing of this thesis. Her tolerance and encouragement have done much to make its production possible.

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INTRODUCTION

WATER UPTAKE BY THE PLANT

The state of water in the plant will be described in this thesis in terms of potential, defined as the work that must be done to transport unit quantity of water from the energy level of a pure, free water surface to a point in the plant/water system whose potential is to be described. If unit quantity is taken as being unit volume, then the potential can be measured in units of pressure; and in most instances in the plant, this potential is negative.

Taking, initially, a non-transpiring plant in equilibrium with the soil at a uniform potential throughout, let us assume that evaporation occurs from the leaves, thereby causing a drop in leaf potential. This drop in potential sets up a gradient between the soil and the leaf along which water moves. This movement persists as long as evaporation continues.

Much theoretical work has been based upon the assumption represented by the equation of Van den Honert (1948), that the flux is proportional to the potential gradient and inversely proportional to the resistance of the pathway, providing the plant water content remains constant .

$$Q = \frac{\Psi_s - \Psi_r}{Rs} = \frac{\Psi_r - \Psi_L}{Rp} = \frac{\Psi_L - \Psi_a}{Rt} \quad \text{(1)*}$$

Q = rate of water flow through the plant
Ψ_s = soil potential
Ψ_r = root surface potential
Ψ_L = leaf water potential
Ψ_a = bulk air potential
Rs = soil resistance
Rp = plant resistance
Rt = transpiration pathway resistance

* This equation assumes that the soil solute potential is negligible.

Since the potential gradients normally found in the transpiration pathway are much larger than those found between the leaf and the soil, it follows that herein lie the main determinants of flux through the soil/plant atmosphere system (Cowan, 1965).

Thus the flux automatically adjusts to equal the evaporation rate by a change in the potential gradient between leaf and soil i.e. by a fall in leaf water potential until the limiting conditions of wilting are reached. The potential gradient necessary to maintain flux equal to the transpiration rate depends on the resistance of the soil and plant.

Thus leaf water potential is determined by the transpiration rate, by the water potential in the soil, and by the resistances to water movement between soil and leaf.

Van den Honert (1948) distinguished two separate sources of resistance in the liquid pathway, those of the plant and of the soil. This distinction remains, but the soil resistance has recently been further sub-divided into rhizosphere and pararhizal resistances. The former is situated in the zone of soil immediately surrounding and between the roots, while the latter is encountered when water moves into the rooting zone from, for example, a water table or soil horizon beneath the roots. This definition conforms to the terminology of Newman (1969a).

These three resistances will be further examined.

1. Soil Resistance and the Movement of Water to the Root

a) Rhizosphere Resistance

The potential at the root surface must be less than that in the soil at all times if there is water movement to the roots. In order to determine the difference between these two potentials under specified conditions, Gardner (1960) solved the flow equation in the soil to give

$$\Psi_s - \Psi_r = \Delta\Psi = \frac{q}{4\pi k} \ln \left(\frac{b}{r}\right)^2 \quad \text{(2)*}$$

Where:-

q is uptake rate per unit root length

k is capillary conductivity of the soil appropriate to the geometric mean of Ψ_r and Ψ_s

b is half the average distance between roots

r is the average root radius

* The components of the equation $\frac{1}{4} \ln\left(\frac{b^2}{r^2}\right)$ used by Gardner (1960) to describe the geometry of the system are the subject of an effectively similar, but more complex expression derived by Cowan (1965).

The potential difference between the root surface and the bulk soil, $\Delta\Psi$, is mainly a function of q and k while the logarithmic term is of smaller significance.

The uptake rate, q, varies during the day as transpiration rises and falls.

The capillary conductivity of the soil, k, declines continuously as the soil dries.

Thus $\Delta\Psi$ can be represented as a sinusoidal curve reflecting the diurnal fluctuations of q about an ever rising mean as the soil dries and k decreases.

The value q is itself a compound factor of transpiration rate and total root length. Gardner (1960) attributed a value of 0.1cm ^{3} cm $^{-1}$ day^{-1} to q when he calculated that Ψ_r appreciably exceeded Ψ_s when Ψ_s reached "a few bars" and became very large at -15 bars. Cowan (1965) also used a similar value of q.

The distance over which water is drawn through the soil to the root increases as the square root of time, and to move more than a few centimetres would take an impossibly long time (Gardner, 1960).

Thus the value given to root density is of importance in determining $\Delta\Psi$, operating through both q and b in equation(2).

Gardner (1960) implied that the main resistance to water movement in the gradient from soil to leaf occurred in the soil, and this view has been held by other workers as follows.

Cowan (1965) calculated that the gradients of moisture and potential are of some magnitude and that little indication of the state of water at the root surface can be obtained by the measurement of that in the bulk soil.

Etherington (1967) found growth to be depressed by relatively small decreases of soil water potential, and speculated whether a high resistance to water movement in the soil under conditions of high transpiration might be as important as low soil water potential in limiting carbon assimilation by stomatal closure, though with little direct evidence for this possibility.

Slatyer (1967) also considered that as Ψ_s and hence k fall, the value of $\Delta\Psi$ needed to maintain water flow increases rapidly and may cause critical values of Ψ_r to develop, even when the soil mass is moist.

Macklon and Weatherley (1965) compared the leaf water potentials of plants growing in water, osmoticum and soil. Ψ_L was little affected as transpiration rate increased in water.

It fell with falling potential of an osmoticum, but was still little affected by changes in transpiration rate. In soil, however, Ψ_L fell rapidly with transpiration rate. They interpreted this as an indication that the source of the fall in leaf water potential lay in the soil, and not in the root or other tissues of the plant.

Sykes and Loomis (1967) compared the potential at permanent wilting point of two soils with differing conductivities. The soil with the higher conductivity was found to be at a lower potential at permanent wilting point, so suggesting that soil resistance was appreciable at these potentials of -7 to -40 bars.

The evidence for a high value of $\Delta\Psi$ has recently been critically reviewed by Newman (1969a, 1969b). He found most previous work to be invalid, in many cases because a pararhizal and not a rhizosphere resistance was involved. He showed that this former resistance could often be large, even at high soil water potentials, and doubted whether high values of rhizosphere resistance, calculated or inferred, often occurred in practice.

His view is supported by Andrews and Newman (1968,1969) who severed a portion of wheat root systems and failed to find any increased sensitivity to drought.

Newman's argument is that Gardner and Cowan were led to the conclusion that rhizosphere resistance was appreciable by the use of values of q in their calculations which were much larger than those found in practice.

It has already been mentioned that q is the quotient of transpiration rate divided by total root length, and it is inaccuracies in the measurement of the latter which have given rise to a gross overestimation of q. Gardner (1960) based his work on the data of root length of Ogata, Richards and Gardner (1960) who, by their own admission, measured only a small fraction of the roots present.

The value for q of $0.1 cm^3\ cm^{-1}\ day^{-1}$ is derived from a root density (LA) of less than 10cm of root beneath one square centimetre of ground. Newman (1969a) points out that this is very rare in practice and occurs only in a few woody plants. In most cases, LA is between one and two orders of magnitude higher. He shows that Rs would not become appreciable (defined as when $Rs > Rp$) until near or beyond the permanent wilting percentage at root densities normally found in herbaceous field plants, and only rarely in some woody plants of exceptionally low rooting density.

Jarvis and Jarvis(1963) detected larger differences between Ψ_L and Ψ_S at the point of stomatal closure in conifers compared with broad leaved trees, and attributed this to lower rooting densities.

Consequently, doubt has been cast on the belief that the soil resistance is the major one on the uptake pathway as the soil dries. Unfortunately, it is not possible at present to measure ψ_r directly and so confirm this. It should be noted that this conclusion is based on the assumption that water uptake is fairly uniform throughout the root system. This might be a false assumption, either if uptake were confined to the root tip zone, thus reducing the effective root length, or if the topsoil were too dry to allow uptake of appreciable amounts of water. In this situation, uptake by sparser, deep roots might give rise to appreciable soil resistances.

b) Pararhizal Resistance

Newman (1969a) examines the contrasting geometry of water movement in rhizosphere and pararhizal zones and considers that even in soil not much drier than field capacity, the pararhizal resistance could be significant, even over quite short distances.

The reasons for this are twofold. Water movement in the rhizosphere is convergent and the further it comes from, the lower the resistance with distance from the root. There is little or no convergence along a pararhizal gradient and the resistance is constant throughout, excepting changes in k.

Additionally, the drop in potential along a pararhizal gradient is proportional to the length of this gradient (Darcy's Law) which is usually many times greater than the length of a rhizosphere gradient in which the distance occurs as b in equation (2).

Newman (1969b) shows that this pararhizal resistance has often been confused with a rhizosphere resistance.

Macklon et al. (1965) and Tinklin et al. (1968) found a large drop in potential between the bulk soil and the plants which they attributed to a high perirhizal (rhizosphere) resistance, which Tinklin et al. (1968) considered to give rise to most of the ecologically important water stress in plants. Newman (1969b) points out that they were in fact measuring a pararhizal resistance, and that most of the potential drop occurred between the bulk soil and the rooting zone, which were separated in the various experiments by a few, up to many centimetres.

The importance of this pararhizal type of water movement has been widely confirmed.

Long and French (1964) used a neutron meter to sample soil water content to 90cm depth during the course of a day's transpiration

by barley. Water was found to be abstracted from the main root zone during the day and this was followed by movement of water from below the rooting zone to replace that lost in transpiration.

Wind (1955a) calculated that 3-4mm water per day rose by capillarity into the root zone in a heavy clay soil.

On balance, the evidence, therefore, suggests that the importance of rhizosphere resistance has been over-estimated in circumstances in which water uptake can take place through most of a root system of normal length. On the other hand, pararhizal resistances may often be appreciable where water moves towards a rooting zone over a relatively large distance, even in wet soil.

2. Plant Resistance and the Movement of Water Through the Plant

The movement of water through the plant has not so far been exposed to precise mathematical description, as has that in the soil.

It is well substantiated that the major resistance lies in the roots, while the stem offers relatively little impedance to water movement.

Tinklin and Weatherley (1966) imposed a high transpiration rate on plants rooted in soil in a wind tunnel, and measured the depression of leaf water potential. They then excised the leaves and immersed their petioles in water. Under the same evaporative conditions, their potential did not fall below the base level representing water saturation. The main resistance was similarly shown to lie below the stem.

Kramer (1938) measured uptake rates through the roots under a vacuum applied to the cut stems. There was a large rise in uptake when the roots were cut off. Uptake rates were depressed by cooling the roots, followed by a large rise when the roots were severed. The stem was found to offer little resistance compared with the roots.

Wind (1955b) related uptake rates to xylem vessel radius and calculated that when transpiration rate was 1mm per day, most of the water being used from below 10cm moved upwards in the soil since the roots offered a greater resistance. As transpiration rate increased, the depth from which water moved upwards through the root in preference to the soil increased. Above this critical depth, the denser rooting habit offered less resistance than the soil.

Jensen, Taylor and Wiebe (1961) investigated water movement through the plant by applying differential pressures to the roots and tops. They found that the roots offered the greatest resistance and speculated that this was caused by the barrier imposed by the suberised endodermis.

Slatyer (1967) considers that the Casparian strip renders the cell walls impermeable to water, making passage through the protoplasm of the endodermis necessary for water to enter the vascular tissue. He points out that the evidence for this theory is corroborated by the similarity between the permeability per unit area of roots and of single cells.

Popislova (1969) measured the variation in water saturation deficit between the margin and the centre of the large laminae of cabbage and banana and found a considerable gradient. This enabled her to estimate the resistance of the leaf to water movement and calculate a high value which she concluded was responsible for the water stress in the leaf.

The change in soil resistance with water content can readily be calculated from capillary conductivity data, but the behaviour of plant resistance has not yet been established with certainty.

Cowan (1965) and Gardner and Ehlig (1962) assumed, in the absence of evidence to the contrary, that plant resistance remained constant over relatively short periods of the growth cycle. Newman (1969b) interprets the data as showing that plant resistance rose as water potential fell, and this is confirmed by Poposlova (1969) who calculated the resistance of leaves at a range of water saturation deficits and found the calculated value to rise proportionately with the leaf suction.

Evidence to the contrary is provided by Tinklin and Weatherley (1966) who tried to establish a relationship between transpiration rate and leaf suction in water culture. After rising steadily during the initial increases of transpiration, leaf suction then remained constant in spite of further increases in transpiration rate. They could only conclude that Rp was falling proportionately as uptake increased, so maintaining plant suction constant. The only explanation coming to mind is that the operative amount of the root system increased with further rises in transpiration rate, so lowering plant resistance. Such a response in the root system has been reported by Brewig (1936) and Brouwer (1965).

Andrews et al. (1968) also suggested a declining plant resistance to be a possible explanation for the lack of increased sensitivity

to drought of wheat plants with partially severed root systems.

It is not difficult to make an approximate guess as to the magnitude of Rp. Cowan noted that plants wilted in moist soil at a transpiration rate of 30cm day^{-1} when the leaf potential might be expected to be -15 bars (-15×10^3cm). This leads to a calculated value of Rp of 5 bar days cm^{-1} or 5×10^3 days. Newman (1969a) calculates values of a similar magnitude from other data sources.

Both Gardner and Cowan have assumed constant values of Rp which are relatively low compared with Rs when constructing their models of water uptake.

Gardner et al.(1962) claim to show that Rp is less than Rs, even at soil potentials as high as -0.1 bars. Newman (1969b) comments on this experiment and purports to show that the interpretation is incorrect since they neglected a probably appreciable vertical movement of water in the soil.

Ehlig, Gardner and Clark (1968) performed a similar experiment to Gardner et al. (1962), which when analysed by Newman's approach, suggests that Rs did not exceed Rp until Ψ_s was of the order of -10 bars.

Newman (1969a) calculated that for Rs to exceed Rp when total root length exceeded 100cm cm^{-2} ground area, Ψ_s would have to be less than -25 bars.

Thus the possibility arises that the resistance of the plant may be the major resistance influencing the movement of water to the transpiring surfaces at soil potentials above the wilting point.

THE EFFECT OF LEAF WATER POTENTIAL ON GROWTH PROCESSES

Perhaps the most neglected area in the field of plant/water relationships is the investigation of the effects of leaf water potential on plant growth. The existence of such effects is widely acknowledged. "Because of the complexities of such detailed studies, very little progress has been made to date" (Gates,1968)

Much of the difficulty in studying this subject revolves round the fact that so many separate processes, each with its own controls, are involved in the overall phenomenon of growth, and the difficulty occurs in trying to isolate each individual process for investigation.

Lawlor (1969) demonstrated the effects of falling water potential on growth parameters. He grew four species of plant in polyethylene glycol osmotica for two weeks and measured extension growth, dry weight gain, leaf area, net assimilation rate, relative growth rate and relative leaf growth rate. It should be noted that the plants were subjected to the stress suddenly and Janes (1966) suggests that this makes the effects more drastic than if the onset is gradual, as in natural conditions. In addition, the osmoticum was found to enter the plant via damaged roots, with deleterious effects. Osmotic potentials from -1.1 bars to -8.0 bars were found to reduce all growth parameters, and growth had ceased in all species except Lolium at a potential of -10 bars. A subsequent increase in growth parameters in the second week suggests that the plants were able to adapt to the lowered potential, given time, and that the effects were exaggerated by the sudden imposition of the stress.

It is difficult, however, to draw any definite conclusions from this type of experiment as to the precise mechanisms being implicated in the reduced growth. These can be conveniently divided into the direct effects of water potential on growth processes and the indirect effects via restricted carbon dioxide supply through stomatal closure, and they will be considered under these two headings.

1. The Direct Effects of Leaf Water Potential on Cell Growth and Physiology

Many components of cell growth processes are directly affected by falling leaf potential.

At the molecular level, the nature of the hydration shell surrounding proteins may have an important bearing on the properties of the proteins themselves, and denaturation may follow the disruption of this shell.

It is probable that the integrity of the specific protein/water structures is essential for the normal functioning of most physiological processes at maximum rates (Slatyer,1967). Different reactions of various species to stress may reflect the varying tolerance of their individual metabolic systems to dehydration. Since it is difficult to disentangle the direct effects of leaf potential on photosynthesis from those due to stomatal closure, Slavik (1965) chose to work with the hepatic, Conocephallum conicum, which does not possess stomata. He found an immediate decline in net photosynthesis as the potential of the thallus fell. The conclusion that this is an effect of water potential on metabolism assumes that permeability of the epidermis to CO_2 is unaffected by water content.

Working on tobacco, Slavik (1963) measured photosynthetic rates at the apex and base of the leaves and found a gradient which corresponded to the differences in hydration, again suggesting a direct relationship between photosynthesis and hydration, providing stomatal aperture was constant along the leaf.

Scarth and Shaw (1951) and Pisek and Winkler (1956) measured photosynthesis and stomatal opening of leaves with varying water deficits. With equal stomatal opening but different leaf deficits, different rates of photosynthesis were found, photosynthesis at low deficits being about three times as great as at high deficits suggesting a considerable direct effect of water deficit on photosynthesis.

Net photosynthesis may be reduced by water stress directly reducing gross photosynthesis or increasing respiration rate, and both effects have been found.

Boyer (1965) grew cotton in sodium chloride osmotica and found a decline in gross photosynthesis while respiration remained unchanged. It is difficult to see how chemical effects of the sodium chloride could be distinguished from the osmotic effects.

Nieman (1968) found that sodium chloride osmotica increased respiration rates, and Troughton and Slatyer (1968) similarly found that dehydration effects were due to enhanced respiration rather than reduced gross photosynthesis. It has been found that a rapid increase in water stress may cause an initial rise in respiration rates followed by a decline as the plant adjusts and this initial rise may be absent in the case of gradual imposition of stress (Slatyer,1967).

The rate of increase in stress may, therefore, determine the observed effect on respiration rate.

It is important to distinguish changes in net assimilation rate from those in leaf expansion rate.

The importance of turgor in cell extension has been demonstrated by Ordin (1958,1960) and Plaut and Ordin (1961). By manipulating the osmotic and turgor components of leaf potential, they were able to show that the turgor component was the main agent in cell expansion. Reduced turgor affected both cell wall metabolism and elongation, and Ordin proposed that some aspect of cellulose synthesis might have been responsible for the reduction of elongation at low turgor.

It has widely been found that the plant organs growing most rapidly at the time of water stress are the ones most severely affected (Denmead and Shaw,1960; Aspinall, Nicholls and May,1964; Aspinall,1965). Gates (1968) examined apical development in tomato and lupin and found the most juvenile tissue was the most sensitive to stress, and yet the most resistant in its ability to resume growth upon re-watering. In other words, suspension rather than impairment of function was apparent under water stress, and the apex did not show a response of protein hydrolysis as did older tissue.

The metabolism of the plant may also be altered at the organisational level.

Gates (1955,1968) analysed the growth of the tomato as influenced by a drying and re-wetting cycle. He describes the changes which occur as a senescent decline during wilting and rejuvenation after re-watering. These changes were manifested in the hydrolysis and translocation of nutrients from particularly the older laminae to the stem. This increase in the labile nutrient pool of the plant further depressed phosphorous and nitrogen uptake from the soil. The younger tissues were least affected by this sequence of events, which commenced before any reduction in dry weight occurred.

The evidence, therefore, suggests that both the synthetic and organisational activities of the plant are adversely affected by water stress, and there is some suggestion that this might occur at a relatively early stage of water stress.

2. The Relationship between Stomatal Aperture and Growth

Stomatal mechanisms have been widely investigated and reported (Stalfelt,1955,1961,1962; Meidner and Mansfield,1968). The mechanism of their response to the falling leaf potential of the droughted plant is not fully understood. It has been shown that stomata close under stress corresponding to a leaf potential of -10 to -15 bars (Ehlig and Gardner,1964), and some relationship to changes in carbon dioxide (CO_2) concentration has been suggested. Slatyer (1967) concludes from available data that decreasing photosynthetic rates and increased respiration under stress initiate rising CO_2 levels which cause eventual closure. There is some evidence that respiration rates only increase when water stress is imposed rapidly. In other cases the plant is able to adjust. Meidner et al. (1968) discuss the observation that increased sensitivity to CO_2 is shown by stressed cells and so this might be responsible for causing closure. Perhaps a change in cell membrane permeability to CO_2 occurs under stress.

The evidence for the above mechanisms remains unsubstantiated.

When the stomata are closed, cuticular transpiration may continue at a rate up to 20% of the potential rate (Ehlig et al., 1964), depending on the species involved. Carbon dioxide exchange through the cuticle, however, appears to be much more severly reduced, probably to negligible proportions (Holmgren,Jarvis and Jarvis, 1965; Barrs,1968). Thus the plant is dependent on open stomata for the gas exchange processes involved in growth.

In order to determine the stage of drought stress likely to reduce growth, the relationship between leaf potential and stomatal aperture must be considered.

This has been investigated by Gardner and Ehlig (1963) and Ehlig et al. (1964). Turgid leaves of several species were suspended in a standard evaporative environment and the rate of water loss with decreasing turgidity was measured. The stomata closed over a fairly narrow range of water content corresponding to the -10 to -15 bar leaf suction range.

A similar comparison on a whole plant basis revealed a more gradual decline in transpiration as leaf potential fell. This was probably because all the leaves were not at the same potential on/ an entire plant.

Therefore the stomata of leaves at the lowest potential began closure when the average plant potential was still quite high, and the stomata closed on leaves of above average potential when the average potential was lower. Thus the range of potential over which closure occurred appeared much wider than in the case of single leaves at uniform potential. The single leaf value does indicate at what leaf potential a cessation of photosynthesis due to inhibited gas exchange may be expected.

Bange (1953) showed that stomatal control of transpiration was negligible in still air except at very small apertures, and that they appeared to operate with little more than an on/off effect. In windy conditions, fine control was possible throughout the range of stomatal aperture. This is explained by the effect of wind speed on air resistance (r_a). In still air, r_a is the major resistance in the diffusion pathway and stomatal resistance (r_s) changes are able to exert little effect on total diffusion rates. Windy conditions reduce r_a to such an extent that r_s becomes the controlling factor, so giving the stomata a high degree of transpiration control.

The question arises as to whether stomatal control affects transpiration and CO_2 diffusion equally.

Gaastra (1963) showed that under well-illuminated conditions, diffusion of CO_2 was the factor limiting photosynthesis. Since CO_2 supply is so critical, any sensitivity of supply to stomatal aperture is of importance.

The diffusion pathway of water is usually considered to commence at the mesophyll cell surfaces, where the air is saturated at leaf temperature, and to extend through the stomata to the bulk atmosphere. That of carbon dioxide is the same, in reverse, as far as the mesophyll surface, but here is interposed a further liquid diffusion pathway which, being liquid, may be of a relatively large resistance (r_m) compared with r_s. Monteith (1963) identifies carboxylation and exitation resistances in the chloroplasts and only after these have been passed does CO_2 concentration become effectively zero. They are normally included in measured values of r_m.

If it is true that $r_m > r_s$ then stomatal aperture may be relatively ineffective in reducing CO_2 uptake compared with water loss, so making carbon assimilation less sensitive to partial stomatal closure than transpiration.

Gaastra (1963) calculated values of r_m of 5-7 sec cm^{-1} for a minimal r_s value of 3-4 sec cm^{-1} in turnips and sugar beet.

Holmgren et al. (1965) found r_m between 2.3 and 14.3 sec cm^{-1} for a wide variety of plants while r_s was variably rather smaller, generally in the range of 50% to 100% of the corresponding value of r_m.

El Sharkawy and Hesketh (1964) measured net photosynthesis rates at increasing water deficit on several species. They found that photosynthesis was not affected until the leaves were visibly wilted, and some wilted leaves still maintained maximum photosynthesis rates, thereby suggesting that partial stomatal closure had relatively little effect on photosynthesis compared with transpiration.

The comparative figures which have been quoted for r_m and r_s (Gaastra,1963; Holmgren et al.,1965; El Sharkawy and Hesketh, 1965) were calculated for maximal stomatal apertures when r_m did appear to exceed r_s. Any diminution in aperture would, however, cause an appreciable rise in r_s which would rapidly exceed r_m, so it seems unlikely that transpiration and photosynthesis are very differently affected by stomatal aperture. More recent work has confirmed this hypothesis.

Barrs (1968) found the ratio of transpiration to net photosynthesis remained constant over a wide range of gas exchange rates induced by stomatal closure. Stomatal aperture seemed to be the only factor involved.

Willis and Balasubramaniam (1968) measured transpiration and photosynthetic rates in leaves of Pelargonium and found that stomatal resistance, rather than mesophyll resistance, appeared to be the limiting factor in both cases.

Shimshi (1963) found a reduction in both transpiration and photosynthesis as the soil dried which could not be attributed to stomatal closure, and which appeared to result from a rise in mesophyll resistance with falling leaf potential. It has not been reported elsewhere that mesophyll resistance can affect water vapour diffusion, but Shimshi's results imply that evaporation takes place below the mesophyll cell walls, thus imposing a gaseous diffusion pathway resistance strictly within the mesophyll. However, Meidner et al. (1968) calculated that the drop in leaf potential necessary to withdraw the water menisci into the pores of the cell walls could be shown to be such as to make the simultaneous death of the cell inevitable (Meidner et al.,1968).

Troughton and Slatyer (1968) were unable to demonstrate any effect of water potential or temperature on mesophyll resistance to CO_2 diffusion, so it seems unlikely that plant water stress materially alters the magnitude of r_m.

The evidence, therefore, suggests that growth and transpiration are affected similarly by closure, and this reduction commences at leaf potentials of the magnitude reported by Ehlig et al. (1964). Restriction of growth can consequently be related to the drying characteristics of the soil in a field situation. A sandy loam, releasing most of the available water at low tensions, may sustain transpiration and growth through the depletion of most of its available water, followed by a sharp decline as potential falls rapidly. A clay soil would cause a more even and gradual decline in plant water potential since soil water potential is more nearly linearly related to water content (Gardner et al.,1963).

Thus growth and transpiration may be restricted by stomatal closure at an earlier stage of drought in a clay soil, but continue longer at the reduced rate because of the conservation of available water supplies by the earlier restriction in transpiration.

It seems reasonable to conclude from this examination of the effects of leaf water potential on physiological processes and on gas diffusion rates that the former are the first to be affected by the onset of drought, and that growth restriction by limitation of the CO_2 supply does not occur until the plant approaches the wilting point and stomatal control of transpiration takes place.

THE EFFECTS OF DROUGHT ON NUTRIENT AVAILABILITY

It is many years since Weaver (1926) first suggested that drought might operate through adverse effects on mineral nutrition of the plant when the soil dried. There have been many comments on this possibility since, but virtually no systematic work on the subject until the last decade. This section will first consider the likely mechanism of low nutrient uptake rates in dry soil, then review recent work on the subject.

1. Some Aspects Relating to Nutrient Availability

Many observers have found that water is removed first from the surface horizons, followed by extraction from progressively deeper zones as the top layers are dried out (Russell, Davis and Bair, 1940; Weaver, 1926; Doss Ashley and Bennett, 1960; Olson, Hanway, and Drier, 1960; Stiles, 1965). Thompson(1957) and Volk (1947) ascribe this to the combined effects of root concentration and surface evaporation. Stiles and Garwood (1963) found that the surface soil was depleted of available water in only a few days of dry weather. It seems all the more surprising, therefore, that so large a proportion of plant roots is present in this surface soil which can be rapidly depleted by evaporation, and it is reasonable to seek some explanation.

It has been noted that higher fertility increases root proliferation and so may increase water extraction (Viets, 1962; Russell, 1966; Drew, 1959). The presence of nutrients seems a likely explanation for the concentration of roots in the surface soil (Stiles and Garwood, 1963), especially since the few roots present at a depth of three feet under a pasture were found sufficient to extract all water requirements of that sward at the potential rate.

Winters and Simonson (1951) compared fertility levels in subsoils and top soils and found that although there was little difference in total phosphorous and potash, they were much more available in the top soil. Most of the nitrogen (N) was found in the surface layers. Peterson and Attoe (1965) believed that appreciable movement of nitrogen to lower depths was unlikely to occur. Garwood (1963) found that most of the 156 pounds of N applied to swards protected from rain was still in the surface two inches at the end of the season.

The plant appears to rely, therefore, on the extraction of nutrients, especially N, from the surface layers of soil, and it is to this end that the roots are concentrated here. In addition, this zone is the first to be depleted of water.

Growth might be expected to decline in proportion to transpiration if restriction of stomatal diffusion of CO_2 were the cause of depression, and finally cease at permant wilting percentage.

Recent work, on grass swards particularly, suggests that growth depression occurs at very low deficits, as little as 0.5", and well before there is any divergence between potential and actual transpiration (Stiles and Williams, 1963, 1965; Russell, 1966).

The evidence strongly points to grasses' furnishing their water requirements for transpiration from the deeper soil during drought, while being prevented by some other factor from making growth. Stiles (1965) suggests that the reason is likely to lie in nutrient distribution in the profile, especially that of nitrogen, which is concentrated towards the surface and becomes unavailable when top soil dries.

It seems reasonable to assume that the ability of the plant to take up nutrients may be partly dependent on the ability of the roots to extend and proliferate.

Volk (1947) found that corn roots grew into soil at below permanent wilting point and absorbed nitrogen and potash but not phosphorous.

Other workers have disputed this. Weaver (1926) believed that, where the soil was very dry, root development was greatly retarded or even ceased.

Kramer (1949) reviewed the root/dry soil relationship. Most roots in dry soil ceased elongation and became suberised to the tip. It seemed unlikely that any significant root growth occurred under field conditions below the permanent wilting percentage. The chief absorption zones of water, and particularly salts, appeared to be located near the root tips which might be inactive under dry conditions.

Thus it appears that roots in dry soil are not in the necessary active growing state for active nutrient uptake.

If the roots cannot extend into dry soil, then they must be dependant on the movement of nutrients to them.

Transport in the transpiration stream was observed by Fried and Shapiro (1961), and the greater this water movement, the higher the mean concentration of ions, carried in the transpiration stream, at the root interface during the growing season. Nye (1968) states that in drier soils, mass flow may be the major factor responsible for carrying mobile nutrients to the root, but only if the water flux can be maintained.

As the soil dries towards the permanent wilting percentage, uptake of water from zones thus affected has been shown to be reduced, and so the movement by mass flow of ions will similarly fall. Simultaneously, the water films surrounding the particles will become thinner and eventually discontinuous, so preventing simple diffusion towards the root (Peters and Russell, 1960; Danielson and Russell, 1959; Nye, 1968). Cooke (1963) points out that nitrate is the only major nutrient ion not strongly absorbed onto the colloids so that it can be transported relatively freely in the soil by diffusion or mass flow, but only if there are continuous water films and appreciable flux.

In dry soil, therefore, after ions in the immediate vicinity of the root have been utilised, there will be no incoming flow to replace them, and since root growth outwards has also been restricted, nitrogen starvation seems a real possibility.

The foregoing paragraphs have outlined the classical argument for nutrient unavailability's being responsible for the primary droughting effect at low water deficits.

A number of recent experiments which purport to confirm this effect will be critically examined.

2. Some Recent Experiments on Nutrient Availability.

Garwood and Williams (1967a) investigated the growth of a perennial ryegrass sward and the pattern of water use as the soil dried.

They found that water extraction from the soil commenced in the top and that, when this was dried, it continued at greater depth. The rate of extraction was as great from the second and third foot as from the surface foot. At a deficit corresponding to the drying of the top foot, shoot growth almost ceased in a mature sward. Although a seedling sward was also examined, yield measurements for this were not given.

This is unfortunate since the seedling sward showed a rather different pattern of root growth, in that active roots were present throughout the profile throughout the season, whereas the mature dry sward only had white roots near the surface early in the year, and these were confined to progressively deeper horizons as the season progressed.

Coinciding with the fall in yield of the mature swards was a large fall in tiller numbers compared with the controls. When the swards were irrigated back to field capacity, the tiller number increased to exceed that of the controls. This was attributed to the utilization of a heavy accumulation of fertilizer, which they showed was still confined to the surface three inches of soil, by new white roots which appeared within a day of re-watering and which were already present in the controls which were irrigated.

The events responsible for the phenomena observed in this experiment must now be considered. The sward was cut at four-weekly intervals during the course of the experiment. The cessation of production in the dry treatment coincided with the flowering period of a vernalised sward. It is well established that tillering declines at the period of ear emergence and then begins again after flowering in the June-September period to produce the majority of the succeeding year's new tillers. The apical meristems of the flowering tillers would presumably have been removed by the cutting, thus preventing their further growth. Any dry matter yield subsequent to this time would therefore be largely dependent on new growth of new vegetative tillers from the bases of the old ones. The data presented show that these new vegetative tillers were able to develop and so were responsible for the increased production in the wet controls. They did not develop in the dry sward and the reasons for this difference must be sought.

It is unfortunate that leaf water potentials were not measured in this experiment. The root system was mainly located in the top foot of the soil and it is possible, therefore, that there had been a fall in the potential of the leaves to maintain water uptake from the few deeper roots as water uptake was shown to continue at the previous rate from the deeper soil. It is not known, however, whether this might have been large enough to inhibit tillering.

Greenway and Kepper (1969) found that a fall in plant potential from -0.4 to -5.4 atmospheres considerably reduced P and Br transport to the shoot but this was attributed to a decreasein water flow through the plant. It is difficult to see how such a phenomenon could have been responsible for reduced tillering in Garwood and Williams experiment, where transpiration rate (and this implies water flow through the plant) remained the same.

The sward had been defoliated and so any labile pool of nutrient ions within the plant would be severly depleted. The production of new tillers is extremely dependent on nitrogen supply (Aspinall,1960) and there is little evidence for apical dominance in grasses (Jewiss,1966). Davidson and Milthorpe (1966) showed that the older leaves were an important reservoir of labile nutrients for re-growth, but were of little importance in the supply of assimilates. Since this labile pool was removed, re-growth is likely to have been dependent on renewed uptake of nutrients from the soil.

The question arises as to whether this uptake occurs by the old root system followed by translocation to the new tillers, or whether new adventitious roots must first arise.

Regarding first uptake by the old system, Williams (1960) claimed that in the flowering tiller, translocation from the roots ceased at a fairly early stage. If this is the case, the old root system is unlikely to be of much consequence in enabling the necessary supply of, particularly, nitrogen to reach the new tiller initials. Davidson and Milthorpe (1966) say that defoliation is followed by a severe declinein theactivity of the roots, their respiration rate falling by two-thirds and phosphorous uptake by four-fifths. This is probably the result of the curtailment of carbohydrate supplies from the shoot on which the roots seem to be particularly dependent.

Oswalt, Bertrand and Teel(1959) found that Dactylis had to grow a new root system before uptake commenced afresh after defoliation, while the old system decomposed. The removal of all the old root system did not alter the rate of re-growth after defoliation under optimum soil moisture conditions.

Thus it seems probable that any appreciable growth of new tillers is dependent on the establishment of a new adventitious root system to supply these tillers.It is a matter for conjecture whether the dry top soil may have prevented such growth.

Garwood and Williams, and Stiles and Garwood (1963) noted that re-watering of the dry sward was followed by the immediate production of new roots which, they say, took up the now available nitrogen which had accumulated in the top soil and so enabled the top growth to exceed that of the controls which had these roots from the beginning. This suggests, since the roots were produced within 24 hours of re-watering, that the dry top soil was responsible for the lack of growth by preventing the development of new adventitious roots able to supplement the tiller nutrient supplies, and so any claimed "nitrogen unavailability" was a direct effect of suppressed rooting and not unavailability as such. This concept is supported by the subsequent experiment of Newbould (1968), described more fully later. This showed that the response to nitrogen, deep placed in a wet zone, was very much less than to irrigation, thus suggesting that the inability to produce new roots in a dry top soil, or some other factor resulting from water stress, is of overriding importance.

In order to test their hypothesis that nutrient unavailability was responsible for cessation of growth, Garwood and Williams (1967b) carried out further experiments involving the injection of nutrients into the soil at 18" and 30" depth at the time at which the sward, protected against rain, was currently extracting water from these depths. An immediate visible response in the greenness of the grass was produced and the yield was greatly increased, as was the nitrogen recovery compared with a surface nitrogen application. Subsequent re-watering gave further quantities of growth which were greatest from the plots of deepest nitrogen application. It was claimed that this experiment demonstrated that uptake can be just as efficient from depth and that nitrogen deficiency was responsible for the restriction of growth.

It cannot be denied that the deep nitrogen injections increased growth. The importance of this effect cannot be estimated, however, since there was no fully watered control, and so there is no evidence that the effect might not be relatively minor compared with the drought effect. Additionally, it does not seem logical to argue that growth ceased due to a nitrogen shortage while the tissue nitrogen level was higher than that present in the re-growth, made in abundant quantities, after re-watering. Clearly, some other factor must have been involved. (Nitrogen percentages calculated from yield and N uptake data presented in their paper, using mean of the two dry harvests).

The most serious objection lies in the method of application of the surface nitrogen to the control. This was simply applied to the surface in a minute (0.76mm) quantity of water. Penetration could be expected to be minimal in the absence of any rainfall and the distribution zone would be negligible. The deep nitrogen was applied down tubes on a six-inch grid in sufficient water to give a "reasonable distribution" in the soil.

It seems unreasonable to draw a comparison between two such different fertilizer distributions. There seems no reason why the surface application could not have been injected below the surface in the same manner as the deeper application, but after the top soil had dried, though it is admittedly difficult to obtain a "reasonable distribution" in dry soil without using appreciable quantities of water.

The validity of these two criticisms is vindicated by subsequent experiments carried out by Newbould (1968), and by Russell and Newbould (1968), who adopted a similar experimental technique. Nitrogen was injected in wet (control) and drying plots at 7.5 cm and 45 cm, or placed on the surface. For reasons already explained, the surface N application is not considered a valid treatment for comparison and will be ignored. This leaves a comparison of placement at 7.5cm in dry soil and at 45cm in the current zone of moisture extraction. While the deeper placement gave superior production during the dry period, the difference was insignificant, and it came nowhere near to equalling the response obtained by watering the plots. This is further evidence that nitrogen uptake <u>per se</u> is of only minor importance in pasture growth during dry spells compared with the importance of water.

Simultaneously with the nitrogen injection in the above experiment, tracers were injected in order to measure the uptake of phosphorous and calcium as affected by water regime. The extent of P absorption was markedly affected by water content of the soil. At the 7.5cm depth, uptake was three times as great from the wet as from the dry regime. The subsequent addition of water greatly increased uptake.

This observation compared with that of Eck and Fanning (1961) who found that P uptake ceased before the soil reached the permanent wilting point, whereas N uptake continued, even from soil containing little of no moisture.

The question of uptake cannot be left here, however, since it is a process actively controlled by the plant. While uptake may be limited by low availability, it can also be limited by low demand. Several workers have found that drought-induced stress causes an increase in hydrolysis relative to synthesis, particularly of phosphorous compounds, and their translocation from the leaves to the stem(Gates, 1968; Greenway, 1969; Williams and Chapter, 1955), thereby increasing the concentration of P in the labile pool and probably thereby reducing uptake by the roots. Gates (1968) found these effects to occur at a very early stage of drought, before dry weight had been reduced. This work was done mainly on the tomato plant which cannot truly be compared with a defoliated sward. It does, however, offer an explanation for the observations of Eck and Fanning (1961), mentioned above, who worked with corn plants which were not of course, defoliated.

Thus the experiments on nutrient availability described above must remain largely inconclusive and offer circumstantial evidence which can be interpreted in other ways. Without exception, the information was obtained from mature, defoliated swards which were in the vernalised condition and so dependent on their adventitious root system.

The response of the root system to environmental factors will next be considered.

THE RESPONSE OF ROOT GROWTH TO ENVIRONMENTAL FACTORS

The extent and diversity of the roots of the Gramineae were examined and reported by early workers, whose investigations have now become classics in this field (Weaver,1926; Weaver and Zink,1945,1946; Dittner,1938; Troughton,1951). Garwood (1967,1968a,1968b) has made the most recent investigations using similar methods to these workers, and his results will be considered here, largely in preference to the earlier work.

The newly sown grass plant is first dependent on the seminal root system for water and nutrient uptake, but the development of the adventitious nodal system rapidly supercedes it, and the relative importance of the two at this stage is demonstrated by Russell (1970) who shows that the nodal system rapidly assumes a dominant role in uptake. Weaver et al. (1945) found that the seminal system was alive and functioning after four months from germination and was capable of supporting the plants if new nodal roots were excised. Annual grasses could rely completely on the seminal system, especially if the dry top soil prevented the development of the secondary system. The length of the life of a root is very variable, depending on soil and plant conditions, but seems to be of the order of four to eight months, the latter figure being the longest surviving root reported by Garwood. Thus the root system of perennial grasses must be in a state of continual replacement by new members.

Swards can, on this basis, be classified into the establishing phase, where the nodal system is in the process of replacing the seminal roots in function, but where all roots are active, alive and functional; and the established sward, where a cycle of death and replacement is in operation. The transition point to the replacement cycle, while no doubt being very variable, might be expected to be in the period of four to eight months after germination. These two phases were clearly identified, with little comment, by Garwood and Williams (1967a), who describe the presence of active, white roots with an intact cortex, throughout the full thirty-six inches, but particularly in the top nine, of the rooting profile of a seedling Lolium sward during the summer following sowing. The absence of active roots in the upper horizons of an old sward in summer was observed, and one

can speculate on the way in which swards with these differing root systems might respond to drought. Kristensen (1961) found that first year grass/clover swards could extract 60-70% of available water before any decline in growth, whereas second year swards were more sensitive to drought, and dry matter production declined after 50% extraction.

The larger part of a root system is generally confined to the surface horizons, Wright (1962) finding 70% of Blue Panic-grass roots in the top two feet. However, the data of Garwood et al. (1967a) show that total root weight and active root weight may have little relationship, and at times, the entire active root system may be confined to the deeper horizons. The total rooting depth, rather than the density, may be of importance in determining the quantity of water available to the plant (Garwood et al.,1967a). Although the general distribution of roots under the Gramineae has been examined, little information on inter-specific differences has been reported.

Garwood (1967a,1970) reports roots of Lolium down to four feet depth, while those of Phleum and Poa were more restricted, the latter being able to accumulate a maximum soil water deficit of about one inch less than Lolium. Goode(1956b) reports similar results where Lolium fully utilised soil water to three feet depth while Phleum had a compact root system, largely extracting water from the surface twelve inches, and Poa was even more restricted to the top six inches. Burton, De Vane and Carter (1954) found wide variations in the root distributions of American grasses. Burmuda grass had the deepest roots, though least in total weight, and was considered the most drought resistant. Garwood (1960a) reports a comparison of Lolium, Dactylis, Poa trivialis and Agrostis tenuis where they showed little difference in their ability to take up water from depth. Zone of water use may not, however, be an accurate indicator of root distribution, due to upwards diffusion in the soil.

A marked seasonality of root growth has been observed by most workers. Baker(1957b) found that the weight of a seedling Lolium sward increased throughout the first season, declined in winter a little, then rose again the following spring. Garwood (1967a) improved the precision of this type of investigation by observing the number of new adventitious roots, since he considered that total root weight reflected only the balance of growth and decay.

He found that new roots of four grass species were produced in increasing numbers during late winter and early spring, falling again in April or May to a very low level for the summer. There was a small increase again in autumn, but the rate of elongation was slow. Elongation rates were highest in the deep roots produced during the summer. The differences were not great amongst the species studied. Beard and Daniel (1966), Ueno and Yoshihara (1967), and Stuckey (1941) report a similar cycle of growth in various common species, and all find that high soil temperatures best explain the fall in root production in summer. Garwood (1968b) investigated this effect of temperature in controlled experiments and found that the number of new roots produced, and their thickness, was greater at low temperatures (48°F), but there was more branching at higher temperatures (85°F) in Lolium.

Weaver (1926) reported that if the soil became very dry, both young roots and root hairs died and root development was greatly retarded, or even ceased. Russell (1970) observed that a short period of desication caused collapse of the root cortex, the presence of which was of greater consequence to phosphorous uptake than the physical age of the root,

Wright (1962) found a considerable decline in root weight under soil moisture stress, but the rather dubious value of weight as a measure of root growth has been discussed by Garwood (1967a). Weaver et al. (1945) observed that dry top soil conditions restricted the development of the nodal root system. Newman (1966) found a reduction in root growth in Flax at -7 bars soil water potential, and this fell to 20% of the rate before drying, at -15 bars. Some limited growth was observed in soil with a water potential below -20 bars. Growth in each layer did not appear to be influenced by the water potential in other layers.

Garwood (1967b) measured a lower weight of root under mature irrigated swards of several species of grass and he attributed this to higher decomposition rates under irrigated conditions. Further experiments (Garwood,1968b) showed that irrigation produced a small significant increase in the production of new white roots, but multiple regression analysis could only show a significant inverse relationship between white root number and soil temperature.

Lambert (1967) observed increased root weights under irrigated seedling swards of Phleum, but this turned into a decrease two years later in the established phase.

Ueno et al. (1967) found a considerable fall in the root growth of Lolium and Dactylis at high temperatures, even though they were irrigated.

Beard et al. (1966) found that temperature showed the highest correlation with root production, followed by light intensity, then soil water conditions, and this appears to be in agreement with the results of most workers on the topic.

The above reference to light intensity and hence, presumably, to photosynthesis and carbohydrate supplies, leads to the question of defoliation and root production.

Jewiss (1968) found that compensation point was re-attained within two days of defoliation, and both he and Dilz (1966) concluded that the crude protein reserves were probably most important in regrowth, and carbohydrate levels less so. Davidson and Milthorpe (1966) thought that carbohydrate reserves were critical for regrowth at high external nutrient levels. It is quite conceivable, therefore, that following defoliation, the internal level of compounds for regrowth might be critically low, and diverted mainly to the regrowth of the shoots until such time as reserves were replenished (Brouwer,1965).

All Garwood's experiments were defoliated, usually at four week intervals. The few investigations which have been made by other workers show that this probably had at least some effect on the subsequent root growth, caused by the diversion of assimilates to new top growth.

Pavlychenco (1942) found that spaced plants produced more adventitious roots than swards. This could well be due to the higher assimilate levels to be expected in the non-competitive situation. Baker (1957a), working similarly with spaced Lolium plants, found that cutting reduced both root weight and the rate of root elongation. This effect disappeared after a single cut, but several cuts caused the plants to enter the winter with reduced rootsystems and this was reflected in lower top growth in the following spring. There was an inverse relationship between cutting frequency and root weight.

Wright (1962) found a similar inverse relationship with cutting height, no doubt connected with the creation of a sink for assimilates in the shoots in preference to the roots.

Goode (1956a) has reported reduced maximum soil water deficits attained by roots of defoliated swards, indicative of reduced root extension or activity.

The placing of factors affecting root growth examined by Beard et al. (1966) in the order of importance; temperature, light intensity (through its effect on photosynthesis and also in relation to competition within swards) and lastly water supply, would seem to be supported by the experiments considered above. The effect of cutting is a further factor, partly confounded with the light intensity factor, but also related to the creation of preferential sinks for assimilates, which further complicates the interaction of all the above factors.

The complexity of these interactions must impose great difficulties in the experimental investigation of the relationship between soil nutrients, water and the growth of the grass plant. Davidson (1969) has recently put forward a hypothesis which may go far to anticipating the effects of environmental factors on root/shoot ratios, though whether the relationship is spurious remains to be seen. He suggests, in agreement with others (Brouwer and de Wit, 1969), that there is a characteristic ratio of root to shoot in any given set of environmental conditions. If defoliation takes place, all further assimilation is directed towards restoring this balance. If the environment changes, then assimilates are directed towards achieving the appropriate new ratio. For example, the application of N increases the proportion of shoot since assimilatory ability becomes of more importance than the nutrient uptake ability of the root system. Conversely, a nutrient deficiency diverts assimilates to root growth since this is now the limiting factor in the nutrient/assimilation balance of the plant. A similar relationship can be proposed for the effects of temperature and soil water.

The control of root and shoot growth by cytokinins is also the subject of recent investigations, and there seems little doubt that their production by the roots is closely related to the metabolic state of the roots as determined by their activity and current stress factors (Vaadia and Itai, 1969).

It seems likely from these recent investigations that a break-through is imminent in the understanding of the relationship between the root and the environment and that a causal mechanism will be isolated to explain the present multitude of descriptive observations.

EXPERIMENTAL SECTION

Examination of Experimental Techniques

1) The Water Potential and Conductivity (k) Characteristics of Silwood Soil and Perlite.

The relationship between water potential, water content and capillary conductivity (k) of the Silwood Soil and Perlite used in these experiments was determined using a fifteen bar ceramic pressure plate. Undisturbed core samples, 5cm thick, were taken from the experiments and placed, still in the metal extraction rings, on the ceramic plate. After being saturated, they were allowed to equilibrate at 0.2 bars pressure. The pressure was then increased by predetermined steps ranging from intervals of 0.1 bar initially to several bars at higher pressures and the rate of outflow was measured. When outflow ceased, the next pressure increment was applied. The outflow from a second plate was measured simultaneously and deducted from that from the first plate to give the net outflow from the samples. The final water content and the dimensions of the samples were then determined. The water content/matric potential characteristics on a volume and weight basis were calculated from this data.

The capillary conductivity between each pressure was calculated by the method of Gardner (1956) and agrees well with the measurements made by Lawlor (1967) on the same soil, but using a pressure membrane apparatus.

The method has been criticised by Jackson, Van Bavel and Reginato (1963) who concluded that the results could be inaccurate by an order of magnitude. The technique assumes constant diffusivity during the outflow from each increment of pressure. This assumption is only valid if the increment is small. Small increments give rise to difficulties in measuring accurately the resulting small outflow, and so a compromise must be reached. The method also assumes the plate resistance to be negligible compared with that of the sample. The ratio of sample resistance to plate resistance was increased by using thick soil cores. A disadvantage was the long period of time required for equilibrium to be attained.

Fig. 1A

Water Release Characteristics of Silwood Soil

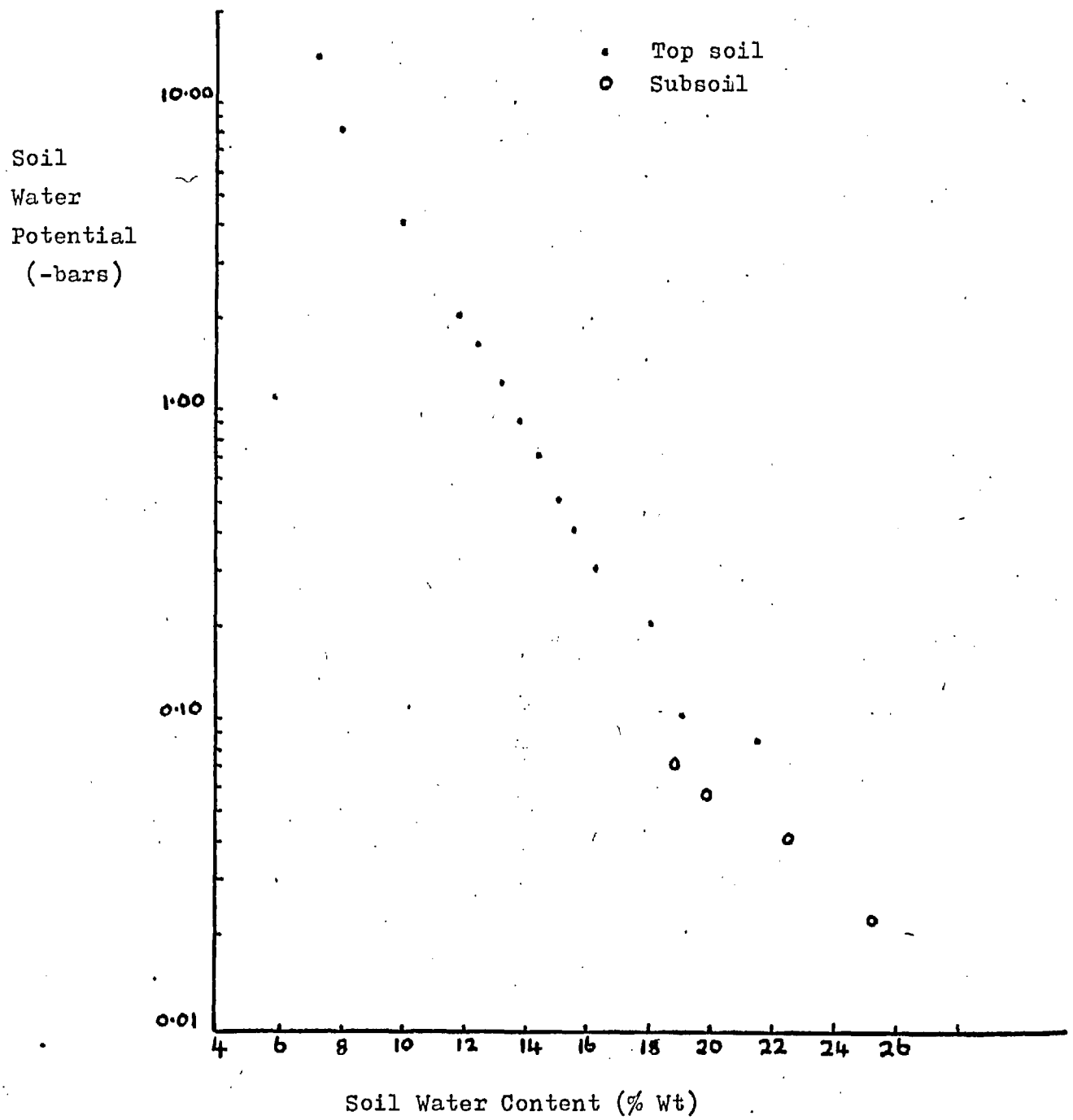


Fig. 1 B

Water Release Characteristics of EUP 130 Perlite

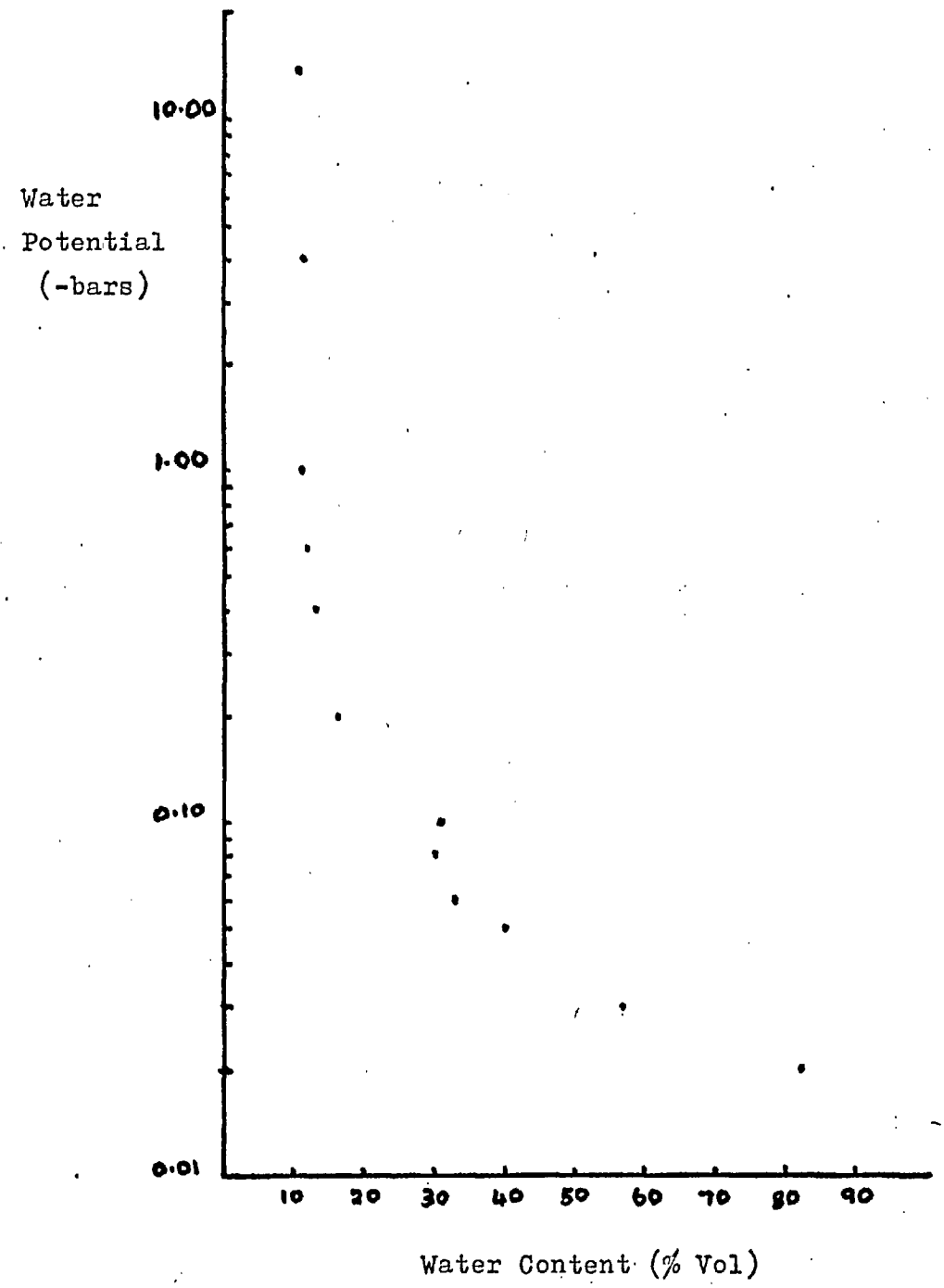


Fig. 1C

Relationship between Matric Water Potential and Capillary Conductivity of Silwood Top Soil

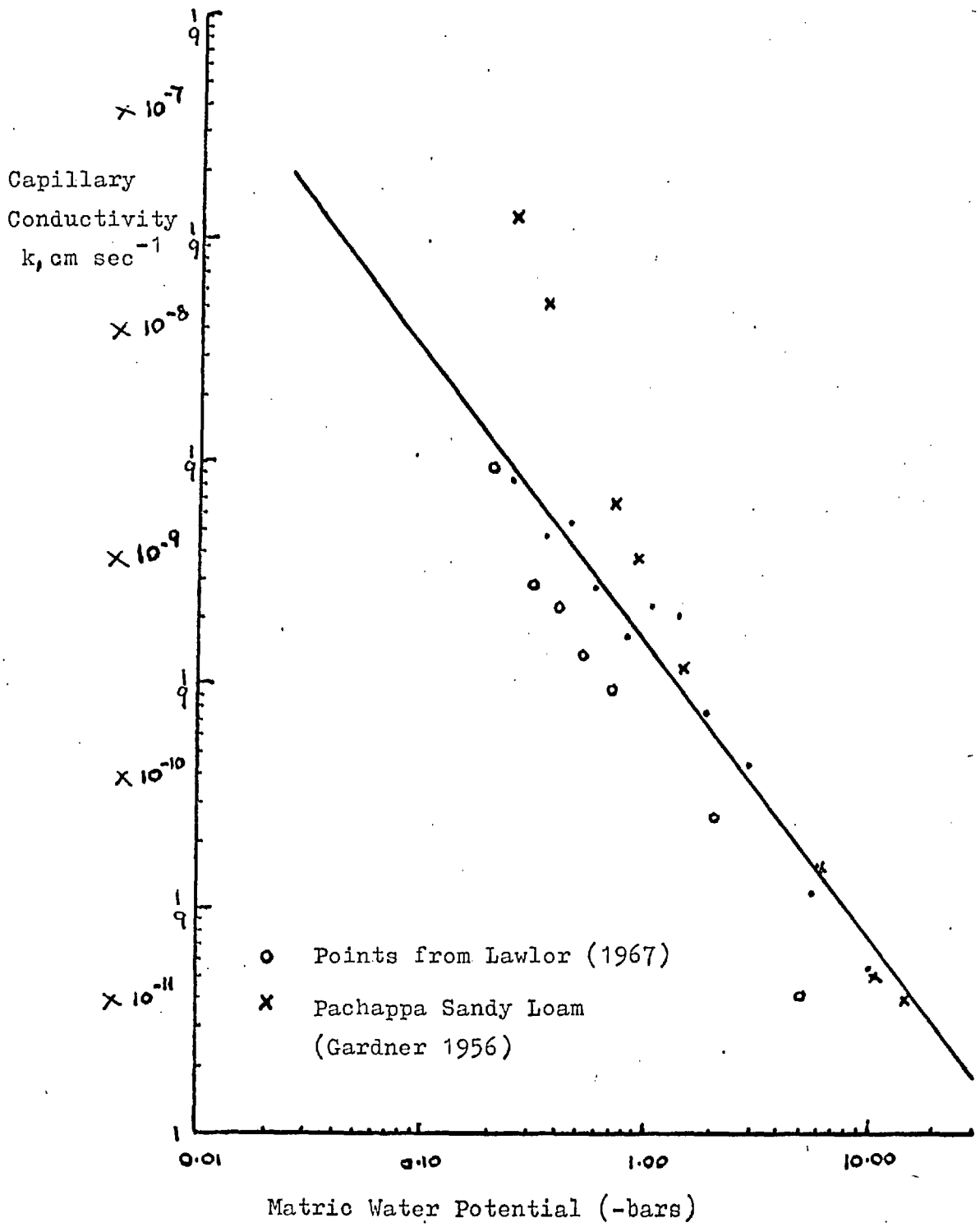
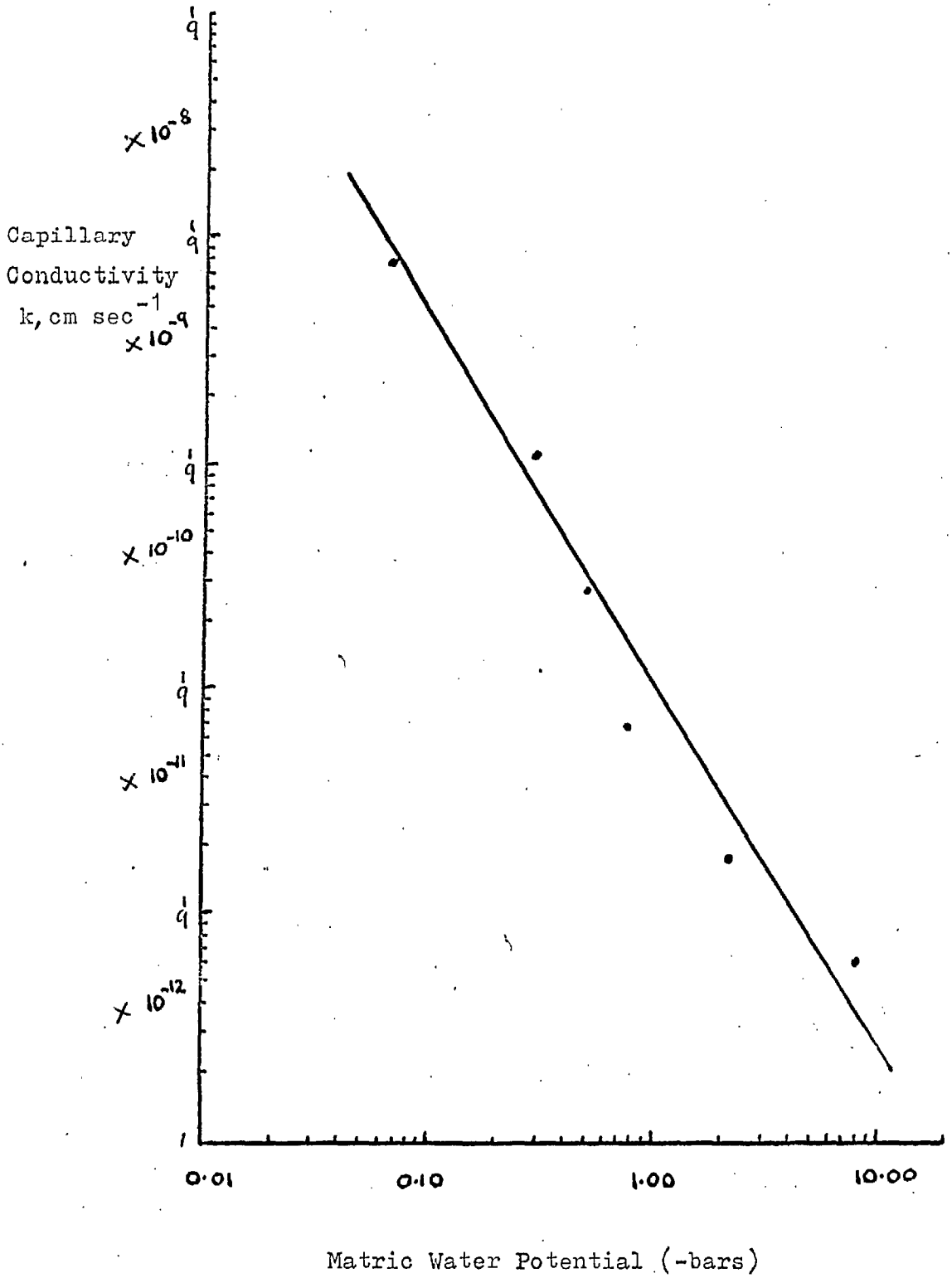


Fig. 1D

Relationship between Matric Water Potential and Capillary Conductivity of Perlite EUP 130



Peck (1966) describes an alternative method of calculating k to eliminate plate resistance which involves matching outflow rates over an initial short period of time to a theoretical curve. It was not possible to measure outflow accurately over a sufficiently short time with the available apparatus and so this method could not be used.

The calculated points and regression lines are shown in Figs.1 A,B,C,D.

The extrapolation of this line seems justifiable since Gardner (1960) determined these characteristics for a similar sandy loam and found the line to be almost linear below a soil water potential of about -50cm.

Values determined by Gardner (1956) for Pachappa sandy soil and by Lawlor (1967) for this same Silwood soil, are also plotted in Fig.1C. No data could be found for Perlite.

The data of Lawlor show very close agreement. They were determined by the use of a ceramic pressure plate down to -1 bars and thence in a Visking membrane apparatus down to -5 bars. He was similarly unable to separate the resistance of the membrane.

The conductivity of the ceramic plate was estimated by covering the saturated plate with water and measuring the outflow rate. The calculated value was 3.86×10^{-9} cm sec^{-1}. This probably gave rise to an appreciable underestimate of soil conductivity but there is still close agreement with values determined by Lawlor (1967) and Gardner (1956).

It is emphasised that any underestimate of conductivity can only add weight to the conclusions derived from the calculations involving these measurements in a later section.

The behaviour of Perlite was found to be unusual in that there was a marked point of change in the water release characteristics. This could probably be associated with a change from the release of water from between the particles to release from within the pores of the particles.

The low conductivity predicted by Warren-Wilson and Tunny (1965) was confirmed at about an order of magnitude lower than sandy loam.

2) Measurement of Leaf Water Potential

The potential of the grass leaf blade was measured with a pressure chamber in the manner described by Scholander, Hammel, Bradstreet and Hemmingsen (1965).

A compression gland was constructed to hold the leaf blade within the pressure bomb without crushing the tissue, while the cut end protruded by a fraction of a centimetre. The chamber was connected to a pressure gauge and compressed air cylinder and the pressure raised by approximately 100cm $cm^{-2} sec^{-1}$ while the cut end of the leaf was observed through a binocular microscope. The pressure at which water exuded from the xylem vessels was noted. Further trimming of the leaf after it has been cut from the plant, or allowing more than the minimum of unpressurised leaf to protrude from the chamber would introduce an appreciable error into the method.

Boyer (1967) found that calibration against a thermocouple psychrometer was necessary for accurate use of the pressure method. He pointed out that the method did not take account of xylem sap potential and that tissue other than the xylem became filled with liquid during measurement, introducing further error.

Waring and Cleary (1967) found agreement of the technique with Slatyer's vapour equilibrium method to within one atmosphere in the range -5 to -20 atmospheres.

The facility and rapidity with which measurements can be made, and the close agreement between actual and anticipated results at either end of the range are a strong recommendation for the field use of the method.

3) Diffusion Porometer

A diffusion porometer, designed and built by Dr. P. Robins of Imperial College and based on similar principles to one described by Meidner et al.(1968) was used to measure the degree of stomatal opening. This apparatus operates by measuring the changes in electrical conductivity of a sulphonated polystyrene strip which are caused by vapour diffusing out of the stomata. The machine was still in a developmental state and had not been calibrated. It did, however, allow comparative measurements of vapour flow and hence stomatal aperture to be made in arbitrary units.

4) The Measurement of Root Length

Newman (1966) describes a method of estimating the length of a sample of root by the interception technique.

The number of intercepts between randomly distributed straight lines of known length (in this case the cross wires of a binocular microscope) and roots spread out in a dish of water were counted.

Then the length of the root sample was estimated from the formula $R = \frac{\pi NA}{2H}$

where: R = total length
N = number of intercepts
A = area of dish
H = length of cross wires

Spreading the root sample evenly and using both wires of the cross to count intercepts so as to compensate for any directionality in the root layout, greatly reduced the number of random locations at which intercept counts were necessary. Counting more than ten locations was found to give little greater accuracy provided the above precautions were observed. Trial measurements on cotton of known length indicated an accuracy better than $\pm$ 20%.

It should be noted that the method does not include the root hair length in the estimate of total length as these are not visible under a low power dissecting microscope. Estimates of intercepts made under a higher power indicated that the root hairs contributed two to three times the length of the root axes.

5) Analysis of Tissue Mineral Content

Determinations of N,P,K and Ca were made by the method described by Varley (1966) on the Technicon Auto-Analyser.

6) The Pipe Technique

This method was evolved to enable uniform conditions to be applied and accurate control and measurement of experimental factors to be made. This is difficult to achieve with field plots. It has frequently been criticised on the grounds that the roots generally follow the outside of the containers. This has not been observed in these experiments.

Each pipe of 15cm internal diameter was cut longitudinally and then reassembled using a collar and wire. The lateral slits were sealed by P.V.C. tape. When stood in a bucket from which outflow could be extracted, the pipe made an easily manipulated lysimeter. It could be weighed on a 50 kg x 10 gm yard-arm balance to determine water loss by transpiration. The roots could be extracted by splitting the pipes and transfering the contents to a nail board for washing.

In an attempt to reduce advective heating, the pipes in outdoor experiments subsequent to the second one were stood in a trench with their tops flush with the surrounding grass. The pipes were stacked together to form a nearly continuous sward, and the blocks were arranged to remove variance between outside and centre rows. Guard rows were positioned at the exposed ends of the blocks, and when pipes were removed for harvest, the gaps were closed up again.

7) Perlite Rooting Medium

Perlite was used in Pipe Experiments I and III as a substitute for subsoil. (Perlite grade EUP 130)

Its defects are considered by Warren Wilson et al. (1965) to be a low hydraulic conductivity and the production of deformities in some seedling types. They conclude that these defects should not be over estimated.

Some characteristics are given by White and Mastalerz (1966); Morrison, McDonald, and Sutton, (1960); and Green, (1968).

Perlite is of volcanic origin and after treatment has a fine, light crumb structure. Each crumb is permeated by fine capillaries, enabling moisture retention in a manner similar to soil.

It has many advantages. It is completely uniform, is much lighter and easier to handle than soil, easier to wash off the roots, and in the case of these experiments, virtually nutrient free.

Roots produced in Perlite tended to be of rather larger diameter and slightly denser than those formed in natural subsoil. A comparison of Pipe Experiment III and Pipe Experiment IV, the former using Perlite and the latter subsoil, showed that at comparable ages, the total root lengths were similar.

The hydraulic conductivity and moisture characteristics of Perlite have been dealt with in a previous section.

8) The Lysimeters

The detailed construction and design of the lysimeters used in these experiments has been described by Etherington (1962). They numbered 28 in two parallel banks orientated north/south. Each concrete tank measured 2yd x 1yd x 1yd and contained the original Silwood soil removed during excavation for their construction. Drainage water was conducted into the trench which separated the two rows of lysimeters. Hinged transparent covers could be put into place during rainfall to protect the plots if required.

A preliminary test crop of wheat indicated a gradient of fertility, possibly related to a low soil pH to which wheat is rather sensitive. While grasses are less sensitive, the future layout of statistical blocks was based on the test cropping results.

9) Growth Analysis by Computer

Growth analysis calculations were performed using a computer programme compiled by Hughes and Freeman (1967) for the purpose of the analysis of data obtained from a

series of sequential harvests. The programme and details of the mathematical principles were obtained from the Authors.

The method involves fitting cubic regression curves on time to the log transformed data of dry weight and leaf area obtained at sequential harvests, a standard error being calculated for each curve at each harvest. The programme computes the growth parameters from the slope of the line obtained by differentiating the equation at each harvest, rather than over a longer time interval as used in conventional formulae. The standard errors for each parameter at each harvest are simultaneously calculated using the standard errors of the harvest points on the fitted curves.

PIPE EXPERIMENT 1

It is widely reported that different species of grass exhibit varying degrees of drought tolerance within the conditions of the British climate. This initial experiment was designed to obtain preliminary information on any morphological differences, particularly of the root system, in common agricultural species of grass which account for differences in drought resistance; and to test whether these differences could readily be reproduced in experiments. The experiment also served as an initial test of the technique of growing grass in pipes, which has already been described.

Method and Materials

Four species of grass were grown under four treatments in which their continued water supply was either obtained from soil at field capacity or else was dependent on the ability of their roots to reach and exploit a water-table which, in the extreme treatment, was 90cm below the surface. In order that the nutrients available to the plants should be the same in every case, each pipe contained 23cm of soil separated from the water-table by an appropriate depth of Perlite. Capillary rise from the water-table into the Perlite was prevented by a layer of coarse gravel, a few centimetres thick.

The experiment was conducted in a heated greenhouse using mercury vapour lights to enhance illumination, commencing in January, 1968. It consisted of four randomised blocks arranged in parallel rows so that edge effects and differences in illumination were spread as evenly as possible along each block.

Each block consisted of the following sixteen factorial combinations-

Four Water Treatments	X	Four Grass Species		
Field capacity	(FC)	Dactylis glomerata	S37	(CF)
30cm Water-table	(30WT)	Lolium perenne	S23	(RG)
60cm Water-table	(60WT)	Festuca arundinacea	S170	(TF)
90cm Water-table	(90WT)	Phleum pratense	S48	(T)

The pipes for the field capacity treatment were 30cm long and the remaining pipes were cut to the length of the corresponding water-table depth and then stood in buckets placed on concrete blocks so that the tops of the pipes were all at the same height. A few centimetres of coarse gravel were put in the bottom of each bucket to prevent capillary rise from the water-table. This was maintained through side-tubes attached to the buckets at one end while the other was attached to a funnel supported in a wooden frame at a height corresponding to the water-table. The FC pipes had a drainage tube from which any surplus water could be collected and returned to the surface soil. The 60WT and 90WT pipes were filled with fine grade EUP 130 Perlite to within 23cm of the top. All pipes were then filled to the top with an equal weight of Silwood top soil (described by Etherington, 1962). A gypsum soil-moisture block was buried at 10cm depth in each pipe and these were read at intervals during the course of the experiment using a resistance meter.

0.15gm of seed of each species was sown in the appropriate pipes on 17 January and the plants were kept well watered after emergence until 21 February by which time they were several centimetres tall. All pipes were then watered to field capacity. All further water additions were to the soil surface in the FC treatments or to the funnels in the WT treatments. The quantities added were recorded.

By 28 March, considerable top growth had been made and this was cut at 2cm above soil level and dried (Harvest1). Subsequently, the pipes were rewatered to field capacity after disconnecting the water-table tubes and then fertilizer was added in 50cm^3 water estimated to be equivalent to the nitrogen removed in the top growth harvested. The grasses were permitted to regrow without subsequent watering except for the FC treatment. The water tables having been disconnected, this meant that the second stage of the experiment tested the ability of the species to maintain growth by extraction of the water held by different depths of Perlite.

When two of the four replicates of each treatment showed permanent wilting, all four were harvested on the assumption that growth had ceased (Harvest 2). Wilting occured first in Lolium and in Festuca, Dactylis and Phleum in order, and first in the 30WT followed by the 60WT and 90WT depths over a period of six weeks from 18 April to 29 May.

Two replicates of the FC treatments were harvested at the time of the 30 WT harvest, and the remaining two replicates at the time of the 90WT harvest.

After this harvest, gravimetric measurements were made of the water content of the pipes at two depths in the soil and two in the Perlite, then sample root systems were washed out of each species and each pipe depth.

The nitrogen content of the plant shoots in each treatment at each harvest was determined after bulking the replications with the exception of the FC treatments at Harvest 2, the replicates of which were not all harvested simultaneously.

Results

Until Harvest 1, the WT treatments were dependent for water on the storage capacity of the soil and Perlite plus extraction from the water-table if the roots were able to reach it.

The yields of the three water-table depths, which were harvested simultaneously, were not significantly different. The mean yield, therefore, of the three WT treatments and that of the FC treatments is presented in Table 1.

Table 1. Pipe Experiment 1

Dry Matter Yield of Foliage at Harvest 1 (gm)

	CF	RG	TF	T
FC	10.6	16.0	12.6	8.9
WT (mean)	5.1	8.1	6.8	2.9

L.S.D.=1.2

The yield was depressed in the WT treatments compared with the controls consistently by about 50% as a result of the soil and Perlite being dried (except in the case of Phleum which was even more severly depressed) even though unlimited water supplies were available from a water-table. The nitrogen concentration of Harvest 1 foliage is shown in Table 2. Since the replications were bulked, no statistical analysis was possible.

The mean concentration in the WT treatments for all species except Phleum was higher than in the controls at field capacity. The percentage was inversely related to the yield of foliage in wet and dry treatments.

Table 2. Pipe Experiment 1

Nitrogen Concentration in Foliage at Harvest 1 (%)

	CF	RG	TF	T
FC	3.1	2.5	3.0	3.9
30WT	3.3	2.3	2.9	3.5
60WT	3.3	3.5	3.5	3.5
90WT	3.2	3.6	3.2	3.6
Mean of WT treatments	3.3	3.1	3.2	3.5

The mean dry matter yields at Harvest 2, shown in Table 3, were not analysed statistically since the replication was split in time for the FC treatments. The variability between replications was small. As at Harvest 1, the depression in yield relative to the controls was considerable. At the time of the harvest of the 30cm pipes, Phleum was least depressed and there was little difference between the other three species. At the harvest of the 90cm pipes, Lolium and Festuca showed considerably less depression relative to the controls than Dactylis and Phleum, and had made considerably more growth from the additional water available in the extra depth of the 90cm pipes since the harvest of the 30cm treatments.

The interpretation of this result is difficult. The superior performance was by the two species which exhausted total supplies first, and also had the deepest root systems as shown later. These two species were able to explore the full depth of the pipe and remove available water, whereas Dactylis and Phleum had more restricted rooting depths. It is suggested that these last two species were able to avoid permanent wilting (at which point they would be harvested), while being ina state of acute water shortage, by virtue of the still moist Perlite at the lower fringe of their root system. This would allow more time for their FC controls to continue growth, so making the growth depression appear larger. On the other hand, the Lolium and Festuca depleted

the pipes of all available water rapidly and then suddenly reached permanent wilting point and were harvested, so allowing little time for further growth of the controls. This would give the appearance of a smaller depression in growth.

Lolium and Festuca were able to make most growth using the water they were able to extract from a 90cm profile, Dactylis rather less and Phleum least.

Table 3. Pipe Experiment 1

Dry Matter Yield of Foliage at Harvest 2 (gm)

	CF	RG	TF	T
FC	8.9	9.8	8.2	5.3
30cm pipes	4.2	4.3	3.4	3.3
FC	25.7	26.0	16.9	11.6
90cm pipes	10.7	16.5	13.0	3.9

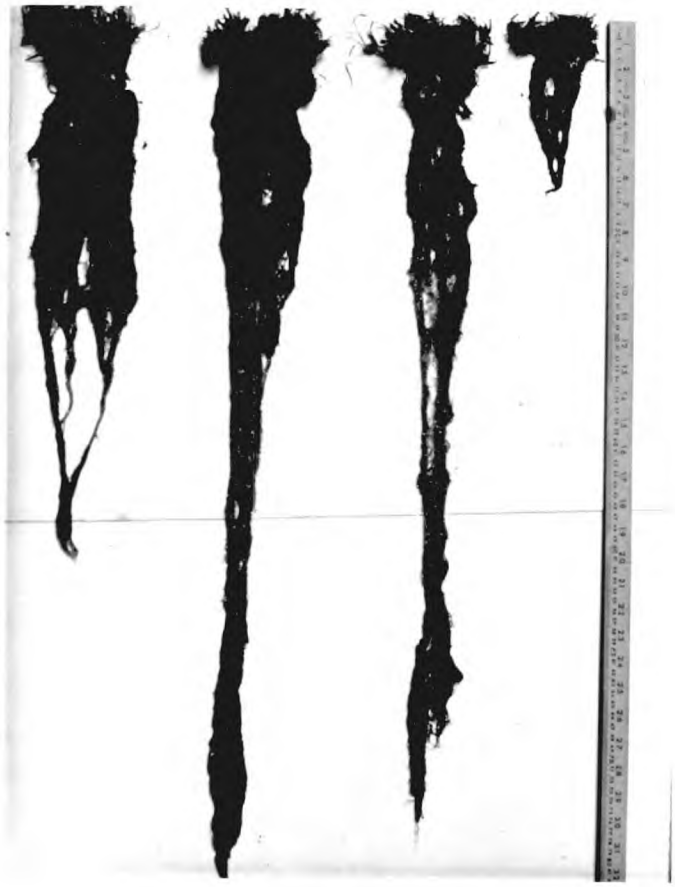
The total nitrogen uptake in the top growth (available only for the drying treatments) at the second harvest (Table 4) shows that appreciable further nitrogen uptake occurred after the top soil was dried to wilting point as shown by the wilting of the 30cm pipes and confirmed by the resistance block readings. This uptake occurred when the two deeper treatments were relying on the Perlite for water. If it can be assumed that leaching of nitrogen into the nutrient-free Perlite was negligible, this nitrogen must have come from the dry top soil.

This effect is not apparent in the case of Phleum since the harvest intervals were very close.

Table 4. Pipe Experiment 1

Total Nitrogen Uptake in Foliage at Harvest 2 (mg)

	CF	RG	TF	T
30cm pipes	146	163	127	121
60cm pipes	227	224	220	130
90cm pipes	184	269	225	118



a b c d

Plate 1

The root systems of:

a) Dactylis

b) Lolium

c) Festuca

d) Phleum

Taken from 90cm pipes, Experiment I.

The rooting pattern of the 90cm pipes is shown in Plate 1. The Dactylis, Lolium and Festuca roots had reached the bottom of all the shallower pipes. Phleum had not reached the 30 cm level. The Lolium and Festuca roots showed considerable proliferation at the bottom of the 90cm pipes and so could presumably have penetrated deeper. Dactylis penetrated to 75cm, Phleum to 20cm. Thus considerable diversity of rooting habit was shown in this experiment. These rooting patterns at wilting were parallelled by the distribution of moisture in the soil and Perlite at the end of the experiment (Table 5).

Table 5. Pipe Experiment 1

Moisture Content of Soil and Perlite in 90cm Pipes at Harvest 2 (% Volume)

		CF	RG	TF	T
Soil	0-10cm	7.8	8.6	11.6	11.7
	10-20cm	10.1	13.1	16.9	15.6
Perlite	23-60cm	20.5	7.6	11.7	23.5
	60-90cm	26.6	13.5	18.5	43.1

Dactylis was most successful in exploiting the top soil, and much less so than Lolium or Festuca in exploiting the 23-90cm depth. Phleum was least successful in extracting water from greater depths; Lolium was most successful.

This experiment showed that the pipe technique was capable of supporting growth by the grasses in a manner which appeared typical of natural conditions, while enabling much better control of the experiment than would be possible in field plots. The roots grew vertically down the pipes and showed no tendency to follow the perimeter as happens to many plants grown in containers. This might be a function of the rooting habit of grasses in that lateral spread is limited, or of the easily penetrable and well aerated nature of the soil used.

These preliminary results showed a considerable morphological difference between the root systems of the species, Phleum being particularly notable in this respect. It was decided, however, to confine further investigations to Lolium and Dactylis. Besides being the two most common agricultural grasses in this country, they are widely described as being drought susceptible and tolerant respectively.

PIPE EXPERIMENT II

The first pipe experiment had shown that drying of the top soil had a severe effect on the growth of grass.

The next experiment was designed to test the hypothesis that placement of fertilizer in deeper, moist zones of the soil might to some extemt alleviate the drought effect by increasing the nutrient availability after the top soil had dried. It was initially intended to test the response of an uncut, seedling sward but the profuse growth of the leaves in response to the fertilizer treatment made trimming necessary on one occasion during the growth period. Secondly, a more detailed comparison of the response of Lolium and Dactylis to water stress was undertaken.

Methods and Materials

The experiment was conducted in an open-sided greenhouse until 18 September, 1968, when the remaining pipes were moved to a heated greenhouse equipped with mercury vapour lighting. The degree of shading early and late in the day in the open greenhouse was considerable, and this combined with the effects of the very dull, wet weather of the late summer to cause rather low transpiration rates compared with subsequent pipe experiments, of the order of 2-4mm day^{-1}.

The experiment consisted of four randomised blocks split into three main harvests, and an initial pre-treatment harvest.

The following treatments were factorially combined.

(I) Two species a) Dactylis S37(CF) and Lolium S23(RG)

(II) Two regimes: a) Field capacity (W) in which the grasses were regularly watered to maintain the initial weight of the pipes. b) Unwatered (D) where the grass was dependent on the water present in the soil after initially being brought to field capacity. This treatment resulted in a gradually increasing degree of drought, culminating in the exhaustion of available water at a 21cm deficit.

(III) Two fertilizer placement depths: All pipes received the equivalent of 190 kg ha^{-1} of nitrogen and 40 kg ha^{-1} each of phosphorous and potassium. This was applied in $40cm^3$ of water, either as surface nutrients (NS) or as distributed nutrients (ND), achieved by placing $10cm^3$ on the surface and $10cm^3$ down each of three tubes extending to 30,60 and 90cm below the soil surface.

(IV) Three harvests: These were taken when the average water deficit in the drying pipes of each species reached 7cm (H1), 14cm (H2) and 21cm (H3). It should be noted that the two species lost water at differing rates and so their respective harvests did not coincide.

Four extra pipes of each species were utilised for an initial pre-treatment harvest (H0).

The experiment was conducted in 120cm pitch-fibre pipes standing in buckets. Each pipe was filled with Silwood sandy subsoil to 30cm from the top, followed by Silwood top soil to the top. Three glass tubes, 30, 60 and 90 cm deep were inserted in the centre of the ND treatment pipes to permit fertilizer injection.

The entire experiment was surrounded by insulation board, 120cm high, surmounted by 15cm of perforated zinc to prevent absorption of radiation by the black pipes and advective heating of the foliage.

Twenty-five seeds per pipe of Dactylis or Lolium were sown on 24 June,1968 and allowed to grow with regular watering and the occasional addition of Long Ashton culture solution in small quantities until 25 July. Then all the pipes were brought to field capacity and weighed. The fertilizer and water treatments were then imposed after the initial harvest of eight pipes.

Subsequent harvests were carried out at the prescribed deficits determined by weight loss. At Harvest 1, the luxurious top growth had become unmanageable and it was decided to defoliate the Harvest 2 and Harvest 3 pipes also and allow regrowth.

On 18 September, the Harvest 3 pipes were moved to a heated and illuminated greenhouse since transpiration rates outside had declined to a very low level.

Harvests were taken 33, 77 and 103 days after zero harvest in Dactylis and 31, 60 and 83 days after zero harvest in Lolium.

The harvest procedure was as follows: On the day prior to harvest at 10 a.m. and 3 p.m., leaf samples were taken from all the pipes to be harvested for relative turgidity measurements. At the same time, porometer readings were taken twice on three leaves of each pipe.

On the following harvest day, the pipes were weighed and the shoots were then cut at soil level. The pipe contents were extracted and the core of soil cut into sections of 30cm length. The top 30cm was further sub-divided into 15cm sections. Samples for moisture determinations were taken vertically through the centre of each core in the drying (D) pipes. The cores were soaked overnight and the roots were then washed out, dried, cleaned and weighed. The total lengths of the roots at Harvests 1 and 3 were determined by unreplicated sub-sampling for Newman's root length technique.

Sub-samples of the top growth were divided into leaf and sheath, and the areas and weights determined.

Nitrogen determinations were made on the top growth and roots, again bulking the replicates, at Harvests 1 and 3.

Results

The total dry-matter yield and its shoot and root components are shown in Table 6. There was no significant effect of fertilizer placement and so the mean of the two is used to simplify the table.

There was a significant interaction of species x water x harvest in the case of total and shoot production. The interaction was confined to water treatment x harvest in the roots though the second order interaction is also shown in Table 6 for completeness.

The production of both root and shoot was lower in the dry treatments than the controls at all harvests but did not reach significance until Harvest 3.

The total production of the two species under the dry treatment was substantially the same at a 21cm soil water deficit at Harvest 3.

The significantly higher yield of the wet Dactylis at Harvest 3 is accounted for in the longer growing period, and disappears when expressed on a daily growth basis.

Analysis showed the overall production rate of Lolium to be significantly higher than that of Dactylis.

Pipe Experiment II Table 6.

Dry-matter Production to Harvest (gm) (x 562=kg ha^{-1})

1) Total (P=0.05)

	CF		RG	
	W	D	W	D
H1	12.16	10.79	13.91	13.23
H2	17.07	15.46	19.28	18.46
H3	43.36	21.48	33.87	23.74

L.S.D.=5.48

II) Top growth (P=0.01)

H1	7.21	6.81	8.23	8.17
H2	11.34	10.44	12.68	12.41
H3	27.04	15.66	20.95	15.66

L.S.D.= 2.00

III) Root (not significant)

H1	4.95	3.97	4.41	5.06
H2	5.67	5.01	6.60	6.05
H3	16.32	5.82	12.92	8.08

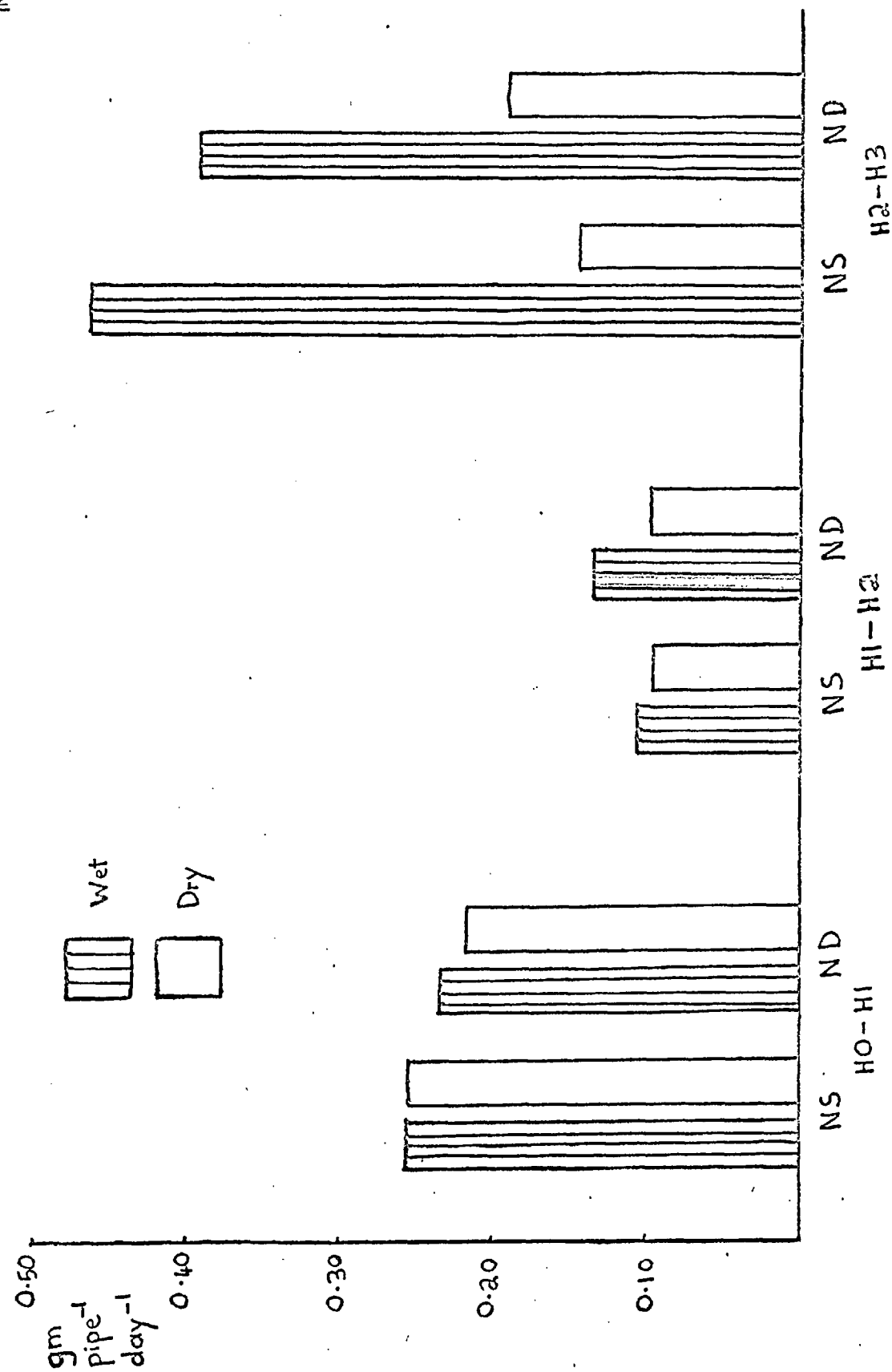
1V) Root (P=0.001)

		W	D
(Mean of the two species)	H1	4.68	4.52
	H2	6.13	5.53
	H3	14.62	6.95

L.S.D.= 2.48

The interaction between harvest, fertilizer placement and water just reached significance at the 5% level for daily dry matter production between harvests. By the time of the third harvest, deep fertilizer placement proved to be less effective than surface placement in the wet treatment and more effective in the dry (Fig.2).

Fig.2



Daily Shoot Dry Matter Production Between Harvests (Species Mean)

The total leaf and sheath area is shown in Tables 7 and 8. The interaction of water x species x fertilizer placement x harvest was significant at the 5% level, but to simplify the complexity of the interaction, the mean of the fertilizer placement treatments is given in Table 7, while the interaction of water x fertilizer placement x harvest is shown in Table 8, again significant at the 5% level.

There was an immediate decline in the area of leaf + sheath of the dry pipes relative to the wet pipes, reaching significance at Harvest 2 in Dactylis and at Harvest 3 in Lolium (Table 7).

Table 7. Pipe Experiment II

Total Sheath and Leaf Areas per Pipe (cm^2)

	CF		RG	
	W	D	W	D
H1	2208	2067	2616	2490
H2	1519	995	1219	932
H3	4084	1312	3609	1881

L.S.D.= 434

Table 8. Pipe Experiment II

Total Sheath and Leaf Areas per Pipe (cm^2)

	W		D	
	NS	ND	NS	ND
H1	2502	2321	2533	2024
H2	1213	1525	943	985
H3	4065	3628	1442	1751

L.S.D.= 434

Reference to Table 8 suggests a benefit from distribution of the ferilizer at later stages of drought, and an initial disadvantage in a manner similar to that shown by daily dry matter production, and also consistant in both species at Harvest 3. This benefit is small, however, compared with that of an ample water supply.

The relative decline in total leaf and sheath area of the dry treatments was rather greater than that in dry weight, and this can be seen in the area/weight ratios (Table 9) which decline considerably as the drying proceeds compared with the controls, suggesting a failure of the leaves to expand in proportion to their increase in weight.

Table 9. Pipe Experiment II

Area/Weight Ratios of Shoots (cm^2 gm^{-1})

	CF		RG	
	W	D	W	D
H1	287	305	323	296
H2	330	269	313	278
H3	213	155	307	264

This hypothesis is supported by the leaf/sheath weight ratios which show a significant harvest x species x water interaction at the 5% level, while harvest x water was significant at the 0.1% level and is presented in Table 10. By Harvest 2, dry-matter was clearly being stored in the sheath while the lamina failed to increase proportionately in the drying treatments.

Table 10. Pipe Experiment II

Leaf lamina Weight/Sheath Weight Ratio

	W	D
H1	2.44	2.32
H2	2.66	2.21
H3	2.33	1.71
		L.S.D.= 0.33

Lolium was notable for the rate and depth of exploration of the soil profile by the roots (Table 11).

Table 11. Pipe Experiment II

Rooting Depth of Dactylis and Lolium (cm).

	CF	RG
H1	42.8	66.4
H2	58.1	90.8
H3	80.5	104.1
		L.S.D.= 6.5cm

The root system of Lolium was considerably deeper than that of Dactylis at all times and this is reflected in the water extraction pattern of each species in the drying pipes (Fig.3). The current major zone of water extraction was always deeper in Lolium, probably a function of the denser roots at depth (Table 12). Dactylis was notable for the dense proliferation of roots in the top soil under wet conditions, though this might be partly attributed to the additional 18 days of growing period.

Table 12. Pipe Experiment II

Root Density at Harvest 3 (cm cm^{-3})

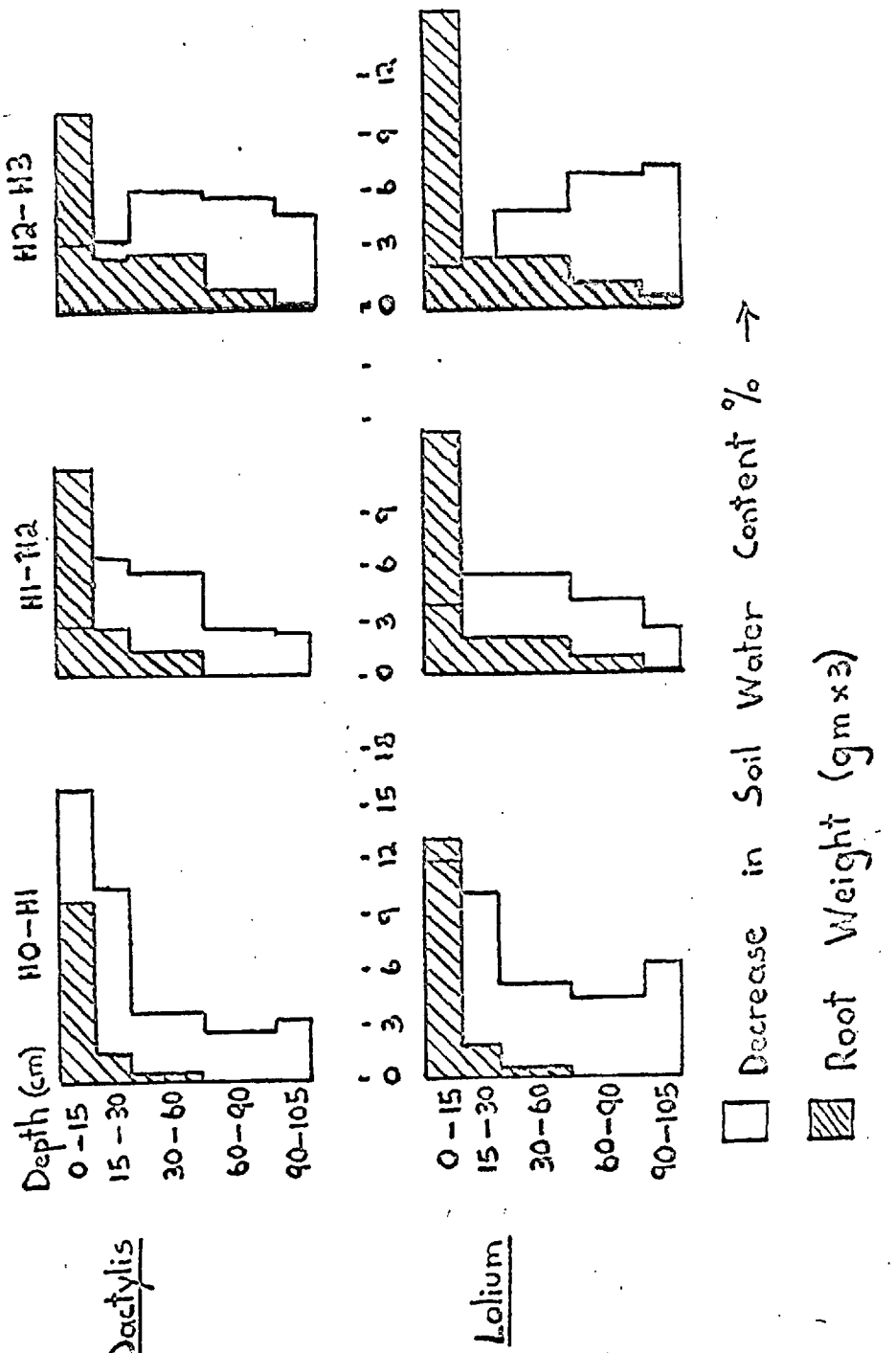
	CF		RG	
	W	D	W	D
0- 15cm	33.6	13.3	19.1	10.1
15- 30cm	12.1	7.6	11.0	7.5
30- 60cm	4.6	3.1	5.4	3.9
60- 90cm	1.5	1.3	4.9	3.9
90-105cm	0.0	0.0	3.4	3.0

The main difference between wet and dry treatments in root density occurred in the top 30cm of soil where the proliferation of roots in the dry soil was greatly reduced. A comparison of wet and dry pipes at each harvest reveals that root density had not changed appreciably since Harvest 1 in the upper regions of the dry pipes and that the rather small increase in total root weight during thisperiod might be accounted for by thickening of the upper roots and continued downward extension.

Fig.3

Water Uptake and Root Distributions in Drying Soil Profiles

(Mean of Nitrogen Placements)



There was no significant difference between the relative turgidities measured in the morning and afternoon. There was an interaction between harvest and water treatment significant at 0.1% level (Table 13a). This has been expanded to include species in Table 13b though the interaction with species was not significant. It does show, however, that relative turgidity in Dactylis appears to be the rather more sensitive to water stress.

Table 13 Pipe Experiment II

Mean Relative Turgidity of Two Species (%)

Table 13a

	W	D
H1	93.7	93.7
H2	96.1	95.7
H3	97.1	93.2

L.S.D.= 1.7

Relative Turgidity (%)

Table 13b

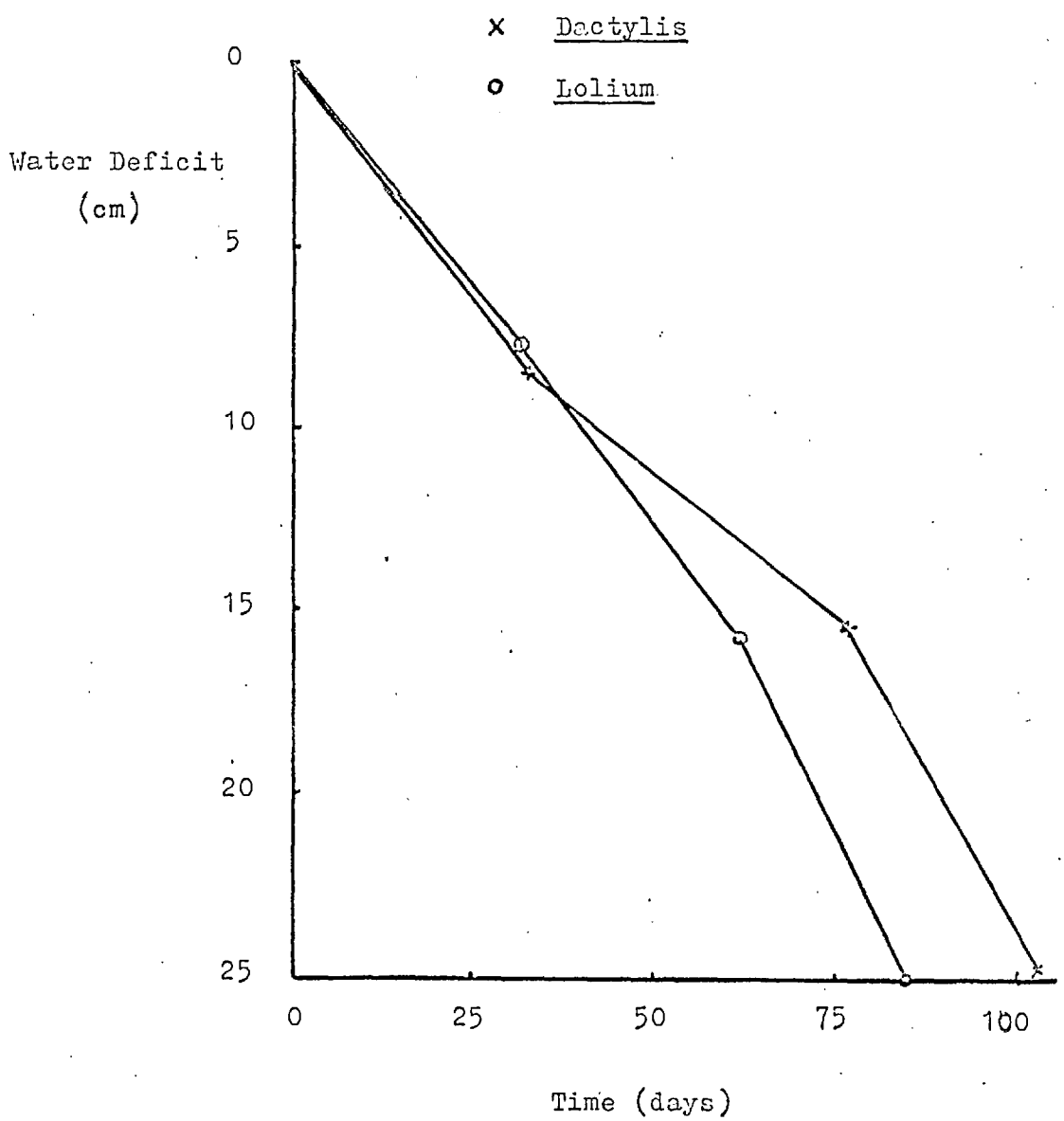
	CF		RG	
	W	D	W	D
H1	95.4	94.6	92.2	92.7
H2	97.4	95.5	94.8	95.7
H3	97.9	92.6	96.4	93.8

The measurement of stomatal diffusion rates using the diffusion porometer was not entirely successful. The apparatus was found to be extremely sensitive to temperature and often ceased to function on a cold morning. The readings must, therefore, be regarded with caution. They are not without interest, however, especially those obtained under greenhouse conditions at Harvest 3, when the readings of the controls indicated sufficient light for full stomatal opening, and the higher temperature ensured correct functioning of the apparatus.

On this third harvest occasion, the stomata of the dry Lolium were found to be still open, though less so than those of the controls. Those of Dactylis were almost entirely closed (Table 14). This is consistent with the tendency of Lolium to deplete the soil of water at a much higher rate, as shown in Fig.4, in the more advanced stages of drought.

Fig.4

Development of Water Deficit in Drying Pipes



The leaf areas (Table 7) of the two species remained similar until Harvest 2 when that of Lolium increased more rapidly to a value about 40% higher in the dry treatments at Harvest 3 than those of Dactylis Even though the ground cover was complete, if a large proportion of the heat transfer was advective, this extra leaf area might explain the difference in the rate of water use. Account must also be taken, however, of the apparent closure of Dactylis stomata at an earlier stage, combined with or related to its reduced ability to explore the profile and so reach new regions for water extraction. The rapid drying of the top soil and the continued growth of the roots to greater depths strongly suggest that extension is an important factor in continued water uptake during a drying cycle, and this is supported by the manner in which the Lolium exhausted available water supplies more rapidly, perhaps as a result of its greater rate of root extension downwards. The downward penetration of Lolium roots was, of course, limited by the depth of the pipes, and in a profile of greater depth, there seems no reason why it should not have continued root extension, so continuing to take up water and grow for the same length of time as Dactylis. The latter appeared to have commenced water economy measures at a smaller deficit, thus enabling it to grow longer, time-wise, into the drought, since it had not reached the bottom of the pipe as had Lolium.

Table 14. Pipe Experiment II

		Rate of Stomatal Diffusion*			
		CF		RG	
H1	a.m.	157	156	270	168
	p.m.	135	172	271	174
H2	a.m.	142	100	106	93
	p.m.	147	118	109	72
H3	a.m.	87	6	74	20
	p.m.	81	7	55	22

* These rates are expressed in arbitrary units calculated from the reciprocal of the time taken for a given deflection of the galvanometer needle. Comparisons cannot be made

between harvests because of changing characteristics of the apparatus due to temperature differences. The Harvest 3 readings are considered reliable because of the uniform greenhouse conditions. The results were not suitable for statistical analysis, but the close correlation between morning and afternoon values suggests considerable consistency.

The nitrogen percentage of the dry matter and the nitrogen uptake were measured separately for the tops and roots. Both showed similar responses to treatment, but the nitrogen percentage in the roots was about 50% lower than in the tops. The two species behaved similarly regarding nitrogen uptake and since the measurements were from bulked replicates, the mean uptake values in roots and tops are presented in Table 15.

Table 15. Pipe Experiment II

Total Nitrogen Uptake in Roots and Tops (kg ha^{-1})

	W		D	
	NS	ND	NS	ND
H0-H1	252	221	265	223
H0-H3	492	433	382	364

At all times, uptake from deep placement was lower than from a surface application. After the first harvest, uptake in the drying pipes fell behind that in the controls, but was still an average of 80% of the latter at Harvest 3.

The nitrogen percentage in the shoots is shown in Table 16. It should be remembered that the figure for Harvest 3 is that of the re-growth since harvest 1, for which the grass was dependent on new uptake.

Table 16. Pipe Experiment II

Nitrogen Percentage in Dry-matter

	W		D	
	NS	ND	NS	ND
Shoot H1	4.15	3.75	4.43	4.20
Shoot H3	1.98	1.81	2.50	2.50
Root H3	1.19	1.09	1.21	1.27

The dry treatments, even at Harvest 1, show an appreciably higher concentration of nitrogen than the wet ones. This difference is accentuated at Harvest 3, in the re-growth made at a deficit of between 7 and 21cm of water. Thus at no time could it be said that the dry plants were internally deficient in nitrogen, compared with the controls, despite having to grow new shoots after defoliation at Harvest 1. The nitrogen percentage in the shoots of the deep fertilized plants is less than that of the surface treated plants in three out of the four comparisons.

The nitrogen percentage in the roots did not change appreciably during the course of the experiment, and seemed virtually unaffected by treatment. This could not, therefore, have been a source of nitrogen for re-growth.

Conclusions regarding the comparative drought resistance of these two species must depend on the basis of comparison. Both were able to make a similar quantity of growth while using a fixed amount of available water in the drying treatments. Had the pipe length not limited further downward growth of Lolium roots, however, into new, untapped zones of water, then there seems no reason why it should not have continued growth as long as Dactylis and so produced more dry matter in a given time but using more water in the process. The fact that it's root system was able to explore the soil environment so much more rapidly seems responsible for the much higher rate of production of Lolium up to the limiting 21cm soil moisture deficit.

In neither species was dry matter production seriously affected by drying until a 14cm deficit had been exceeded, but the leaf area, especially of Dactylis showed signs of considerable restriction at the deficit of 7cm at Harvest 2.

There was some suggestion that distribution of the fertilizer through the profile had been of advantage both to leaf weight and area towards the end of the drying cycle in both species. The higher nitrogen percentage in the droughted plants suggested, however, that some factor other than nitrogen uptake, was largely responsible for limiting growth.

LYSIMETER EXPERIMENT I

This experiment was designed to test the response of a mature sward of each species to a drying cycle, in the vernalised and hence flowering condition. The swards were defoliated frequently and so their ability to continue to take up nitrogen as the drought intensified could also be studied.

Method and Materials

The experiment took place in the lysimeters described at the beginning of this section. The covers were put in place whenever necessary to exclude all but very light rain, and were removed in fine weather. A standard rain gauge in one lysimeter measured any rainfall they received while the covers were not in place.

The swards had been sown the previous summer and were fully established.

The design was of six blocks, each consisting of four adjacent lysimeters. Block treatments consisted of Lolium S23 (RG) and Dactylis S37 (CF) factorially combined with two methods of fertilizer application. There were insufficient lysimeters to allow a watered control treatment.

The fertilizer was a granular compound containing the equivalent of 500 kg ha^{-1} of nitrogen, 107 kg ha^{-1} of phosphorous and 208 kg ha^{-1} of potash. The lysimeters were watered to field capacity and in the surface fertilizer treatment(NS), the compound was then distributed on the surface. In the deep fertilizer treatment (ND), the fertilizer was first applied, and then the lysimeter was leached with a total of 5cm of water applied at intervals over a week. From the data of Aylmore and Mesbahul (1968), this latter treatment was calculated to leach the nitrogen component of the fertilizer into the profile to a depth of at least 30cm.

The fertilizer was applied on 21 March 1969, before growth had started in a late spring. It was observed that the heavy fertilizer dressing caused severe scorching of the leaves on the lysimeters which were not watered following its application. The herbage was cut at intervals of

7-14 days depending on the rate of regrowth until growth ceased in midsummer. Growth from the outside edges was discarded and a sample of $1m^2$ was taken from the centre of each lysimeter.

By 9 July, all growth had ceased and the tops were showing considerable wilting and scorching in the very hot weather of this period. On 17 July, the lysimeters were watered and exposed to all rainfall. On 15 August, all the resulting regrowth was harvested (H8).

The dry weight of each sample and the nitrogen content of bulked replicates of harvested material was measured.

Over the next 12 weeks, all lysimeters were watered back to field capacity and the water required was recorded.

Results

A curve of log cumulative dry weight of each treatment was fitted by the computer method of Hughes and Freeman (1967) and the L.S.D. determined for each harvest date. The fitted log data was then retransformed and plotted in Figs. 5 and 6 for each species. The yield of the fertilizer treatments differed significantly from the first harvest and continued to do so throughout on a cumulative basis. When the dry-matter production between harvests is considered, however (Figs.7 and 8), it can be seen that this cumulative difference is accounted for almost entirely by a significantly higher rate of production during the first two harvest intervals. This lower early production by the treatments which received no water after the fertilizer application can certainly be partly attributed to the severe leaf scorch which ensued. After Harvest 3, there was no advantage in the ND treatment in Lolium and only a small, non-significant advantage throughout in Dactylis. The total production of Dactylis was significantly lower than (Table 17) in Lolium, accounted for by a lower rate of production after Harvest 3. The decline in production by Dactylis was much more severe at Harvests 6 and 7 than in Lolium.

Both species responded similarly to the two fertilizer treatments and there was no significant interaction.

Fig.5

Cumulative Dry-matter Production

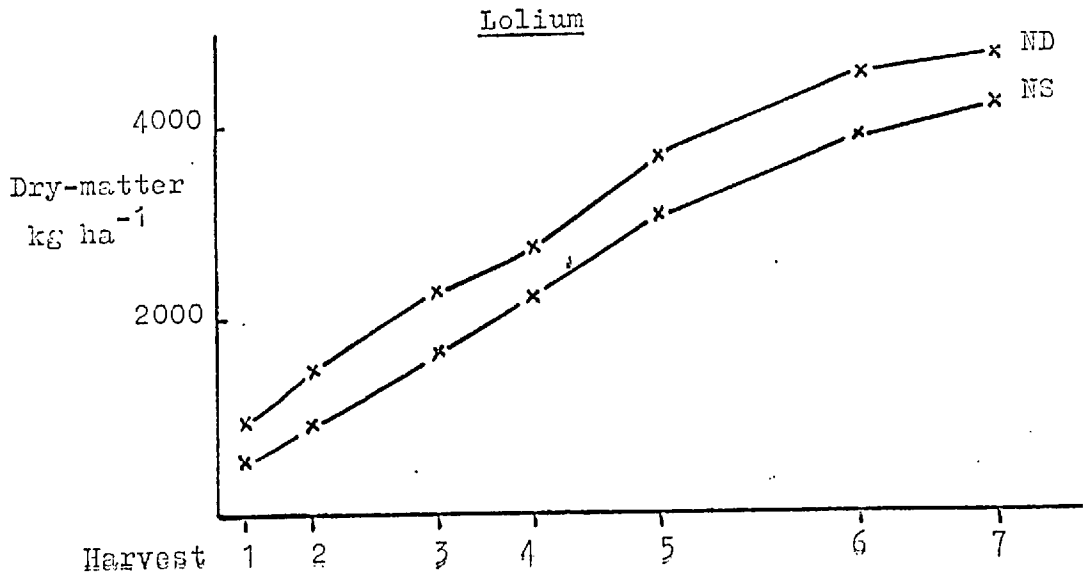
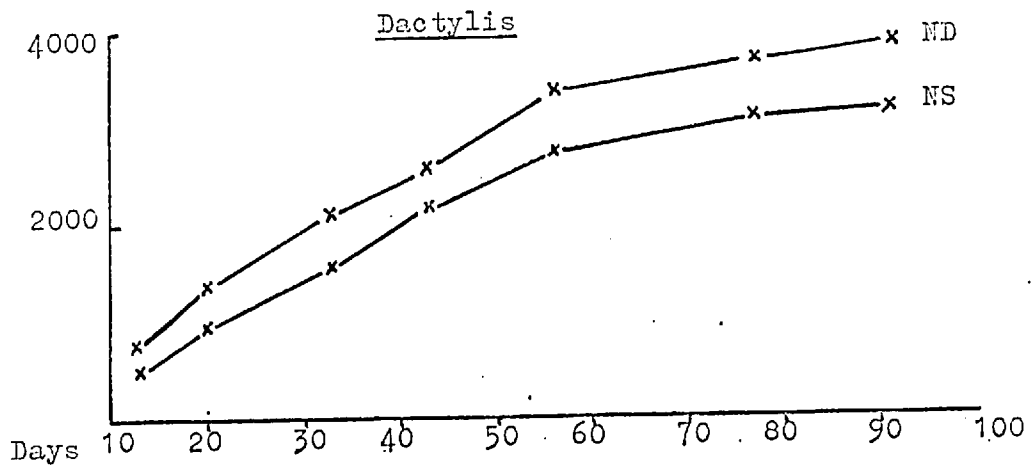
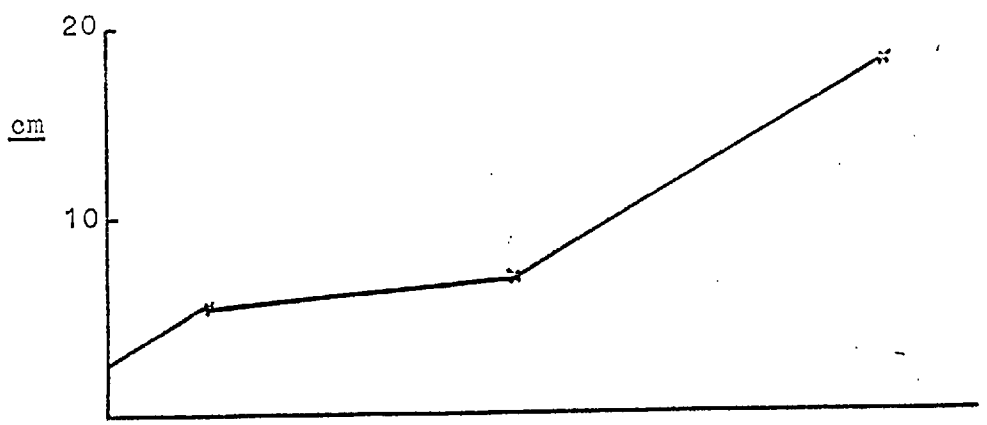


Fig.6





Calculated soil moisture deficit

Fig.7

Daily Dry-matter Production Between Harvests

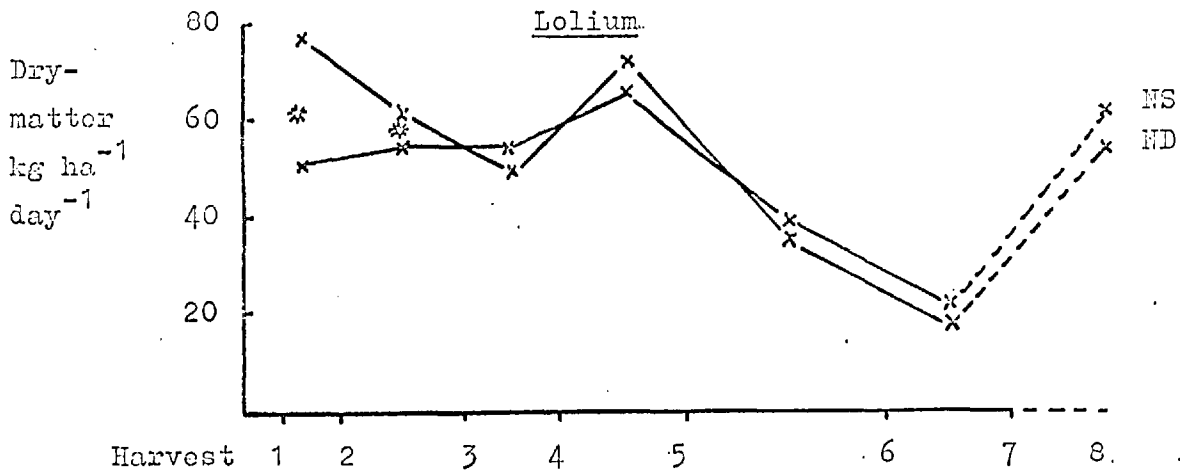
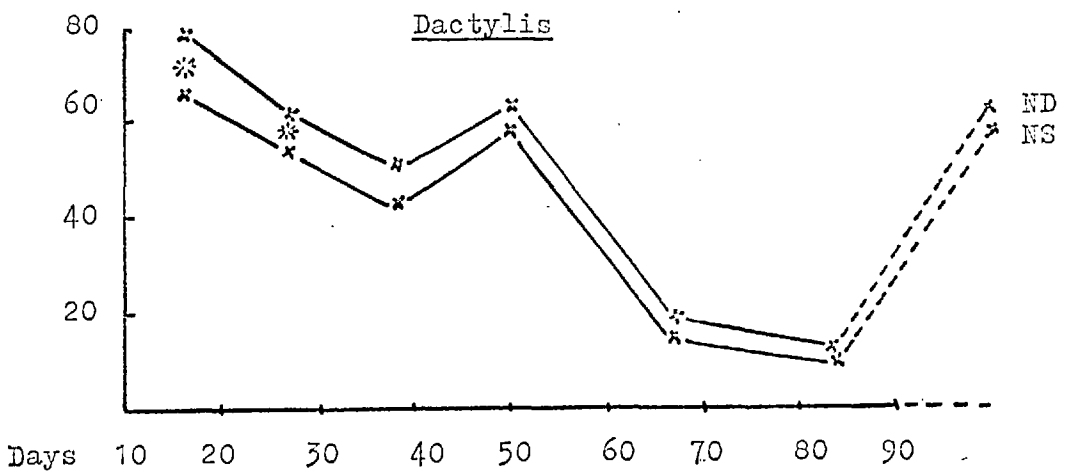
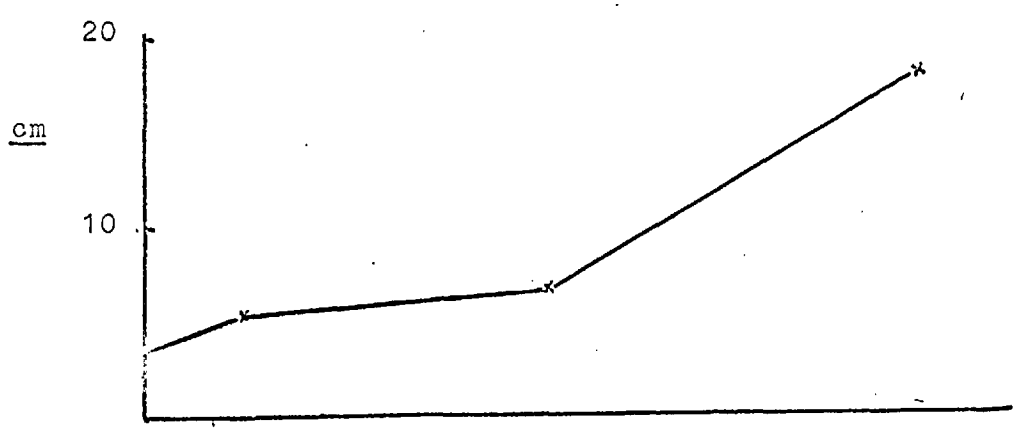


Fig.8





Calculated Soil Moisture Deficit

Lysimeter Experiment I. Table 17

Total Cumulative Dry-matter Production (kg ha^{-1})

	RG	CF
NS	4200	3190
ND	4740	3900

L.S.D.=740

Upon rewatering, all treatments returned to a rate of growth comparable with the early part of the drying cycle of 50-60 kg ha^{-1} day^{-1}.

Nitrogen was taken up at a fairly steady rate until Harvest 5 (Figs. 9 and 10) after which there was a rapid decline until growth ceased. After rewatering (Harvest 8), uptake rate rose again to a level almost corresponding to the earlier parts of the drying cycle. It can be seen from a comparison of nitrogen uptake rate and growth rate that the two are extremely closely related. The question must arise as to which is the causal factor in the relationship. The nitrogen in the NS treatment was confined to the surface of the soil, a zone which would dry in the first few days of the drought cycle. There was little indication of a serious decline in uptake until after Harvest 5, however, corresponding to a calculated water deficit of 8cm indicating the removal of available water to a depth of about 45cm.

The decline in nitrogen uptake rate did not therefore appear to be related to the drying of the surface centimetres of soil where the nitrogen was applied and so it seems unlikely that the fall in growth rate was the result of a decline in nitrogen uptake rate. It seems much more likely that some other factor was becoming an important influence in reducing the growth of the sward and this reduced growth caused a simultaneous reduction in nitrogen uptake. This is supported by the observation that the more severe decline in growth of Dactylis at Harvest 6 and 7 was accompanied by a similarly more severe fall in nitrogen uptake. It seems improbable that this might be related to some sudden difference in nitrogen availability to the two species in the surface zones where the nitrogen was located, and more likely to be due to the differing abilities of the two species to

Fig.9

Rate of Nitrogen Uptake in the Shoots

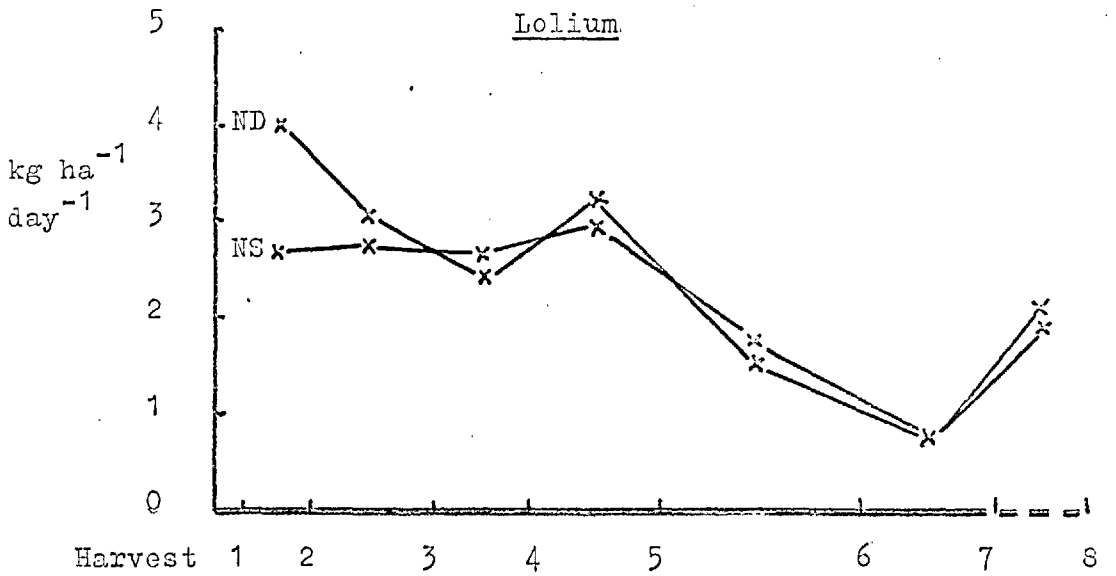
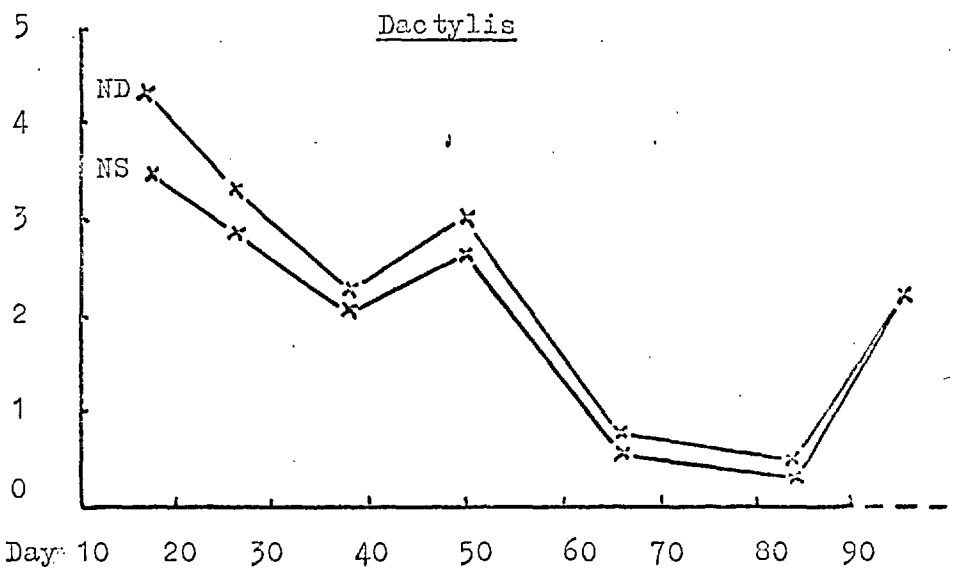


Fig.10



utilize the water at depth where it was currently being extracted, or withstand some other physiological stress.

Examination of the nitrogen percentage in the harvested growth further confirmed this view. This content was at a very high level initially (Table 18), and in spite of frequent harvesting, the regrowth was always able to maintain a nitrogen content comparable with what would be considered as a high level in the field (Whitehead, 1966).

Lysimeter Experiment I. Table 18.

Percentage Nitrogen in Dry-matter (%)

	NS	ND
H1	5.60	5.80
H2	5.25	5.35
H3	5.10	5.25
H4	4.80	4.90
H5	4.50	4.65
H6	4.30	4.35
H7	3.80	3.95
H8	3.65	3.60

The nitrogen content of the regrowth fell upon rewatering, and there was no evidence that the renewed water supply had made the possibly large residual quantity of fertilizer nitrogen available again in such a way as to restore the high tissue levels shown at the beginning of the experiment. It is possible to calculate the approximate deficit during the experiment from the local (Meteorological Office, Bracknell) figures for potential transpiration.

Rainfall and water additions required to restore the profile to field capacity after the end of the experiment were equivalent to 43cm of water. Transpiration during rewatering, assuming the potential rate, amounted to 19.1cm. Water use before rewatering commenced i.e. during the experimental period was therefore

$$43.0-19.1=23.9\text{cm}$$

This figure is similar to that for potential transpiration during the treatment period.

The actual soil moisture deficit at Harvest 7 would be less than 23.9cm by the 5.0cm of light rain that was allowed to reach the soil during the experimental period. The maximum deficit was thus 18.9cm at Harvest 7. The potential deficit after rainfall deductions for each month is plotted in Figs. 5-8.

The data obtained from this experiment suggest that Dactylis is less able to continue growth into drought conditions than Lolium, but lack of a watered control means that other effects such as that of flowering cannot be eliminated.

Both species were able to continue growth at a steady rate until a water deficit of 8cm was exceeded, when the growth of both declined rapidly, particularly in Dactylis.

Regrowth after each harvest was dependent on fresh nitrogen uptake, previous experiments having indicated that root storage was negligible, and there was no evidence that this uptake was in any way impeded by drying of the surface zones where the fertilizer was situated; rather that any decline in uptake was due to reduced internal demand. Some factor other than nitrogen shortage thus appeared to cause the decline in growth rate when an 8cm deficit was exceeded.

PIPE EXPERIMENT III

Experience gained with previous pipe experiments suggested a number of improvements to the technique.

Having established in previous experiments that nitrogen unavailability seemed of little importance compared with the effects of water stress, the former aspect was dropped from the treatments and the growth analysis approach was improved by increasing the replication and the number of harvests.

Development of a pressure apparatus with which to measure the water potential of the leaf made it possible to follow the water balance of the plant during the development of a drought in detail.

Difficulty was experienced in obtaining a subsoil from which roots could be washed easily and which at the same time did not itself contain old roots. The alternative adopted was to use Perlite which had shown itself capable of supporting fairly normal root growth when compared with a sandy subsoil, but whose water release characteristics were not known.

Method and Materials

The experiment was conducted in a trench 6m x 2m x 1.2m deep over which movable covers could be placed during rainfall. The trench ran east-west, as did the experimental blocks, thus giving an even intensity of illumination and exposure. When the pipes were in position, there was a passage along the north side for ease of access for weighing. The trench surrounds were covered in grass, and as harvests were removed, the exposed ends of the blocks were protected by a guard row.

It was hoped that this arrangement, in which the tops of the pipes were level with the surrounding grass-covered land, would reduce advective heating and give 'natural' transpiration rates.

The experimental design was similar to Pipe Experiment II with the omission of the fertilizer treatment. The two grass species (*Dactylis* and *Lolium*) were factorially combined with irrigated and drying treatments (W,D) in five randomised blocks split for five main harvests of twenty pipes each, and an initial harvest of four pipes (H0-H5).

The top 30cm of each pipe was painted white to reduce radiation absorption.

Each pipe was filled with EUP 130 grade Perlite to within 30cm of the top followed by a weighed quantity of Silwood top soil to the top.

Alongside the pitch-fibre pipes, four light-weight 'Marley' plastic drain pipes, 120 x 10cm, were similarly filled. These were light enough to be weighed on a large 'Mettler' balance to record hourly transpiration losses to 0.1gm. These pipes received the same treatment as the large pipes for the duration of the experiment and were assumed to be at the same stage of drought throughout.

Fifty seeds of either Dactylis (CF) or Lolium (RG) were sown on 4 April, 1969 after watering all the pipes to field capacity. Spring was late, emergence slow and early growth poor. The Dactylis germination was about 60% compared with 90% for Lolium. Small quantities of Long Ashton Nutrient Solution were given periodically to encourage growth. The pipes were watered regularly to maintain field capacity and on 6 June, the equivalent of 150 kg ha^{-1} of nitrogen, 32 kg ha^{-1} of phosphorous and 63 kg ha^{-1} of potash were applied in $50cm^3$ of water to each pipe. Field capacity was maintained by light watering until 19 June when the zero harvest was taken. From this date all the wet treatment pipes were watered regularly with known quantities, but it proved difficult at times to maintain field capacity since the exceptionally hot weather caused greater losses by transpiration than could easily soak into the soil. This deficit did not exceed about 4cm and it is assumed that it occurred in the Perlite of the middle zone of the pipe since water was applied to the surface.

When the grass tops reached a height at which they were unable to support themselves, a cylinder of wire-netting was put in position to maintain their vertical orientation.

A dome solarimeter recorded incident radiation until Harvest 4 when it ceased to function.

Harvests of each species were taken simultaneously, and since their water use rates differed, the deficits were different. The deficits, which reached numerically large sizes due to the large water holding capacity of the Perlite, were as follows: (cm)

	H1	H2	H3	H4	H5
Dactylis	5.4	11.7	16.2	24.9	37.9
Lolium	6.6	12.0	18.1	29.8	40.7

The deficits converged again after Harvest 4 as a result of the exhaustion of available water by Lolium before Dactylis as shown by permanent wilting of the Lolium.

The harvest procedure was as follows: The day (24 hr) prior to harvest was divided into four periods: 9 p.m. - 9 a.m.; 9 a.m.- 1 p.m.; 1 p.m.- 5 p.m.; 5 p.m.- 9 p.m.. Each of these periods corresponds to four hours of daylight. The leaf water potential of each pipe to be harvested was measured at the end of each period, using the pressure method. The stomatal aperture was measured with the diffusion porometer. The pipes were weighed at the beginning and end of the 24 hour period to measure total transpiration losses. The light 'Marley' pipes were weighed initially and after each 4 hour period and the day's total losses from the large pipes divided in the same ratio as from the small pipes. Radiation records were taken between main harvests and during the 4 hour periods.

On the following day, the grass tops were cut at the stem base and the roots were washed out in 15cm sections down the pipe after taking soil samples for moisture determination from each section in the dry pipes. The average diameter of root sub-samples was measured before drying and weighing. The length of weighed sub-samples was determined by Newman's method without replication.

After measuring the apparent leaf and sheath areas, the shoots were dried and weighed and their nitrogen contents determined along with those of the roots using the Technicon Auto-Analyser.

PIPE EXPERIMENT III

Results

The yields of dry-matter and leaf areas of both species were analysed by the computer programme of Hughes and Freeman (1967) as discussed in the section 'Experimental Techniques'.

The actual mean values and the fitted values after transformation from loge figures are shown in Table 19, where comparison shows that the computer was able to fit a cubic curve with very little deviation from the real mean points with the exception of the first three harvests of the Lolium dry treatment. Here there was an inconsistency in the progression of total and root dry weight and leaf area with time in the real data which the fitted curve eliminated.

A comparison of the L.S.D.s for the fitted loge data (Table 19) shows that the variabliity of the Lolium was considerably greater than for Dactylis.

The fitted data after transformation back to the original units shows an immediate depression in weight and leaf area of the dry treatments compared with the controls. This divergence shows a general tendency to increase with time.

The total weight of the dry Dactylis differs significantly at the 5% level from the wet control at Harvest 2, and splitting this into the component top and root weights reveals that it is largely due to a divergence in root weight which reaches significance at Harvest 3. The wet and dry top weights of Dactylis never differed significantly.

In the case of Lolium, the total weight depression was evenly distributed between the tops and roots and was non-significant throughout. This lack of significance, however, may have been due to the larger standard errors. In addition, it must be remembered that the drying cycle commenced much sooner on the growth curve of Dactylis which increased its weight by 650% during the course of the treatment compared with the 370% of Lolium and so it might be expected to have had an effect of greater magnitude on the growth of Dactylis.

Table 19. Pipe Experiment III

Dactylis Dry Weight and Leaf Area per Pipe (gm, cm^2)

		WET				DRY		
		Mean	Fitted	Log_e	Log_e L.S.D.	Log_e	Mean	Fitted
Weight								
Total	H0	10.08	10.29	2.33	0.21	2.33	10.08	10.26
	H1	17.71	17.42	2.85	0.10	2.78	16.58	16.18
	H2	24.54	24.55	3.20	0.10*	3.09	21.36	22.15
x562=	H3	29.91	30.75	3.42	0.09*	3.31	27.89	27.48
kg ha^{-1}	H4	40.98	40.37	3.69	0.13	3.58	35.90	35.96
	H5	59.95	59.92	4.09	0.13*	3.90	49.25	49.37
Shoot	H0	4.41	4.57	1.52	0.24	1.53	4.41	4.60
	H1	10.38	10.05	2.31	0.11	2.24	9.93	9.40
	H2	15.53	15.38	2.73	0.11	2.65	13.60	14.19
	H3	18.17	19.19	2.95	0.10	2.88	17.67	17.88
	H4	23.82	23.15	3.14	0.15	3.10	22.71	22.37
	H5	33.89	33.88	3.52	0.16	3.44	31.30	31.35
Root	H0	5.21	5.32	1.67	0.30	1.65	5.21	5.23
	H1	7.33	7.07	1.95	0.17	1.87	6.66	6.51
	H2	9.01	9.28	2.23	0.16	2.09	7.75	8.11
	H3	11.73	11.74	2.46	0.09*	2.28	10.22	9.84
	H4	17.16	16.90	2.82	0.19*	2.58	13.22	13.25
	H5	26.07	25.96	3.25	0.20*	2.88	17.94	17.93
Leaf	H0	869	912	6.81	0.33	6.82	869	927
Area	H1	1754	1694	7.43	0.16	7.33	1630	1535
	H2	2260	2188	7.68	0.15	7.57	1966	1954
x56=	H3	2123	2344	7.75	0.13	7.67	1964	2153
m^2ha^{-1}	H4	2329	2223	7.70	0.21	7.68	2262	2173
	H5	2437	2449	7.80	0.22	7.61	2025	2042

		Wet	Dry
Leaf Area Index	H0	4.82	4.82
	H1	9.74	9.05
	H2	12.55	10.92
	H3	11.79	10.91
	H4	12.93	12.56
	H5	13.53	11.25

Table 19. Pipe Experiment III

Lolium Dry Weight and Leaf Area per Pipe (gm, cm^2)

		WET				DRY		
Weight		Mean	Fitted	Log_e	Log_e L.S.D.	Log_e	Mean	Fitted
Total	H0	16.09	17.06	2.83	0.38	2.88	16.09	17.90
	H1	28.93	26.63	3.28	0.18	3.20	28.74	24.52
x562=	H2	32.09	34.38	3.53	0.17	3.42	27.16	30.83
kg ha^{-1}	H3	39.68	39.77	3.68	0.16	3.59	36.02	36.31
	H4	47.67	46.50	3.84	0.22	3.80	46.68	44.80
	H5	65.81	66.01	4.19	0.26	4.01	55.05	55.52
Shoot	H0	6.15	6.53	1.88	0.38	1.95	6.15	7.06
	H1	13.82	12.75	2.54	0.18	2.46	14.19	11.76
	H2	16.68	17.88	2.88	0.18	2.77	14.20	15.97
	H3	20.73	20.95	3.04	0.15	2.95	18.15	19.09
	H4	23.98	23.32	3.15	0.24	3.12	24.23	22.70
	H5	30.93	31.01	3.43	0.25	3.28	26.32	26.56
Root	H0	9.94	10.59	2.36	0.43	2.38	9.94	10.79
	H1	15.11	13.70	2.61	0.20	2.53	14.54	12.61
	H2	15.42	16.46	2.80	0.19	2.70	12.96	14.86
	H3	18.75	18.84	2.93	0.18	2.84	17.87	17.24
	H4	23.69	23.01	3.13	0.27	3.08	22.47	21.89
	H5	34.88	34.94	3.55	0.29	3.36	28.73	28.89
Leaf	H0	1045	1054	6.95	0.41	7.06	1045	1167
Area	H1	2165	2133	7.66	0.21	7.48	2069	1786
	H2	2698	2793	7.93	0.18*	7.73	2043	2296
x56=	H3	3002	2944	7.98	0.20	7.86	2545	2618
m^2ha^{-1}	H4	2669	2679	7.89	0.33	7.93	2950	2812
	H5	3279	3289	8.09	0.37*	7.64	2096	2094

		Wet	Dry
Leaf Area Index	H0	5.80	5.80
	H1	12.02	11.49
	H2	14.98	11.35
	H3	16.67	11.13
	H4	14.81	16.38
	H5	18.21	11.64

The apparent leaf area of the drying treatments of both species fell below the controls by Harvest 1, but became significant only in Lolium. At Harvest 5, it was largely attributable to the rolling of the leaves as the plants wilted, so causing a large decrease in apparent leaf area. The significant difference at Harvest 2 which is not confirmed at subsequent harvests may be fortuitous in view of the discrepencies already discussed in the data at this period. It thus seems unlikely that the true leaf area of either species was significantly lower in the dry treatments than in the controls.

The net assimilation rate of both species as computed from the fitted data is shown in Fig. 11. The L.S.D.s are included for Dactylis, those of Lolium being larger in every case. The dry treatments did not deviate significantly from the controls in either species, though the rapid separation of the curves at Harvest 5 suggests that this might soon have been the case had the plants continued in the wilted condition.

Root growth followed a similar pattern in the Perlite to that found in the subsoil of Pipe Experiment II (thus confirming that Perlite did not induce any serious abnormality in rooting behaviour). Lolium roots reached the bottom of the pipe by Harvest 2, Dactylis roots did so at Harvest 5.

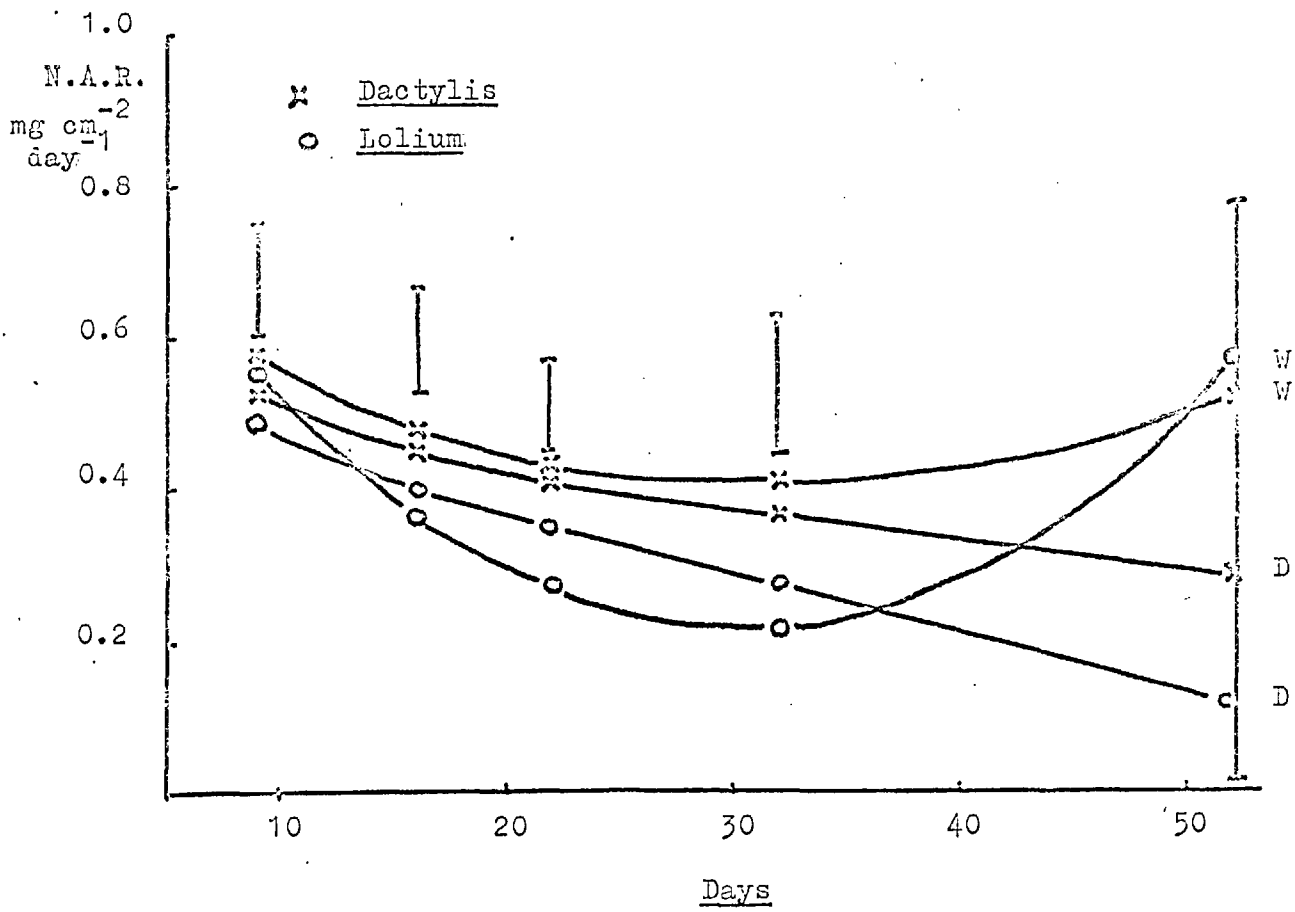
Statistical analysis of the root weights in each zone at each harvest was not possible because of the absence of roots in several zones, especially at earlier harvests. Analysis was therefore confined to the final harvest when all zones were occupied. Lolium produced a significantly greater weight of root than Dactylis, but there was no difference in the way they responded to water. There was an interaction both of species and of water treatment with depth, both significant at the 0.1% level (Tables 19a, 19b).

While the root weight was significantly below the controls in the top 15cm zone of the dry pipes, there was little difference between 15 and 45cm, then at all depths below 45cm, the root weight was greater in the dry pipes.

The greater root weight of Lolium was most pronounced near the surface, possibly because of a greater plant density, and also below the 75cm level. There was little difference in the middle zones.

Fig.11

Fitted Net Assimilation Rates (indicating L.S.D.for Dactylis only)



Tables 19a,b. Pipe Experiment III

Root Weight of 15cm Zones (Log_{10} x 100)

19a

	Wet	Dry
1	3.21	2.86
2	2.69	2.68
3	2.28	2.27
4	2.24	2.31
5	2.22	2.31
6	2.09	2.26
7	1.96	2.15
8	1.85	1.89

L.S.D.=0.1

19b

	CF	RG
1	2.94	3.14
2	2.62	2.76
3	2.28	2.27
4	2.27	2.28
5	2.23	2.31
6	2.10	2.26
7	1.85	2.26
8	1.47	2.27

L.S.D.=0.1

The root density was calculated from unreplicated subsamples and so statistical analysis was not possible (Table 20). The final density was two to three times greater than in Pipe Experiment II, probably because better environmental conditions and more available water caused more vigorous growth. At intermediate harvests, however, when the root density in the top soil of the two experiments was comparable, then the root density in the Perlite was also comparable with that in the subsoil.

The root density of the dry treatments became increasingly less than that of the controls as the soil dried. This difference was confined largely to the two upper horizons, especially the surface 15cm where the increase in density during the course of the experiment was relatively small in the dry treatments compared with the increase in the controls in this horizon.

The root density was similar in the two species, though the accumulation of roots in the lowest horizon in Lolium may indicate an ability to extend even deeper.

Analysis of the leaf water potential data showed an interaction of harvest x water x species x time of day, significant at the 5% level (Fig12). For clarity, this has been simplified into lower order interactions, all significant at the 0.1% level (Figs.13 14, 15).

Table 20. Pipe Experiment III

Mean Root Density in 15cm Zones (cm cm^{-3})

	Horizon	H0	H1	H2	H3	H4	H5
Dactylis Wet	1	23.6	29.1	35.3	42.1	62.5	95.3
	2	8.0	12.5	15.5	22.1	36.7	56.2
	3	1.4	3.2	4.6	6.1	7.2	15.0
	4	0.1	0.4	1.7	4.7	7.1	14.0
	5	-	-	0.2	1.7	4.9	12.2
	6	-	-	-	0.1	1.6	8.3
	7	-	-	-	-	0.2	5.1
	8	-	-	-	-	-	4.2
Dactylis Dry	1	23.6	23.2	25.7	30.1	34.2	33.4
	2	8.0	14.0	13.0	16.6	19.2	23.8
	3	1.4	3.1	4.9	6.5	7.3	10.8
	4	0.1	0.5	2.2	4.8	7.3	11.1
	5	-	-	0.4	1.5	5.0	10.6
	6	-	-	-	0.2	2.0	9.1
	7	-	-	-	-	0.2	5.6
	8	-	-	-	-	-	3.4
Lolium Wet	1	34.3	45.0	46.3	54.9	69.7	112.2
	2	6.2	26.5	24.4	34.0	40.0	56.4
	3	2.9	4.9	4.1	5.3	6.1	6.8
	4	1.6	3.4	3.9	4.9	6.0	6.0
	5	0.7	2.2	3.4	4.9	6.0	6.5
	6	0.1	0.7	2.0	3.6	5.5	5.5
	7	-	-	0.6	1.8	5.2	5.5
	8	-	-	0.1	0.4	6.7	11.9
Lolium Dry	1	34.3	55.7	41.4	48.9	49.0	42.6
	2	6.2	21.0	20.3	25.2	30.2	40.2
	3	2.9	3.5	3.4	5.7	6.0	5.8
	4	1.6	2.6	3.3	5.3	6.0	6.8
	5	0.7	2.0	2.8	5.0	6.3	7.3
	6	0.1	0.8	1.4	4.4	6.0	6.9
	7	-	0.1	0.4	2.3	6.1	6.9
	8	-	-	0.1	0.8	6.2	13.8

Daily Course of Leaf Water Potential during a Drying Cycle

o Wet
× Dry

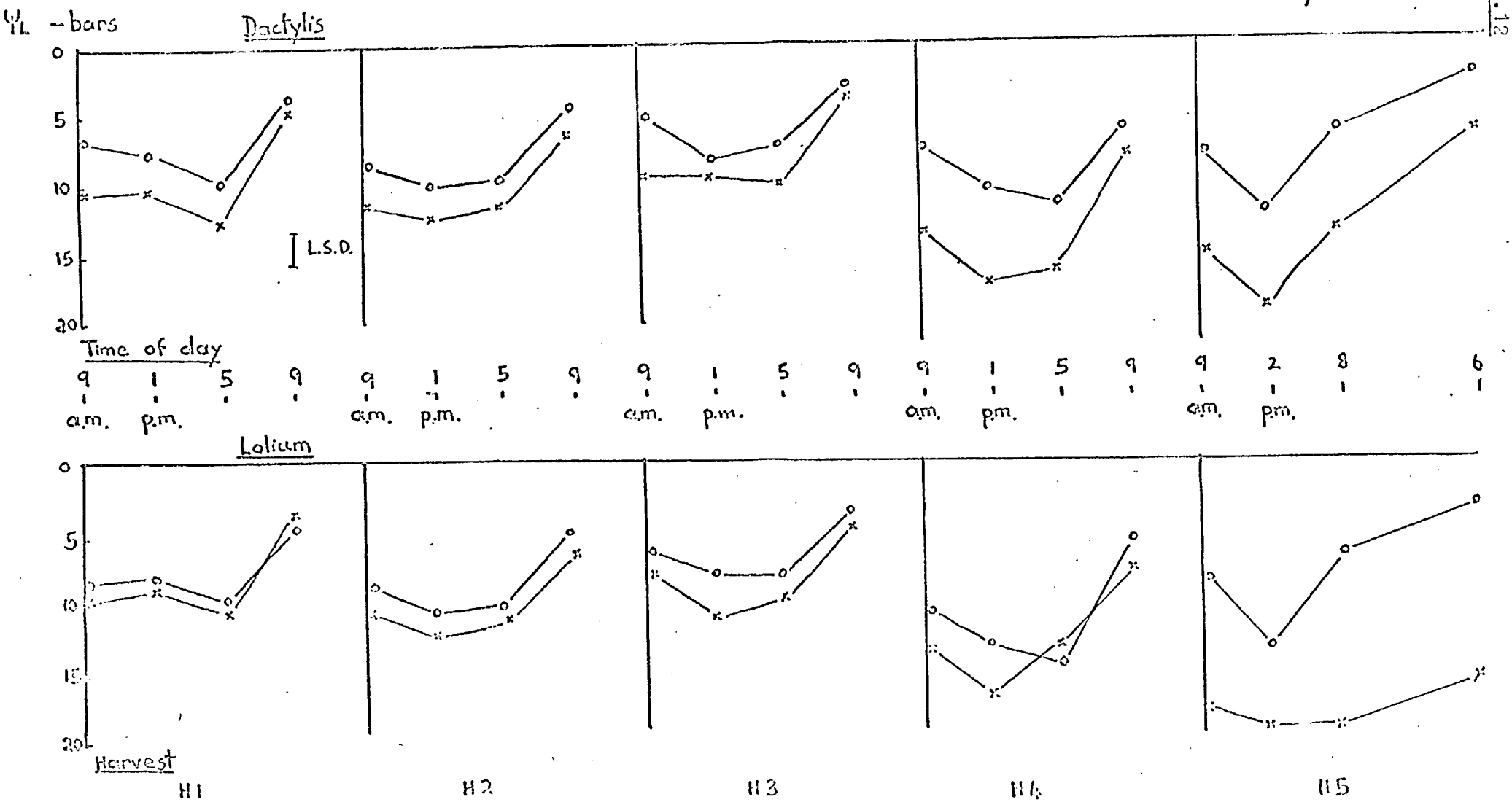


Fig.13

Daily Course of Leaf Water Potential in Wet and Dry Treatments

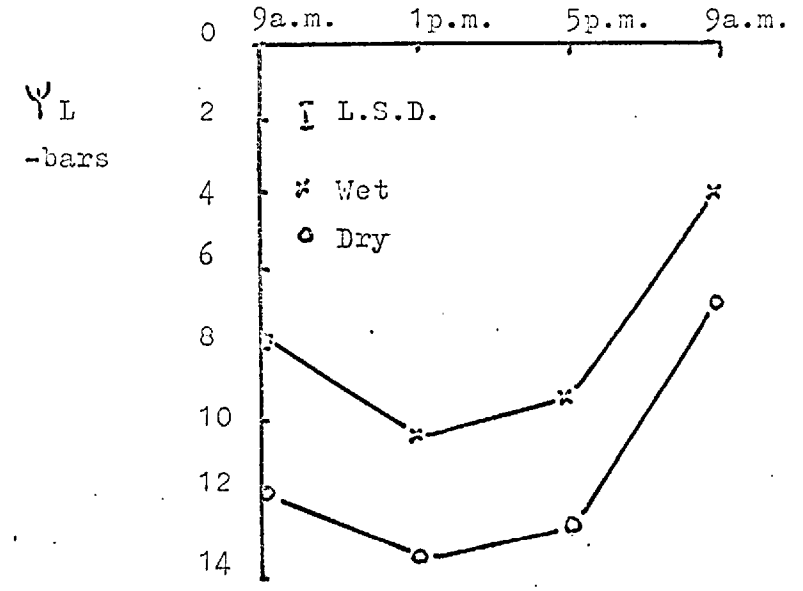


Fig.14

Mean Daily Leaf Water Potential during Course of Drying Cycle

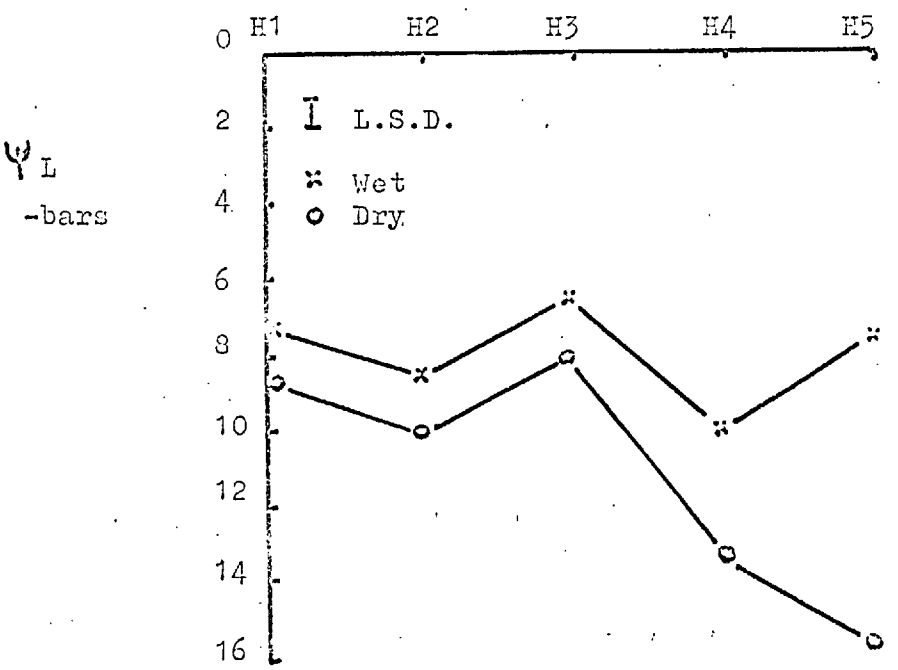


Fig.15

Mean Daily Leaf Water Potential during the Course of a Drying Cycle

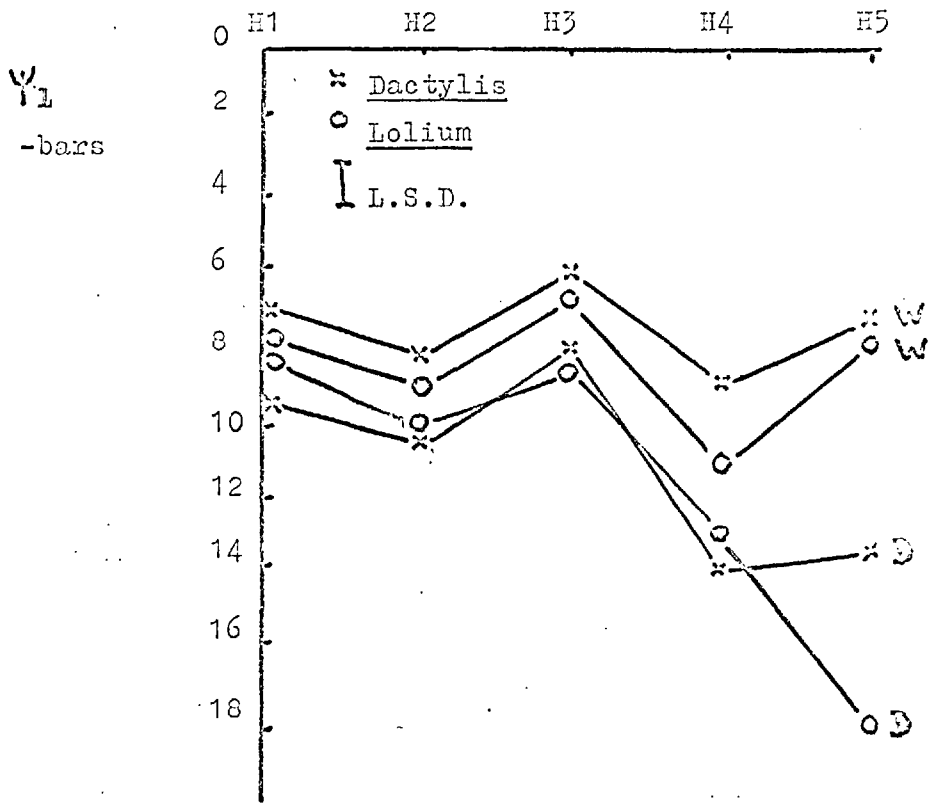
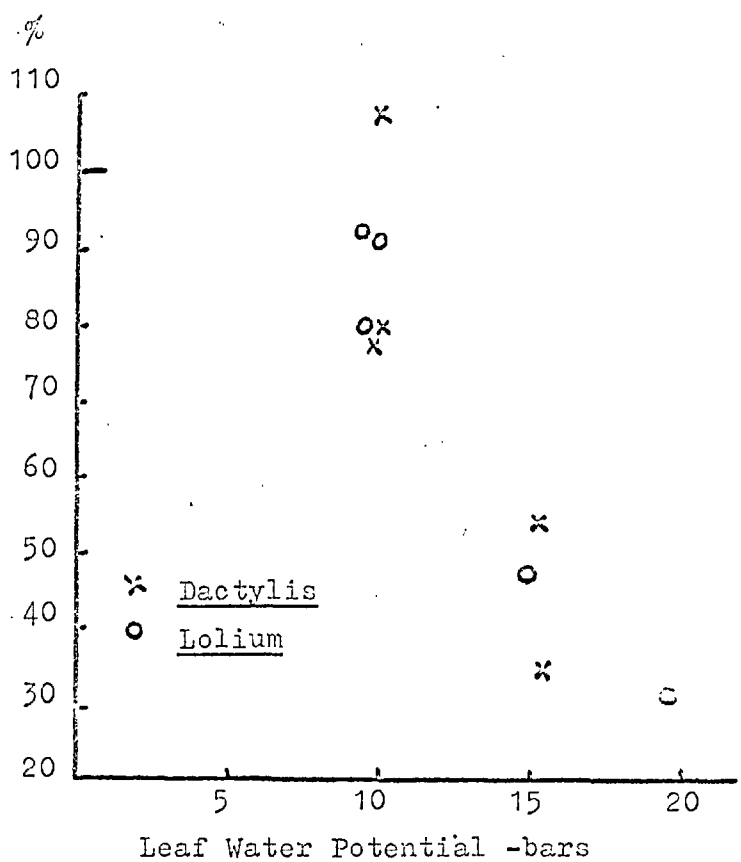


Fig.16

$$\frac{\text{Dry Treatment Stomatal Diffusion Rate}}{\text{Wet Treatment Stomatal Diffusion Rate}} \times 100$$



The daily march of leaf potential is shown in Fig.13. The wet and dry treatments did not show any significant interaction with time of day. The potential was closely correlated with radiation and by 9a.m. had shown an appreciable fall from night-time levels if these can be assumed to be above those at 9p.m. on the same day. The potential fell rapidly to peak with the radiation levels, as measured by the solarimeter, around mid-day and then rose again particularly rapidly as the sun was setting. Measurements taken at Harvest 5 (Fig 12) at 6a.m. showed that levels of -2 to -3 bars were attained by the controls during the night, and individual leaves gave readings of virtually zero. Wilting, particularly in Lolium , was observed when the potential fell below -15 bars. Lolium exhibited permanent wilting at Harvest 5 in the dry treatment and failed to recover during the night (Fig 12).

The potential of the wet and dry treatments at successive harvests is illustrated in Fig 14. The potentials remained parallel until Harvest 3 after which a significant divergence had developed by Harvest 4 and this increased rapidly to Harvest 5.

The behaviour of the individual species can be examined in Fig 15. This must be considered in the light of the more rapid use of water by Lolium, whose soil water deficit was greater than that of Dactylis by about 5 cm at Harvest 4 and 3cm at Harvest 5.

From Harvest 1, Dactylis showed signs of being more sensitive to the increasing water deficit, and this became most marked at Harvest 4, inspite of the higher soil water deficit of Lolium. Their behaviour after Harvest 4 can be explained by the exhaustion of available water supplies by Lolium and subsequent permanent wilting, whereas several centimetres of water were still available to Dactylis which had not extended its root system to the bottom of the pipe until Harvest 5.

The diffusion porometer did not prove entirely reliable again, though the sensitivity to temperature had been partly corrected. A considerable number of measurements of stomatal diffusion were obtained, however, at various times during the course of the pre-harvest day on each harvest occasion.

These readings are given after averaging over the course of a day in Table 21, expressed in arbitrary units as in Pipe Experiment II.

Since leaf water potentials were measured simultaneously, these could be related to stomatal diffusion rates. The water potential of the dry treatments is plotted against the diffusion rate from the dry treatment expressed as a percentage of that from the controls for each harvest in Fig.17. This suggests that stomatal control starts to operate when leaf water potential falls below about -10 bars in both species.

Examination of the porometer data suggests that an appreciable degree of stomatal restriction had begun to appear by Harvest 4. This coincides with a fall in leaf potential to -10 to -15 bars. There is little indication of a major difference between the two species, bearing in mind that the soil water deficit of Lolium was the greater by about 5cm at Harvest 4, while its stomata appear wider open. By Harvest 5, the exhaustion of available water by Lolium had resulted in permanent wilting and presumably almost complete stomatal closure, whereas Dactylis was still able to regain turgor during the night.

Table 21. Pipe Experiment III

Mean Daily Stomatal Diffusion Rates*

	CF,W	CF,D	RG,W	RG,D
H1	156	124	135	125
H2	164	177	185	169
H3	167	130	106	83
H4	93	32	177	86
H5	103	56	143	45

* See Pipe Experiment II

As in previous pipe experiments, the rate of water use from the drying Lolium pipes exceeded that of Dactylis, reaching a difference in the accumulated deficit of nearly 5cm by Harvest 4, then declining again as Lolium reached permanent wilting point first.

Since the difference in leaf area between wet and dry treatments did not reach significance except in Lolium at Harvest 5, it is possible to confirm the point of stomatal restriction of transpiration by plotting the water loss from the dry treatments as a percentage of that from the wet (Fig. 17). No precautions had been taken to prevent water loss from the soil surface, however, and this could give rise to considerable differences as the topsoil of the drying treatments dried. Exploratory experiments were therefore performed in which water loss from a pipe with a wet soil surface under grass was compared with that from a pipe with a surface which had been waxed. The wax treatment restricted water loss to about 60% of the control.

It is, therefore suggested that the initial depressson in water use by the drying pipes relative to the controls occurred as a result of falling water loss from the soil surface of the drying pipes. Once the surface had dried, the level of about 60% was maintained until after Harvest 4 when there was a sudden rapid decline. This corresponds to the indication of relative stomatal restriction shown by the porometer readings and also to the fact that it was at Harvest 4 that the leaf potentials of the dry treatments first began to fall appreciably below -10 to -15 bars (Fig.12) for part of the day. It thus appears that these two species are able to withstand a substantial drop in leaf potential to a figure approaching -15 bars before there is any marked stomatal restriction.

Water loss from the drying Lolium was less restricted compared with controls than in Dactylis throughout (Fig.17) until the wilting of Lolium at Harvest 5 caused a convergence. This difference is not apparent in the porometer data.

The nitrogen content of the top growth was generally slightly higher in the dry treatments (Table 22). The difference in the roots was negligible. There was no suggestion of a difference between species.

Table 22. Pipe Experiment III

Nitrogen Percentage of Shoots (Mean of both species)

	H0	H1	H2	H3	H4	H5
Wet	2.55	1.90	1.60	1.40	1.10	1.05
Dry	2.55	2.00	1.65	1.50	1.25	1.15

Fig. 17

Water Use of Two Species

Relative to Controls

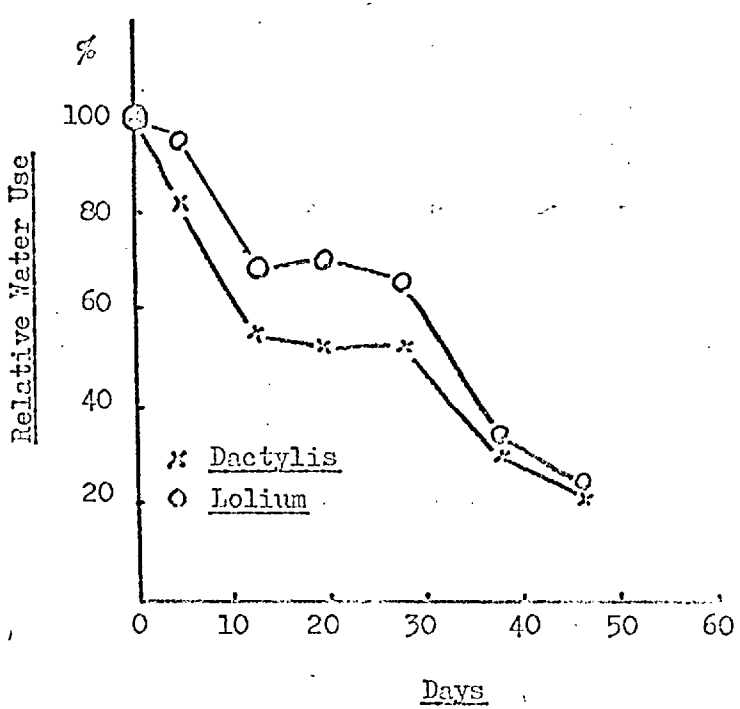
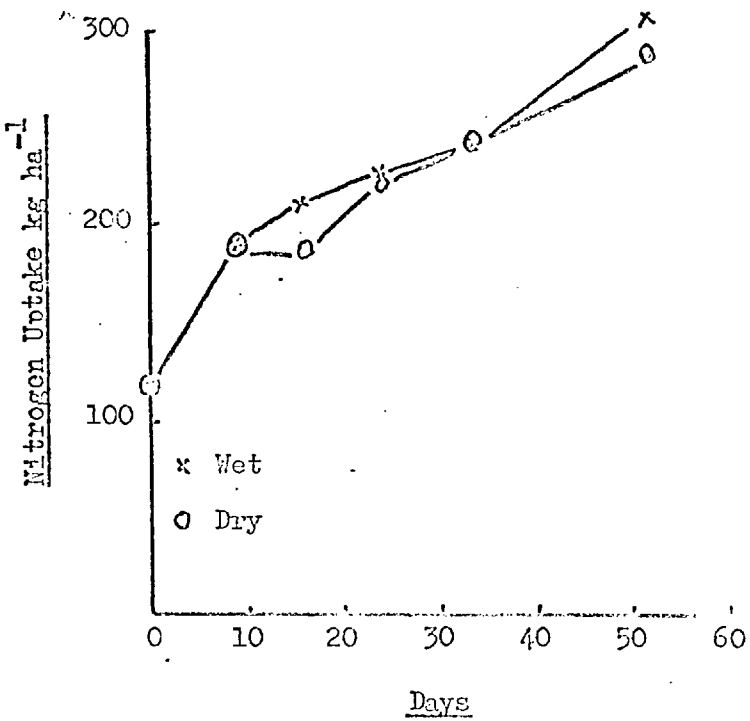


Fig. 18

Total Nitrogen Uptake,

Root and Shoots



The level in the roots was about 50% of that in the tops.

The total recovery of nitrogen in roots and tops is plotted in Fig. 18. There is little suggestion that the wet treatment differed significantly from the dry. Nitrogen uptake continued throughout the experiment and approximately trebled in this time. There is no evidence that drying of the topsoil at an early stage had restricted nitrogen uptake in the dry treatments, assuming that this is where most of the nitrogen was located.

The most surprising outcome of the experiment was the small effect of water stress on all aspects of growth. All were affected at a very early stage but by a relatively small amount throughout. The apparently greater susceptibility of Dactylis might well be explained by the imposition of the treatment at a relatively earlier stage in its growth cycle. It was notable in both species, especially in Dactylis, that little further root growth occurred in the top 30cm when this region had dried.

The data on the water balance of the plants was of particular interest, and calculations based on this are presented in a later section.

The magnitude and rapidity of the changes in leaf potential with changing radiation levels were most notable. Even at the earliest stages of stress the potential diverged from the controls and fell towards the wilting point at mid-day. The stomata seemed virtually unaffected until wilting point was approached. The two species showed little difference in this respect, though there was some suggestion that Dactylis showed a rather greater sensitivity, perhaps as a result of its less well developed root system.

It seemed unlikely that nitrogen unavailability in the dry top soil was of any significance.

PIPE EXPERIMENT IV

The previous pipe experiment showed little significant difference between Dactylis and Lolium in their growth response to water stress

It was decided, therefore, to confine this experiment to the former species which showed greater uniformity and was not so restricted in rooting by the limited depth of the pipes.

The purposes of the experiment were twofold. Study of the water balance was previously done in Perlite which had rather unusual water release characteristics. It was felt desirable to repeat this water balance analysis in normal soil and the results are reported in a later section.

Secondly, the experiment was designed to study in detail the failure of roots to develop in dry top soil; and to confirm the suggestion of the previous experiment that root development was more seriously affected than top growth by drought in an establishing sward.

Method and Materials

The experiment was conducted in a heated greenhouse using mercury vapour lights to increase illumination. This was sufficient to give a transpiration rate of 5-6mm day^{-1}.

The experimental design consisted of three randomised blocks, each of six pipes, plus an additional two pipes for a pre-treatment harvest, H0.

Each block contained three pairs of pipes, one pair for each of three harvests (H1, H2, H3) in a split plot layout. Field capacity (W) and drying treatments (D) were applied to each pair as in previous pipe experiments.

120x15cm pipes were filled with Silwood sandy subsoil followed by a 30cm surface zone of Silwood top soil. After watering to field capacity, each was sown with 30 seeds of Dactylis, S37 in August 1969. Field capacity was maintained until 18 October when the initial harvest (H0) was taken and the drying treatment commenced. The remaining harvests were taken after 16, 29 and 43 days at deficits in the dry pipes of 9.3cm (H1), 14.0cm (H2), and 18.8cm (H3).

The final plant density was approximately 25 per pipe.

The leaves were maintained in a vertical position by wire-netting tubes as in the previous pipe experiment.

The harvest procedure was also similar. The leaf water potentials were measured at 10a.m., 1p.m. and 4p.m. during which time there was little change since the main contribution to radiation came from the lights. The pipes were weighed at the first and last of these times and the 6 hour weight loss calculated.

The six pipes were then opened and the contents extracted in 15cm horizons from which samples for soil moisture determination were taken in the dry pipes. The roots were then washed out, dried after measuring the average diameter of some samples, and then the length of subsamples was determined by Newman's method.

The shoots were cut off at the base, the apparent leaf areas measured, and then dried and weighed and separated into tillers and main shoots. The nitrogen content of each was measured with the Auto-analyser. The number of main root axes leaving the base of the plants was counted and the weights and areas of the main shoots and tillers were determined separately. A careful comparison was made of the type of root and tiller development in the wet and dry treatments.

Results

The computer method of Hughes and Freeman (1967) was again used to analyse the results. The fitted log values of total dry weight, top and root weight, and leaf area, with the appropriate Log. L.S.D.s are presented in Table 23. The real mean data and the fitted data after transformation back from the log values are also shown. The fitted, retransformed data are plotted in Figs. 19 and 20.

As in previous experiments, the weights and leaf area fell below those of the controls as soon as drying commenced. The total weight and that of the roots in the dry treatments almost reached a significant depression at Harvest 2 and did so at Harvest 3. The depression in the dry treatment shoots compared with controls never approached significance. Thus the lower total dry weight is accounted for largely by a lower root weight.

Table 23. Pipe Experiment IV

Dactylis Dry Weights and Leaf Areasper Pipe
(gm, cm^2)

		WET				DRY		
					Log_e			
Weight		Mean	Fitted	Log_e	L.S.D.	Log_e	Mean	Fitted
Total	H0	7.15	7.10	1.96	-	1.96	7.15	7.10
	H1	14.78	14.76	2.69	0.20	2.59	13.26	13.24
x562=	H2	21.30	21.33	3.06	0.20	2.87	17.87	17.70
kg ha^{-1}	H3	26.75	26.79	3.29	0.20*	3.07	21.67	21.63
Top	H0	4.30	4.30	1.46	-	1.46	4.30	4.30
	H1	9.05	9.04	2.20	0.35	2.14	8.53	8.50
	H2	13.39	13.40	2.59	0.35	2.47	12.01	11.82
	H3	17.40	17.42	2.86	0.35	2.70	15.03	14.93
Root	H0	2.85	2.79	1.03	-	1.03	2.85	2.79
	H1	5.73	5.73	1.74	0.35	1.55	4.73	4.73
	H2	7.91	7.91	2.07	0.35	1.76	5.86	5.84
	H3	9.36	9.38	2.24	0.35*	1.89	6.63	6.64
Leaf	H0	1182	1191	7.07	-	7.07	1182	1191
Area	H1	1438	1457	7.28	0.27	7.19	1334	1334
x56=	H2	2192	2193	7.69	0.27*	7.36	1594	1578
m^2ha^{-1}	H3	2164	2161	7.68	0.27*	7.39	1635	1626

		Wet	Dry
Leaf Area Index	H0	6.56	6.56
	H1	7.98	7.41
	H2	12.17	8.85
	H3	12.02	9.08

Fig.19

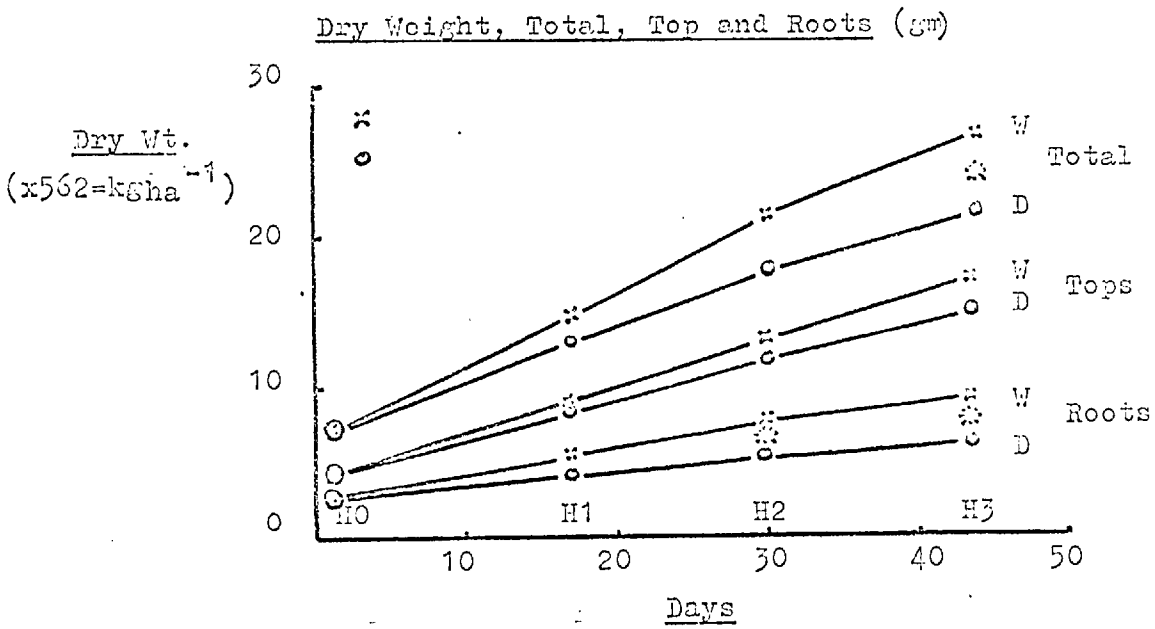

Dry Weight, Total, Top and Roots (gm)
Dry Wt.
(x562=kgha⁻¹)
30
20
10
0
W
D
Total
W
D
Tops
W
D
Roots
H0
H1
H2
H3
10
20
30
40
50
Days

Fig.20

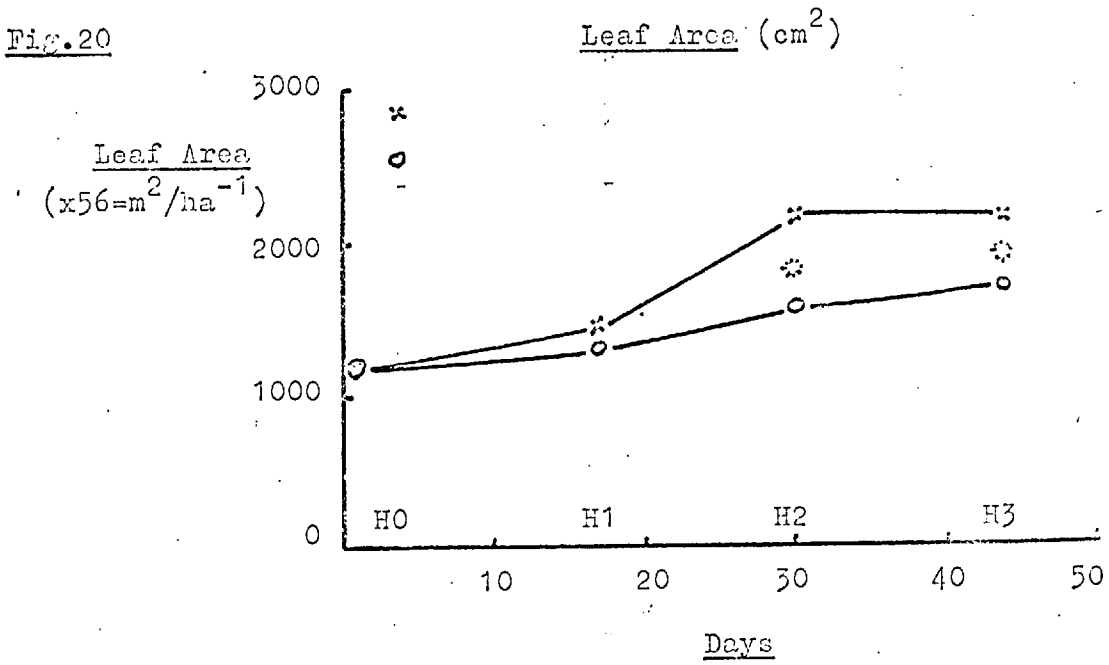

Leaf Area (cm²)
Leaf Area
(x56=m²/ha⁻¹)
3000
2000
1000
0
H0
H1
H2
H3
10
20
30
40
50
Days

Fig.21

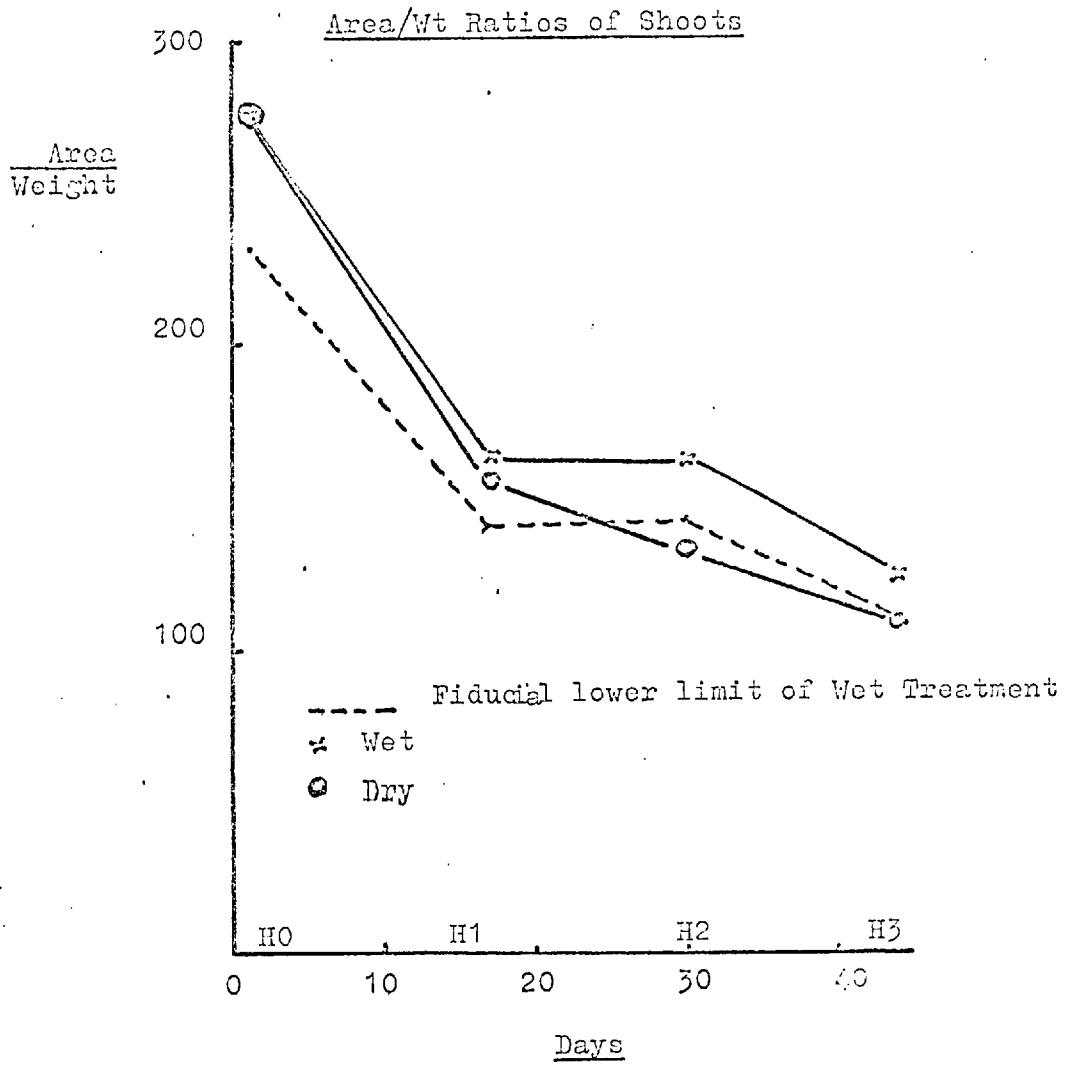
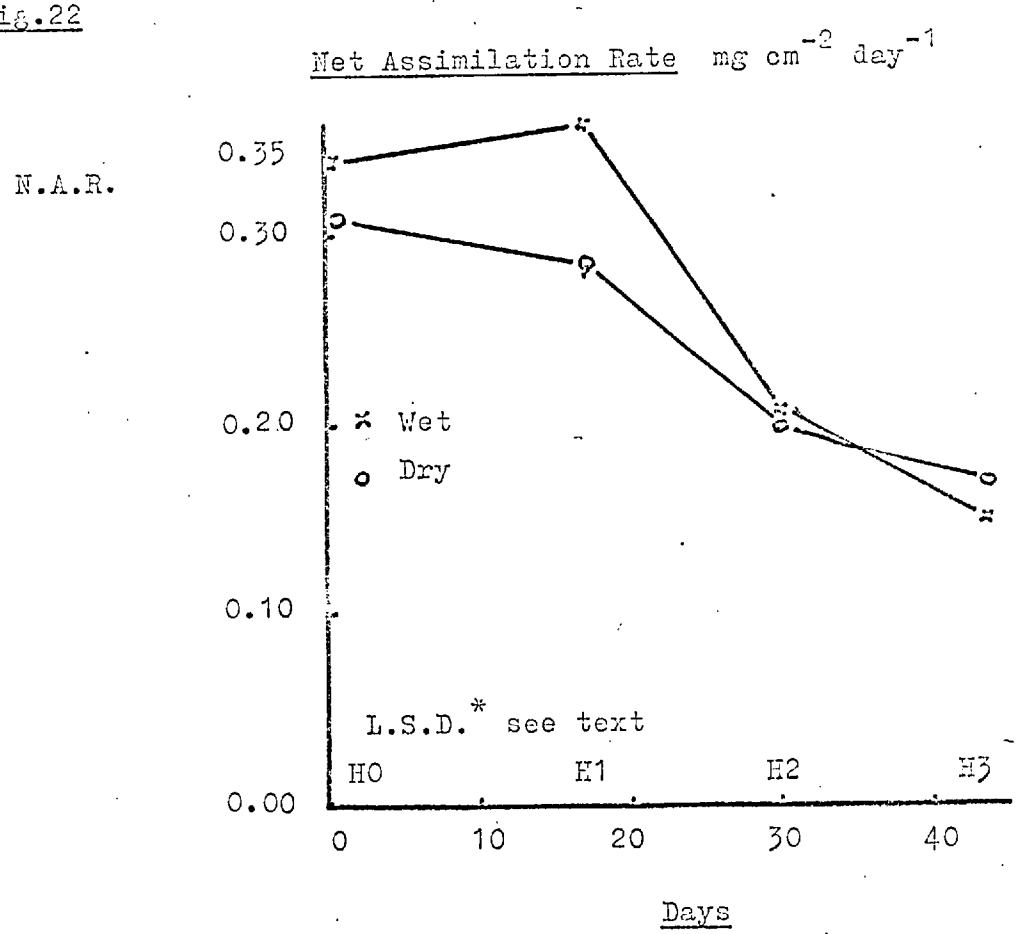

Area/Wt Ratios of Shoots
Area
Weight
300
200
100
Fiducial lower limit of Wet Treatment
Wet
Dry
H0
H1
H2
H3
0
10
20
30
40
Days

Fig.22


Net Assimilation Rate mg cm^{-2} day^{-1}
N.A.R.
0.35
0.30
0.20
0.10
0.00
Wet
Dry
L.S.D.* see text
H0
H1
H2
H3
0
10
20
30
40
Days

The leaf area, however, fell significantly compared with controls by Harvests 2 and 3. This fall in area without a correspondingly large fall in leaf weight accounts for the significant fall in area/weight ratio at Harvests 2 and 3. (Fig.21). The top growth appeared visibly poorer by Harvest 2 in the dry treatments, and considerably so at Harvest 3. This, it appears , was due almost entirely to a fall in apparent leaf area rather than leaf weight. There was little difference in the net assimilation rate(Fig. 22) between the two treatments. The computed L.S.D.s were larger than the actual N.A.R. values and so could not conveniently be included in the Fig.22.

A detailed examination of the morphology of the plants revealed that the number of tillers per plant increased at the same rate in wet and dry treatments throughout the growth period (Table 24).

Table 24. Pipe Experiment IV

Tiller Numbers per Plant at Harvest

	Wet	Dry
H0	0.75	0.75
H1	1.01	1.13
H2	1.37	1.37
H3	1.84	1.97

The small and non-significant depression in weight of the main shoots and tillers of the dry treatment was similar, but the leaf area of the main shoots was relatively more depressed than that of the tillers (Table 25). A 't' test showed a barely significant difference between wet and dry main shoot area/weight ratios (P=0.05). The difference between the wet and dry tiller ratios did not approach significance.

Table 25. Pipe Experiment IV

Area/weight Ratios of Tillers and Main Shoots at Harvest 3

($cm^2 gm^{-1}$)

	Wet	Dry
Main Shoots	112	88
Tillers	147	140

The most striking difference between the treatments was to be found in the nature of the root system. The number of main axes arising on the droughted plants was only 60% of the number on watered plants. Both treatments had a similar number of what appeared to be the original seminal axes amd some decorticated adventitious roots. These were supplemented by thick, white, adventitious roots in the wet plants, extending from a few to many centimetres into the soil, and obviously still being formed in considerable numbers. It was not possible to distinguish whether they were of tiller or main shoot origin. They were, however, completely absent from the dry treatment plants. Clearly, therefore, the wet plants were able to produce new adventitious roots in to the damp soil, whereas the droughted plants were completely inhibited from doing so. This accounts for the fact that the lower root weight in the dry treatments was confined entirely to the top zones of soil.

Analysis of the measurements of leaf water potential revealed a significant difference (0.1% level) between the wet and dry treatments on and after the first harvest (Table 26). This large initial difference in leaf water potential corresponds to the drying of the top soil where most of the root system was located. There was little further fall in potential until the point of incipient wilting at Harvest 3.

Table 26. Pipe Experiment IV

Leaf Water Potentials (-ve bars)

	Wet	Dry
H1	5.7	9.4
H2	6.1	9.6
H3	5.8	13.6
		L.S.D.= 2.9

There was no significant change in potential during the day, probably because the major radiation source was constant from the mercury vapour lights.

The unreplicated nitrogen analyses suggest that the dry treatment main shoots were deficient in nitrogen compared with the wet controls, whereas the tillers were unaffected (Table 27).

Table 27. Pipe Experiment IV

Nitrogen Concentration of Shoot Dry Matter (%)

	Main Shoot		Tillers	
	Wet	Dry	Wet	Dry
H1	1.4	1.4	1.8	1.5
H2	1.5	1.0	1.3	1.2
H3	1.2	0.9	1.2	1.2

The overall nitrogen percentages were low since there had been no preliminary fertilizer additions.

This experiment confirmed that in an establishing seedling sward of Dactylis, root weight increase was more severely affected than top weight by drought and this was found to be due to the failure of the dry treatments to produce new adventitious roots once the top soil dried. The visibly poorer shoot growth was caused by a failure of leaf area, largely of the main shoots, to expand. This was reflected in a fall in their area/weight ratio. Tillering appeared unaffected.

The main shoots of the dry treatments also appeared to be subject to a depression in nitrogen percentage whereas the tillers were unaffected. In the absence of fertilizer additions, the plants would be dependent on mineralization of soil nitrogen, a process very dependent on soil water content.

PIPE EXPERIMENT V

Previous experiments had failed to confirm that nitrogen unavailability in the soil was of importance in producing a drought effect in undefoliated, seedling swards. Shoot growth was not seriously affected until intense levels of water shortage were experienced by the plants, but new root growth into drying zones of the soil was inhibited from an early stage. A discrepancy was, therefore, apparent between the results of these experiments and those reported by The Grassland Research Institute. It seemed possible that this difference might be due to the defoliation regime they applied. This experiment was designed as a preliminary to more detailed investigations on outdoor swards, to determine the effects of defoliation and any consequent modifications to root growth on the susceptibility of grasses to drought. A check on whether any factor resulting from defoliation had increased susceptibility to nutrient deficiency was introduced by comparing the response to drying with either nutrients evenly distributed through the profile or an application confined to the surface 30cm.

Method and Materials

The experiment was conducted in 120 centimetre pipes in a heated greenhouse during the winter of 1969-70 and using mercury vapour lights to enhance illumination. Four randomised blocks each contained the same two water regimes as previous experiments (W,D) factorially combined with two nutrient distribution treatments. These were either the normal soil profile of 30cm of Silwood top soil then sandy subsoil (T/S), or top soil throughout the profile (T). It was intended that these distributions of top soil would similarly distribute nutrients, especially nitrogen.

Thirty seeds of Dactylis S37 were sown in each pipe on 7 November and were watered regularly. Nitrogen in the form of ammonium sulphate was applied at the rate of 75 kg ha^{-1} on 15 December. All the plants were cut at 2-3cm above soil level when 15-20cm high on 27 January. The water treatments then commenced and the surface soil covered with 2cm of expanded polystyrene granules to reduce surface evaporation.

The regrowth was harvested at water deficits of 8.1 and 13.8cm (Harvests 1,2) in the drying pipes, as determined by weighing, on 21 February and 24 March.

The apparent leaf areas were measured for all treatments, and a visual estimate made of the greenness of the foliage.

One week after Harvest 2, all treatments were accidently watered, and this error was discovered on April 15, by which time some recovery of the dry treatments was becoming apparent. It was, therefore, necessary to terminate the experiment,

The roots were washed out immediately in sections from the 0-30cm and 30-120cm depths. The main root axes and short white roots were counted at the bases of the tillers. The numbers of main plants and tillers were counted; then the shoots were discarded.

Nitrogen analyses were performed on the bulked replicates of the top growth from Harvest 2.

Results

An analysis of variance on the dry weight of the shoots at Harvests 1 and 2 showed an interaction between water treatment x soil distribution x harvest, significant at the 5% level. This is simplified in Table 28 to the water treatment x soil distribution interaction, significant at the 0.1% level; and the water treatment x harvest interaction significant at the 1% level in Table 29.

Table 28. Pipe Experiment V

Dry Weight of Shoots per Pipe (gm)

(Mean of H1 and H2)

	T	T/S	
W	4.51	2.11	
D	2.47	1.58	L.S.D.=0.46

Table 29. Pipe Experiment V

Dry Weight of Shoots per Pipe (gm)

(Mean of T and T/S treatments)

	H1	H2	
W	2.90	3.73	
D	2.30	1.76	L.S.D.=0.46

The regrowth of the dry treatments had fallen significantly behind that of the controls by Harvest 2. The yield of the dry pipes containing only top soil was nearly twice as severely depressed at both harvests as that of the pipes with a subsoil, relative to their watered controls.

There was no significant difference between the root weights of any of the treatments, above or below the 30cm depth, at the final harvest. (Table 30).

Table 30. Pipe Experiment V

Mean Root Weight at Final Harvest per Pipe (gm)

0-30cm	30-120cm
2.53	0.60

Measurement of the apparent leaf areas at Harvest 2 showed an interaction of water treatment x soil distribution significant at the 2.5% level (Table 31). The depression in the dry treatment with topsoil throughout was considerably more severe than in the topsoil/subsoil, relative to controls.

Table 31. Pipe Experiment V

Leaf Area per Pipe at Harvest 2 (cm^2)

	T	T/S	
W	1880	919	
D	731	594	L.S.D.=414

The area/weight ratios of the shoots did not differ significantly between treatments.

As in Pipe Experiment IV, the morphology of the plants was carefully examined at the final harvest.

The number of tillers per plant was unaffected by the drying treatment but the higher fertility levels of the top soil treatment gave increased numbers compared with the top soil/subsoil treatment (Table 32).

Table 32. Pipe Experiment V

Tillers per Plant at Final Harvest

T	T/S	
4.6	3.2	L.S.D.=1.3

The number of root axes leaving the bases of the plants is shown in Table 33. There were considerably more in the wet than the dry treatments, and no soil treatment effect.

Table 33. Pipe Experiment V

Mean Root Axes per Pipe at Final Harvest in Wet and Dry Treatments

W	D	
574	335	L.S.D.=80

The size of the differenceis hard to correlate with the absence of any difference in root weight, but many of the roots in the wet treatments were classified as 'recent roots' and appeared to have developed to a very limited depth. They may have accounted for the increased numbers while making little contribution to total weight in the wet treatments. The actual number of new white roots was limited to about one per plant in the wet treatments and they were completely absent in the dry treatments. Decortication of existing roots was observed to be in progress.

Analysis of the shoots for nitrogen content at Harvest 2 confirmed a visual assessment of the greenness of the shoots. The dry treatments were both very dark green and had a higher level of nitrogen than their controls. The shoots of the wet subsoil treatment were pale green and had a much lower nitrogen percentage than the other treatments (Table 34).

Table 34. Pipe Experiment V

Nitrogen Content in Shoots at Harvest 2 (%)

	T	T/S
W	3.6	1.9
D	3.9	3.0

This experiment, where the grass was cut, revealed some interesting morphological differences from the uncut situation.

The regrowth was reduced in the dry treatments by a significant amount at an early stage. The difference in the root weight in the upper zones between wet and dry treatments observed in previous uncut experiments was not found in this instance. The rate of production of new roots seemed very low, and the total root weight was a fraction of that of uncut plants at a similar stage of growth, while breakdown of the root cortices was proceeding at an appreciable rate.

It thus appeared that cutting, through its influence on root growth and morphology, might have a significant effect on the ability of the plant to regrow in dry soil.

Once more, no evidence for a nitrogen deficiency could be found in the dry treatments.

PIPE EXPERIMENT VI

Pipe experiment III had shown that a drying cycle had little effect on the growth of either Dactylis or Lolium, when uncut, with the exception of the root growth of Dactylis. These results had been confirmed in Dactylis by Pipe Experiment IV using a natural subsoil in place of Perlite. It was felt desirable to repeat the experiment with Lolium and obtain additional information on any changes in the root morphology due to drying of the soil.

Further data were collected simultaneously for the water balance calculations of a later section.

Method and Materials

The experiment was located in the trench used for Pipe Experiment III, in early summer of 1970.

The design was of simple split plots for four harvest dates. During the course of a drying cycle for half the pipes (D), the remainder were watered frequently to field capacity (W). The whole was replicated three times.

Twenty-one pipes, 120cm x 15cm, as used in previous experiments, were part filled with Silwood sandy subsoil and the top 30cm with top soil. Thirty-two seeds per pipe of Lolium S23 were sown on 30 April, 1970, and these emerged on 7 May with about 70% germination. On 21 May, 50cc of Long Ashton Nutrient Solution were added to each pipe, and the equivalent of a further 75 kg ha^{-1} of nitrogen as ammonium sulphate on 1 June. The plants were watered regularly throughout this period, and by the zero harvest on 11 June, were at field capacity, as confirmed by run-through from the pipes. The zero harvest was taken when the plants were 10-15cm high. Then the drying cycle commenced on half the pipes. They were weighed initially and at each harvest to determine the water deficit. The remaining pipes were maintained at field capacity.

Further harvests were taken at deficits in the drying pipes of 10.2, 14.3 and 20.1cm, which closely corresponded to the harvest deficits for Dactylis in Pipe Experiment IV. These deficits were attained after 14, 22 and 32 days respectively, representing an evapo-transpiration rate of about 6mm per day.

On the day preceding harvest, the pipes were weighed at 5 a.m.. Leaf potential measurements were made with the pressure apparatus after taking a porometer reading on the same leaf, at two hourly intervals until dusk. Radiation measurements were made simultaneously with a dome solarimeter. The pipes were then reweighed, and harvested the following day.

On the harvest day, the pipes were split and the contents exposed. Cores were taken horizontally for soil moisture determination from the centre of each 15cm zone, then the profile was split into sections of this length and the roots washed out and cleaned. The roots, still attached to the shoots, were examined carefully. The total number of axes and the number of short white roots were counted. The average diameter was measured on a sub-sample from each depth then all the roots were dried, weighed and the total lengths estimated, using a factor determined by Newman's method.

The tops, severed from the roots at their base after counting the number of tillers, were split into laminar and sheath components. The area of a laminar sub-sample was measured on an Eel leaf-area meter and then the shoots were dried and analysed for nitrogen, phosphorous, potassium and calcium.

Results

The dry weights and leaf areas were analysed statistically by the computer method of Freeman and Hughes (1967). The fitted curves are shown in Fig.23 and the fitted, actual, and loge means and L.S.D. in Table 35.

As in previous experiments, there was an early decline in dry weight and leaf area parameters of the drying treatment below the level of the controls, and this persisted throughout. At Harvest 2, the difference in total weight and root weight was significant, but the significance disappeared again at the final Harvest 3. The Harvest 3 wet pipes showed a lower root weight than the preceding Harvest 2 pipes. No explanation can be given other than experimental variation. If the trendline of the wet pipes had continued to Harvest 3, then the significant difference would have been maintained.

Table 35. Pipe Experiment VI

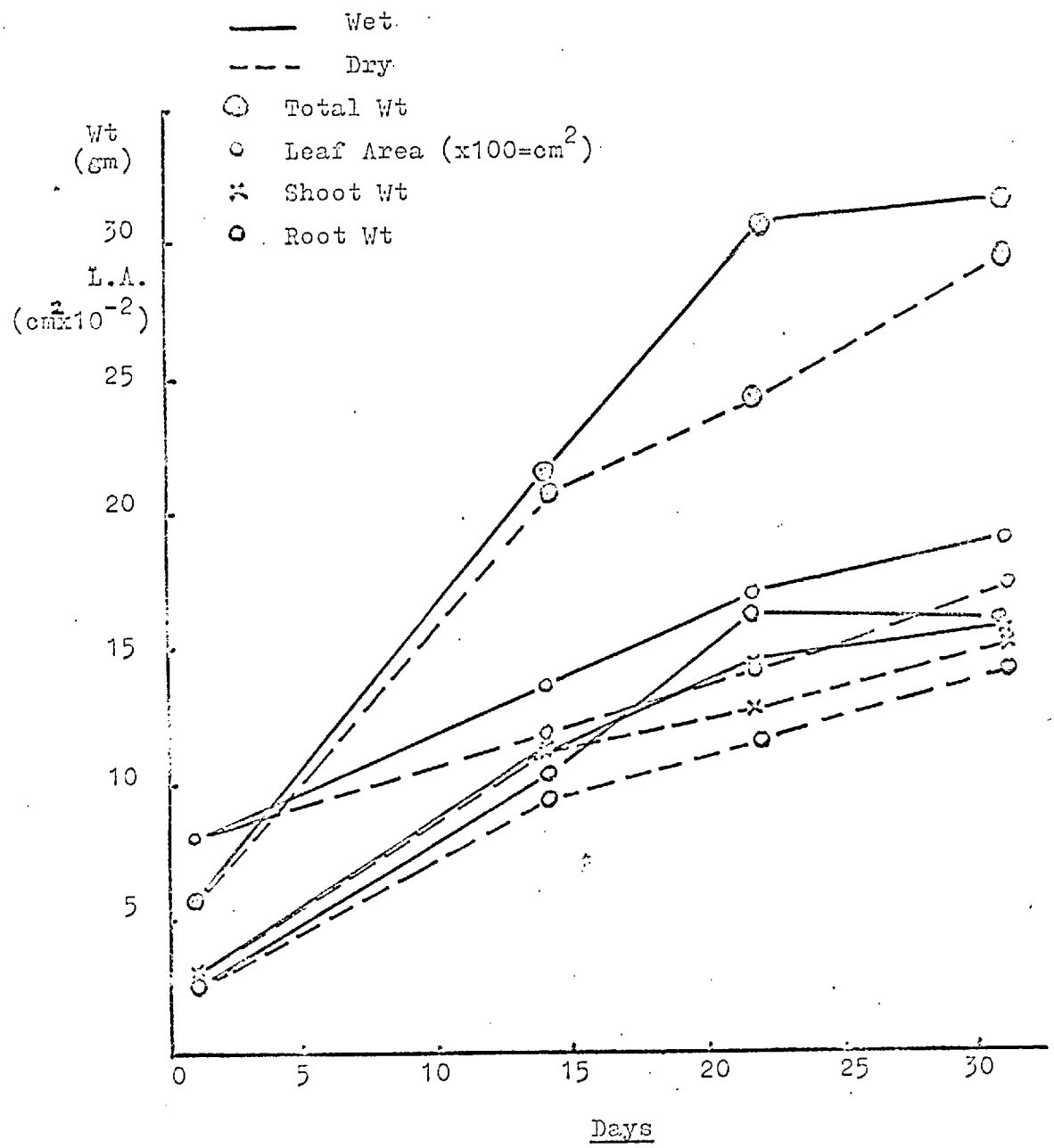
Dry Weight and Leaf Area per Pipe (gm, cm^2)

		WET				DRY		
Weight		Mean	Fitted	Log_e	Log_e L.S.D.	Log_e	Mean	Fitted
Total	H0	5.76	5.68	1.73	0.21	1.73	5.76	5.68
	H2	21.51	21.58	3.07	0.21	3.03	20.64	20.70
x560=	H2	30.65	30.69	3.42	0.21*	3.18	24.12	24.55
kg ha^{-1}	H3	31.41	31.55	3.45	0.21	3.38	29.39	29.48
Shoot	H0	3.16	3.13	1.14	0.21	1.14	3.16	3.13
	H1	11.10	11.11	2.41	0.21	2.42	11.22	11.25
	H2	14.38	14.34	2.66	0.21	2.54	12.65	12.67
	H3	15.74	15.74	2.75	0.21	2.72	15.21	15.25
Root	H0	2.59	2.51	0.93	0.27	0.93	2.59	2.53
	H1	10.42	10.40	2.34	0.27	2.24	9.42	9.44
	H2	16.28	16.33	2.79	0.27*	2.44	11.47	11.47
	H3	15.68	15.68	2.75	0.27	2.65	14.17	14.20
Leaf	H0	801	794	6.67	0.26	6.67	801	794
Area	H1	1359	1368	7.21	0.26	7.07	1180	1187
x56=	H2	1698	1691	7.42	0.26	7.25	1412	1419
$m^2 ha^{-1}$	H3	1902	1910	7.55	0.26	7.47	1754	1769

Leaf Area Index	Wet	Dry
H0	4.5	4.5
H1	7.6	6.6
H2	9.4	7.8
H3	10.6	9.7

Fig.23

Dry Wt of Total Plant, Shoots and Roots and Leaf Area per Pipe at Harvest



Thus the result appears to confirm that roots are more severely affected than shoots by drying of the soil under the conditions of this experiment.

The leaf area of the dry pipes remained below that of the controls from Harvest 1, but this depression never became significant.

The area/weight ratios of the laminae just differed significantly from controls at Harvest 1, but this difference disappeared at subsequent harvests and was probably fortuitous.

The ratio of lamina weight/sheath weight was lower in the dry treatments at all harvests by a non-significant amount.

The root weights from the different zones were analysed for effects of the water treatments after transformation to Log_{10} values. A significant interaction of water treatment x depth (P=0.001) was of particular interest (Table 36). The mean root weight in the two surface zones was higher in the controls, but in all subsequent zones, it was higher by a small amount in the dry treatments, thus following the pattern of Pipe Experiment III. The total root weights were rather higher in the latter experiment but the growing period was also longer.

Table 36. Pipe Experiment VI

Root Weight (Log_{10} x 100) per Horizon. Harvest Mean

	Wet	Dry
Horizon 1	2.85	2.71
2	2.46	2.34
3	1.94	1.98
4	1.89	1.94
5	1.92	1.95
6	1.83	1.85
7	1.73	1.82

L.S.D.=0.07

The root densities at Harvest 3 were similar to those in previous experiments (Table 36a).

Table 36a. Pipe Experiment VI

Estimated Root Densities at Harvest 3 (cm cm^{-3})

		Wet	Dry
Horizon	1	61.9	53.2
	2	25.8	19.8
	3	7.7	8.4
	4	7.4	8.0
	5	8.2	8.1
	6	6.9	7.2
	7	8.5	9.0

The number of tillers arising from each original plant remained constant after Harvest 1 at about 11 tillers per plant. There was no difference between the treatments. There was, however, a depression, relative to controls, in the average number of root axes leaving the bases of the drying plants and the interaction with harvests was significant at the 5% level(Table 37).

Table 37. Pipe Experiment VI

Main Root Axes per Tiller

	H0	H1	H2	H3
Wet	1.9	2.3	2.3	2.7
Dry	1.9	1.9	1.6	1.9

L.S.D.=0.4

The number of root axes increased by nearly 50% during the experiment in the wet treatments, but showed no change in the dry treatments. This was a similar pattern to that observed in Dactylis in Pipe Experiment IV, but the similarity did not extend to the number of new short white roots present (Table 38). There were more present in the dry treatments at all harvests after Harvest 1 (P=0.01) and examination of these roots in the dry treatments showed all except the tip to be ensheathed in a rather fibrous layer. All were very short, usually about 0.5cm long, and gave the impression of being in a state of suspended growth. The lower numbers in

the controls might be attributed to the continued growth of these roots, thus coming outside the 'short root' category and accounting for the increased number of total axes in the wet treatments.

Table 38. Pipe Experiment VI

Number of New White roots (0-4cm long) per Pipe

	Wet	Dry
(Mean of Harvests)	94	127

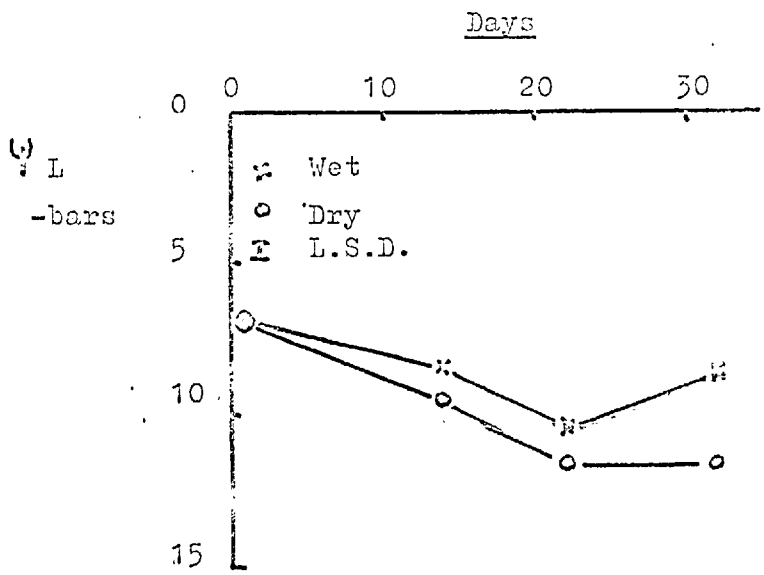
L.S.D.=21

The leaf water potentials behaved similarly to previous experiments, diverging significantly from controls at all harvests after the treatments commenced then remaining almost parallel until the final harvest when the divergence increased again (Fig.24). The two curves remained parallel during the day and there was no significant interaction between time of day and water treatment (Fig. 25).

Stomatal diffusion rates were measured with the diffusion porometer immediately before the measurement of leaf water potential. Readings could not be taken early in the morning because the high air humidity at this time caused a full scale deflection. Comparisons were not possible between harvests or times of day because of temperature fluctuations affecting the apparatus. Direct comparisons between wet and dry treatments revealed a difference at Harvest 3 which, when the data were analysed, proved to be significant (P= 0.01) (Table 39). No measurement of leaf temperature at the time of the porometer reading was attempted, and any difference between wet and dry treatments due to their differing transpiration rates may have influenced the figures. As in previous experiments, the readings from the dry treatments suggested a narrower stomatal aperture from an early stage in the drying cycle, and this difference was significant at the final harvest.

Fig.24

Mean Daily Leaf Water Potential



Mean Daily Course of Leaf Water Potential

Fig.25

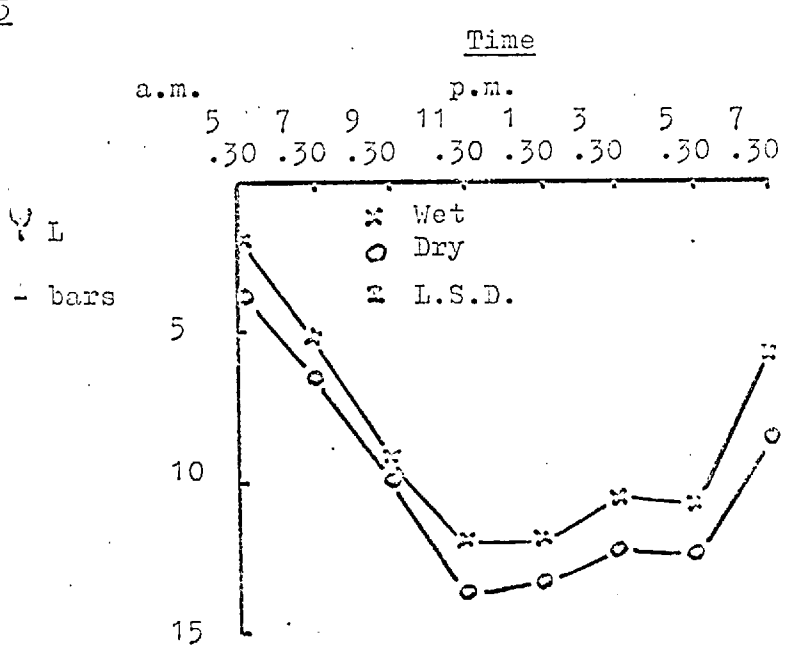


Table 39. Pipe Experiment VI

Harvest 3, Stomatal Diffusion Rates (Arbitrary Units)*

Time	9.30a.m.	11.30	1.30p.m.	3.30	5.30	7.30
Wet	45	62	34	38	37	36
Dry	34	30	16	22	25	19

*See Pipe Experiment II.

Calculation of the uptake of nitrogen in the shoots during the course of the experiment showed no significant difference between wet and dry treatments, and their tissue nitrogen level was also similar.

Analysis for the other macro-nutrients was carried out for the first time in this experiment and showed an effect of water treatment on phosphorous uptake significant at the 0.1% level (Table 40).

Table 40. Pipe Experiment VI

Phosphorous Uptake by Shoots to Harvest (kg ha^{-1})

	H0	H1	H2	H3
Wet	10.7	23.0	23.6	25.8
Dry	10.7	20.8	19.1	18.0
				L.S.D.=1.7

Phosphorous uptake continued in the wet treatment but showed a small apparent decline in the dry treatments, perhaps due to translocation to the growing root system.

Potassium and calcium levels in the shoots showed no appreciable divergence from controls throughout the experiment (Table 40a)

This experiment confirmed that root axis production was the first factor to be affected by the onset of drying of the soil profile, but once again, the overall effect of water stress on growth was small. There was further evidence that compensatory root growth occurred at deeper levels in dry treatments, suggesting, perhaps, that it was some factor of the dry surface soil which prevented root growth rather than a shortage of assimilates.

Table 40a. Pipe Experiment VI

Macro-nutrient levels in the shoots (% Dry Weight)

		H0	H1	H2	H3
N	Wet	4.8	2.4	1.8	1.5
	Dry	4.3	2.2	1.7	1.5
P	Wet	0.62	0.37	0.29	0.29
	Dry	0.62	0.33	0.27	0.21
K	Wet	5.0	3.0	2.4	2.5
	Dry	5.0	2.8	2.7	2.4
Ca	Wet	0.47	0.35	0.39	0.42
	Dry	0.47	0.36	0.40	0.41

New evidence was produced that phosphorous uptake ceased when the surface zones dried, while nitrogen, potassium and calcium uptake appeared unaffected.

There was little to suggest that Lolium differed greatly from Dactylis in its morphological response to drying, or that the use of Perlite for Pipe Experiment III had in any way influenced the results when compared with soil.

PIPE EXPERIMENT VII

Pipe Experiment V, performed on Dactylis during the winter, had suggested that a cutting regime could exert an overriding influence on root growth causing a severe depression compared with an undefoliated sward. This experiment was designed to confirm this effect on Lolium.

Method and Materials

The experiment was carried out alongside Pipe Experiment VI during early summer, 1970. It consisted of three randomised blocks, split for harvest date. There were wet and drying water treatments, and two harvests plus an initial harvest, in a similar manner to previous pipe experiments.

Thirty-two seeds of Lolium S23 were sown on 30 April, 1970, in pipes 120cm deep containing Silwood subsoil and 30cm of Silwood top soil. After emergence on 7 May, they were watered frequently, and received 50cc of Long Ashton Nutrient Solution on 21 May and ammonium sulphate equivalent to 75 kg ha^{-1} on 1 June. The initial harvest was taken on 11June and further harvests on 28 June and 24 July at deficits of 8.3 and 15.9cm of water respectively in the drying pipes. At each harvest, all the remaining pipes were defoliated at 2cm height.

On the day preceding harvest, the pipes were weighed at 6a.m. then leaf water potentials and porometer readings were taken at three-hourly intervals until 9p.m. on the following evening, when the pipes were reweighed. Radiation levels were recorded simultaneously on an integrating solarimeter.

On the following day, the pipes were opened and soil samples taken for moisture determinations from 15cm sections, before washing out the roots. Plant, tiller and root axis counts were made before measuring leaf/sheath ratios, leaf areas, then drying and weighing all samples.

Estimates of total root length were made using a factor determined by Newman's method, and the shoots were analysed for nitrogen, phosphorous, potassium and calcium using the Auto-analyser.

Results

The yields of dry matter and the leaf areas at each harvest are shown in Table 41.

Table 41. Pipe Experiment VII

Dry Weight and Leaf Area per Pipe (gm, cm^2)

		WET			DRY	
Weight		Mean	Log_e	Log_e L.S.D.	Log_e	Mean
Total	H0	9.51	2.23	0.33	2.23	9.51
x560=	H1	12.13	2.50	0.33	2.49	12.20
kg ha^{-1}	H2	15.89	2.76	0.33	2.59	13.31
Shoot	H0	5.21	1.64	0.29	1.64	5.21
	H0-H1	5.59	1.72	0.29	1.72	5.66
	H1-H2	6.61	1.89	0.29	1.66	5.31
Root	H0	4.30	1.43	0.42	1.43	4.30
	H1	6.54	1.88	0.42	1.87	6.54
	H2	9.28	2.22	0.42	2.08	8.00
Leaf	H0	801	6.67	0.34	6.67	801
Area	H0-H1	599	6.38	0.34	6.26	535
x56=	H1-H2	412	6.02	0.34	5.80	331
$m^2 ha^{-1}$						

Leaf Area Index	Wet	Dry
H0	4.4	4.4
H0-H1	3.3	2.9
H1-H2	2.3	1.8

Statistical analysis of the $\log_e$ values failed to show any significant differences between wet and dry treatments. Examination of the actual means shows a divergence of 15-20% in all four parameters at Harvest 2. The weight differences were negligible at Harvest 1.

The total root weight of the dry treatments continued to increase during the drying cycle at a rate comparable with the controls. The total root weight present at the end of the experiment was, however, much lower than that of the comparable Pipe Experiment VI, despite the longer growing period.

Analysis of the root weights present in each 15cm zone revealed a similar picture to Pipe Experiment VI where there was a significant depression in the dry treatments in the surface zones and compensatory growth at all greater depths (Table 42).

Table 42. Pipe Experiment VII

Root Weights (Log_{10} x 100) at Final Harvest

Depth	Wet	Dry
1	2.58	2.49
2	2.18	2.11
3	1.76	1.72
4	1.65	1.69
5	1.72	1.82
6	1.62	1.69
7	1.59	1.67

L.S.D.=0.08

The estimated root densities were about 50% of those reached in the uncut Pipe Experiment VI, even though the growing period was longer (Table 42a). The average root diameters were similar in the two experiments.

Neither the laminar area/weight ratios nor the lamina /sheath weight ratios differed significantly from controls.

The total number of tillers did not increase after Harvest 1, but considerable mortality occurred in both wet and dry treatments after this harvest, reducing the number of live tillers in both treatments by about 30%. There

Table 42a. Pipe Experiment VII

Root Densities at Harvest 2 (cm cm^{-3})

Depth	Wet	Dry
1	37.7	27.0
2	13.5	11.2
3	5.3	4.3
4	4.0	4.3
5	4.7	6.3
6	4.1	4.4
7	5.4	6.2

was no difference between treatments in the number of live or dead tillers at Harvest 2.

The number of root axes continued to increase during the experiment in the wet treatments, but showed no significant change in the dry ones. The water treatment x harvest date interaction was significant at the 5% level (Table 43).

Table 43. Pipe Experiment VII

Root Axes per Tiller

	H0	H1	H2
Wet	1.87	2.03	2.67
Dry	1.87	1.80	2.00

L.S.D.=0.35

There were short white roots present in the dry treatments, and the water treatment x harvest interaction was significant at the 5% level (Table 44)

Table 44. Pipe Experiment VII

New White Roots (0-4cm) per Tiller

	H0	H1	H2
Wet	0.80	0.30	0.28
Dry	0.80	0.48	0.51

L.S.D.=0.15

The majority of these white roots were very short and appeared to be dormant.

The effect of water treatment on leaf water potential was significant at the 1% level, and the interaction with harvest date at the 2.5% level. The leaf water potential of the drying plants fell below that of the controls at Harvest 1 and increasingly so at Harvest 2 (Fig.26).

There was no significant interaction between water treatment and time of day (Fig.27).

While the stomatal diffusion rates from the dry treatments fell below those from the controls at Harvest 1 and increasingly so at Harvest 2, this effect was not quite significant.

Analysis of the shoot nitrogen levels and uptakes showed no significant difference between wet and dry treatments (Table 44a). There was no suggestion that the drying treatments had been unable to take up appreciably less nitrogen than the wet treatments. The percentage of nitrogen

Table 44a. Pipe Experiment VII

Nitrogen Uptake in the Shoots Between Harvests (kg ha^{-1})

	H0	H1	H2
Wet	84	62	48
Dry	84	56	44

in the shoot dry matter at Harvest 2 was slightly higher in the dry treatments, that of phosphorous was significantly lower (P=0.01), while no difference was apparent in the levels of potassium and calcium (Table 44b).

Table 44b. Pipe Experiment VII

Macro-nutrient Content of Shoots at Harvest 2 (% of Dry Matter)

	N	P	K	Ca
Wet	1.3	0.31	2.0	0.57
Dry	1.5	0.27*	2.0	0.57

Fig.26

The Course of Leaf Water Potential

1) During a Drying Cycle

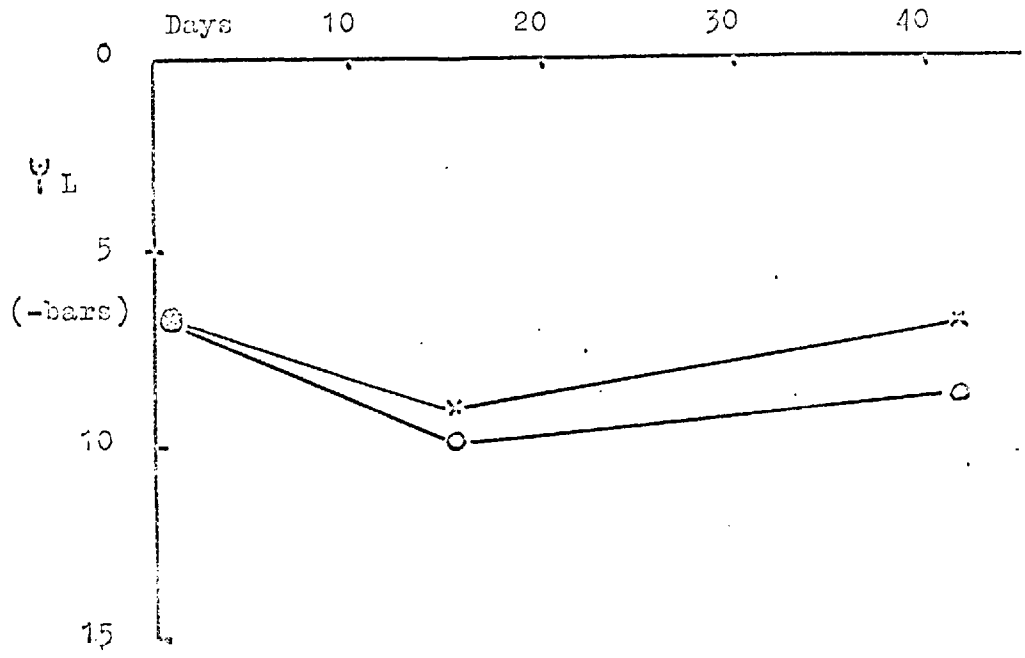
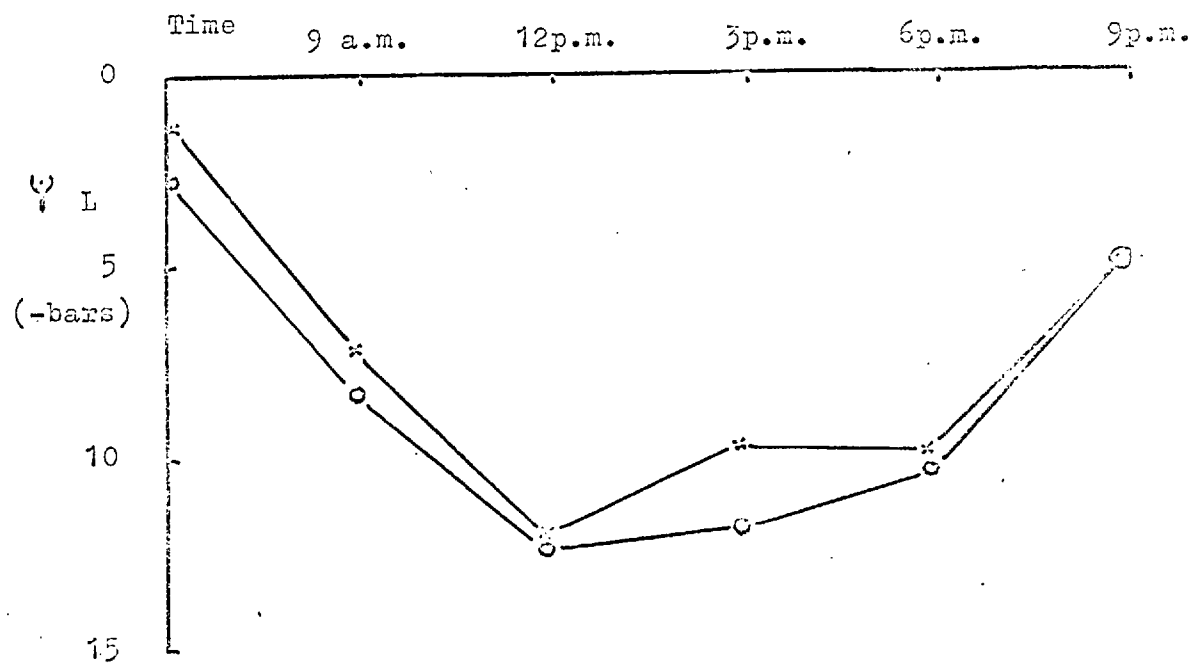


Fig.27

2) During the Day (Harvest mean)



This experiment showed little effect of water stress on growth under the cut regime, though the deficit was much slower to accumulate because of the limited leaf area, and harvesting took place at rather lower deficits. It did, however, confirm the considerable adverse effect of cutting on root development and also showed, again, the compensatory deeper root development when the surface soil dried.

The depression in phosphorous uptake which was apparent in the previous experiment was demonstrated again.

LYSIMETER EXPERIMENT II

The manner in which Lolium and Dactylis had tolerated apparently severe levels of drought in the pipe experiments had been surprising in view of the widely reported depression of growth at small water deficits.

It was thought possible that this insensitivity to drought might be due to the vigorously extending system of new roots under the uncut seedlings in the pipes. Pipe Experiments V and VII had already revealed that cutting seriously retarded root development, compared with an uncut sward. It also seemed likely that an established sward might have a considerably less dense system of active root. If this were so, their responses to drought might differ, and this lysimeter experiment was designed to test the response of mature and seedling swards in the cut and uncut conditions to drought.

Method and Materials

The experiment was conducted on the lysimeters, using Dactylis only, during spring, 1970. The Lolium swards used for the 1969 Lysimeter Experiment I were sprayed with 'Paraquat' in the previous autumn. After removing the dead top growth, the surface was dug over. The plots of Dactylis remaining from 1969 constituted the established swards for the purposes of this experiment, and the seedling swards were sown on the dug plots.

The established (E) and seedling (S) sward treatments were factorially combined with an uncut treatment (U) or a defoliation regime (C), and also with a watered (W) or drying (D) treatment. The whole factorial combination of eight treatments was replicated three times, leaving four spare lysimeters for initial sampling of the roots.

The seedling swards were sown on 23 March, 1970. The spring was exceptionally late and cold, giving patchy and delayed germination three weeks later. Light raking of the surface after sowing the seed also appeared to have contributed to the unevenness, combined perhaps with heavy rain and then dry winds. The very dense patches of seedlings grew comparatively well, but where the seed was thinner on

the ground, the germinating seedlings were small and weak, and many died out altogether, increasing the unevenness of the sward. The statistical blocks were arranged to compensate as far as possible for the variability of the seedling swards.

The established swards commenced growth very late, on 28 April, and the first flower heads were emerging within ten days. Since the seedling swards were not sufficiently advanced to start the treatments until 8 June, the experiment had to be run as two independent sections for established and seedling swards.

1) Established Swards

The equivalent of 190 kg ha^{-1} of nitrogen, 40 kg ha^{-1} of phosphorous and 80 kg ha^{-1} of potash were applied in the form of a compound fertilizer early in May, and the lysimeters were watered to field capacity on 7 May, when the drying cycle commenced. Further rainfall was excluded by placing covers in position as necessary. On the 8 May, the cut treatment plots were all defoliated (H0) giving initial yield data for both cut and uncut treatments. Root samples were taken from the two spare established lysimeters in four cores 10cm diameter at successive 12.5cm depths. Soil moisture samples were taken from the dry treatment lysimeters from the depths 0-30, 30-60, and 60-90cm.

All wet treatments were watered to field capacity at regular intervals.

On 20 May, the cut treatments were again defoliated at 3cm height (H1).

On 2 June, all the cut treatments were again defoliated. One half of each of the uncut lysimeter plots was also cut (H2). There was a visible longitudinal gradient of growth, but no lateral difference other than edge effects, and so the plot was split for cutting along its longer axis.

Root and soil moisture samples were taken as at the zero harvest from the treatment plots and the density of live tillers was counted.

On the day preceding harvest, leaf water potentials were measured with the pressure apparatus and diffusion porometer readings were taken simultaneously on the same leaves.

It was observed on 9 June that there was very little regrowth on the dry, cut plots and the cut halves of the uncut plots. Good regrowth occurred on the wet plots. Defoliated flowering tillers did not regrow.

The soil temperature at 2cm depth was measured under all established sward treatments at 2 p.m. on 9 June, a very hot day.

By 15 June, the uncut, dry treatments were largely wilted, and growing tillers were very sparse on the cut, dry plots. The leaf water potentials were measured during the day and porometer readings taken; then on the following day the shoots were harvested (H3), root and soil moisture samples taken, tiller density counted, and the proportion of lamina, sheath, flowering stem and dead material estimated.

Although this section of the experiment was designed to finish at this point, further root samples were taken on 16 July (H4) and the tops were cut again. The plots were then exposed to rainfall until 3 August when further leaf samples and root samples were collected (H5).

2). Seedling Swards

The treatments took the same general form as for the established swards.

The initial harvest (H0) of the cut treatments was carried out on 8 June when the swards had formed a reasonably vigorous and dense cover and tillering was starting in the less dense areas. There was insufficient regrowth to require an intermediate trim (equivalent to Harvest 1 in the established swards) and when it was established that half the available water had been removed on 30 June, Harvest 2 (H2) was carried out. Already, wilting was apparent in the uncut, dry treatments. The final harvest (H3) took place on 15 July, when considerable wilting and die-out had occurred in the dry treatments.

The plots were then exposed to rain and on 3 August, further leaf and root samples were taken.

The following common harvest procedure was adopted at both Harvests 2 and 3:-

On the day preceding harvest, the leaf water potentials were measured at sunrise, mid-morning, early afternoon and sunset. Before the potential was measured, a diffusion porometer reading was taken on the same leaf except in the case of the first and last times of day when the atmosphere was too humid for the porometer to function properly.

On the harvest day, the plots were cut and the herbage collected and dried after partitioning samples into leaf, sheath, and flower stem and dead material where appropriate. This material was subsequently analysed for nitrogen content.

Cores of 10cm diameter were taken from denser areas of tillers in 12.5cm zones down to 50cm. The roots were extracted by washing, the dry weights, number of axes, number of new white roots and the proportion of roots with an intact cortex were determined for each sample.

The water deficit at each harvest was determined from samples taken from each 30cm horizon.

The number of live tillers was counted at random locations with a $100cm^2$ quadrat.

Results

1) Established Swards

Table 45. Lysimeter Experiment II

Yields of Shoot Dry Matter (gm per plot; x 5 = kg ha^{-1})

		WET		Log_e	DRY	
		Mean	Log_e	L.S.D.	Log_e	Mean
Uncut, (yield at harvest)	H0	149	4.99	0.32	4.99	149
	H2	904	6.80	0.32	6.62	759
	H3	1153	7.04	0.32*	6.71	824
Cut, (Cumulative yield)	H0	149	4.99	0.17	4.99	149
	H1	346	5.87	0.24	5.78	337
	H2	596	6.41	0.24	6.18	499
	H3	753	6.65	0.27*	6.29	555
Cut, (Individual harvest yields)	H0	149	4.99	0.17	4.99	149
	H1	197	5.26	0.24	5.23	188
	H2	250	5.52	0.24*	5.09	162
	H3	157	5.06	0.28*	4.02	56

Table 46. Lysimeter Experiment II

Calculated Soil Water Deficits at Harvest in Dry Treatments(cm)

	H0	H2	H3
Uncut	0	8.5	10.6
Cut	0	7.1	8.0

The yields of dry matter in the harvested material are presented in Table 45 and the corresponding water deficits in Table 46.

The total yields of the shoots in the dry treatments had fallen appreciably behind those of the controls by Harvest 2 and this difference became significant in both uncut and cut treatments at the final harvest. When the production on a non-cumulative basis is considered in the cut treatments, significance was reached at Harvest 2.

There was no significant difference between any treatments in the number of live tillers, which averaged 26 per 100 cm^2.

Large, but unreplicated samples of the shoots had the following distribution of dry weight at Harvest 3 (Table 47).

Table 47. Lysimeter Experiment II

Distribution of Shoot Dry Weight at Harvest 3 (%)

	Leaf		Flower	Dead
	Lamina	Sheath	+ stem	Material
Wet Uncut	58	13	29	–
Dry Uncut	56	12	32	–
Wet Cut	92	8	–	–
Dry Cut	54	18	–	28

Any reduction in weight of the dry treatments compared with controls in the uncut swards seemed to have been equally distributed between all the components of total top weight.

The tillers of the wet, cut swards formed new leaves in rapid succession and these expanded quickly. This was reflected in their high proportion of the total weight. The dry, cut tillers continued to expand the existing leaves

whose tips were severed by defoliation, but generally failed to produce new leaves, so giving a high proportion of sheath and less lamina. There were considerable quantities of dry, dead material present.

Statistical analysis of the root weights at each depth showed a significantly greater total weight of root (P=0.001) under the dry treatments, accounted for largely by greater weights in the two deepest sampling zones (Table 48). The greater weights of the dry treatments showed a progressive increase at successive harvests.

Table 48. Lysimeter Experiment II

Mean Root Weight (Log_{10} x 100) in 12.5cm Zones

Depth	1	2	3	4
Wet	2.50	1.60	1.10	0.99
Dry	2.51	1.62	1.33	1.19

L.S.D.=0.10

There was no overall effect of cutting, but there was a significant reduction in root weight (P=0.01) under the cut swards at Harvest 3 (Table 49).

Table 49. Lysimeter Experiment II

Mean Root Weight (Log_{10} x 100)

	H0	H2	H3
Uncut	1.36	1.68	1.84
Cut	1.36	1.69	1.71

L.S.D.=0.08

There is a contradiction of the effect of water treatment in these results and those of previous pipe experiments. It may, however, be explicable in terms of the fact that this was an established sward with roots that had been produced over a period of the last two years. Many of these would be in a state of decay, and the rate of this decay might be related to the moisture content of the soil. Root samples were examined microscopically at the third harvest,

therefore, to determine the proportion of live roots with an intact cortex in the total sample which constituted the weights recorded above.

The proportion of live roots in the total was significantly higher in the wet and in the uncut treatments at the 0.1% and 5% levels respectively. The non-significant interaction of these two factors is shown in Table 50.

Table 50. Lysimeter Experiment II

Roots with Intact Cortex as Percentage of Total Roots at Harvest 3

	Uncut	Cut
Wet	57	50
Dry	39	34

L.S.D.=7

An investigation of the rate of production of new roots was made by counting the number of axes and new white roots at each harvest and then relating them to the number of tillers.

There was no significant difference in the number of root axes between either harvests or treatments, at a mean value of 9.2 axes per tiller. There was only the occasional new white root present. It appears, therefore, that from Harvest 2 until Harvest 4 there were almost no new roots produced. This coincided with a period of very hot, dry weather. After Harvest 4, the weather became cool and dull, and when further root samples were taken at Harvest 5, considerable production of new white roots was visible, particularly in the dry plots which had been exposed to rainfall since Harvest 4. They had produced two or three times the number of new white roots that were present in the controls. In addition, extensive branching and production of new, white lateral roots from the old axes was observed.

Soil temperature has been implicated as a factor influencing the rate of new root production, and the soil temperatures as measured at2·p.m. at 2cm depth on a hot day are presented in Table 51.

The temperature of the soil in the cut plots was considerably higher since more of the radiation reached the

soil surface, and also the wet plots were cooler. All temperatures were very high.

Table 51. Lysimeter Experiment II

Soil Temperatures Under Established Swards 9 June 2p.m.
(C^{o} at 2cm)

	Uncut	Cut
Wet	19	25
Dry	23	27

The nitrogen percentage in the shoots and the nitrogen uptake as determined from bulked samples are presented in Tables 52 and 53.

Table 52. Lysimeter Experiment II

Nitrogen Content of Shoots (% of DM)

		H0	H1	H2	H3	H4	H5
Uncut	Wet	3.8	-	3.5	2.0	1.9	1.7
	Dry	3.7	-	2.9	1.8	2.4	3.0
Cut	Wet	3.8	5.3	3.0	3.0	2.1	2.8
	Dry	3.7	5.0	3.8	2.9	2.8	4.8

The standard error of previous replicated (rather than bulked sample) determinations was 0.29 for a sample mean of 2.54% nitrogen. Assuming a similar coefficient of variation of 11.5%, the standard error for the above data would be 0.36. This suggests that only at Harvest 5 did the wet and dry treatments differ significantly, no doubt because the shoot growth of the dry treatments had left more residual nitrogen in the soil which was subsequently taken up when growth recommenced. Similarly, the reduced total growth of the cut treatments resulted in a higher tissue nitrogen percentage compared with the uncut treatments.

The total uptake of nitrogen in wet and dry treatments follows very closely the pattern of growth in the two

treatments. No explanation other than translocation to the roots can be offered for the apparent decline in total uptake from Harvests 2 to 3 in the uncut treatments (Table 53).

Table 53. Lysimeter Experiment II

Nitrogen Uptake in Shoots (kg ha^{-1})

(At harvest)		H0	H1	H2	H3
Uncut	Wet	28	-	159	115
	Dry	28	-	110	75
(Between harvests)					
Cut	Wet	28	51	38	24
	Dry	28	47	31	8
Total Uptake					
Cut	Wet	141			
	Dry	114			

The levels of P, K and Ca (Table 54) were generally higher in the cut than the uncut treatments. The level of P was considerably lower in the dry treatments, while that of K was higher, both these differences being greater in the cut treatment. The Ca level was considerably higher in the wet, cut plots.

Table 54. Lysimeter Experiment II

Level of Macro-nutrients in the Shoot at Harvest 3 (% of DM)

		P	K	Ca
Uncut	Wet	0.25	2.0	0.43
	Dry	0.20	2.1	0.42
Cut	Wet	0.39	2.0	0.60
	Dry	0.27	2.7	0.47

The leaf water potentials were analysed separately at Harvests 2 and 3 since at the former harvest there were only three measurement times, whereas there were four at all other lysimeter harvests.

At Harvest 2 there was a difference between wet and dry treatments and cut and uncut treatments, both significant at the 0.1% level, and an interaction between the water and cutting treatments (P=0.01). The same pattern was present at Harvest 3 except that the interaction was not significant. The water x cutting interaction for both harvests is shown in Table 55.

Table 55. Lysimeter Experiment II

Harvest 2

Mean Daily Leaf Water Potential (-bars)

	Uncut	Cut	
Wet	4.6	4.6	
Dry	8.0	5.3	L.S.D.=1.0

Harvest 3

	Uncut	Cut	
Wet	6.7	6.5	
Dry	10.1	7.7	L.S.D.=1.7

The uncut treatments were very much more sensitive, in terms of leaf potential, to drying of the soil, no doubt because of their larger transpiring surface. The difference in water deficit (Table 46) does not seem an adequate explanation.

There was no significant interaction of water treatment and time of day at either harvest, and the daily march of potential was similar to previous experiments.

No porometer data were collected at Harvest 2, but replicated readings were available at Harvest 3. There was a significant difference in both water and cutting treatments and the interaction is shown in Table 56 (P=0.05).

Table 56. Lysimeter Experiment II

Porometer Readings of Stomatal Rate at Harvest 3.*

*See Pipe Experiment II

	Uncut	Cut	
Wet	92	97	
Dry	35	97	L.S.D.=29

The diffusion rates of the dry, uncut plants were considerably restricted compared with the other treatments. There was no difference between the cut, wet and cut, dry plants.

Examination of the plots at the end of August showed a complete recovery of growth and tiller numbers in the formerly dry treated plots. Abundant tillering and new white root production had taken place and the foliage was much healthier and darker green than that found in the wet plots. Apart from the colour difference between wet and dry treatments, no easily visible difference was present between any of the treatments.

Results

2) Seedling Swards

Table 57. Lysimeter Experiment II

Dry Weight of Shoots (gm per plot; x 5 = kg ha^{-1})*

		WET		Log_e	DRY	
		Mean	Log_e	L.S.D.	Log_e	Mean
Uncut	H0	283	5.65	0.18	5.65	283
(Yield at	H2	708	6.56	0.18	6.43	621
harvest)	H3	885	6.78*	0.18	6.35	574
Cut	H0	283	5.65	0.24	5.65	283
(Cumulative	H2	569	6.35	0.24*	6.06	434
yield)	H3	661	6.47	0.24*	6.16	478
Cut	H0	283	5.65	0.25	5.65	283
(Individual	H2	286	5.65	0.25*	5.01	151
harvest	H3	92	4.50	0.25*	3.77	44
yields)						

*There was no Harvest 1 as in the cut established swards, but the same nomenclature is used for ease of comparison.

The interpretation of the seedling sward results must be made in the content of the severe inter-plant competition which developed during the course of the experiment. The mature swards had developed an equilibrium tiller density during the two years of their existance, but no 'natural' density had time to become established before treatment started in the seedling swards. The uneven establishment has been explained before. The superior growth in the dense areas of sward rapidly changed to a situation of intense competition after the treatments had started.

In the cut treatments, after the first cut, regrowth was limited to the number of tillers which the particular environmental situation could support. i.e. all the cut, wet tillers survived because water and light were adequate, but considerable mortality occurred in the cut, dry treatments, no doubt due to competition for water.

Though extremely dense, most plants survived in the wet, uncut treatments, but heavy mortality occurred in the dry, uncut treatments while the remaining plants grew relatively healthily leaving an under-storey of wilted and dying plants.

While giving an interesting insight into the effects of water stress and competition on an establishing sward, the objectives of the experiment were partly confounded by this phenomenon.

The yields of shoots in both dry, uncut and dry, cut treatments fell behind those of the controls by Harvest 2, but by a significant amount only in the case of the cut treatments (Table 57). The corresponding soil water deficits at each harvest are given in Table 58.

Table 58. Lysimeter Experiment II

Soil Water Deficit at Harvest (cm).

	H0	H2	H3
Uncut	0	6.6	7.6
Cut	0	5.2	6.4

The lower yield could be attributed to the death of a proportion of the plants in the drying plots and does not necessarily imply growth depression due to drought in the surviving plants.

This is illustrated by the number of live tillers in each treatment (Table 59). There were significantly fewer in the dry treatments (P=0.001), and in the uncut treatments (P=0.01). The lack of water stress had allowed a much higher survival rate on the watered treatments, and the reduced competition, presumably for light, had enabled better survival in the cut swards. These tiller densities make an interesting comparison with those of the established swards which averaged 26 per 100cm^2 in all treatments and those of the pipes given elsewhere.

Table 59. Lysimeter Experiment II

Number of Live Tillers at Harvest 3 (per 100cm^2)

	Uncut	Cut
Wet	48	62
Dry	15	32

L.S.D.=15

The distribution of the dry matter of the shoots is given in Table 60, from large unreplicated samples. A high proportion of the weight was in the leaf lamina in the cut treatments, and more in the sheaths in the dry treatments.

Table 60. Lysimeter Experiment II

Distribution of Shoot Dry Weight at Harvest 3 (%)

	Leaf Lamina	Sheath	Dead Material
Wet Uncut	67	16	17
Dry Uncut	51	23	26
Wet Cut	88	12	—
Dry Cut	57	12	31

Statistical analysis of the Log_{10} root weights from each root zone showed no overall effect of water treatment but a significantly lower weight in the cut treatments (P=0.05). (Table 61).

Table 61. Lysimeter Experiment II

Mean Root Weights of Uncut and Cut Treatments at Harvest

(Log_{10} x 100)

	H0	H2	H3
Uncut	1.55	1.68	1.58
Cut	1.55	1.57	1.44

L.S.D.=0.11

The interaction between water treatment and depth (P=0.01) confirmed that reduced growth in the surface zones on drying was at least partially compensated for by increased weight at depth (Table 62).

Table 62. Lysimeter Experiment II

Mean Root Weight (Log_{10} x 100)

Depth (cm)	0-12.5	12.5-25	25-37.5	37.5-50
Wet	2.29	1.71	1.10	1.03
Dry	2.17	1.75	1.26	1.18

L.S.D.=0.13

The root weights were increased by the dead remains of the roots of the previous sward which had not decomposed. These were estimated to constitute 65% of the total root length present, showing no significant difference in the proportion present under different treatments.

Examination of the number of root axes from each tiller revealed a significantly higher number in the wet treatments (P=0.05), while cutting had no effect (Table 63).

Table 63. Lysimeter Experiment II

Mean Number of Root Axes per Tiller, Mean of Harvests

Wet	Dry
3.8	2.7

L.S.D.=0.9

It was noted at the two later harvests that short white roots were confined to the few dominant plants present in each treatment, and the small plants which had suffered most from competition had no new white roots. The competitive stress suffered by the plants, therefore, seemed to have been the major factor in determining new root production, and no treatment effect was distinguishable.

The percentage of nitrogen in the shoots and the uptake data are presented in Tables 64 and 65.

Table 64. Lysimeter Experiment II

Nitrogen Content of Shoots (% of DM)

	H0	H2	H3	H5
Uncut Wet	-	2.3	2.3	2.5
Dry	-	2.7	2.5	3.8
Cut Wet	4.4	2.7	2.8	2.6
Dry	3.8	4.0	3.3	4.1

The standard error for the nitrogen percentage, estimated as for the established swards, would be about 0.36.

The drying treatments showed a consistent tendency to a higher nitrogen percentage compared with controls, as did the cut treatments. The difference between wet and dry treatments was again particularly marked when the latter had been rewatered after Harvest 3. At Harvest 2, samples of healthy and wilting plants were taken from the dry, uncut plots and analysed. The nitrogen percentage in the wilting plants was 155% of that in the good plants.

The nitrogen uptake in the shoots was at a slightly lower level than in the established swards but followed an otherwise similar pattern, being closely correlated with the yield of dry matter.

The level of P in the shoots was considerably lower in the dry treatments than in the controls at Harvest 3. The levels of K and Ca showed small irregular variations (Table 66).

Table 65. Lysimeter Experiment II

Nitrogen Uptake in the Shoots (kg ha^{-1})

(To harvest)	H0	H2	H3	
Uncut Wet	56	81	102	
Uncut Dry	56	84	72	
(Between harvests)				Total
Cut Wet	56	39	13	108
Cut Dry	56	30	7	93

Table 66. Lysimeter Experiment II

Level of Macro-nutrients in the Shoot at Harvest 3 (% of DM)

	P	K	Ca
Uncut Wet	0.30	2.5	0.67
Uncut Dry	0.22	2.8	0.72
Cut Wet	0.41	2.8	0.68
Cut Dry	0.26	2.4	0.70

The effect of the drying treatments was to lower the leaf water potential significantly below the control level, while cutting made the reduction less severe (Table 67).

Table 67. Lysimeter Experiment II

Leaf Water Potentials, Mean of Harvests and Times of Day(-bars)

	Uncut	Cut
Wet	8.3	7.4
Dry	10.7	8.9

L.S.D.=1.4

This was the only experiment to show a significant interaction (P=0.001) of water treatment and time of day (Table 68). The drying plants were able to effect an almost complete recovery of leaf water potential when radiation levels fell in the evening.

Table 68. Lysimeter Experiment II

The Effect of Drying on the Course of Leaf Water Potential through the Day (- bars)

	5.30a.m.	10a.m.	1p.m.	9p.m.
Wet	1.9	12.3	12.8	4.2
Dry	1.6	14.8	17.5	5.0

L.S.D.=1.4

Analysis of the porometer data at Harvest 3 showed a significantly lower rate of stomatal diffusion in the dry treatments (P=0.01). The stomata appeared to be less affected in the dry, cut treatments than in the dry, uncut treatments. (Table 69), showing a similar pattern to the leaf water potentials.

Table 69. Lysimeter Experiment II

	Stomatal Diffusion Rates at Harvest 3*	
	Uncut	Cut
Wet	132	132
Dry	71	110

L.S.D.=36

* See Pipe Experiment II

The plots showed complete recovery in a manner similar to the mature swards by the end of August.

This experiment confirmed reports from elsewhere that growth of a mature sward is depressed at relatively small water deficits. It was not possible, unfortunately, to confirm in field conditions that a seedling sward, with a new and expanding root system, was relatively insensitive to drought. The level of competition was clearly an important factor in determining the development of the seedling plants, and there seems little point in trying to draw comparisons with the pipe situation.

This experiment served, most of all, as a reminder of the numerous factors which combine to determine the response of grasses to drought, and the near impossibility of controlling and combining them all, simultaneously, in a way which would enable valid conclusions, applicable to any general situation, to be drawn.

THE WATER BALANCE OF DACTYLIS AND LOLIUM

The Measurement of Plant Resistance to Water Flow

Present knowledge of the nature of plant and soil resistances has been discussed in the introduction to this thesis. Calculation of the distribution of the total resistance along the pathway from soil to leaf has been handicapped by the inability to measure water potential at the root surface and so estimate the relative importance of the soil and plant components of the total resistance.

A method of calculating the water potential at the root surface has been derived from Gardner's (1964) mathematical model of water uptake by a root system, with a minor modification from Cowan's (1965) treatment.

Symbols Used (C.G.S. units)

Unless otherwise stated, the symbol refers to a uniform horizon. The addition of a bar to the symbol (e.g. $\bar{R}_s$) indicates that the value has been extended, as explained in the text, to encompass the entire root profile.

U	$cm^3\ cm^{-2}\ sec^{-1}$	rate of uptake from total root depth
E_t	$cm^3\ cm^{-2}\ sec^{-1}$	transpiration rate
Q	$cm^3\ cm^{-3}\ sec^{-1}$	rate of soil water depletion
ψ_s	cm	water potential in bulk soil
ψ_r	cm	water potential at root surface
ψ_L	cm	mean leaf water potential
R_p	sec	resistance to water flow from root surface to leaf evaporating surface
R_s	cm sec ($\bar{R}_s$ sec)	resistance to water movement from unit soil volume to root surface
k	$cm\ sec^{-1}$	capillary conductivity of soil
k'	$cm\ sec^{-1}$	geometric mean of k values appropriate to the potentials at each end of potential gradient
L	$cm\ cm^{-3}$	root density
B		a dimensionless function of root system geometry (Gardner 1964)

α cm^2	a similar function to B, derived by Cowan (1965)
r_1 cm	root radius
r_2 cm	radius of cylinder of soil effectively occupied by a root

The overall calculation is based on the equation of Van den Honert (1948), adapted for the situation of varying conditions through the rooting zone.

$$U \text{ (assumed} = E_t) = \frac{\bar{\psi}_s - \bar{\psi}_r}{\bar{R}_s} = \frac{\bar{\psi}_r - \psi_L}{R_p} = \frac{\bar{\psi}_s - \psi_L}{\bar{R}_s + R_p} \quad \text{---} \quad (1)$$

Whence $$R_p = \frac{\bar{\psi}_s - \psi_L}{U} - \bar{R}_s \quad \text{---} \quad (2)$$

In order to elaborate these equations, uptake from uniform horizons of unit thickness is first considered.

$$Q = \frac{\psi_s - \psi_r}{R_s} \quad \text{---} \quad (3)$$

The calculation of R_s

Gardner expressed soil resistance as

$$R_s = \frac{1}{BkL} \quad \text{---} \quad (4)$$

Hence $$\psi_s - \psi_r = \frac{Q}{BkL} \quad \text{---} \quad (5)$$

Cowan derived the similar equation

$$\psi_s - \psi_r = \frac{Q\alpha}{k} \quad \text{---} \quad (6)$$

thereby setting α equal to $\frac{1}{BL}$

$$\text{Cowan sets } \alpha = \frac{r_2^4}{2(r_2^2 - r_1^2)} \ln\left(\frac{r_2}{r_1}\right) - \frac{3r_2^2 - r_1^2}{8} \quad \text{(7)}$$

whereas Gardner used, in effect,

$$\alpha = \frac{1}{2} r_2^2 \ln\left(\frac{r_2}{r_1}\right) \quad \text{(8)}$$

Equation 7 was used in the present treatment. For the rapid derivation of α from given values of r_1 and r_2, a graphical representation of equation 7 can be used.

In order to derive R_s from equation 4, a value of k appropriate to the potential gradient ψs to ψr is required, and this is assumed after Cowan to be the geometric mean.

$$(k_{\psi_s} k_{\psi_r})^{\frac{1}{2}} = k' \quad \text{(9)}$$

The evaluation of equation 9 requires the calculation of ψ_r.

Combining equations 3, 4 and 9,

$$Q\alpha = k' (\psi_s - \psi_r) \quad \text{(10)}$$

A graphical representation of equation 10 can be constructed to enable the derivation of ψ_r for given values of $Q\alpha$ and ψ_s (Fig.28).

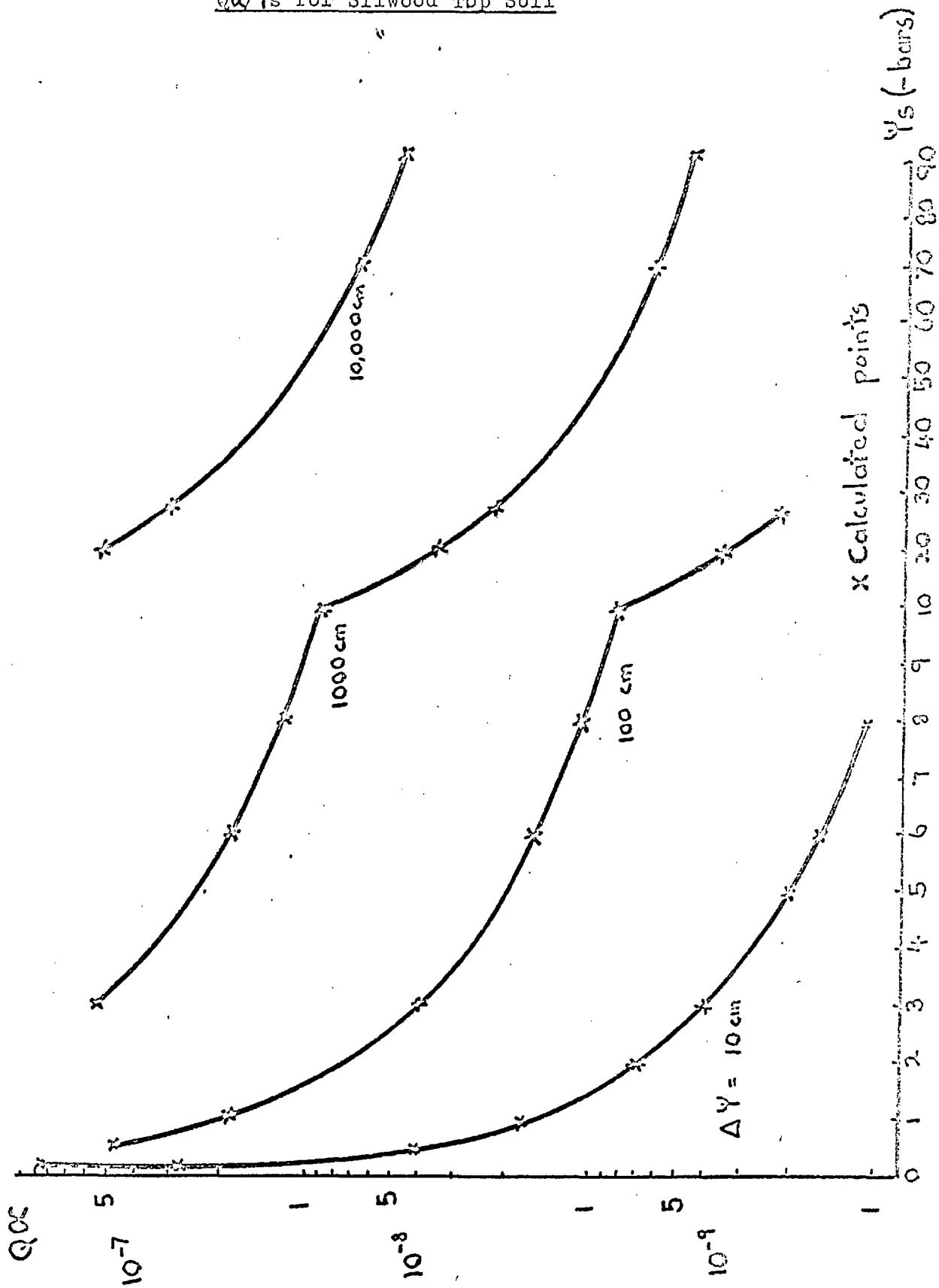
Now, extending the calculation to n horizons, each of thickness hcm, the total uptake of water

$$U(=\Sigma Qh) = h\left[\frac{(\psi_{s_1} - \psi_{r_1})}{\alpha_1} k'_1 + \cdots\cdots \frac{(\psi_{s_n} - \psi_{r_n})}{\alpha_n} k'_n\right]$$

$$= h\left[\left(\frac{\psi_{s_1} k'_1}{\alpha_1} + \cdots\cdots \frac{\psi_{s_n} k'_n}{\alpha_n}\right) - \left(\frac{\psi_{r_1} k'_1}{\alpha_1} + \cdots\cdots \frac{\psi_{r_n} k'_n}{\alpha_n}\right)\right]$$

Fig.28

Qα/Ψs for Silwood Top Soil



$$= h \left[\sum_{n=1}^{n} \left(\frac{\psi_s \, k'}{\alpha} \right) - \sum_{n=1}^{n} \left(\frac{\psi_r \, k'}{\alpha} \right) \right] \qquad \text{(11)}$$

The integrated conductance from the soil to the root surface over the whole profile

$$\text{where} \quad K = \sum_{n=1}^{n} \left(\frac{k'}{\alpha} \right)$$

$$\text{is} \quad h K = \frac{1}{\bar{R}_s} \qquad \text{(12)}$$

Then combining equations 11 and 12

$$U = \frac{1}{\bar{R}_s} \left[\sum_{n=1}^{n} \left(\frac{\psi_s \, k'}{\alpha \, K} \right) - \sum_{n=1}^{n} \left(\frac{\psi_r \, k'}{\alpha \, K} \right) \right] \qquad \text{(13)}$$

The terms inside the brackets of equation 13 have the dimensions of potential and represent mean values of bulk soil and root surface potential respectively, weighted by permeability and root density so that regions of high permeability and root density contribute most to the mean potential.

Equation 13, therefore, gives the terms to be entered in equation 2, and, knowing ψ_L, hence to calculate Rp.

The above calculations were incorporated into a computer programme with the following modifications in place of graphical solutions.

1) The value of α was calculated for each horizon from the data.

2) The appropriate value of k was calculated each time from a regression equation of k on ψ_s described in a previous section.

3) An iterative procedure was used for the calculation of ψ_r. The potential gradient between the bulk soil and root was increased from zero by successive increments of 0.1cm of water until the value of Q, calculated from equation 10 on the basis of this assumed gradient, first exceeded the real experimental value of Q. At this point, the true value of ψ_r had been approximated.

The programme also calculated real uptake from each horizon from the experimentally determined apparent uptake values by a method described in a following section.

The calculation of apparent uptake

From the harvest data measurements

1) The average daily change in the volume of water present in each horizon during the period from the preceding harvest to the following harvest* was calculated, thereby giving approximate values to the distribution of water removal between horizons on the harvest day.

2) The measured total transpiration during the harvest period was divided between the horizons in the ratio of the uptake distribution as estimated in 1).

* This procedure was modified for the final harvest by using the distribution of uptake as calculated from average uptake between the pen-ultimate and final harvests, there being no harvest following the final one.

This method assumes a linear fall of the soil water content with time in each horizon, and also, in Pipe Experiment III where the day's uptake was further subdivided, that the distribution of uptake between horizons remained constant during that day. This can only be justified by refering to Gardner's (1964) suggestion that uptake pattern is insensitive to uptake rate. Others (Brouwer, 1965) suggest that the operative amount of root varies with uptake rate.

Apparent uptake rates were then corrected to allow for movement within the soil into and out of adjacent horizons at lower or higher water potentials respectively.

The estimation of real uptake by the roots

Real uptake from each horizon was determined from apparent values by means of the equation

$$Q\ \text{Real}_2 = Q\ \text{Apparent}_2 - \left(\frac{\psi_{s_2} - \psi_{s_1}}{h}\right) k' + \left(\frac{\psi_{s_3} - \psi_{s_2}}{h}\right) k'$$

where the subscripts refer to horizons 1, 2, 3, when 1 is at a lower potential and 3 at a higher potential than 2. Evaporation from the soil surface was assumed negligible.

Negative uptake rates calculated for the bottom horizon and, occasionally elsewhere, may have resulted from incorrect extrapolation of the ψ_s/water content/k graphs. This extrapolation was normally only necessary for the surface and bottom horizons.

The calculation of R_p in Pipe Experiment III was done by a simplified method because the computer was not programmed to handle the different capillary conductivities of soil and Perlite. On the basis of preliminary calculations, it was assumed in this experiment that $\psi_s \simeq \psi_r$, thereby eliminating the part of the calculations involving k.

Similar simplified calculations of R_p were made for the corresponding wet treatments, and since the distribution of uptake was unknown, it was assumed that $\psi_s = \psi_r = 0$ throughout the pipe.

Thus for the wet treatments, equation 2 becomes

$$R_p = -\frac{\psi_L}{U}$$

The data required for these calculations were obtained during the course of Pipe Experiments III, IV, VI and VII by methods described in the appropriate sections. The mean of replications was used in the first two experiments in view of the rather variable data, but improved techniques enabled results to be calculated for individual pipes in the last two experiments.

Anomalies in the data which were revealed when the Perlite water contents were converted to water potentials precluded examination of the results of Pipe Experiment III after the first two harvests in the dry treatments.

Results

An example of the computer output for each harvest in Pipe Experiment VI is shown in Table 70.

Plant Resistance

The calculated plant resistances are summarised in Table 71. Replication permitted an analysis of variance in experiments VI and VII and showed a significant effect of water treatment ($P=0.001$), R_p being higher in the dry

Table 70. Pipe Experiment VI

Water Balance Analysis

Lolium Uncut, Dry Treatment Harvest 1 Pipe 1 (15cm horizons)

r_1	r_2	Ψ_s	Q	k'
0.0045	0.095	-8000	1.57×10^{-7}	1.06×10^{-10}
0.0043	0.157	-5800	1.34×10^{-7}	1.61×10^{-10}
0.0041	0.197	-6400	2.61×10^{-7}	1.40×10^{-10}
0.0041	0.232	-1800	4.67×10^{-7}	7.44×10^{-10}
0.0041	0.218	- 170	2.58×10^{-7}	1.71×10^{-8}
0.0048	0.289	- 38	4.10×10^{-7}	1.24×10^{-7}
0.0054	0.495	- 10	-4.32×10^{-7}	7.23×10^{-7}

Ψ_r	q
-8015	0.45×10^{-8}
-5829	1.04×10^{-8}
-6513	3.18×10^{-8}
-1856	7.91×10^{-8}
- 171	3.86×10^{-8}
- 39	1.08×10^{-7}
- 10	3.32×10^{-7}

$\bar{\Psi}_s$	-83.3
$\bar{\Psi}_r$	-84.0
Ψ_L	-9059
U	1.88×10^{-5}
Rp	5.5×10^{3}
$\bar{R}s$	0.3

UNIT KEY

r_1 cm
r_2 cm
Ψ_s cm
Q $cm^3\ cm^{-3} sec^{-1}$
k' cm sec^{-1}
Ψ_r cm
q $cm^3\ cm^{-1} sec^{-1}$

$\bar{\Psi}_s$ cm
$\bar{\Psi}_r$ cm
Ψ_L cm
U $cm^3\ cm^{-2} sec^{-1}$
Rp days
$\bar{R}s$ days

Table 70, Pipe Experiment VI

Water Balance Analysis

Lolium Uncut, Dry Treatment Harvest 2 Pipe 1 (15cm horizons)

r_1	r_2	Ψ_s	Q	k^1
0.0036	0.888	-8900	0.31×10^{-7}	0.92×10^{-10}
0.0037	0.110	-7500	0.29×10^{-7}	1.15×10^{-10}
0.0036	0.202	-8300	0.41×10^{-7}	1.00×10^{-10}
0.0038	0.202	-7200	1.02×10^{-7}	1.21×10^{-10}
0.0037	0.207	-5700	3.13×10^{-7}	1.63×10^{-10}
0.0045	0.212	-1600	9.85×10^{-7}	8.59×10^{-10}
0.0050	0.243	- 68	-3.48×10^{-7}	5.77×10^{-8}

Ψ_r	q
-8903	0.77×10^{-9}
-7504	1.08×10^{-9}
-8328	5.30×10^{-9}
-7256	1.31×10^{-8}
-5835	4.23×10^{-8}
-1680	13.89×10^{-8}
- 68	-6.44×10^{-8}

$\bar{\Psi}_s$	-363.6
$\bar{\Psi}_r$	-366.0
Ψ_L	-11923
U	1.73×10^{-5}
Rp	7.74×10^{3}
$\bar{R}s$	1.17

Table 70. Pipe Experiment VI

Water Balance Analysis

Lolium Uncut, Dry Treatment Harvest 3 Pipe 2 (15cm Horizons)

r_1	r_2	Ψ_s	Q	k'
0.0027	0.078	-13000	4.39×10^{-8}	0.56×10^{-10}
0.0031	0.127	-10700	3.50×10^{-8}	0.72×10^{-10}
0.0031	0.205	- 7600	-1.31×10^{-8}	1.13×10^{-10}
0.0036	0.220	- 7000	2.78×10^{-8}	1.26×10^{-10}
0.0034	0.223	- 5700	2.60×10^{-8}	1.65×10^{-10}
0.0043	0.228	- 3800	6.00×10^{-7}	2.74×10^{-10}
0.0045	0.201	- 550	2.10×10^{-7}	3.63×10^{-9}

Ψ_r	q
-13006	0.83×10^{-9}
-10712	1.76×10^{-9}
-7600	-1.73×10^{-9}
-7018	4.21×10^{-9}
-5712	3.72×10^{-9}
-3985	9.83×10^{-8}
- 554	2.66×10^{-8}

$\bar{\Psi}_s$	2620.3
Ψ_r	2632.2
Ψ_L	10983
U	1.39×10^{-5}
Rp	6.94×10^{3}
$\bar{R}s$	9.95

Table 71

Plant Resistance (x 10^3 days)

		H1	H2	H3
IV	Wet	6.4	9.2	5.2
	Dry	8.6	10.9	18.0
VI	Wet	4.6	7.7	3.5
	Dry	7.4	12.1	5.0
				L.S.D.= 1.8
VII	Wet	9.0	7.7	-
	Dry	9.6	17.2	-
				L.S.D.= 4.0

III		CF				RG				
9-9a.m.	H1	H2	H3	H4	H5	H1	H2	H3	H4	H5
Wet	6.5	10.0	6.4	8.6	15.3	7.6	10.5	10.1	8.8	10.0
Dry	-	-	-	-	-	-	-	-	-	-
9-1p.m.										
Wet	4.5	4.6	5.0	3.1	4.2	5.1	4.8	5.2	4.4	4.1
Dry	9.3	6.3	-	-	-	5.9	5.9	-	-	-
1-5p.m.										
Wet	4.5	4.2	3.6	3.3	5.2	4.6	4.4	3.9	4.2	6.3
Dry	7.3	5.7	-	-	-	5.8	6.0	-	-	-
5-9p.m.										
Wet	5.6	5.7	7.3	5.3	-	7.2	6.1	12.3	6.1	-
Dry	8.5	7.4	-	-	-	6.6	7.6	-	-	-

treatments of both experiments. There was an interaction between harvest and water in Pipe Experiment VII (P=0.01) and this same effect was apparent in Experiment IV, but absent from Experiment VI.

In Pipe Experiment III, R_p showed a diurnal cycle, falling to a minimum at maximum uptake rates during the middle of the day, then rising again in the evening. Plots of R_p and U incorporating all available data show falling resistance in both wet and dry treatments as U increases, though the rate of decline decreases rapidly when U exceeds 1.16 x 10^{-5}, equivalent to E_t = 1cm day^{-1}.

The accuracy of the calculation of R_p is most dependent on the reliability of the measurement of U and Ψ_L.

Considering U first, the evaporation of water directly from the surface of the soil, restricted to an unknown extent by the polystyrene barrier, might have been responsible for the recorded interaction between harvest and water treatment. Soil evaporation in the wet treatments might be assumed to contribute a constant proportion to U, whereas the continually drying top soil of the dry treatments might be expected to contribute a decreasing amount to total water loss at successive harvests, thereby reducing the measured value of uptake towards its true value and causing a proportional increase in the estimate of R_p. Up to 40% of evapo-transpiration from pipes under grass was shown to occur from the wet soil surface in pilot experiments, but no data was obtained regarding the effectiveness of a polystyrene granule vapour barrier.

The daily fluctuations in R_p in Experiment III could not be attributed to this cause, however, since the method of estimating U eliminates the possibility of soil evaporation being the fluctuating factor, unless there was also a diurnal fluctuation in the relationship between total evapo-transpiration and soil evaporation. Alternatively, the method of partitioning daily transpiration using the small pipes might have introduced a cyclic error in U, so accounting for this result. The fact that the basic inverse relationship between R_p and U holds both within a day and between harvests does, however, strongly suggest a real relationship.

The measurement of ψ_L by the pressure method has been discussed elsewhere and found to show a close correlation with expected results. Any tendency of the technique to overestimate (i.e. towards less negative potentials) ψ_L at low potentials (and hence, normally, low U values), or underestimate (i.e. towards more negative potentials) at high leaf potentials, would create a fortuitous inverse relationship between R_p and U.

The relationship between R_p and U, was explored statistically by Mr. East of U.C.W. (statistics dept.). Regressions were fitted of both linear and quadratic types to the individual sets of data for each species and water treatment, pooled from all experiments.

$$\text{i.e. } \log_e R_p = a + bU$$
$$\text{and } R_p = a + bU + cU^2$$

Both equations were found to describe the data with good precision (R^2 = 70-80%), and both had disadvantages. The quadratic regression gave an upturn in the curve which was not apparent in the data. Since, from basic reasoning, the asymptotic type of curve seems more likely to describe the relationship, the linear regression was further examined for all four treatments. Differences between the slopes and the ordinates were considered.

Comparisons of linear regressions of $Log_e R_p$ on U

Difference between	Slope	Ordinates
Wet Lolium v Dry Lolium	* *	NS
Wet Dactylis v Dry Dactylis	NS	* * *
Wet Dactylis v Wet Lolium	NS	*(*)
Dry Dactylis v Dry Lolium	NS	NS

When the quadratic regressions were compared, then the wet and the dry treatments did not differ between species, and so this enabled the data from each species to be pooled for an overall comparison of the quadratic regressions of wet and dry treatments, and this difference was highly significant (P=0.001). R^2 was 77% in both cases.

The linear regressions of all treatments are presented in Fig.29 and the quadratic regressions of pooled wet and pooled dry data in Fig.30

Integrated Soil Resistance and Water Potential at the Root Surface

The results (dry treatments only) of all experiments showed a similar pattern and they will be outlined in general terms. At Harvest I, real uptake rate (Q) was fairly uniform from all horizons containing roots, becoming increasingly concentrated in the lower horizons as the profile dried. At the final harvest, uptake rates were an order of magnitude higher in the two lowest horizons than in those above. The root density was fairly even throughout the pipe below the two upper horizons. As a consequence, the method of weighting used in the calculation of $\bar{\psi}_s$ gave values strongly orientated towards the horizons of maximum uptake and high soil potential, and only in the later stages

Fig.29

Linear Regressions of $Log_e Rp$ on U

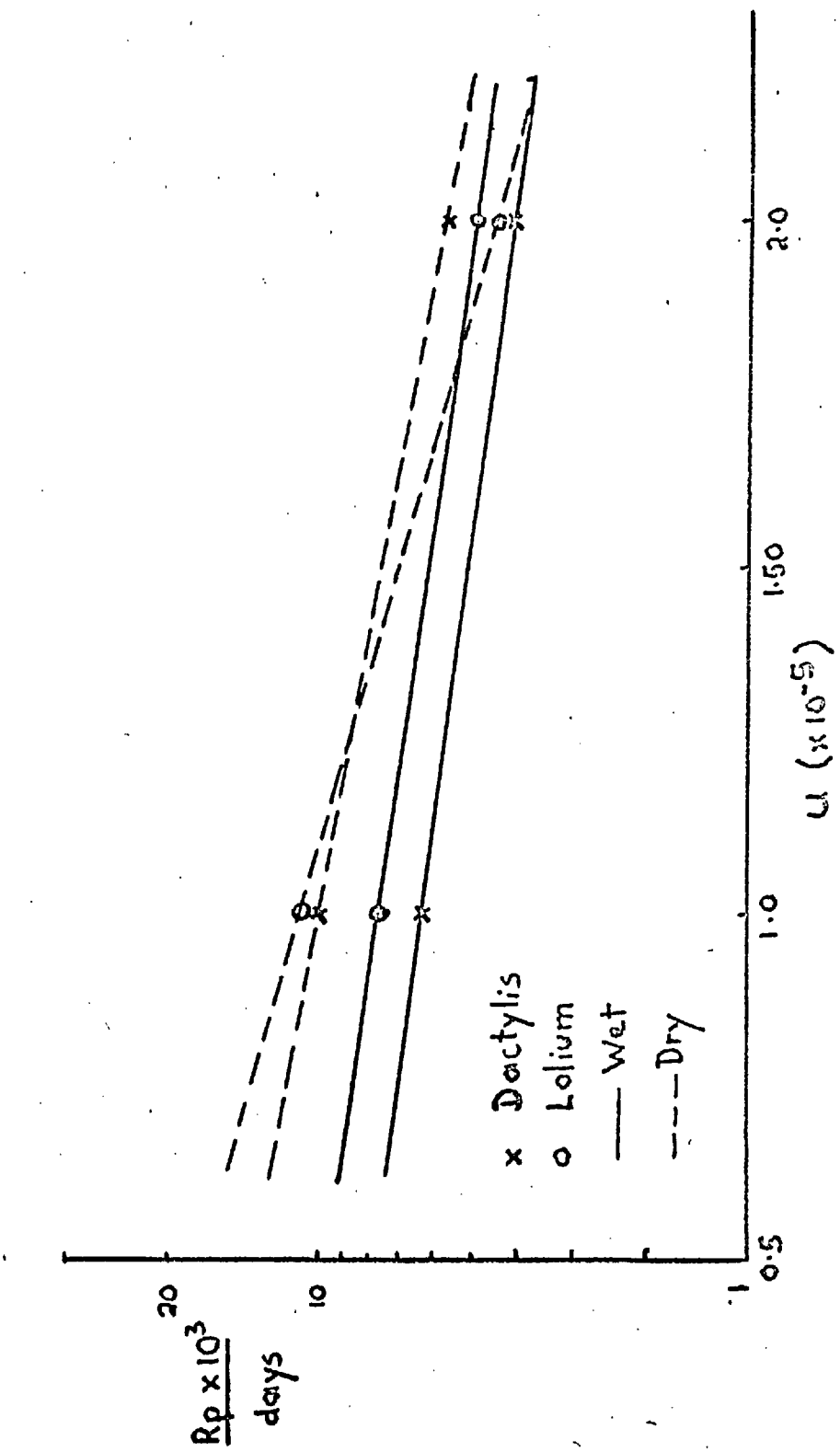
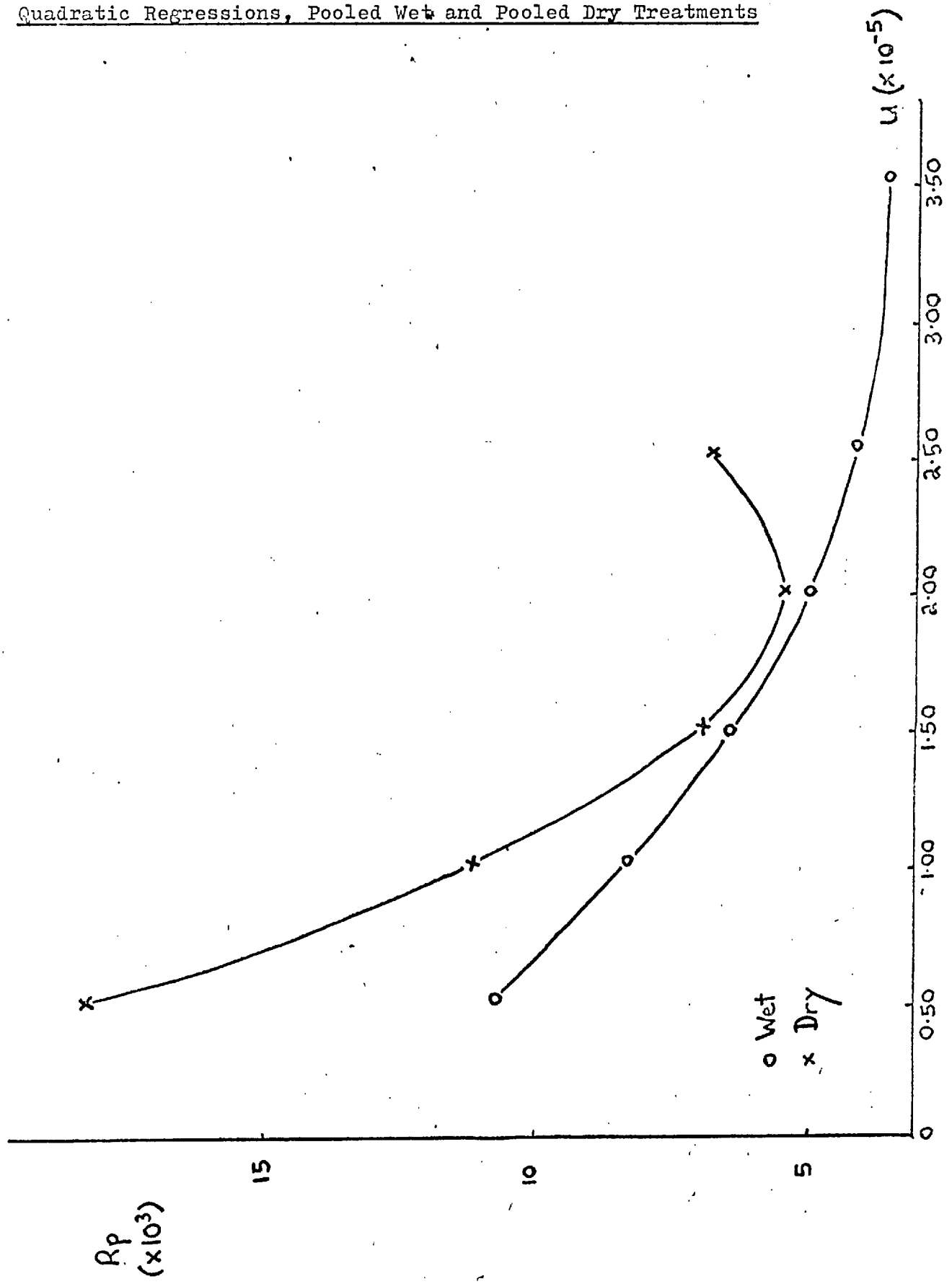


Fig.30

Quadratic Regressions, Pooled Wet and Pooled Dry Treatments



of drying, when the two lowest horizons were subject to rapidly falling potential, did the value of $\bar{\Psi}_s$ fall appreciably below -1 bar. Between Harvests 1 and 2 in Experiment III, $\bar{\Psi}_s$ rose, even though the soil was drying, because root extension was sufficiently rapid to more than compensate for the fall in potential in the upper horizons.

The fact that uptake was always low in zones of low potential (and hence low k) causes the estimated drop in potential between the soil and root surface ($\Delta\Psi$) to be very small at all times, even when the soil was very dry. The range of calculated potential gradients was between 1 and 200cm of water, the highest values being found in horizons of moderate soil potential where uptake was still occurring at an appreciable rate. Further falls in Ψ_s diverted uptake to lower and wetter horizons, so causing $\Delta\Psi$ to fall again. Hence, the difference between $\bar{\Psi}_s$ and $\bar{\Psi}_r$ was small, generally in the range 1-10cm of water, increasing appreciably to a maximum recorded value of 49cm only in the final stages of drying in the lowest horizons. As a consequence, $\bar{R}_s$ remained very small and ranged from four orders of magnitude smaller than R_p in a wet profile to two orders smaller in a dry profile at the point of incipient wilting.

Thus, on the basis of the analysis applied to the conditions of these experiments, the plant appears to offer the major resistance in the flow pathway. In order to help establish why other workers have come to contrary conclusions, the calculated uptake rates per unit root length for each horizon were computed (Table 70).

DISCUSSION

While setting out with limited objectives, the complexity of the interactions of water stress, nutrition and plant response caused a rapid proliferation in the aspects covered by this thesis, all closely inter-related and often little understood. It is convenient to discuss these aspects individually, while bearing their relationships in mind.

The term 'water stress' is used indiscriminately and imprecisely throughout the literature (Slatyer,1967; Kozlowski,1968), and usually without definition. Taylor (1968) describes stress as being water conditions in the plant which are unfavourable to optimum growth. Since these conditions differ between plants, times,and stages of growth, and optimum growth is not specified, this definition adds little to the usefulness of the term.

Using the terminology of water potential, it seems reasonable to regard a plant as being under water stress if its water potential falls below zero, and to ignore any relationship to growth/performance parameters. Thus under all normal conditions, a plant is under some degree of stress and the object of the following section is to examine the normal range and magnitude of stress. Following sections will then examine its relationship to growth response and nutrition.

The Water Balance of *Dactylis* and *Lolium*

1. The Behaviour of Leaf Water Potential and its Implications on Growth Processes

The daily course of transpiration (E_t) is largely a function of solar radiation conditions, and superimposed in these experiments are probably fairly large contributions from reflection and advection from surrounding areas. E_t in the pipe experiments ranged from 0.2-1.5cm day^{-1}, greenhouse experiments in winter and hot, breezy days in summer giving rise to the respective extremes of the range. Soil evaporation probably made an important contribution in the wet treatments, where highest values were recorded. The highest transient rates recorded were 3.4cm day^{-1}.

Average E_t values from the dry treatment lysimeters were 0.2-0.4cm day^{-1},

Thus E_t was generally well above average for the U.K. in the pipe experiments, but fairly normal in the lysimeters. The higher E_t values recorded from the pipes might be expected to cause lower leaf water potentials than on the lysimeters (Cavande and Taylor,1967), but this effect could not be detected. The possible reasons may be either that the plants were all operating in the range of Ψ_L associated with stomatal control, or that the much denser and more rapidly expanding root systems in the pipes gave a lower resistance to uptake, thus permitting higher uptake rates at the same value of Ψ_L . Whatever the reason, soil and xylem flux rates would be correspondingly higher.

Methods in general use are too cumbersome to permit rapid sequences of measurements of leaf water potential, and this possibly accounts for the lack of published records of the daily course of Ψ_L . In these experiments, Ψ_L fell from initial dawn levels in the range 0 to -4 bars, rapidly down tothe range -8 to -14 bars (and sometimes as low as -19 bars towards the end of a drying cycle). This fall was followed by an equally rapid rise as evening approached to within -2 to -4 bars of the dawn level, the balance of the rise taking place during darkness. This course encompasses both wet and dry treatments until the terminal phases of the dry treatments when the plants failed to recover appreciably during darkness (Fig.12).

The size and duration of the fall in Ψ_L is remarkable in view of the extensive literature showing that growth rate falls at potentials below fully turgid levels. Boyer (1968) found that cell enlargement only occurred at potentials above -3.5 bars, hence rapid leaf extension only took place at night when turgor pressure was sufficiently high. Crafts (1968) defined the onset of stress as being in the range 0 to -5 bars, though field and forage crops grew well down to -16 bars. Many authors have described the commencement of adverse effects on photosynthetic and metabolic processes in the range of -5 to -10 bars (Lawlor,1969; Slavik,1965; Boyer,1965). Thus, for much of the day in these experiments, both wet and dry plants were experiencing a level

of stress normally associated with a considerable reduction in extension growth and the suppression of metabolic functions. There was little to suggest that this was simply the result of excessive transpiration rates since the lysimeter plots behaved similarly at normal transpiration rates, and also, Ψ_L fell to these levels after sunrise, before potential transpiration rates had reached very high levels.

Equally surprising, however, was the rapidity with which recovery ensued at sunset, even when uptake was confined largely to the lowest horizons. For most of the night, therefore, plant water potentials could be associated with low levels of stress. How much compensation can be accomplished during darkness for reduced daytime growth processes, is open to speculation. Clearly, lost photosynthetic fixation cannot be regained, but translocation and cell extension can possibly progress at compensatory rates (Boyer, 1968)

2. Stomatal response to stress

Stomatal response to Ψ_L is probably of over-riding importance in determining the response of photosynthetic rates to stress. It is unfortunate that the measurements of diffusion rate in these experiments were relative rather than absolute, and their nature was such that comparisons were only reliable with the provisos made in the discussion of the method. There were signs of stomatal restriction relative to the controls soon after drying commenced in most cases, but the difference was generally small until the end of the drying cycle. The levels of Ψ_L in the controls which were used for comparison of any treatment effects were, however, frequently in the range associated with stomatal restriction (Ehlig and Gardner, 1964) and the small size of the difference in diffusion rate from wet and dry treatments could conceivably be attributed to a similar restriction in both. There is some evidence for this in Table 39 where the daily course was closely followed. Diffusion rates from the wet treatments rose considerably until 11.30 a.m. when there was a sudden fall to a level which persisted through the

remainder of the day. This fall in diffusion rate closely followed a fall in ψ_L to below -10 bars which appears to mark the onset of stomatal restriction (Fig.16 and other unpublished data) and resulted from a sudden fivefold rise in radiation levels when the weather changed. The lower potentials in the dry treatments, resulting from the dry soil, had caused the -10 bar level to be passed earlier in the day, hence the earlier decline in diffusion to lower levels.

It seems conceivable, therefore, that stomatal restriction of CO_2 diffusion may have reduced assimilation in both wet and dry treatments, and growth responses must be considered in this light. It may be of importance that water vapour diffusion was only recorded as being zero on rare occasions when high evaporative demand in the final phases of drying caused ψ_L to fall to very low levels in the range -16 to -19 bars. In view of the apparently wide range of ψ_L over which partial stomatal restriction appears to operate, and the fact that for much of the day, ψ_L was in this range in both wet and dry treatments, then considerable importance must attach to the relative magnitudes of diffusion resistances to water vapour and CO_2. It appears, assuming a similar range and form of ψ_L in field conditions to that found here, that even under optimum soil moisture conditions, plants may be operating in a state of partial stomatal closure. If, indeed, the pathway resistances to water vapour and CO_2 are similarly affected, this means that photosynthesis must inevitably be proceeding at less than the maximum rate. Since the origin of the reduction in photosynthesis appears to lie in low ψ_L rather than low ψ_S, it is possible that irrigation of the foliage (i.e. mist irrigation) aimed at reducing transpiration rate might be more effective than irrigation of the soil in increasing ψ_L, and so increasing CO_2 uptake.

The interaction of cutting and water treatments whereby ψ_L of the drying treatment in the Lysimeter Experiment II swards did not diverge appreciably from that of the wet in the cut treatment, but showed the normal divergence in the uncut treatment, might have been expected in view of the small proportion of evaporating surface on the large root system. The pattern of both ψ_L and stomatal resistance shows a considerable advantage in defoliation as a

means of reducing water stress, but the importance of the metabolic consequences of defoliation must not be over looked since it is conceivable that they may predominate.

Differences between the two species in the behaviour of Ψ_L and R.T. are difficult to detect since simultaneous measurements on both were only made in Pipe Experiments II and III, and they were at slightly different stages of drying. These experiments suggested that Dactylis was rather more sensitive to stress in that under given soil water conditions, the values of Ψ_L and R.T. diverged more from those of the controls than in Lolium (Table 13a, Fig.15). This feature could be related to the different sizes of root system in the two species and this aspect will be discussed in detail later. At similar transpiration rates, differences in Ψ_L between the wet and dry treatments are likely to reflect the overall soil potential, $\bar{\Psi}_S$, as weighted by the distribution of the root system, and this value of $\bar{\Psi}_S$ may be reflected in Ψ_L. A smaller and shallower root system in Dactylis would give a lower value to $\bar{\Psi}_S$ and hence lower Ψ_L.

There appeared to be a difference in the pattern of water use by the two species under stress. In both Experiments II and III it was noted that stomatal diffusion rates were higher in Lolium towards the end of a drying cycle, inspite of the greater water deficit. Cowan and Milthorpe (1968) discuss the effect of different root densities on the pattern of water use with time, and show (after Cowan, 1965) that with a sparser root system, a plant will be more sensitive to soil water stress as reflected in Ψ_L, and so will commence water economy measures at an earlier stage of drought, whereas in the densely rooted crop, E_t falls later but more rapidly; a similar picture to that recorded here. Their calculations were made assuming much lower rooting densities than those recorded here, and so the significance of this phenomenon may be small.

A lower ability of Lolium to control water loss also seems possible. Thaine, Harris and Lesham (1970) comment on the presence of hydrophobic waxes in the cuticle of Dactylis and show that leaves of Lolium exhibit a higher rate of water loss while drying from the turgid condition. The water repellent nature of the leaves of Dactylis was

also noted in this experiment, and it seems a real possibility that a higher cuticular resistance is involved.

Attempts to correlate r_s with ψ_L were largely unsuccessful and certainly were inadequate to reveal any difference between the species which might account for their differing water loss characteristics. The relationship between the two factors showed little correlation from leaf to leaf, and only general relationships were discernible. Bull, Stiles and Wangati (1967) came to the conclusion that there was little relationship, and Andrews and Newman (1968) also comment on this possibility. Stomatal aperture is undoubtedly a function of other factors such as guard cell turgor and CO_2 concentration (Slatyer, 1967) and these bear only an indirect relationship to ψ_L (Gavande et al.,1967). The relationship proposed by Ehlig and Gardner (1964) is probably a gross oversimplification.

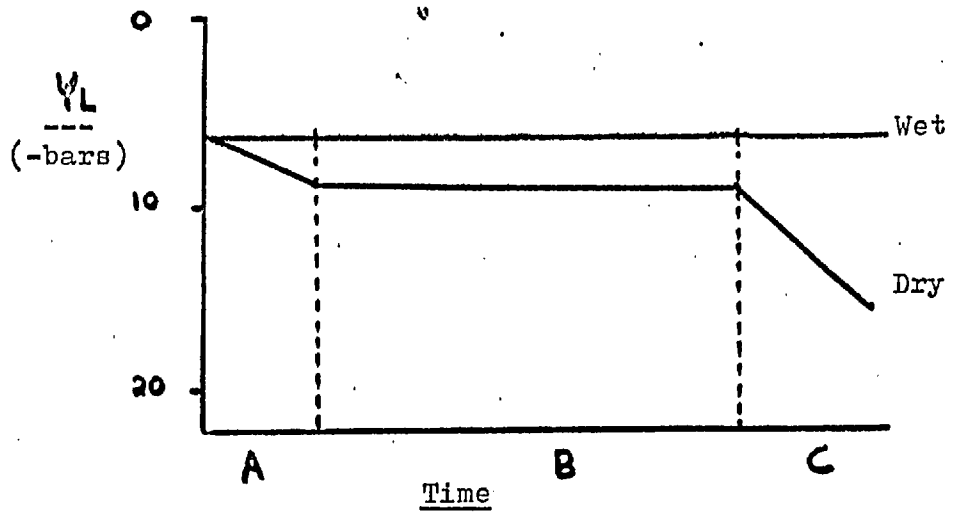
The indications are, from these experiments, that Lolium lost water more rapidly than Dactylis, but the reasons could not be determined with certainty. It is likely that a greater depression in ψ_L in the dry treatment of Dactylis, related possibly to a smaller root system, caused the onset of water economy measures at an earlier stage of drying, and combined with a lower permeability of the cuticle, resulted in a lower rate of water use in this species. The continued transpiration of Lolium at a higher rate resulted in the earlier and more abrupt exhaustion of limited water supplies.

3. The Response of ψ_L to Soil Factors during a Drying Cycle

The course of ψ_L during a drying cycle showed a similar pattern in all pipe experiments with three or more harvests (Fig.31). After an initial small decline below the control level (A), a parallel course, separated generally by 1 to 2 bars difference (B) was followed until the upper part of the pipe was depleted of available water and extraction was confined to the lowest horizons, resulting in a rapid fall of ψ_s in this region. At this point, the leaf water potential resumed its divergence (C) from control levels.

This behaviour suggests that even though the soil water deficit and depth of extraction was increasing through-

Fig.31



A)Initial and relatively small depression of Ψ_L as surface soil dries and, since a high proportion of roots are here, resistance rises.

B)Steady Ψ_L as roots extend down profile, water moves up along potential gradients etc., sufficient water being available to maintain Ψ_L from still wet horizons.

C)Ψ_s of lowest horizons begins to fall; no further root extension or diffusion being possible, Ψ_L falls rapidly.

out the experiment, the stress to which the plant was subject did not increase after initial drying of the top soil, but remained fairly constant until drying of the lowest zones commenced. Clearly, therefore, a simple average of Ψ_s (Taylor,1952) in each zone is likely to be of little value in evaluating the soil component of total stress, since this would give continually rising values through a drying cycle. The pattern of water use and its relation to Ψ_L confirm the necessity of evaluating a single stress value related to zone of water use and root density. Uptake from a restricted part of the profile was sufficient to supply a large part of current E_t requirements and the potential in the wettest zones appeared to be most important in determining stress caused by the state of water in the soil. This is very much in agreement with the conclusions of Slatyer (1967), who said that stress, integrated over the root system by measuring it at the base of the stem, largely reflected Ψ_r in the wettest zone, even though the surface horizons were at very low potentials. In this way, a crop with high root density and deep root zone may only be subjected to a low level of stress so long as part of the root system is in wet soil.

There are difficulties, however, in estimating the soil component of total stress, as it affects the plant, by a simple and reliable method. Measurements of Ψ Xylem taken at the top of the root system (Slatyer,1967) may be of limited value in that they also contain components of total stress due to root resistance unless uptake is zero. Thus Ψ_L as measured at sunrise, while exhibiting a general decline as the soil dried, bore little relationship to $\bar{\Psi}_s$ as calculated here. It did, however, bear a close relationship to the arithmetic mean water potential over all zones.

It had been noted that Ψ_L followed a generally parallel course during the day in wet and dry treatments, and the difference between the two treatments is likely to reflect both any difference in $\bar{\Psi}_s$ as integrated by the root system, and differences in Rp and Rs between the two treatments. Assuming that Rp is similar, and anticipating from evidence in a later section that Rs is negligible, then the difference between the mean values of Ψ_L in wet and dry treatments may be considered as representing stress due to the drying

soil. The relationship to calculated $\bar{\Psi}_s$ was still poor, and was very much less sensitive to changes in soil water status through the profile than the calculated $\bar{\Psi}_s$. It did, however, bear a possibly spurious but nevertheless remarkably close relationship to the simple average of Ψ_s in the soil zones of maximum uptake, these being zones at higher water potential and defined as being where:

a) $Q > 0.2 \times 10^{-6} cm^3\ cm^{-3}\ sec^{-1}$, or

b) $\Psi_s > -6000cm$.

Pipe Experiment 6

Integrated Ψ_s as estimated by various methods (cm)

$\bar{\Psi}_s$ as determined by:	H1	H2	H3
Computer calculation $\bar{\Psi}_s$	-72	-220	-6293
Mean Ψ_s of all depths	-3013	-5156	-8126
Ψ_L wet - Ψ_L dry	-1600	-1700	-3100
Ψ_L at sunrise	-2500	-5500	-6000
Mean Ψ_s in all zones where. $Q > 0.2 \times 10^{-6}\ sec^{-1}$ or $\Psi_s > -6000cm$	-1672(5)*	-1718(3)	-3375(2)

(*) = Number of zones involved.

It is difficult therefore, to determine whether the method of integration proposed by Gardner and used in this paper is a useful contribution towards solving the difficulty of giving a single value to total soil water stress.

4. Soil Resistance

The analysis of water balance made here differs from that reported by many other workers in that the features of the uptake system were integrated over the entire profile in which there were considerable gradients of water content and related parameters, and of root distribution. This is a rather different, and much more realistic picture than that of a small and uniformly dried zone. The present analysis takes into account the changing distribution of uptake as drying proceeds, changes in root distribution with time,

and all the related phenomena of the naturally drying profile which are often ignored in simplified mathematical models.

Newman (1969a) points out that his conclusions, derived from the examination of a single, uniform zone, would be invalid if, in reality, a part of the profile was too dry for uptake to take place. Whereas Newman's and the other models from which it was derived show a picture of a gradual uniform fall in potential in the root zone, a corresponding rise in R_s and $\Delta\Psi$ and hence falling values of Ψ_L, this is not the pattern found in these experiments. The effect of drying of one zone is to shift the principal uptake zone downwards, with little or no fall in Ψ_L, and this shift downwards continues so long as further root/soil zones exist. When the lowermost zone is reached, this being rather an artificial situation in these experiments, since further upward diffusion from zones unexplored by roots in the field might delay or ameliorate its sudden and rapid drying, then the situation comes nearer to resembling that of the single uniform profile situation. Now, Ψ_L starts to fall to maintain uptake against the rapidly falling soil water potential in the bottom zone.

This pattern is only possible where there is sufficient root present to permit a large part of the plant's transpiration demands to be met from a small part of the profile. For example, in Pipe Experiment VI at Harvest 2, (Table 70) 80-90% of total uptake was from horizons 5 and 6. This is the situation in which Newman (1969a) considers that appreciable soil resistance may occur. It is significant, therefore, that in these two zones, two of the largest drops in potential between the soil and root surfaces ($\Delta\Psi$) were calculated, namely 135 and 80 cm respectively, even though k was still relatively high. Uptake was very low from the drier regions, hence $\Delta\Psi$ was correspondingly small. Even so, $\bar{R}s$ was not appreciable, compared with Rp when most of the profile was dried and uptake was confined to a small part of the profile, and values of $\bar{R}s$ were normally 10^2-10^4 times smaller than Rp in these experiments.

The reason for the failure of the predicted large rhizosphere resistances to materialize is undoubtedly, as Newman stated, that root densities are normally much greater than those used to make these predictions. Cowan (1965) used

L_A values of 2.5-10cm root cm^{-2} soil surface. Those found in these species ranged over 500-3000cm cm^{-2}, the former value being reached at HO soon after establishment. Cowan's (1965) values of L_V of 0.125-0.5cm root cm^{-3} soil were lower than any recorded here above the terminal root fringe, by one or two orders of magnitude.

Gardner's (1960) uptake values of $q=0.1cm^3\ cm^{-1}\ day^{-1}$ ($0.116x10^{-5}\ cm^3\ cm^{-1}\ sec^{-1}$) imply root densities ($L_A$) of below 10cm cm^{-2} according to Newman (1969a). This value of q is ten times greater than any recorded here, and on average 10^2-10^3 times greater.

Cowan and Milthorpe (1968) had recognised the unreality of earlier assumptions when they commented that hydraulic conductivity is unlikely ever to limit uptake rate.

5. Plant Resistance

For the purposes of his calculations, Cowan (1965) assumed a constant value of Rp. It is considered to be variable by other authors both in the long and short terms (Cowan et al.,1968; Slatyer,1967).

The overall permeability of the plant is a compound factor made up of the permeabilities of the individual parts in both parallel and series, and many of these are likely to vary. In the short term, Cowan et al. (1968) describe likely changes in both leaf and root conductances related to changes in water potential and flow rate, and caused by the flow of solutes, temperature gradients and the changing geometry of the flow system as E_t varied. Brouwer (1965) found that the operative amount of the root system varied with E_t, and this seems a likely explanation for the possible inverse relationship between E_t and Rp found in these experiments, and reported also by Tinklin and Weatherly (1966), Andrews and Newman (1968) and Cox (1966). The decline in Rp with increasing E_t was less marked at high values of E_t.

In the longer term, Rp appeared to rise as the soil dried, with the qualifications expressed in an earlier section. At all times, it was higher in the dry than the wet treatments. Root resistance could be influenced by numerous environmental factors, suberisation, the effects of aging,

reduced root growth in dry soil which was widely recorded here, differences in soil temperature due to dry soil, and none of these factors can be separated in these experiments. Cowan et al. (1968) have stated that in a soil with 20% water content by volume, the resistance of the roots is five times that of the same roots in water. This probably greatly over-simplifies the situation. Water held on soil particles comes nearer to being in a two dimensional state and so may have a different contact relationship with the root. The curvature of menisci, changing surface tension, and the added complication of root mucigel and root hairs in relation to pore size of the soil particles must all be considered when making predictions of this kind. It seems reasonable, however, to assume that the root/water contact in a drying soil may decrease, hence causing the apparent value of Rp to increase due to a fall in the effective absorbing area of the root system. This factor could be responsible for the overall difference between wet and dry treatments and the continuing rise in Rp during a drying cycle, but the probable inverse relationship previously described between Rp and E_t must be considered as acting simultaneously since E_t fell in the long term.

The importance of the upward diffusion of water and of root extension into previously untapped zones are widely discussed in relation to drought resistance (Kramer and Coile, 1940; Gardner, 1968). The latter feature largely applies to the early part of these experiments before the roots reached the full extent of the profile. In the case of Lolium, this was generally accomplished by Harvest 1. During this period, extension rates of 2cm day^{-1} were generally recorded, sometimes reaching 3.5cm day^{-1} in Lolium. They were similar in sandy subsoil and Perlite. These rates of extension were in close agreement with those of Garwood (1967c) recorded under mature swards of Lolium in the deeper horizons in summer. Assuming 15% by volume of available water in the soil below the root zone, a rate of extension of 2cm day^{-1} would bring 0.3cm day^{-1} of available water into the root zone.

Gardner (1968) integrates the effects of diffusion and root extension to show that the total zone of influence of

the roots can extend well beyond their own physical limits. In these experiments, root extension appears to play the major part in utilizing available water outside the current root range.

In the context of a finite limit to root extension in these experiments, the rapid root extension rate of Lolium, while increasing water availability in the short term, may well have resulted in the more rapid exhaustion of available water and so reduced its ability to withstand prolonged drought since water economy measures did not appear to commence until later than in Dactylis. In the hypothetical case of the short term drought, however, when water supplies are restored before complete exhaustion of the profile, then advantages in transpiring at the maximum rate with fully open stomata may manifest themselves in increased CO_2 assimilation.

The Effects of Water Stress on Growth of Lolium and Dactylis

1) The Source of the Stress Effects

In many previous investigations, water stress has been found to reduce plant growth, manifesting its effects through all the growth parameters normally studied (Lawlor, 1969; Slatyer, 1967) and from an early stage in the course of drying of the soil. In many such experiments, stress was applied either osmotically in culture solution or in a volume of soil which restricted root growth and so dried fairly uniformly. Such conditions may be quite unrepresentative of the field situation where continued root extension is possible and normal such as in annual crops and grasses. Irrigation experiments in the field (Stiles and Williams 1965) have similarly shown an early restriction of growth, but the diversity of growth parameters used which normally only reflect the economic yield of the crop, and possible interactions with other factors such as water and soil temperature or defoliation regimes make interpretation more difficult and the precise role of stress itself undefinable.

The circumstances of the present experiments, in which soil water stress contributed little to plant stress until the deeper horizons of the soil began to dry appreciably, have already been discussed. A major source of stress lay in the natural resistance of the plant itself and its inability to conduct water to the transpiring surfaces at a sufficiently rapid rate, and so both wet and dry treatments were similarly stressed, as judged by leaf water potential. It was concluded that even watered plants may be under stress formuch of the day, and the relatively small effect of drought on growth must be considered in relation to this.

Investigations on natural swards (Garwood et al., 1967a, 1967b; Penman, 1962; Stiles and Williams, 1965) have consistently shown severe growth restriction at relatively minor deficits. The growth restriction was small in the present pipe experiments, even at considerable deficits, slightly greater on the Lysimeters, and greater still under a cutting regime. A conclusive explanation cannot be given for this discrepancy, but some features which may be of possible significance will be considered.

The light, easily penetrable soil in the pipes gave rise to an extensive and vigorous root system which, while not penetrating to atypical depths, appeared to have greater density at depth than in the field situation (Plate 3). This activity at depth was almost certainly enhanced by the fact that the roots of the immature plants would be all operative before the normal cycle of decay and replacement had been initiated. Hence the negligible contribution of soil stress to total stress in these conditions. The quantity of actively functioning root under the established swards was almost certainly smaller, though measurement was impractical due to the difficulty of distinguishing between living, dead and decaying roots. There was some suggestion in the mature swards of Lysimeter Experiment II that the difference in leaf water potential between wet and dry treatments may have been rather larger than in the pipe experiments, and also that the growth restrictions began at a lower soil water deficit. The shallower and less dense root system in the Lysimeters may have been responsible for causing a rather larger contribution from soil stress to total plant stress, hence the rather earlier and greater growth restriction.

Defoliation was found to greatly suppress new root production in the pipes, and this effect was present though more difficult to measure on the lysimeters. The effects of drought on growth were greater and earlier on cut swards in these experiments, and the results of other workers have generally been obtained from defoliated swards. This may suggest that defoliation increases susceptibility to drought. However the fact that defoliation reduced the difference in leaf water potential between wet and dry treatments to an insignificant level suggests that the increased response to drought is not due primarily to increased water stress, nor is there evidence for a nitrogen deficiency (Table 51). It is essential at this point to consider metabolic effects on the plant due to defoliation, drying of the top soil and related influences associated with these treatments. Although differences in temperature, water potential, water content and penetrability of the top soil which occur as the soil dries appear to have rather small effects on plant water stress, they may have considerable physiological and metabolic consequences. They must

be considered in relation to the high proportion of roots in this surface region and the relationship between the condition of these roots and shoot growth as mediated by hormonal balance control mechanisms which remain largely unresolved at present but which have been briefly considered in the introduction to this thesis. It may be postulated that the origin of at least part of the restriction in growth which occurs when the top soil dries may lie in the physiological reaction of the plant's growth control processes to the adverse physical environment of the dry soil. Such investigations were beyond the scope of this thesis and must render the interpretation of the causal mechanisms behind the growth responses largely inconclusive. In addition, no specific factors could be isolated as being responsible for the differences in the magnitude of the growth response in these experiments compared with those of some other workers.

2) The Nature of the Growth Response to Water Stress

The dry treatments in all the present experiments showed some decline in growth relative to controls from an early stage. These effects rarely reached significance until near the end of the pipe experiments, but tended to be greater and occur at a lower soil water deficit in the lysimeters. Their form was, however, consistent throughout, and their onset coincided with the initial drying of the top soil which depressed γ_L below control level before Harvest I.

Etherington (1962) reports one of the relatively few examples of growth analysis applied to grasses undergoing different water treatments. There was a reduction with stress in total yield and tillering, but not in leaf numbers. The area/weight ratio of the leaves fell, and also the net assimilation rate. Hence the reduced area and efficiency of the assimilating surfaces contributed to the reduced total yield. Garwood (1963) also reported a severe fall in live tiller density compared with controls in a ryegrass sward protected from rain. These results are in general accord with those reported here, except that tiller numbers were not affected by stress, except in the seedling

swards of Lysimeter Experiment II, where considerable plant mortality occurred. In the pipe experiments, tiller numbers had largely been initiated prior to or early in treatment.

The absence of any relative reduction of tiller number by drought in the cut swards is surprising since defoliation killed the flowering tillers and it may be that no new tillers were formed in either wet or dry treatments after flowering, which occurred very early in the treatment period. The inhibition of tillering by flowering is widely reported (Jewiss,1966). Although visual inspection suggested a much lower tiller density in the dry, cut lysimeters, close examination revealed that there were still green parts present at the cut end of the sheaths, and that these had failed to expand, while no new leaves were produced. Suppression of leaf extension rather than complete mortality of the tiller appeared, therefore, to be occurring in the dry, cut treatment in this experiment. For reasons explained, no attempt was made to draw conclusions from the seedling sward densities on the lysimeters.

There was a consistent trend towards reduced leaf extension in drought in the pipe experiments, always visible to the eye, but showing variable significance in the reduced area/weight ratios of the leaves and the overall reduction in leaf area. Since cell extension is largely dependent on turgidity (Boyer,1968), this effect has been reported as being amongst the first visible indications of stress.

It would be unwise to draw definite conclusions concerning NAR because of the large errors computed for this parameter, but there was little evidence of any appreciable difference between treatments until the final stages of drying when wilting was becoming considerable and the NAR curves for the wet and dry treatments diverged rapidly (Fig 11). D'Aoust and Taylor (1969) found irrigation of Lolium swards increased leaf area but not NAR.

Thus the small reduction in total dry matter assimilation due to drought may be partly attributable to reduced leaf extension. Most of the reduction in weight took place in the dry surface root zones, especially in the early phases, but the presence of a partial compensatory redistribution of

dry weight to the deeper roots again implicates the presence of interacting factors arising from micro-environmental effects on the roots in the dry top soil.

The present experiments and similar ones performed by other workers have clearly been inadequate to unravel the complexities of the situation. It would be unrealistic to attempt to explain the apparent anomalies between the various results in the absence of more precise information on the mechanisms involved.

The Effects of Drought on Nutrient Uptake

This thesis has been concerned with two kinds of macronutrients.

Unbound nitrate ions exist in simple solution and their concentration is directly related to soil water content.

The 'bound' ions phosphate, potassium and calcium are largely attached to the soil particles where they are in dynamic equilibrium with a low concentration in solution in the soil water. Changes in soil water content are countered by adsorption or desorption of ions.

The larger proportion of nutrients must move to the root surface either by diffusion or mass flow in the transpiration stream before they can be absorbed. Only a small quantity of the soil is in direct contact with the root surface (Wiersum, 1969).

The effectiveness of diffusion extends over short distances, depending on ion mobility, concentration gradient and cross-sectional pathway. The dimensions of the pathway depend on soil water content. Since the concentration of non-absorbed ions does likewise, the falling size of pathway and increasing concentration gradient tend to counteract each other. On the other hand, ions in the exchange complex remain at a level concentration and so their diffusion rate depends mainly on the area of the pathway. Thus falling soil water content primarily affects the diffusion of adsorbable ions and may have little effect on unbound nitrate ions.

Mass flow in the transpiration flux is important over much greater distances, and its effectiveness is proportional to transpiration rate. It has been calculated that this flow carries calcium, potassium and phosphorous in descending order of importance (Barber, 1962).

Thus the entire nitrate pool in the soil solution is available to the plant. Root density is unimportant since water movement takes place over relatively long distances, and Garwood et al. (1967b) found the most efficient uptake of nitrogen from soil depths of low root density.

Root density becomes increasingly important to the uptake of exchangeable ions of decreasing mobility.

Uptake may take place over a greater part of the root length than was previously believed. Phosphorous, which has largely been studied to date may require an intact cortex. When the cortex collapses, bacterial immobilisation may occur (Russell,1970). Nitrogen has not lent itself to isotopic investigation, but its greater mobility and the manner in which the plant can accumulate it in its tissue with little apparent selectivity suggests that an intact cortex may be less necessary than is the case for phosphorous. In the present experiments, the seedling plants subjected to drying were found to still possess intact cortices and root hairs, but it seems probable that this is fairly unusual (Russell,1970). The cortex had largely collapsed on most older roots in mature swards. Water uptake may be largely unimpeded through suberised and decorticated roots (Newman,1969a) and there is the possibility that N uptake may be also.

Thus the 'nitrogen unavailability' recently proposed by Garwood et al. (1967b) has little apparent theoretical basis in terms of immobility in the drying soil. The inhibition of mineralisation of organic matter in dry soil may, however, substantially reduce nitrogen supply from dry horizons.

On the other hand, phosphorous migration to the root surface may be substantially reduced by a decline in soil water content and uptake rate in a dry zone, and real unavailability may be considered probable. Calcium and potassium would occupy intermediate situations. The changing contributions of diffusion and mass flow to overall ion migration complicate the issue and may account for the wide spectrum of reported results.

The total uptake of nutrients may not be the best indicator of nutrient stress because uptake may be a function of demand rather than supply, as Gates (1968) showed in the case of phosphorous. Nitrogen uptake appears to occur irrespective of demand up to high concentrations (Whitehead, 1966) and is normally the factor most limiting growth. Uptake is unlikely to be reduced through lack of internal demand unless translocation from the roots is prevented. Williams (1960) found this was the case due to internal factors in flowering tillers . Garwood was working with swards in the flowering phase.

The nutrient concentration in the plant tissue relative to a watered control may, therefore, be a better basis for comparison of the effects of water stress in the soil on availability, and this method of expression has been widely used for experimental comparisons (Jenne et al.,1958).

Comparison of the N contents on this basis has yielded rather variable results both in the literature and the present experiments, and here they have ranged from slightly reduced to increased concentration relative to watered controls. The nitrogen uptake was generally reduced by only a small amount inspite of the fact that nitrogen was confined to the topsoil either by the use of subsoils poor in humus, or in Experiment III a 'subsoil' of perlite, and by surface placement of fertilizer nitrogen.

It is possible that mineralisation phenomena are involved in producing conflicting results but that where they are small, as was probably the case here, there is little evidence in theory or practice for nitrogen unavailability.

The other elements are theoretically more liable to reduced availability in the decreasing order calcium, potassium and phosphorous, and this is largely confirmed in later experiments where the appropriate analyses were performed. The calcium and potassium content of the shoots showed only small random variation, and since transport to the root surface may be in excess for calcium (Wiersum, 1969), the tissue level may be determined more by demand than supply. In all cases, the phosphorous concentration was reduced, and significantly where statistical analysis was possible, in the drying treatments. This has been predicted on theoretical considerations, but a reduced internal demand as suggested by Gates (1968) cannot be precluded.

Garwood and Williams (1967b) considered that defoliated swards could be at a disadvantage in drought conditions because of the absence of nutrients for recirculation, and imply that the effect would be less serious in uncut conditions. Greenwood and Titmanis (1968) investigated the effects of defoliation on nitrogen stress and its relation to leaf nitrogen in young plants of Lolium. The reduction

in photosynthate due to defoliation caused nitrogen stress to be reduced to half the control level, even after four defoliations (stress was measured as the percentage reduction in relative growth rate compared with unstressed controls). This is confirmed by the results of the present experiments where, on the lysimeters, the concentration of nitrogen and phosphorous in the cut plants was greater, often considerably so, than in the uncut plants (Table 52), even in dry conditions. The method of measuring stress adopted by Greenwood et al. eliminates the dilution factor inherent in the comparison of tissue nutrient concentrations where the production of dry matter by the uncut plants is greater overall.

In conclusion, there are no theoretical grounds for a relationship between soil water content and nitrogen availability other than via mineralization phenomena from the soil organic nitrogen pool. The experiments of Garwood et al. (1967a,b) had basic defects in the techniques they used which appear to invalidate their conclusions. It is widely accepted (Whitehead,1966; Henzell,1970) that grasses are amply supplied with nitrogen at tissue concentrations above 2% of the dry matter, and further increases in concentration have very little effect on relative growth rate. The nitrogen contents of the herbage produced by Garwood et al. was never as low as 2%. This is not compatible with their statement that after defoliating a sward in dry weather, "the depression in growth can be attributed more to a deficiency of plant nutrients than to a lack of water". Indeed, the nitrogen level in the abundant growth following rewatering of the droughted plants was no greater than the concentration present when growth had ceased due to the supposed nitrogen deficiency.

Thus their experiments appear to do no more than demonstrate that fertilizer applied to the surface of a dry soil remains in this situation until washed in by rainfall. The present experiments indicate that adverse physical factors present in a dry top soil reduce growth by their effects on metabolic and physiological processes in the plant.

Plate 2.

A general view of Pipe Experiment III illustrating the weighable pipes standing in a trench flush with ground level. The portable protective covers are visible in the background. Wire-netting cylinders maintain the vertical leaf orientation.

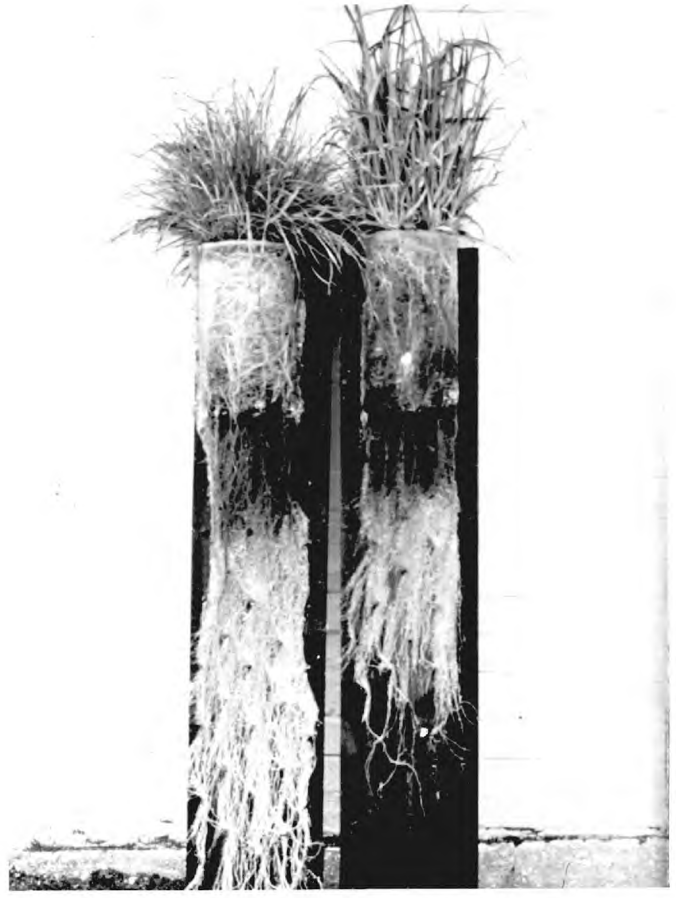


Plate 3.

The partially exposed root systems of Lolium (left) and Dactylis grown with a Perlite subsoil in Pipe Experiment III, Harvest 5.

Plate 4.

Lysimeter Experiment II.

Established, wet, uncut Dactylis sward at Harvest 3

Plate 5.

Lysimeter Experiment II

Established, dry, uncut Dactylis sward at Harvest 3

Note the under-storey of dying and wilted plants dominated by relatively few large plants, still turgid.

Plate 6.

Lysimeter Experiment II

Established, wet, cut Dactylis swards illustrating vigorous extension of the laminae following defoliation.

Plate 7.

Lysimeter Experiment II

Established, dry, cut Dactylis swards illustrating the failure of the existing laminae to extend and the absence of new laminae growing from the sheaths.

SUMMARY

Simulated swards of Dactylis glomerata S37 and Lolium perenne S23 were grown in large lysimeters or vertical pipes of 15cm diameter, both being sufficiently deep to allow largely unrestricted root development.

Flowering and non-flowering (seedling) swards, subjected to cut and uncut treatments, were allowed to dry the profile from 'field capacity' until exhaustion of available water supplies, and were compared with watered controls.

Sequential harvests made during a drying cycle enabled the effects of an increasing soil water deficit on the growth, water balance and nutrient uptake to be followed.

The rate of total dry weight increase was reduced from an early stage, but never by a large amount. The cause appeared to be reduced leaf expansion rather than a decline in net assimilation rate. The root weight was reduced more than the shoot weight, particularly in Dactylis. New adventitious roots ceased elongation immediately the top soil dried. There was some compensatory growth at deeper levels, suggesting that a physical/physiological impediment to root growth due to dry top soil rather than a deficiency of assimilates caused the surface roots to cease growth and diverted assimilates to lower levels.

Defoliation itself severely retarded root growth, largely masking the effects of the drying treatment.

No conclusive explanation could be given for the much greater drought effects on growth reported elsewhere compared with those found here.

Leaf water potential (ψ_L) fell during the day in all treatments and controls to levels which would be expected to have critical effects on growth processes. The stomata rarely closed completely, but there was evidence for some restriction in treatments and controls at these low levels of leaf water potential. Leaf water potential rapidly rose again in the evening to levels which might allow a normal continuation of those growth processes not requiring sunlight.

Defoliation greatly reduced water stress and the restriction of stomatal aperture, but did not reduce the susceptibility to drought.

A poor relationship between leaf water potential and stomatal diffusion suggests that leaf water potential is not the operative factor in stomatal control.

Dactylis showed greater sensitivity to stress in terms of leaf water potential, relative turgidity and stomatal diffusion rate and this caused an earlier onset of water economy measures compared with Lolium. The latter species tended to transpire rapidly until the profile was abruptly exhausted of water at an earlier point in time. The significance of the size and the vigor of extension of the respective root systems is discussed in relation to plant water status and uptake in a drought.

A model was developed (after Gardner,1964; Cowan,1965) to evaluate the water balance of the swards. Root density was adequate to allow the plants to absorb most of their water requirements from a small volume of wet soil. Drying of a horizon had the effect of shifting uptake to the next lower horizon without a simultaneous fall in leaf water potential until the terminal zone was being exhausted. Thus, soil resistance to water flow was negligible compared with that of the plant. Measured uptake rates per unit root length were much lower than those previously used to predict high soil resistance. Plant resistance appeared to fall as transpiration rate rose, and rise as the soil dried. Possible explanations are considered.

Criticisms are made of the techniques used by Garwood and Williams (1967a, 1967b) to show that nitrogen shortage was responsible for the cessation of grass growth in drought. No evidence could be found for critically low tissue N levels as a result of drought in these or Garwood's experiments. Reduced phosphorous uptake was detected, however.

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