A COMPARATIVE STUDY OF PLANT WATER RELATIONS IN *CHLORIS GAYANA* KUNTH AND *SETARIA SPHACELATA* S&H

By

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DECLARATION

I, Kassim Omar Farah, hereby declare that this is my original work and has not been presented in any other University.

Date: 1st Oct. 1982 Signed: ....
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This thesis has been submitted for examination with our approval as University supervisors

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DEDICATION

This thesis is dedicated to my parents who have instilled in me the sense of treasuring education.

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ABSTRACT

The effect of limiting moisture on the germination, establishment, physiological response and dry matter of two important pasture grasses, namely Chloris gayana Kunth and Setaria sphacelata S & H, which occur on the high and medium potential areas of Kenya was investigated. Drought conditions were simulated using osmotic solution of known osmotic potential. Six moisture stress levels ranging from 0 bars to -12 bars were generated using mannitol as an osmotic substrate. The two grass species were germinated in contact with these media on blotter papers in an incubator with its temperature fixed at 25 degrees Celsius. Postgermination survival and physiological response to water stress were studied under greenhouse conditions where differential moisture levels were obtained by withholding water from plots for periods varying from 2 days to 8 days. A further study was conducted to evaluate the effectiveness of straw mulch in conserving soil moisture and hence mitigating the internal water status of the two pasture grasses.

Increased moisture stress reduced the germination rates as well as 24 day total germination percentage of both C. gayana and S. sphacelata. The results of this study indicated that the two species had inherent differences in germination rates which was expressed at all levels of water stress. Water stress influenced the internal water status of both plants as expressed by changes in leaf water potential. Partitioning

the sum of squares of the main effect showed that increasing water stress had proportionally decreasing effects on the leaf water potential of the two grasses. Calculated slope estimates revealed that in the main, C. gayana was more tolerant of drought than S. sphacelata as manifested by the ability of the former to maintain a more favorable leaf water potential over the watering regime studied.

Varying the watering regime modified the degree of the stomatal opening. Lower frequency of watering reduced leaf conductance of both grass species. However, no difference was detected between the species with regards to leaf conductance. Changes in leaf water potential of C. gayana was affected by the time of the day while for S. sphacelata leaf conductance changed with the time of the day.

Increasing soil water stress resulted in lower mean dry matter weights of the shoot and root of both grass species. The response of the two grass species to soil moisture stress, in terms of shoot and root biomass production, were found to be different with C. gayana showing higher production at all levels of the watering regime.

Mulching increased leaf water potential of both grass species. However, mulching was found to be ineffective in raising the production of any of the grasses.

CHAPTER 1

INTRODUCTION

Inadequate water supply under field conditions may cause water stress and thereby influence physiological processes and growth of plants. For this reason soil moisture could be regarded as one of the critical factors in plant establishment, growth and development (Bassirri *et al*. 1977). Water is essential for life and without it no life can exist. The liquid surrounding of an aqueous solution is the *conditio sin quo non* for most of the physiological responses and as such is as decisive for the occurrence of a single enzymatic reaction as it is for the global zonation of world vegetation. It is no wonder therefore that scientists since early times have made every effort to study and understand the functional interrelationships between water and the phenomena of life (Lange *et al*. 1976).

All plants except large trees and shrubs contain more than 80% by weight of water (Pratt and Gwynne 1977).

This compound is the matric of life, contributing as much, if not more to the properties and requirements of life as such complex molecules as carbohydrates, fats and proteins. Water is directly or indirectly required for every life process and chemical reaction. It is the vital component of these reactions, the medium in which they take place, and the solvent for most of the reacting chemicals. It is the continuous phase between the cells and within the cells.

In contrast to the situation in terrestial animals, in all actively growing plants there is a liquid phase continuity from the water in the soil through the plant to the liquid-gas interface (Soil-plant-atmosphere-continuum, SPAC) at the evaporation sites in the leaves. The proliferation of roots in the soil provides an extensive absorbing surface across which passes virtually all the water and mineral nutrients utilized bv the plant (Slatyer 1969).

"Nearly every study of seedling requirement cites the importance for young plants of drought, whether due to lack of precipitation, excessive exposure to drying conditions or in competition with established vegetation. In this regard Sharitz and McCormick (1975), Mack (1976), Cook (1979) have strongly argued that lack of soil moisture is one of the most important sources of mortality for plant seedlings."

Drought is known to limit the germination, growth and development of many plant species. One of the way ,that overall pasture and range condition could be improved would be to identify and utilize grass species that exhibit a higher degree of adaptability to the drought conditions that is so characteristic of most regions of Kenya. Chloris gayana Kunth and Setaria sphacelata S & H form the two most important grass species used in the Kenya Highlands and medium potential areas as pasture leys (Birch 1964, Boonmann 1972a) due to their high herbage productivity and nutritive values (Said

1974). They have been domesticated and seed production is carried out commercially by Kenya Seed Company at Kitale. The use of Chloris gayana commonly known as Rhodes grass has been extended to medium potential areas with the development of certain varieties that have proved to tolerate drier conditions (areas with an average annual rainfall of approximately 600 mm). Little is known about the plant-water relationship of this grass although there appears to be a real possibility of extending adapted ecotypes to the drier areas.

This study was conducted to evaluate the physiological response of Rhodes grass to varying soil watering regimes. Setaria sphacelata was included in this study for comparison as a species which is not drought tolerant and it confined almost exclusively to high rainfall areas where precipitation exceeds 850 mm annually.

1.1 OBJECTIVES

The specific objectives of the study were:

i) To examine on a comparative basis the effect of water stress on the seed germination of Chloris gayana (Rhodes grass) and Setaria sphacelata (Nandi Setaria)

ii) To assess postgermination survival and physiological response of the above species to varying soil water potentials.

iii) To assess the effectiveness of mulch in conserving soil moisture for the growth of the two species.

CHAPTER 2

LITERATURE REVIEW

Probably few environmental factors are as important to the survival and growth of plants as is the availability of water. Range Scientists and managers have, for example, long recognized the vital role of plant-water relations in managing and in manipulating range condition (Brown 1977). The water status of plants as a whole is controlled by cell water stress such that its effects on meristematic tissues are presumably synthetic e.g., synthesis of DNA, RNA and cell wall materials (Kramer 1969). Kramer (1969) argued that the susceptibility of meristematic regions to water stress appeared to vary among species.

Balls (1908) working with cotton, Loomis (1934) and Thut and Loomis (1944) working with corn found that shoot elongation was completely inhibited during periods of high transpiration. In contrast Wilson (1948) and Slatyer (1957) found that stem tips of tomato continued to elongate even when the leaf tissues were wilted. Slatyer (1973) noted that root development affects the size and character of the absorbing system for minimal nutrients while shoot developlent affects rates of carbohydrate metabolism.

Several investigators have shown that considerable hydrolysis of proteins occurs in wilted plants and is accompanied by an increase of amino acids (Barnett and Naylor

1966; Chen et al., 1964; Chibnel 1954; Petries and Wood 1938). Chen et al., (1964) observed three stages in citrus seedling subjected to increasing soil water stress over a period of ten days. In the first stage prior to wilting there was a rapid increase in water content followed by a small increase in protein possibly due to continued RNA synthesis and finally an apparent decrease in protein content of the seedling.

Barnett and Naylor (1966) found a general decrease in soluble protein in water stressed Bermuda grass and also a decrease in protein bound arginine. Shah and Lommis (1965) found a tendency for DNA content per cell, which remained relatively constant with age in expanding beet leaves, to be reduced by water stress only if severe wilting occurred and was protracted. Gardner and Nieman (1964) showed a marked reduction of the rate of increase in DNA content of developing and presumably active cotyledonary leaves of radish at slight stress levels but also found that there was still some increase in DNA level when severe stress was imposed. Together, these results appear to be consistent with a marked sensitivity of cell division to stress, but with cell breakdown occurring in developed tissues and under severe and prolonged stress (Slatyer 1973).

2.1 TERMINOLOGY IN PLANT WATER RELATIONS

2.1.1 WATER POTENTIAL

This is a parameter that presents a large diversity of discussion and proposals, the terminology of which have sometimes led to serious misunderstandings (Lange *et al*. 1976). Lange *et al*. (1976) suggested that only recently has the new concept based on thermodynamic ideas, found increasing general acceptance thereby unifying the expressions which characterize water properties. According to these concepts, the state of water is described by its chemical potential within the system under study in relation to that of pure free water. Taylor and Slatyer (1960, 1961) and Slatyer and Taylor (1960) argued convincingly that the fundamental unit of measurement for describing the status of water should be in chemical potential or partial molar Gibbs free energy. They adopted the term "Water Potential as the fundamental unit from Schofield (1949, in Owen 1952).

Water potential expresses the difference between the chemical potential of pure free water at reference temperature, elevation, pressure and the chemical potential of water in the system (Soil, plant, or atmosphere) (Brown 1977). Among the various forces affecting the chemical potential of water are:

a) Force of capillarity, adsorption, and imbibition from contact of water with the matrix surface (Nielsen *et al.* 1970; Warren Wilson 1967; Taylor and Ashcroft 1972);

b) Force due to the presence of dissolved solute such as salts, in solution with water (Slatyer 1967; Brown 1972);

c) Forces of gravitational attraction (Hillel 1971). The difference in gravitational attraction between reference water and the water in the system are usually quite small if the elevations are small and except for unusual cases, are not considered (Slatyer 1967; Kramer 1969).

The total water potential (ψ_w) is determined by different features of a system, and consists of a series of mutually independent components that result from the above forces.

The total water potential in a biological system is usually negative, that of pure free water being taken as zero. The relationship of the various components of water potential (Total) are empirically interrelated as shown by the equation:-

$$\psi_w = \psi_\pi + \psi_m + \psi_p$$

Where ψ_w = Total water potential of the whole system

ψ_π = Osmotic Pressure

ψ_p = Pressure potential

ψ_m = Matric potential

At equilibrium the energy status of water can be described as the algebraic sum of the various components of water potential (Brown 1977). By considering this parameter we can specify the direction and motion of water. The difference between pure free water (μ_w^o) and that of water bound by solutes (μ_w) is an indication of water under the above conditions to do work compared with pure free water.

2.1.2 TRANSPIRATION

Transpiration is basically a passive physical process involving water vapour transferring along a concentration gradient from the evaporating sites through the plant to the bulk atmosphere (Bange 1953; Gates 1964; Halmgren *et al.* 1965; Slatyer 1966, 1969).

Transpiration is dependent on a) an energy supply to satisfy the latent heat demand, b) a water vapour concentration gradient to provide the driving forces for vapour flow, and c) the diffusive resistance located in the vapour pathway (Rawlings 1963; Slatyer 1966; Molz *et al.* 1968). When the soil water potential is high, transpiration proceeds primarily as a function of the vapour concentration gradient between the leaf surface and the atmosphere. However, as the soil water potential declines, and with consequent decreases in leaf water potential and cell turgor, water vapour in the transpiration stream is met with increased resistance to flow due to the drying mesophyll and reduced stomatal aperture (Gardner and Ehling 1963; Rawling 1963; Ehlig and Gardner 1964; Slatyer 1966). The degree of control exerted by the plant can quantitatively be expressed as the transpiration resistance (Niller and Gates 1967; Slatyer 1967).

2.1.3 DIFFUSIVE RESISTANCE

This is the resistance that a leaf surface presents to air flow through the leaf. It is a parameter that gives an indication of the extent of stomatal opening, resistance to water flow and hence is inversely related to transpiration. It is assumed generally that when the stomata are closed, stomatal resistance is infinitely high and the measured transpiration is that due to vapour flow via the cuticle. Since these cuticular and stomatal pathways are in parallel the resistance they represent may be linked as follows:

$$\frac{1}{r_l} = \frac{1}{r_c} + \frac{1}{r_s} \qquad \text{(Slatyer 1967)}$$

r_l - Total internal resistance

r_c - Cuticular pathway resistance

r_s - Stomatal pathway resistance

When the stomata are open r_s and r_c are in parallel and the proportion of vapour transport along each pathway is inversely proportional to resistance encountered (Slatyer 1969). Typical estimates of cuticular resistance r_c (expressed per unit external leaf area) ranges from <20 sec cm^{-1} for shade plants to 20 sec cm^{-1} for xerophytes (Holmgren *et al.* 1965).

2.2 EFFECT OF WATER STRESS ON SEED GERMINATION

Seeds represent the means for survival and spread of most plants. Although seeds in various states contain some water, the proportion of water in the seeds is usually less than that contained in the cell of the actively growing plant of the same species (Slatyer 1967; Kramer 1969). Imbibition of water largely by the protein component of the seed is stage one of the germination process and thus water deficit will curtail this vital process (Brown 1977). Helmerick and Pfeifer (1954) found that germination and seedling growth of winter wheat decreased with increased osmotic potential of mannitol and that differences between varieties in response to conditions of limited moisture was significant. Rapidity of germination of *Sporobolus aeroides* was delayed and eventually inhibited by increasing water stress (Knipe 1968). Bassirri *et al.* (1977) showed that increased osmotic potential progressively delayed and reduced seed germination, shoot length, fresh and dry weight of both cultivated and wild varieties of safflower. They further demonstrated that germination of the cultivated varieties were completely inhibited between 8 to 18 atm. Parmar and Moore (1968) showed that increasing osmotic potential levels affected corn seeds of low energy a more adversely than those with high energy. McGinnies (1960) working on six range grasses noted that increasing moisture stress delayed germination in 28 days. He also demonstrated that increasing moisture had two major effects on germination:- as moisture stress increased germination was delayed and its rate reduced. The combined result was a lower total germination percentage. McGinnies (1960) noted that these effects were most pronounced at moisture stress level of - 7.5 atmospheres. He observed little difference between 0.33 atm and 5 atm treatment effects.

The germination of lettuce seeds in the soil was totally inhibited when water potential decreased below - 4 bars (Tadmor _et al_. 1968). In the case of ponderosa pine, seed germination was greatly depressed at - 7 bars (Larson and Schubert 1969). Tadmor _et al_. (1968) reported that germination of seeds of most species proceeded when the moisture content in the upper 10 cm of the soil is above wilting point.

Mayer and Poljakoff-Mayber (1975) also demonstrated that there is a species difference and variation in threshold value of water stress beyond which germination is inhibited. The water stress that prevents germination is not necessarily a constant value for a specific kind of seed unless other conditions are kept constant (Levitt 1972).

Gulliver and Heydecker (1973) have found that both germination rates as well as total seedling establishment are dependent on water levels in the substrate. They further argued that there is a minimum water content of the seed below which germination ceases. At progressively higher water levels, germination proceeds more rapidly to an optimal level beyond which reduced aeration and other factors reverse the trend.

2.3 LABORATORY SIMULATION OF WATER STRESS

Several laboratory techniques have been developed to study seed germination and seedling establishment under conditions of limited water availability. Conditions of limited water availability have been simulated using osmotic solutions of sodium chloride (Nieman 1962; Parmar and Moore 1968; Flowers 1972; Ghorashy *et al*. 1972), mannitol (Wiggans and Gardner 1959; McGinnies 1960; Tapia and Schmutz 1971; Jackson 1965; Parmar and Moore 1968) and Polyethyl glycol (Kaul 1966; Parmar and Moore 1968; Sionit *et al*. 1973; Bassirri *et al*. 1977).

Solution of varying concentrations are maintained around the root zone so as to attain a more effective control of water potential fluctuations. Using these techniques Uhvit (1946) reported that at atmospheric pressures greater than -7 atmospheres, germination of alfalfa was retarded more by sodium chloride than by mannitol. Thimann (1954) found mannitol to be more suitable than the other two solutes for limiting water uptake in plants without affecting metabolic action of the plant, although Jackson (1965) found conflicting result which indicated that mannitol is not only absorbed rapidly and metabolically but it causes a marked decrease in the rate of root hair elongation.

Sionit *et al.* (1973) using polyethylene glycol, investigated the effects of varying osmotic potential from 0 to 13 atm on germination of three safflower varieties and concluded that variation in percentage and rate of germination were due to osmotic concentration on the media rather than to water stress *per se*. In this connection Johnson and Assay (1978) showed that the different solution concentrations had a specific effect on germination independent of water potential; consequently this technique may confound the effects of drought *per se* with the direct effect of the osmotic solution on the seeds.

2.4 EFFECT OF WATER STRESS ON OTHER PHYSIOLOGICAL PROCESSES

Naturally plants show a diversity of morphological and physiological adaptations which enable them to escape and tolerate water deficits (Turner 1979). Kaul (1966) reported that in both wheat and barley the root/shoot ratios decreased with increasing osmotic stress while oats showed no clear response. Numerous reports in the literature show that water deficit limits yield. Salter and Goode (1967) utilized this relationship to determine the stage of growth at which crops were most susceptible to water stress. Hsiao (1973), Boyer and Mcpherson (1975), Begg and Turner (1976) and Turner and Begg (1978) in recent reviews, showed that many physiological processes associated with crop growth and development are influenced by water deficits. It is not very clear however, how these interact and integrate to cause a particular reduction in yield or even why one species or variety yields better under conditions of limited rainfall than another (Hsiao _et al_. 1976). One characteristic feature that allows desert ephemerals to resist drought is developmental plasticity which enables them to produce an abundance of vegetative growth, flowers, and seeds in seasons of abundant rain.

In addition to high developmental plasticity, rapid phenological development enables the desert ephemerals to both escape drought and survive long periods without rain (Mulroy and Rundell, 1977). An important aspect of developmental plasticity is the ability of plants to transfer assimilates accumulated priot to seed filling to the grain during the seed filling stage (Gallagher _et al_. 1976). Moderate water deficiencies can result in stunting, distorted development and much reduced crop yields while prolonged drought, can cause complete crop failure (Slatyer 1969). Slatyer (1969) further points out that deleterious effects of water deficit are usually pronounced in tissues and organs which are in stages of most rapid growth. Slatyer (1969) also reveals that differentiation, initiation of vegetative and reproductive primordia in the apical meristems and the enlargement of cell thus differentiated are very sensitive to water stress.

Water stress affects practically all aspects of plant growth, modifying the anatomy, morphology, biochemistry and physiology of plants. Some of these effects are related to decreasing turgor, some to decreasing water potential (Kramer 1969; Slatyer 1960). Kramer (1969) argued that water stress usually had multiple effects on plant growth. Photosynthesis for example, is reduced by closure of stomata, which decreases the supply of carbon dioxide: Water stress also reduces the capacity of the protoplasm to carry out photosynthesis while reduced translocation may hinder it by accumulation of end products. This reduction in photosynthesis, decreased translocation of carbohydrates and growth regulators, and disturbance of nitrogen metabolism, all manifest in poor growth. In turn, reduced growth reduces the photosynthetic surface further decreasing the relative amount of carbohydrate available for growth (Kramer 1969).

There is a general agreement that water stress at certain critical stages in plant causes more injury than at other stages. Slavik (1965) cites Russian work showing the injurious effects of water stress on grain yield when it occurs during tillering, heading and anthesis. Water stress also has effects on plant structure. The differences in leaf structure from the lower and the upper part of a tree and between sun and shade leaves are often attributed to differences in leaf water stress. The xeromorphic structure of leaves growing in bogs is often attributed to physiological drought, but this is questioned by Caughey (1945). This type of xeromorphism is probably related to nitrogen deficiency or other nutrients than just physiological drought _per se_ (Albretch 1940).

2.5 WATER STRESS AND DISEASE RESISTANCE

There is evidence that resistance to disease and insect attacks is sometimes related to the level of plant water stress. Parker (1965) considered water stress itself as a physiological disease and listed various symptoms of drought injury. Bier (1959) reported that the fungus causing bark cankers in willows invaded the bark only when the relative water content was below 80%. Parker (1961) reviewed considerable literature on the relationship between water content and disease incidence concluding that development of bark cankers is usually correlated with decreased water content of the bark.

The incidence of blossom end rot in tomato fruits is said to be higher on plants subjected to severe water stress (Carolus *et al*. 1965).

EFFECT OF MULCH ON MICROENVIRONMENT AND PLANT PRODUCTION

Many manufactured and natural materials are being used as mulches to promote plant growth (Lal 1974). Desirable mulches conserve soil moisture, moderate soil temperature, reduce soil erosion, improve soil properties and usually improve stands and plant production (Willis 1957).

Plant growth is regulated by, *inter alia*, soil moisture and soil temperature, both of which are influenced by mulching. Lower soil temperatures were found under straw mulch (McCalla and Duley 1946; Willis 1957; Maurya and Lal 1981). Mulching tillage studies in the Eastern United States of America have given variable results. In some studies mulch tillage increased yields of maize (Moody *et al.* 1963), whereas in other studies yields were lower than under conventional tillage (Beale *et al.* 1955; Free 1953; Willis 1957). Maurya and Lal (1981) found that straw mulch increased root density and shoot elongation of maize as a result of effective soil temperature regulation.

2.6 CHARACTERISTICS, HABITAT AND GRAZING VALUE OF *Chloris gayana* AND *Setaria sphacelata*

2.6.1 *Chloris gayana* (Rhodes grass)

C. gayana is a prolific, stoloniferous grass which grows naturally in many parts of East, Central and Southern Africa. It is extremely adaptable and can be found growing successfully in many parts of the world under a wide range of conditions. It is one of the most important grasses in many parts of Australia where is was introduced from Southern Africa around the turn of this century. At present it finds its place in nearly all pasture improvement programmes on the African continent. In Kenya it is one of the important grasses used as pasture ley in the high and medium potential areas. It occurs in open and wooded grasslands at medium elevation (Pratt and Gwynne 1977). Seed production is relatively easy and prolific in most ecotypes. Establishment from seed is fast and can be grazed within 4-6 months after sowing. This grass produces numerous tillers and stolons which cover the ground well (Bogdan 1969).

Edward and Bogdan (1951) claimed that its chief habitat is in the scattered tree grassland type of vegetation. Several ecotypes exist which differ in their agricultural values as well as adaptability to various climatic conditions. The variety used in this study was ELBMA RHODES which can withstand relatively drier conditions.

Boonmann (1972a) found that adequate and timely top dressing, close row width and careful choice of harvest data increased seed yield either directly or indrectly by synchronizing maturity. He also demonstrated that in _C. gayana_ establishment, phosphate fertilization failed to increase any yield aspect, while seed rate reduced yield of clean seed and number of heads but increased yield of dry matter significantly. Seed rate and row width did not affect yield of pure germinating seed (PGS) significantly. Shieldrick and Thairu (1975) demonstrated that high rate of growth in ley grasses such as *C. gayana* occurs after the onset of rains. This may be the most feasible time to conserve herbage as silage both in terms of provision of herbage for dry season feeding and as aid to grassland management.

Thomas (1977) found that in a system of beef production based on the dairybred steer, the use of high levels of concentrate feeding in the first dry season are not reflected in high slaughter weight. Maximum performance can be achieved by giving *C. gayana* grass as sole feed in the form of silage. Investigation of the nutritive value of natural pasture in Uganda indicated that calculated starch equivalent is normally adequate for maintenance and some degree of production in local domestic cattle, while protein equivalent can frequently be limited for extended periods of the year (Marshal *et al*. 1961; Bredon and Wilson 1963). More than 200 sample analysis of *C. gayana* have shown that it had an average crude protein level of 5.96% (Long *et al*. 1969). This mean ranged between 3% to 16.79% which is very adequate in meeting the protein demands of most classes of domestic livestock.

2.6.2 Setaria sphacelata (Nandi setaria)

S. sphacelata is a tufted or occasionally rhizomatous perennial, usually 50-150 cm tall. It is native to Kenya and occurs from near sea level to 3200 m in open and wooded grassland, on forest edges and in swampy places, mostly on fertile soils in eco-climatic Zones II and III (Pratt and Gwynne 1977). It originated in the Nandi district of Kenya, and prefers high precipitation and good soil fertility status. The attractive features of this grass are its persistence, productivity, high palatability and relatively good seed production. These valuable features outweigh its negative characteristics, viz its tufted habits and its tendency to go to stem too early. Nandi setaria pasture can last upto four years. This is long enough a period for ordinary ley (Bogdan 1959). This grass species is mainly found growing in highland grassland and scattered tree-grassland and also to some extent in Acacia-Themeda wooded grassland (Edward and Bogdan 1951).

Boonmann (1972b) demonstrated that close width row and nitrogen fertilization boosted the seed yield and dry matter production of Setaria sphacelata. Long et al. (1969) showed that S. sphacelata has an average crude protein of 5.82% and a range of 2.74% to 17.22%.

2.6.3 QUALITY CHANGES OF PASTURE GRASSES WITH SEASON

The chemical composition of tropical forages varies with the season. Bogdan and Kidner (1967) have shown that grass consumed in the dry season contained less available protein and soluble carbohydrate than wet season fresh grass.

Crude protein content of pastures may follow a bimodal seasonal pattern throughout the year that is approximately in phase with rainfall (Kidner 1966; Drau and Harrington (1972). With adequate rainfall, crude protein values can be as high as 20% of the dry matter in young leafy herbage while in periods of inadequate moisture, pastures are usually dormant and contain approximately 5% or less crude protein (Kidner 1966). In this respect *C. gayana* and *S. sphacelata* had a range of 3% to 16.79% and 2.74% to 17.22% crude protein respectively during the two distinct seasons (Long *et al*. 1969). The longer the dry season, the longer the period when the grass is fibrous and of very low crude protein content. Changes in the quality of protein also do occur. Dougall (1963) found that when growth was less restricted under a more favourable water status, the ratio of true protein to crude fibre improved. Proportions of other nutrients are also similarly affected. Seasonal changes in the composition of

Pennisetum clandestinum (Kikuyu grass) indicated an inverse relationship between crude protein and carbohydrate contents (Dougall 1953). French and Ledger (1957) and Elliot and Topps (1963) have suggested that these fluctuations in quality of herbage results in corresponding seasonal variations in animal live weight gains.

CHAPTER 3

MATERIALS AND METHODS

This study was aimed at investigating water relations of two grass species when they are subjected to varying degrees of water stress. The two grass species used were:

i) Chloris gayana - This grass was selected on account of its importance as a pasture ley in medium as well as high potential areas. It shows a wide range of ecological amplitude and is a promising species for use in much drier areas.

ii) Setaria sphacelata - is a high potential grass whose use is restricted to wetter areas with high soil fertility. It is used in this study for comparative purposes under conditions of limited moisture.

Seeds of the grasses were obtained from Kenya Seed Company. The study encompasses three aspects as indicated below.

3.1 LABORATORY STUDY

In this study the effect of limited moisture condition on germination of the two named grass species was assessed. Fully developed, mature and undamaged seeds were selected for germination in 4" petri dishes in a suitable incubator whose temperature was maintained between 24^0 to

26^oC. The temperatures were kept constant throughout the day and night.

The seeds were germinated in the dark save during counting when they were brought out in the light.

Each grass species was replicated four times at six moisture stress levels (0, -2 bars, -4 bars, -6 bars, -8 bars, -12 bars).

The moisture stress levels were obtained using an aqueous solution of mannitol which had been prepared according to Van't Hoff's procedure (1887) as quoted by Salisbury and Ross (1969). Van't Hoff's procedure gives an empirical relationship between osmotic potential and solution concentration. The relationship is given by the equation:-

$$\psi_\pi = MIRT$$

Where ψ_π - Osmotic potential in bars

M - Molality in moles per 1000g of water

I - A constant that accounts for ionization of solute and/or deviation from a perfect solution

R - gas constant (0.083 $\frac{\text{litres bars}}{\text{mole deg K}}$)

T - Absolute temperature in ^oK

<u>e.g.</u> for -4 bars

$t = 24^oC$; $T = 24 + 273 = 297\ ^oK$

$$-4 = M \times 1 \times 0.083 \times 297$$

$$M = \frac{4}{0.083 \times 297} = 0.162M.$$

N.B. For non-ionizing solutes e.g. mannitol i takes a value of 1.

1 mole of mannitol = 182.17 g

0.162 moles = 182.17 x 0.162 = 29.512 g

So to obtain -4 bars of osmotic pressure, dissolve 29.512 g of mannitol in 1000 g of water.

UNITS:

$$\text{Bars} = M \left(\frac{\cancel{\text{Mole}}}{\cancel{\text{Litres}}}\right) \times I \times R \left(0.083 \frac{\cancel{\text{Litres}}\ \text{Bars}}{\cancel{\text{Mole}}\ \cancel{\text{Deg K}}}\right) \times \cancel{T\ (\text{Deg K})}$$

$$\text{Bars} = \text{Bars}.$$

The blotters were immersed in the mannitol solution and the seeds placed on the surface in contact with the solution. 10 ml of the corresponding solution was initially added to every dish. Extra additions were made as necessary to curb down effects of evaporation on the solution concentration. Distilled water was used for the zero water potential treatment. Thiram was dusted on the blotting papers so as to minimize fungal infection. One hundred seeds were planted in each petri dish. Seedling counts were taken from the third day after planting when germination first commenced. Counts were taken on a daily basis for the first 8 days and thereafter counts were performed every other day for a period of 24 days. Germinated seeds were regarded as those whose seed coats had ruptured and primary roots were visible. The final germination percentage was then transformed using arcsin square root of percentage (each square root of percentage ' X ' is transformed to its arcsin-angle whose sine is $\sqrt{X}$ for analysis of variance).

This is done because germination percentage is a binomially distributed parameter and hence does not meet the assumptions of analysis of variance (Zar 1974; Sokal and Rohlf 1969).

The experiment was carried out in two phases with phase one running from January 14th to February 6th 1982 consisting of 2 species and four water stress levels Viz 0 bars; -4 bars; -8 bars, -12 bars, replicated four times. It was found in phase one that optimum germination coincided with moisture stress levels between zero and -6 bars and that germination was negligible beyond -8 bars. So in phase two, it was decided to run germination at 0 bars, -2 bars and -6 bars. The experimental units were arranged in a completely random design. Randomization was performed using "Ten thousand" digit table (Steel and Torrie 1960).

3.2 GREEN-HOUSE STUDY

This study was divided into two parts:-

a) Investigation of the effect of varying soil moisture regime on the physiological and growth response of the two grass species - _C. gayana_ and _S. sphacelata._

b) The role of mulch in conserving soil moisture as reflected in changes of water potential and dry matter production of the two named grasses.

3.2.1 DIFFERENTIAL WATERING REGIME

The grasses were sown in polypots in soils that were obtained from Kiboko - National Range Research Station (Red silty clays). Varying soil water potential was simulated by withholding water for various periods of time as follows:

a) Pots were watered after every other day (T_1) to serve as control.

b) Pots were watered after every four days (T_2)

c) Pots were watered after every six days (T_3)

d) Pots were watered after every eight days (T_4)

250 mls of water were added during each watering time. In total there were eight treatment combinations viz two grass species and four watering times replicated

4 times. The pots were arranged in a completely random design. For all the experimental units the following parameters were measured:-

i) Water potential - measured in bars using a dew point microvoltmeter (HR-33TSN 1774) and pressure bomb (PMS instrument Company, Corvallis, Oregon).

ii) Transpiration rate - Units of measurements is $\mu gCm^{-2}S^{-2}$ using a steady state porometer (Type LI-1600 Licor Ltd.).

iii) Diffusive resistance (Units of measurements is sec/cm) this parameter was also measured using a steady state porometer (Type LI-1600 Licor Ltd.). This parameter was converted to leaf conductance which is its reciprocal. Leaf conductance is given by: $\frac{1}{\text{diffusive resistance}}$. The units of measurement of leaf conductance is cm/sec.

The grasses were sown on 25/1/82 and the measurement of leaf water potential, transpiration and diffusive resistance were conducted after 48 days when all the watering regimes were synchronized. Diurnal changes of leaf water potential and leaf conductance were measured after 112 days at three time periods of the day i.e., 6 a.m. - 10 a.m.; 12-2 p.m., 4-6 p.m.

After 124 days from sowing (15th May, 1982) the shoots were clipped and their fresh weight taken. The fresh shoots were then oven dried at 80°C for 24 hours. The roots were extracted from the pots using a high pressure hose-pipe water. Fresh and dry weights were also taken; weighing and drying was done as above.

The grasses were grown between January and May 1982. This period was characterized by high mean day temperatures reaching a maximum of 35.2°C at 2.30 p.m. in the green house. Relative humidities were low, averaging 65% over the entire period of study.

3.2.2 MULCH STUDY

In this study the role of mulch (made from dried straws of Themeda triandra) in conserving water was being investigated. Conservation of water by mulch should theoretically improve the dry matter yield and influence physiological water status of the grass species named above. The experimental layout consisted of the two grass species replicated four times. The main treatment was mulch verses no-mulch. Half of the polypots, were mulched while the other half were left without mulch material. The mulch material was applied until it formed about 2 cm layer above the soil surface. Watering was administered after every four days, 250 ml being added to every pot. This watering was found to be neither excessive nor limiting to introduce its own influence on the parameters measured. The response variable measured included leaf water potential, diffusive resistance as well as fresh and dry weights of roots and shoots. The former measurements were taken 41 days after sowing and the latter 124 days after sowing.

The grasses were grown between January to May 1982. Fresh and dry weights of shoot and roots were taken 124 days after sowing.

3.2.3 EXPERIMENTAL DESIGN

In this study the experimental design employed throughout was completely random design where the experimental units were arranged in a completely random manner, thus enabling the assignment of treatments to experimental units without any bias. In all studies the treatments were replicated four times (sample size n = 4).

Expected means were worked out for leaf water potential leaf conductance as well as shoot and root dry weight of the two grasses using the value of a calculated slope estimate (a parameter that approximates the coefficient of regression β).

$$\text{Calculated slope estimate (b)} = \frac{C_i \bar{x}_i + \ldots\ldots. + C_n \bar{x}_n}{C_i^2 + \ldots\ldots. + C_n^2}$$

Where $\bar{X}$ - is the observed mean of the parameter under consideration.

C - Cofficient of polynomial value derived from Steel and Torrie (1960).

Expected mean = (C_i x b) + Grand mean.

e.g. Leaf water potential of C. gayana (Appendix 16) calculated slope estimate

$$(b) = \frac{(-3 \times 11.76) + (16.72 \times -1) + (25.28 \times 1) + (29.41 \times 3)}{(-3)^2 + (-1)^2 + (1)^2 + 3^2} = \underline{3.08}$$

$$\text{Grand mean} = \frac{83.16}{4} = 20.79$$

Expected mean

$$= (-3 \times 3.08) + 20.79$$

$$= 11.55$$

Expected means have been worked out to draw a line of best fit (see Figures 3, 6, 9 and 10 and Appendix 16 and 17).

CHAPTER 4

RESULTS AND DISCUSSION

4.1 GERMINATION STUDY

Seeds represent the means for survival and spread of most species of higher plants. Directly or indirectly seeds are the source of life-sustaining nutrients for man as well as other animals. Transformation of a planted grass seed into an established plant is a sequence of developmental stages beginning with seed germination.

Water plays a crucial role in this vital process of germination, one of which is its requirement for the activation of enzymes and RNA systems. Water deficiency impairs germination of seeds and may therefore arrest the perpetuation of plant species. This study was undertaken to determine the response of germination of two important pasture grasses, namely *C. gayana* and *S. sphacelata* to limiting moisture conditions.

4.1.1 SPECIES VARIATION IN TOTAL GERMINATION AT VARIOUS LEVELS OF OSMOTIC POTENTIAL

Changes in germination of *C. gayana* and *S. sphacelata* are presented in Table 1. This data indicates a steady decline in the germination percentage of the two species with increasing osmotic potential (water stress). *S. sphacelata* displayed a significantly ($P \leq 0.05$) higher

TABLE I: MEAN GERMINATION PERCENTAGE OF *C. gayana* AND *S. sphacelata* AT DIFFERENT [1]MOISTURE LEVELS AFTER 24 DAYS

TREATMENT OSMOTIC POTENTIAL (in bars)	SPECIES	
	C. gayana	*S. sphacelata*
0	32.01 ± 3.45*	43.38 ± 2.01
-2	34.21 ± 3.72	37.95 ± 3.08
-4	23.16 ± 3.65	35.01 ± 2.73
- 6	21.97 ± 3.63	25 ± 2.82
-8	11.26 ± 2.57	16.79 ± 3.03
-12	6.34 ± 1.03	9.58 ± 2.61

[1] Moisture level is represented by osmotic potential.

*Means are followed by standard deviations.

germination value upto -4 bars compared to C. gayana (Table 1 and Appendix 1). This difference could possibly be explained by the fact that the seeds of C. gayana were contained within spikelets thus making it difficult to ensure that every propagative unit planted contained a seed; or that S. sphacelata may have been improved for germination percent through selection. The difference in germination percent may also result from modes of propagation of these grasses i.e., the ability to establish vegetatively.

4.1.2 RESPONSE OF GERMINATION OF C. gayana AND S. sphacelata TO INCREASING OSMOTIC POTENTIAL (WATER STRESS)

Response in germination percentage to increasing moisture stress of the two species is given in Table 1 as well as Figures 1 and 2. Germination rates were significantly ($P \leq 0.05$) higher at lower moisture stress levels (Appendix 1). Data presented in table I shows that initially, germination percentages declined significantly in two stages (-2 bars and -6 bars for C. gayana and 0 bars and -4 bars for S. sphacelata). In both stages C. gayana declined at higher moisture stress levels. Over the moisture stress used (0 bars to -12 bars) C. gayana had 27.6% reduction in germination percentages whereas S. sphacelata had 33.6% reduction. These values were found to be significantly different. The inherent differences in germination percent between the two species under study necessitates that a relative approach be used to make an objective comparison in their response to increasing drought. These trends suggest that, in terms of total germination, C. gayana is more tolerant to moisture than S. sphacelata. It appears that the former species can thrive, at least in the early stages of growth, under semi-arid conditions. These findings further suggest superiority of C. gayana over S. sphacelata in tolerance to water stress. They also imply that C. gayana is adaptable to a wider range of moisture condition than S. sphacelata. C. gayana would therefore appear to do well both in humid as well as semi-arid areas while S. sphacelata would presumably be confined to wetter areas only, declining in performance as it is moved to drier regions.

The reduction in percent germination as a result of increasing osmotic concentration of mannitol may be due to two reasons.

Firstly, increasing solute potential (concentration) brings about a decline in water potential and hence creates drought condition. Germination of seeds is dependent upon the water levels in the substrate. There is a minimum level of water content below which germination does not occur (McDonough 1977). In this study germination occurred even at the highest level of water stress employed for both species. At progressively higher water levels, germination rate increased more rapidly to an optimal level declining thereafter. The optimal water level for germination for C. gayana in this study was approximately

FIG. 1: RESPONSE IN GERMINATION OF C. gayana TO SIX MOISTURE STRESS LEVELS

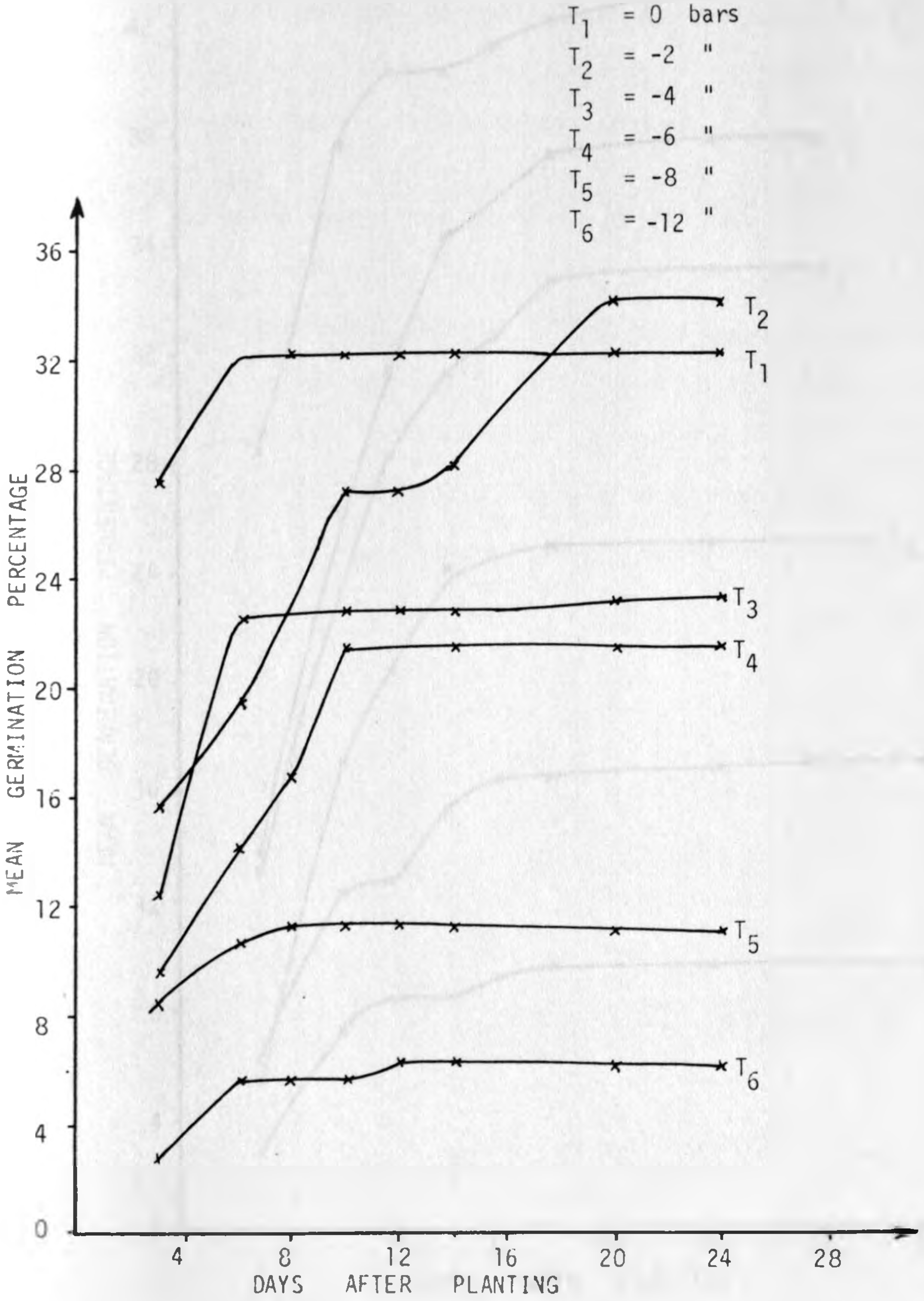
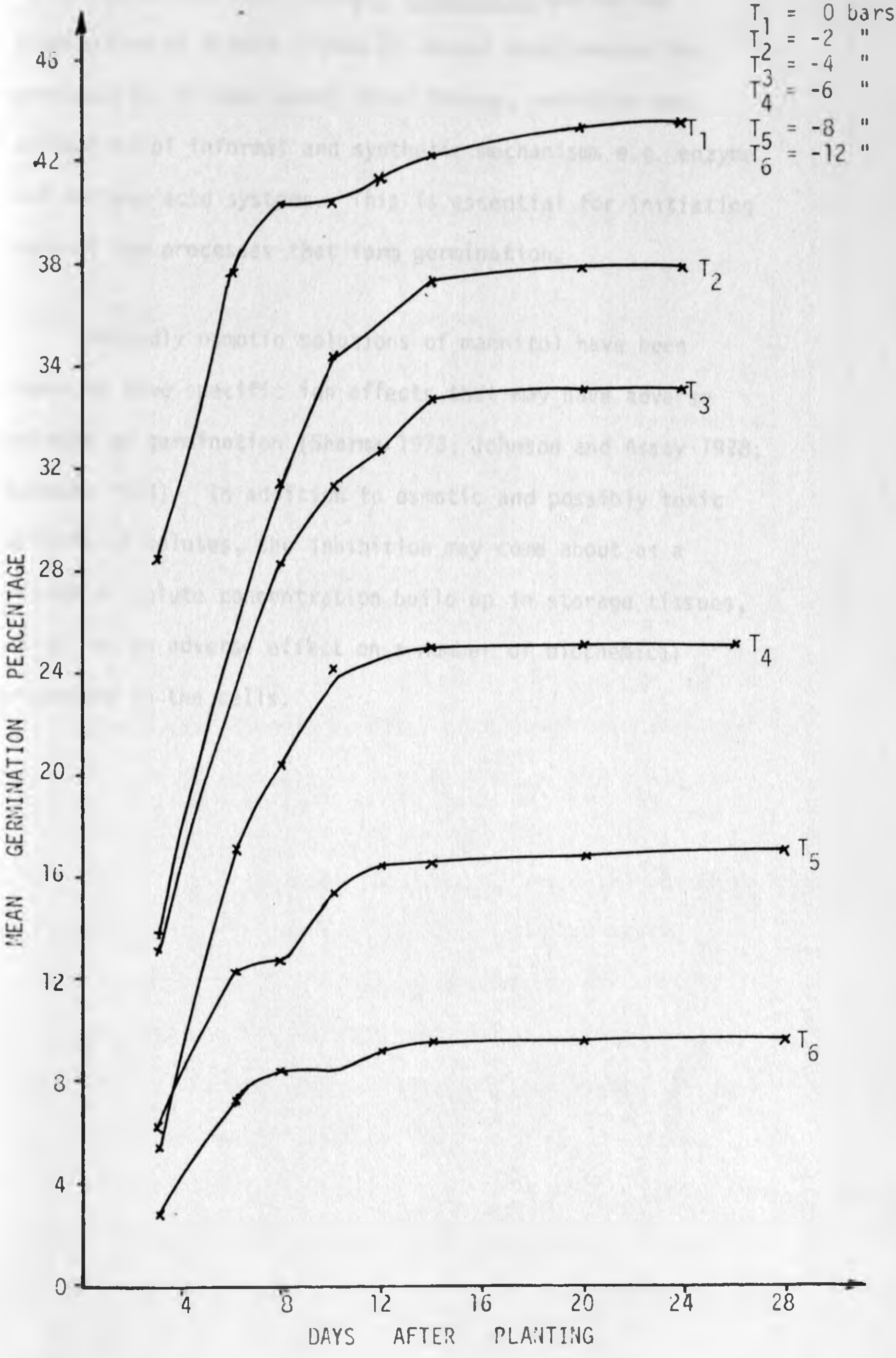


FIG. 2: RESPONSE IN GERMINATION OF *S. sphacelata* TO SIX MOISTURE STRESS LEVELS



-2 bars. On the other hand, S. sphacelata had optimal germination at 0 bars (Table I). Water requirements for germination includes among other things, hydration and activation of informal and synthetic mechanisms e.g. enzyme and nucleic acid systems. This is essential for initiating part of the processes that form germination.

Secondly osmotic solutions of mannitol have been shown to have specific ion effects that may have adverse effects on germination (Sharma 1973; Johnson and Assay 1978; Redmann 1974). In addition to osmotic and possibly toxic effects of solutes, the inhibition may come about as a result of solute concentration build up in storage tissues, which has an adverse effect on a number of biochemical processes in the cells.

4.1.3 CHANGES IN GERMINATION RATES OF C. gayana AND S. sphacelata WITH TIME

Tables II and III show the germination responses of C. gayana and S. sphacelata to water stress at different stages of growth or changes in germination with time from the day of planting. These changes are also represented graphically in Figures 1 and 2 respectively. Both species showed a rapid increase in germination rate initially followed by a decline which eventually levelled off. The germination rates appeared to level off earlier at higher osmotic potentials. This could be due to the depressing effects that both drought per se and specific ion effect have on germination. This would be in agreement with the finding of McGinnies (1960) working with six range grasses in a similar trial where he observed delay in germination and decrease in germination rate when they were subjected to increasing solute potential of mannitol solution. Analysis of variance (Appendix 2 and 3) shows that water stress and time, in terms of day after planting have significant effect ($P \leq 0.05$) on germination percentage. C. gayana reaches its maximum germination percentage by the sixth day whereas for S. sphacelata the highest level of germination was attained by the eighth day for lower osmotic potentials (T_1, T_2, T_3) and sixth day for the higher osmotic potentials (T_4, T_5, T_6). This could be explained by the germination characteristics of the two grass species

TABLE II: CHANGES IN PERCENT GERMINATION OF *C. gayana* ACROSS TIME AT VARIOUS OSMOTIC POTENTIALS

DAYS	T_1*	T_2	T_3	T_4	T_5	T_6
3	27.84 ± 1.32**	15.61 ± 1.68	12.44 ± 1.97	9.45 ± 2.56	8.48 ± 0.77	2.87 ± 1.44
6	31.01 ± 1.89	19.54 ± 2.41	22.54 ± 3.77	14.09 ± 3.48	10.74 ± 1.14	5.62 ± 1.86
8	31.34 ± 3.89	23.07 ± 3.60	22.72 ± 3.87	16.26 ± 3.11	11.26 ± 2.57	5.62 ± 1.86
10	32.01 ± 3.45	27.29 ± 3.79	22.89 ± 2.69	21.51 ± 3.63	11.26 ± 2.57	5.62 ± 1.86
12	32.01 ± 3.45	27.29 ± 3.79	22.89 ± 2.69	21.51 ± 3.63	11.26 ± 2.57	6.24 ± 1.03
14	32.01 ± 3.45	28.16 ± 3.15	23.16 ± 3.65	21.51 ± 3.63	11.26 ± 2.57	6.34 ± 1.03
20	32.01 ±3.45	34.21 ± 3.72	23.16 ± 3.65	21.51 ± 3.63	11.26 ± 2.57	6.34 ± 1.03
24	32.01 ± 3.45	34.21 ± 3.72	23.16 ± 3.65	21.51 ± 3.63	11.26 ± 2.57	6.34 ± 1.03

*T_1 = 0 bars; T_2 = -2 bars; T_3 = -4 bars; T_4 = -6 bars; T_5 = -8 bars
T_6 = -12 bars.

**The numbers following the means are standard deviations.

TABLE III: CHANGES IN PERCENT GERMINATION OF *S. sphacelata* ACROSS TIME AT VARIOUS OSMOTIC POTENTIALS

DAYS	T_1*	T_2	T_3	T_4	T_5	T_6
3	28.49 ± 1.79**	13.84 ± 2.32	13.21 ± 1.19	5.38 ± 2.57	6.35 ± 3.69	2.89 ± 0.11
6	37.80 ± 1.27	25.68 ± 3.44	23.0 ± 2.16	17.05 ± 2.39	12.19 ± 3.45	7.28 ± 2.65
8	40.48 ± 5.01	31.39 ± 4.85	28.33 ± 5.74	20.55 ± 2.15	12.65 ± 2.97	8.39 ± 2.06
10	40.48 ± 5.01	34.36 ± 4.31	31.37 ± 3.88	24.07 ± 3.42	15.35 ± 3.87	8.39 ± 2.06
12	41.35 ± 5.15	35.94 ± 4.02	32.63 ± 3.43	24.59 ± 2.62	16.45 ± 4.72	9.24 ± 1.72
14	42.07 ± 3.26	37.31 ± 3.75	33.66 ± 2.98	25.08 ± 2.82	16.45 ± 4.72	9.58 ± 2.82
20	43.23 ± 3.52	37.95 ± 3.31	35.01 ± 2.73	25.08 ± 2.82	16.79 ± 3.03	9.58 ± 2.82
24	43.23 ± 3.52	37.95 ± 3.31	35.01 ± 2.73	25.08 ± 2.82	16.79 ± 3.03	9.58 ± 2.82

*T_1 = 0 bars; T_2 = -2 bars; T_3 = -4 bars; T_4 = -6 bars; T_5 = -8 bars
T_6 = -12 bars.

** Numbers following mean are standard deviations.

whereby highest germination rates occurred between the 3rd and 6th day. This could also have resulted from confounding effect of germination rate with osmotic potentials. Such confounding effects may have resulted from specific ion effects of the mannitol used. The various solutions used to simulate drought have effects other than that of water stress *per se* (Johnson and Assay 1978; Lagerweff 1969).

4.2 PHYSIOLOGICAL RESPONSE OF *S. sphacelata* AND *C. gayana* TO VARYING SOIL MOISTURE REGIMES (GREEN-HOUSE STUDY)

The response of plants to drought manifests itself in various forms, the most notable of which are a host of physiological changes. A study of the internal water status of leaf tissues will enable one to assess the relationship that exists between the physiological state of the plant and dry matter production.

In the present study attention was mainly focused on the development of internal water deficit of two pasture grasses namely *C. gayana* and *S. sphacelata* following varying soil moisture treatment.

The physiological parameters measured in this study were water potential and diffusive resistance and the experimentation was conducted at the green house located in the field station, Kabete.

4.2.1 LEAF WATER POTENTIAL

This parameter measures the chemical potential of water in a system e.g. in the plant or in the soil. It indicates how much water is available for use within the plant tissues and hence is a useful parameter to measure as it reflects the water status of the plant. The values of this parameter are negative, the standard and highest being that of pure free water which has a value of zero.

4.2.1.1 SPECIES VARIATION IN LEAF WATER POTENTIAL

Changes in leaf water potential are presented in Table IV. The table shows that *C. gayana* had a higher mean leaf water potential than *S. sphacelata* at all watering regimes. This difference was found to be highly significant ($P \leq 0.05$) (Appendix 4).

Withholding water for varying period of time creates a corresponding range in soil water potential which is a main determinant of internal water status of plants. Plants may respond to soil water stress in any of the following ways.

a) Drought tolerance - This represents mechanisms, which allow the plants to survive and produce under conditions of high internal water stress.

b) Drought avoidance - This is a mechanism, which helps maintain a high tissues water status under conditions of water stress.

c) Drought escape - This includes a whole host of behavioural characteristics that allow plants to complete their life cycle before the onset of severe moisture stress (Levitt 1972).

Under the circumstance of the present study it will be difficult to pinpoint what mechanism is employed by the two grass species to react to the varying soil moisture

TABLE IV: MEAN LEAF WATER POTENTIAL (bars) OF _C. gayana_ AND _S. sphacelata_ AT DIFFERENT WATERING FREQUENCIES

WATERING FREQUENCY (days)	LEAF WATER POTENTIAL	
	C. gayana	_S. sphacelata_
2	-11.76±1.10*	-13.27±1.41
4	-16.72±0.68	-19.57±1.06
6	-25.28±1.49	-29.47±1.52
8	-29.41±0.10	-33.28±0.95

*Numbers following means are standard deviations.

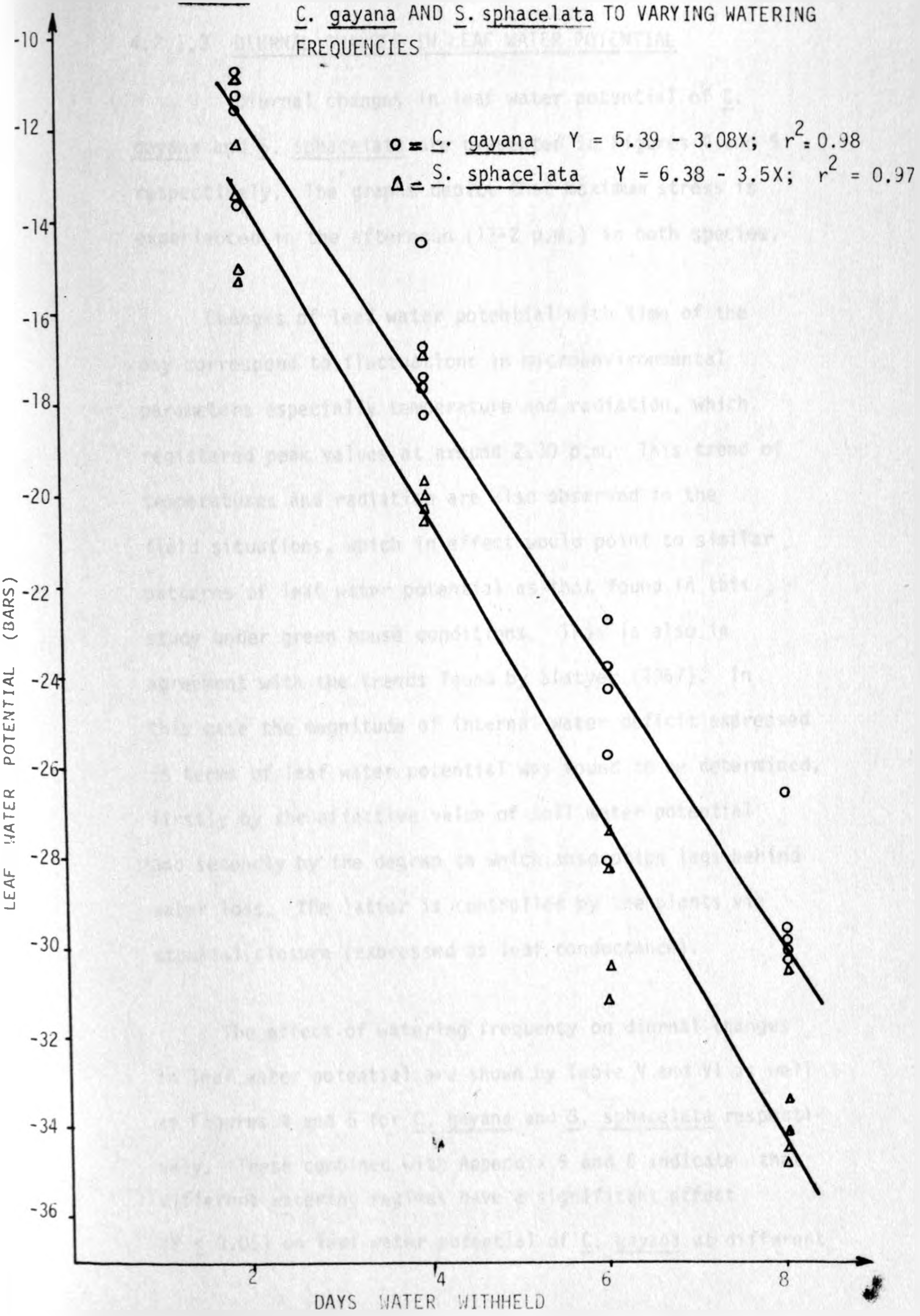
regime because situations of high internal water stress was not achieved. However since both are perennial grasses, drought escape is unlikely to be the mechanism that is in operation. The explanation most likely lies in differences in drought avoidance or drought tolerance or some combination of the two.

Whatever the mechanism evolved C. gayana, in this study had shown superior abilities for maintaining higher leaf water potentials under similar condition of soil moisture stress than S. sphacelata. C. gayana appears to have evolved certain mechanisms that enabled it to resist rapid fluctuation of leaf water potential as a result of changing soil water potential.

4.2.1.2 EFFECT OF WATERING FREQUENCY ON LEAF WATER POTENTIAL

The difference in response of leaf water potential of the two species to varying soil moisture regime is indicated in Figure 3. From this fugure we also note that C. gayana had a lower coefficient of regression (3.08) than S. sphacelata which strengthens the hypothesis that the former was more adaptable to fluctuating soil moisture regime.

<u>FIG. 3</u>: REGRESSION LINES RELATING LEAF WATER POTENTIAL OF <u>C</u>. <u>gayana</u> AND <u>S</u>. <u>sphacelata</u> TO VARYING WATERING FREQUENCIES



4.2.1.3 DIURNAL CHANGES IN LEAF WATER POTENTIAL

Diurnal changes in leaf water potential of C. gayana and S. sphacelata are presented in Figures 4 and 5 respectively. The graphs depict that maximum stress is experienced in the afternoon (12-2 p.m.) in both species.

Changes of leaf water potential with time of the day correspond to fluctuations in microenvironmental parameters especially temperature and radiation, which registered peak values at around 2.30 p.m. This trend of temperatures and radiation are also observed in the field situations, which in effect would point to similar patterns of leaf water potential as that found in this study under green house conditions. This is also in agreement with the trends found by Slatyer (1967). In this case the magnitude of internal water deficit expressed in terms of leaf water potential was found to be determined, firstly by the effective value of soil water potential and secondly by the degree to which absorption lags behind water loss. The latter is controlled by the plants via stomatal closure (expressed as leaf conductance).

The effect of watering frequency on diurnal changes in leaf water potential are shown by Table V and VI as well as Figures 4 and 5 for C. gayana and S. sphacelata respectively. These combined with Appendix 5 and 6 indicate that different watering regimes have a significant effect ($P \leq 0.05$) on leaf water potential of C. gayana at different

FIG. 4: CHANGES IN LEAF WATER POTENTIAL OF *C. gayana* WITH TIME OF THE DAY AT FOUR LEVELS OF WATERING REGIMES

MORNING - 6-10 a.m.
AFTERNOON - 12-2 p.m.
EVENING - 4-6 p.m.

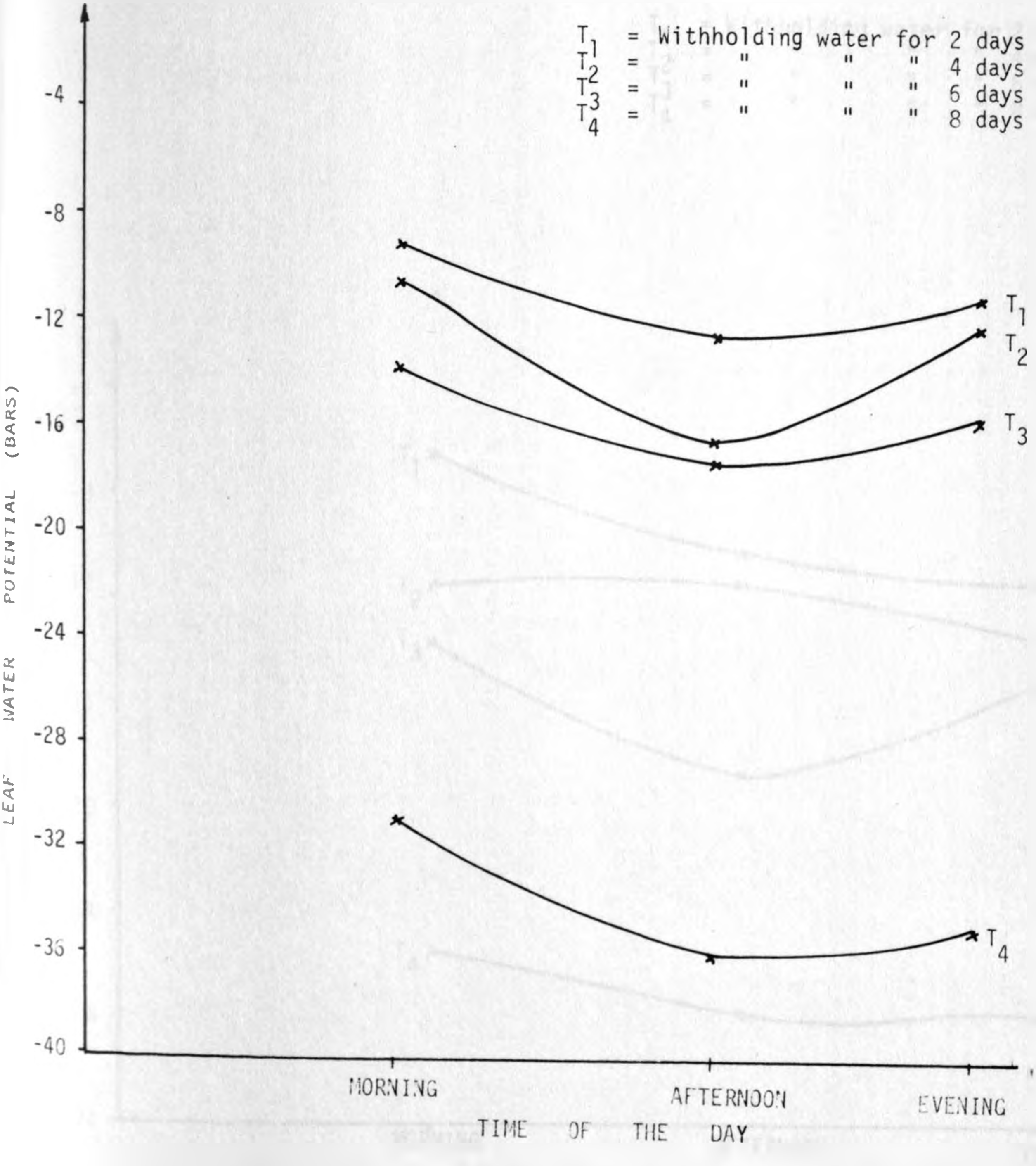


FIG. 5: CHANGES IN LEAF WATER POTENTIAL OF *S. sphacelata* WITH TIME OF THE DAY AT FOUR LEVELS OF WATERING REGIMES

MORNING - 6-10 a.m.
AFTERNOON - 12-2 p.m.
EVENING - 4-6 p.m.

T_1 = Withholding water for 2 days
T_2 = " " " 4 days
T_3 = " " " 6 days
T_4 = " " " 8 days

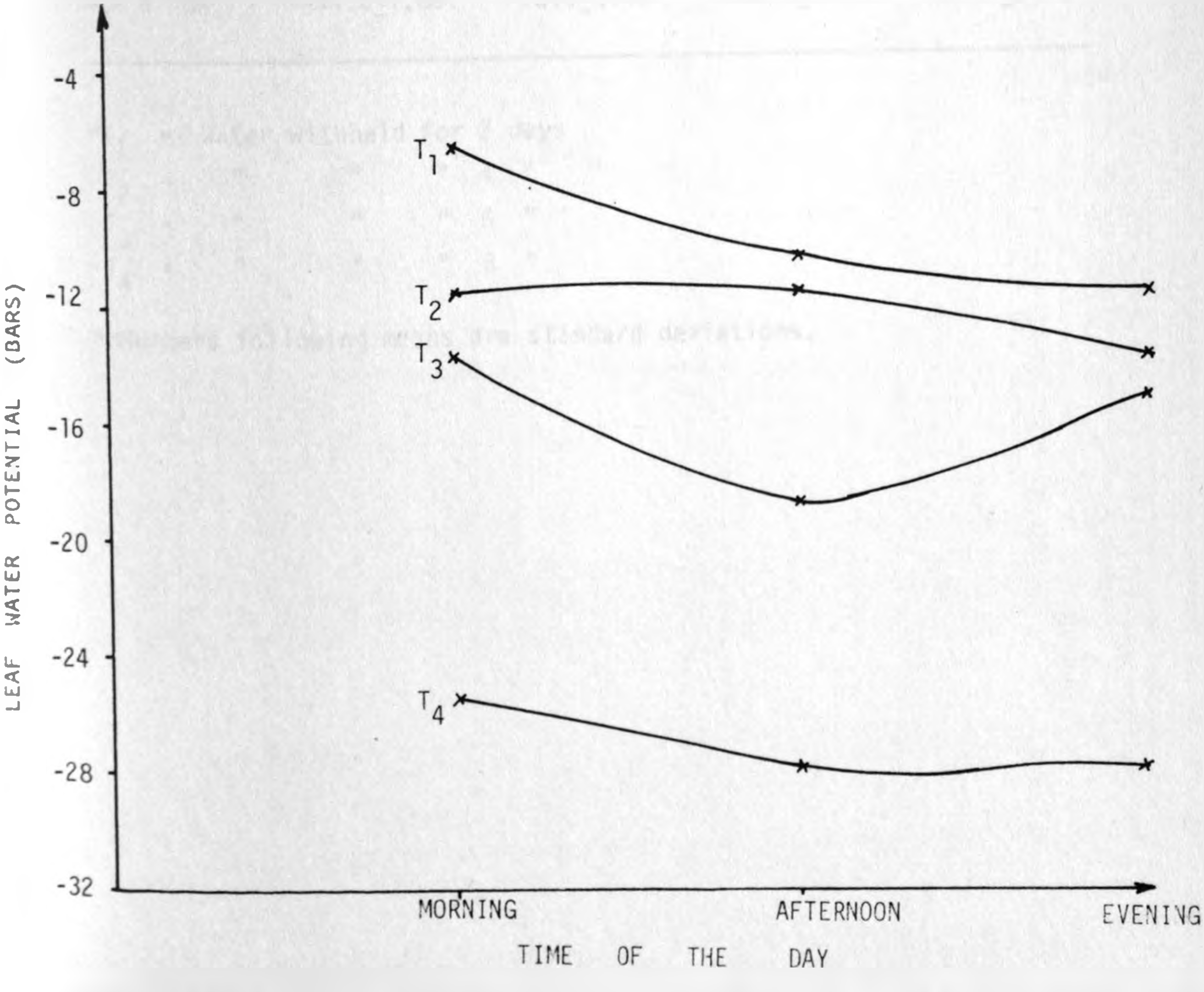


TABLE V: CHANGES IN MEAN LEAF WATER POTENTIAL (bars) OF *C. gayana* AT VARYING WATERING REGIMES WITH TIME OF THE DAY

TIME OF THE DAY	T_1*	T_2	T_3	T_4
6 - 10 am	-8.88±1.41**	-10.13±2.17	-13.88±1.25	-30.66±2.16
12 - 2 pm	-12.25±2.03	-16.38±2.35	-17.33±2.58	-36.17±2.44
4 - 6 pm	-11.0±1.86	-12.0±2.40	-15.66±1.73	-35.17±2.03

*T_1 = Water withheld for 2 days
T_2 = " " " 4 "
T_3 = " " " 6 "
T_4 = " " " 8 "

**Numbers following means are standard deviations.

TABLE VI: CHANGES IN MEAN LEAF WATER POTENTIAL (in bars) OF *S. sphacelata* AT VARYING WATERING REGIMES WITH TIME OF THE DAY

TIME OF THE DAY	T_1*	T_2	T_3	T_4
6 - 10 am	-6.38±3.87**	-11.38±2.63	-13.50±4.69	-25.66±3.20
12 - 2 pm	-10.13±2.15	-11.38±3.22	-18.75±3.72	-27.13±2.73
2 - 6 pm	-11.0±2.69	-13.63±2.94	-15.75±3.18	-27.75±3.10

*T_1 = Water withheld for 2 days
T_2 = " " " 4 "
T_3 = " " " 6 "
T_4 = " " " 8 "

**Numbers following means are standard deviations.

times of the day. Appendix 6 shows that changes of water potential at the three times of the day with varying water regimes was not significant.

However Figures 4 and 5 clearly illustrate that differential watering regime lowers the leaf water potential of both grasses at the three selected times thereby indicating that whereas certain times of the day present desirable conditions for favourable internal water status of the plants, frequency of watering does have a substantial effect on the degree of tissue dehydration. What this would suggest is that a certain minimal threshold value of soil moisture is necessary before diurnal benefits are realised i.e. plants subjected to prolonged water stress appeared to have less diurnal fluctuations.

The primary factor controlling stomatal aperture appears to be intercellular space concentration of carbon dioxide. Below a certain level of this concentration, which varies between species, opening movements are initiated. The degree of opening or closing which follows depends on the magnitude of the concentration change. In light, the reduction of carbon dioxide in photosynthesis means that a closing movement results in internal carbon dioxide concentration, which in turn tends to cause reopening (Slatyer 1967). In theory, therefore, there tends to be some overshooting and cyclical stomatal responses which are gradually damped out to lead to a new steady state situation in which stomatal aperture and internal carbon dioxide concentration are once again in balance. The data for _C. gayana_ and _S. sphacelata_ do not appear to conform to this scheme. This may have resulted from a combination of effects of water stress on cell turgor, which tends to close stomata, and the need to adjust water loss (this aids transpiration pull and hence water absorption) and carbon-dioxide exchange with the external environment.

TABLE VII: [1]MEAN LEAF CONDUCTANCE OF *C. gayana* AND *S. sphacelata* AT DIFFERENT WATERING FREQUENCIES

WATERING FREQUENCY (days)	LEAF CONDUCTANCE (cm/sec) *C. gayana*	LEAF CONDUCTANCE (cm/sec) *S. sphacelata*
2	0.24±0.01	0.20±0.03
4	0.17±0.02	0.18±0.01
6	0.12±0.01	0.1 ±0.01
8	0.07±0.02	0.07±0.02

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[1] Means are presented with their respective standard deviations.

4.2.2.2 EFFECT OF WATERING FREQUENCY ON LEAF CONDUCTANCE

Analysis of variance (Appendix 7) shows that leaf conductance of both C. gayana and S. sphacelata are significantly affected by altering watering frequency ($P \leq 0.05$). More frequent watering results in higher leaf conductance than less watering frequencies (Table VIII). Within the limits of the experimental range this relationship is generally linear (Figure 6 and Appendix 8).

Leaf conductance has a high and positive functional dependence on watering frequency as revealed by the magnitude of the R^2 values (Figure 6). The influence of differential watering regime, which determines soil moisture level, on leaf conductance is therefore substantial.

The grasses responded to decreasing moisture regime by adjusting their leaf conductance. At higher and favourable soil water levels, the grasses maintained a correspondingly high leaf conductance whereas when the soil water regime levels down, the grasses displayed decreased leaf conductance. This lowers transpiration rate, a process that plays an important role in internal water balance of the plants. The grasses' behaviour would point to possession of certain adaptive features that allows them to vary leaf conductance with the time so that at around 2 p.m. when the environmental conditions, especially ambient

TABLE VIII: CHANGES IN [1]MEAN LEAF CONDUCTANCE (in cm/sec) OF *C. gayana* AT VARYING WATERING REGIMES WITH TIME OF THE DAY

TIME OF THE DAY	T_1*	T_2	T_3	T_4
6am-10 am	0.32±0.01	0.37±0.02	0.13±0.12	0.11±0.01
12-2 pm	0.18±0.04	0.22±0.10	0.20±0.01	0.12±0.01
4 pm - 6 pm	0.28± 0.04	0.22±0.09	0.13±0.17	0.07±0.06

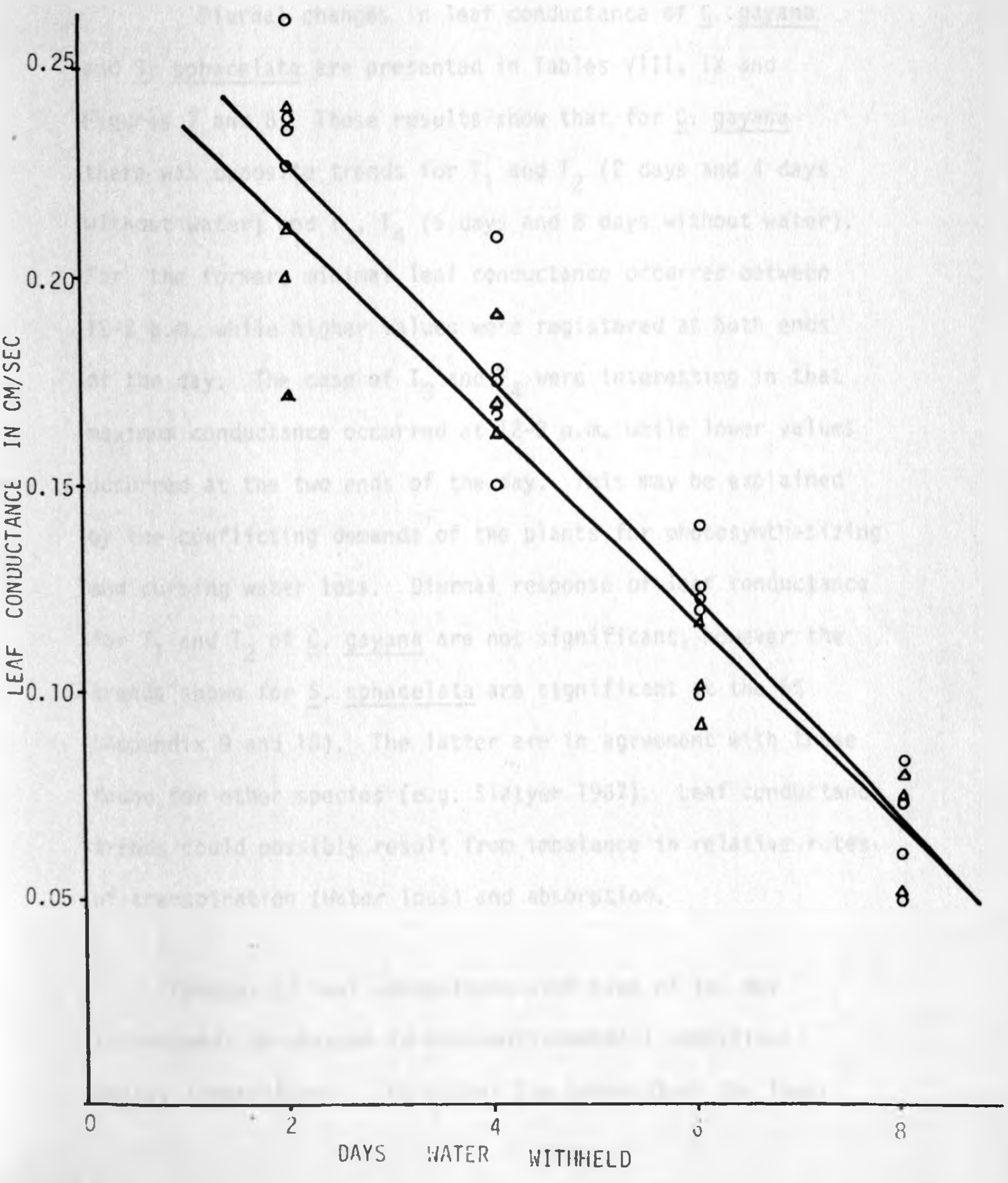
[1] Means are followed by respective standard deviations.

*T_1 = Water withheld for 2 days;
T_2 = Water withheld for 4 days
T_3 = Water withheld for 6 days
T_4 = Water withheld for 8 days

FIG 6: REGRESSION LINES RELATING LEAF CONDUCTANCE OF C. gayana AND S. sphacelata TO VARYING FREQUENCIES OF WATERING

○ = C. gayana $Y = 0.29 - 0.028X$; $r^2 = 0.92$

△ = S. sphacelata $Y = 0.26 - 0.026X$; $r^2 = 0.90$



temperature and radiation are at their peak. The leaf conductance tends to a minimal value (0.07 cm/sec for both species). This indicates closure of stomata in order to have a greater control over transpiration.

4.2.2.3 DIURNAL CHANGES IN LEAF CONDUCTANCE

Diurnal changes in leaf conductance of C. gayana and S. sphacelata are presented in Tables VIII, IX and Figures 7 and 8. These results show that for C. gayana there was opposite trends for T_1 and T_2 (2 days and 4 days without water) and T_3, T_4 (6 days and 8 days without water). For the former, minimal leaf conductance occurred between 12-2 p.m. while higher values were registered at both ends of the day. The case of T_3 and T_4 were interesting in that maximum conductance occurred at 12-2 p.m. while lower values occurred at the two ends of the day. This may be explained by the conflicting demands of the plants for photosynthesizing and curbing water loss. Diurnal response of leaf conductance for T_1 and T_2 of C. gayana are not significant, however the trends shown for S. sphacelata are significant at the 5% (Appendix 9 and 10). The latter are in agreement with those found for other species (e.g. Slatyer 1967). Leaf conductance trends could possibly result from imbalance in relative rates of transpiration (Water loss) and absorption.

Changes in leaf conductance with time of the day corresponds to changes in microenvironmental conditions, mainly temperatures. The higher the temperature the lower

TABLE IX: CHANGES IN [1]MEAN LEAF CONDUCTANCE (in cm/sec) OF *S. sphacelata* AT VARYING WATERING REGIMES WITH TIME OF THE DAY

TIME OF THE DAY	T_1*	T_2	T_3	T_4
6 am - 10 am	0.15±0.03	0.27±0.02	0.14±0.04	0.09±0.01
12 - 2 pm	0.15±0.1	0.17±0.02	0.10±0.01	0.08±0.01
4 pm - 6 pm	0.14±0.01	0.12±0.06	0.09±0.02	0.07±0.02

[1] Means are followed by respective standard deviations

*T_1 = water withheld for 2 days
T_2 = water withheld for 4 days
T_3 = water withheld for 6 days
T_4 = water withheld for 8 days

FIG. 7: CHANGES IN LEAF CONDUCTANCE OF C. *gayana* WITH TIME OF THE DAY AT FOUR LEVELS OF WATERING REGIMES

MORNING - 6-10 a.m.
AFTERNOON - 12-2 p.m.
EVENING - 4-6 p.m.

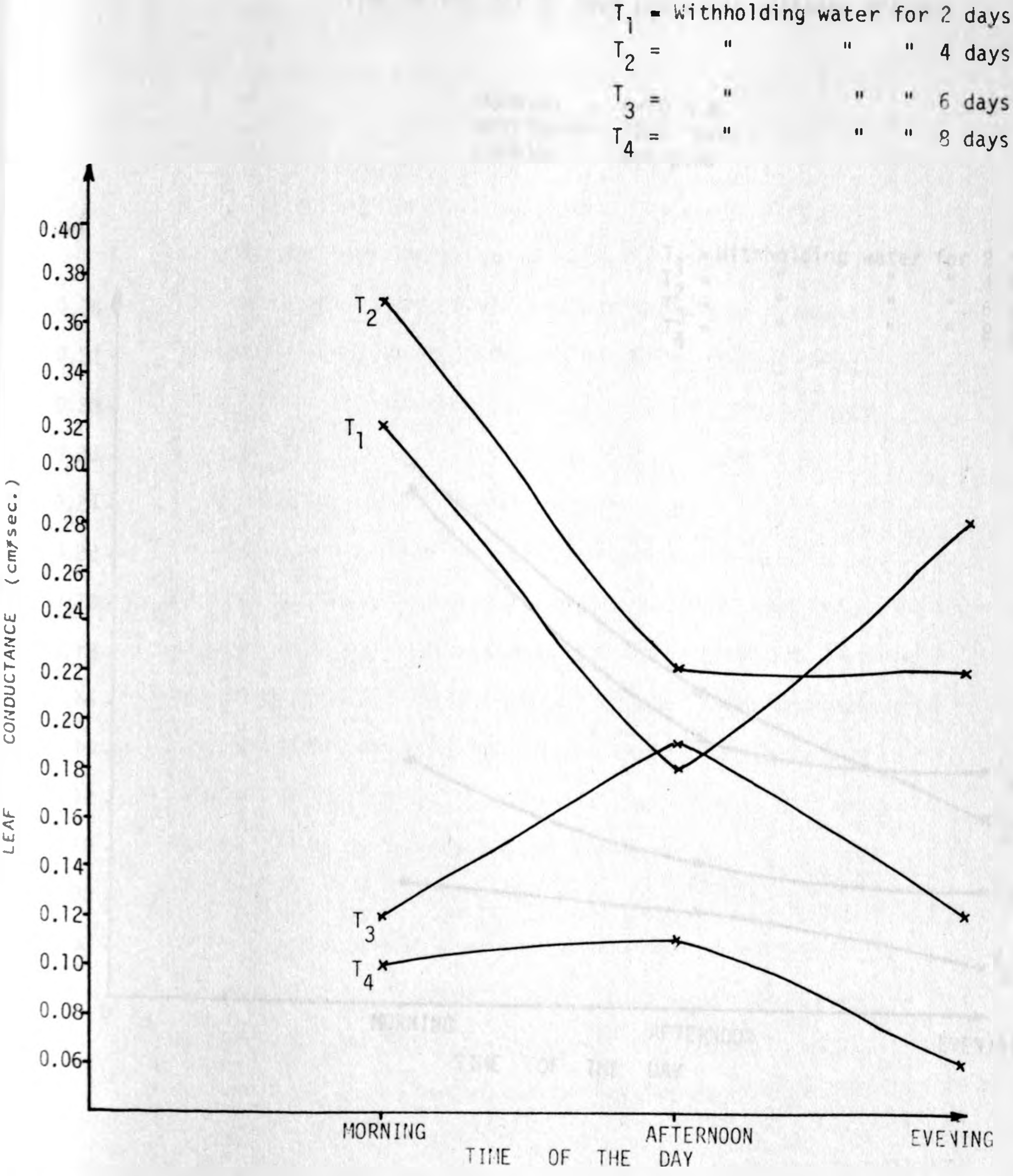
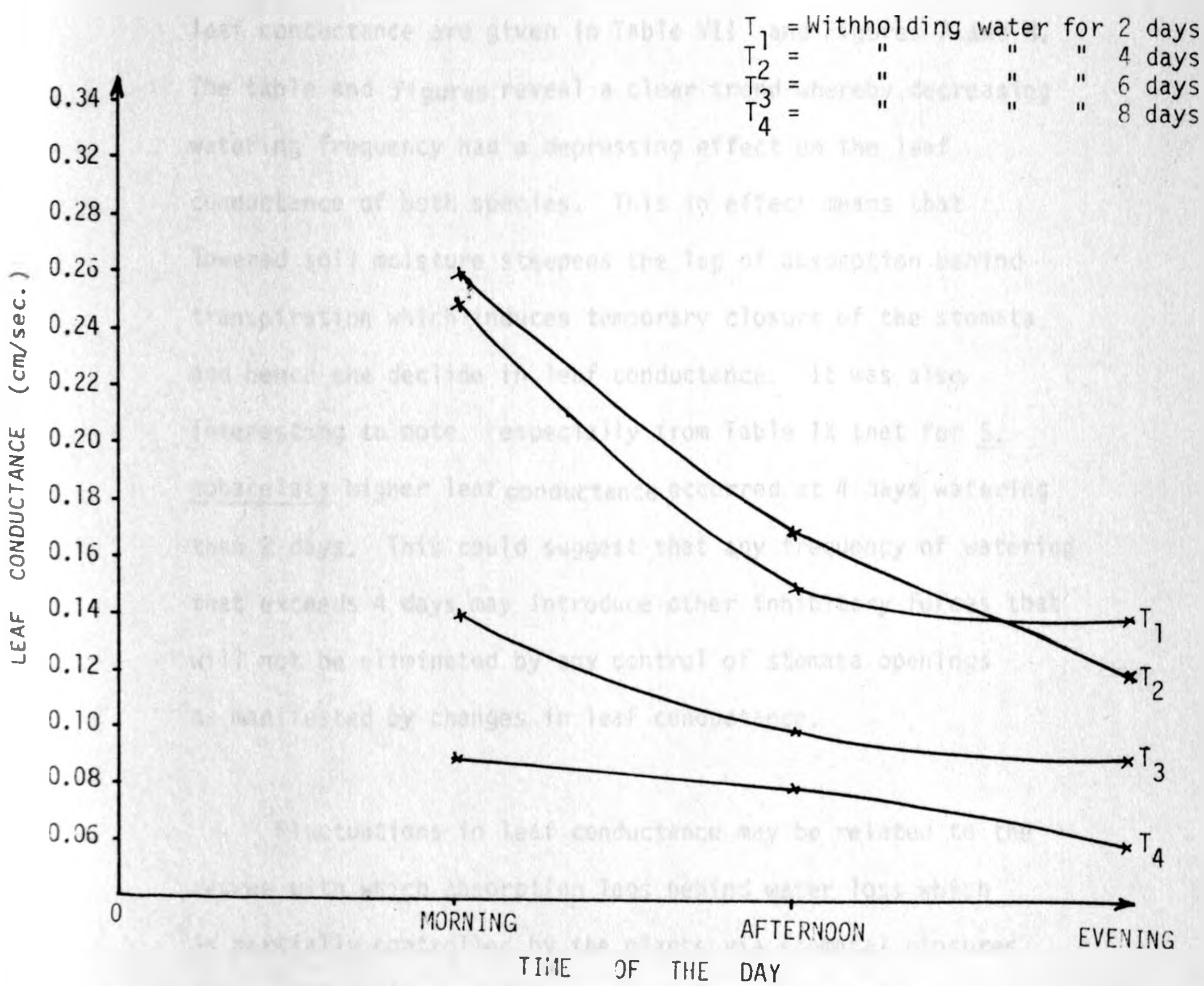


FIG. 8: CHANGES IN LEAF CONDUCTANCE OF S. sphacelata WITH TIME OF THE DAY AT FOUR LEVELS OF WATERING REGIMES

MORNING - 6-10 a.m.
AFTERNOON - 12-2 p.m.
EVENING - 4-6 p.m.



the leaf conductance. Such pattern will best be appreciated when looked at from the point of view of the need to control water loss in the advent of decreasing soil water and increased availability of latent heat for vaporising water and hence facilitating its loss via the stomata. Decreased leaf conductance indicates a response of the plant to have greater control over water loss or excessive transpiration.

Effect of frequency of watering on diurnal changes in leaf conductance are given in Table VII and Figures 7 and 8. The table and figures reveal a clear trend whereby decreasing watering frequency had a depressing effect on the leaf conductance of both species. This in effect means that lowered soil moisture steepens the lag of absorption behind transpiration which induces temporary closure of the stomata and hence the decline in leaf conductance. It was also interesting to note especially from Table IX that for S. sphacelata higher leaf conductance occurred at 4 days watering than 2 days. This could suggest that any frequency of watering that exceeds 4 days may introduce other inhibitory forces that will not be eliminated by any control of stomata openings as manifested by changes in leaf conductance.

Fluctuations in leaf conductance may be related to the degree with which absorption lags behind water loss which is partially controlled by the plants via stomatal closures (expressed as leaf conductance). Stomatal control of transpiration leads to an interesting diurnal pattern in leaf conductance. Under extreme conditions of either greater demand or reduced water supply, the extent to which the water potential gradient through the plant would have to be steepened to satisfy demand, may be associated with reduction of leaf water potential to a value which induces a degree of stomatal closure. It is under these conditions that regulatory functions of the stomata becomes apparent and serves to prevent flow to be maintained at lower potential of the leaves.

4.3 EFFECT OF DIFFERENT WATERING REGIMES ON DRY MATTER PRODUCTION OF *C. gayana* AND *S. sphacelata*

Water is an essential factor for the life and performance of pasture grasses. This study has placed a focus on the response of *C. gayana* to variable soil moisture levels. In so doing it would be possible to determine the range of soil moisture potential as reflected by frequency of watering that will sustain enough primary production to support adequate livestock production. This kind of experimentation will also enable the pasture agronomist to evaluate dry matter yield of *C. gayana* in various ecological zones of Kenya. *S. sphacelata* is used as a comparison since it represents a species that is highly sensitive to fluctuating moisture and therefore can be described as drought intolerant. The latter species has a narrow ecological amplitude for soil moisture levels.

4.3.1 SPECIES VARIATION IN DRY MATTER PRODUCTION

Species differences in shoot production of *C. gayana* and *S. sphacelata* at different watering regimes are given in Table X. This coupled with Appendix 11 show that *C. gayana* had higher shoot weights at all levels of watering regime. This would suggest that it has better ability to produce adequate herbage under a wide soil moisture range. It also would imply that this species is more desirable in conditions of limiting moisture than *S. sphacelata*.

TABLE X: MEAN SHOOT DRY WEIGHT OF _C. gayana_ AND _S. sphacelata_ AT DIFFERENT WATERING REGIMES.

WATERING FREQUENCY (days)	SHOOT DRY WEIGHT (gm/pot)	
	C. gayana	_S. sphacelata_
2	11.80±2.0*	4.70±1.65
4	10.97±1.39	3.75±0.60
6	5.08±0.68	2.30±1.04
8	3.17±0.69	1.50±0.5

*Means are followed by standard deviations.

Table XI and Appendix 12 indicate the effect of varying soil moisture regime on root production of the two grass species. *C. gayana* a had a significantly ($P \leq 0.05$) higher mean root production than *S. sphacelata* at most levels of watering frequency. This difference in root weight may be interpreted to mean deeper and spreading rooting characteristic in favour of *C. gayana.* The difference in biomass production, especially root production under conditions of limiting moisture would tend to suggest existence of different water-use mechanisms among the two species studied.

4.3.2 EFFECT OF WATERING FREQUENCY ON DRY MATTER PRODUCTION

Decreasing the soil moisture levels was found to significantly ($P \leq 0.05$) lower shoot and root dry matter production (Appendix 11 and 12). There was a significant ($P \leq 0.05$) difference in shoot weights of the two species. *C. gayana* shows much higher dry weights at all levels of watering regime for both the shoot and root. Tables X and XI and Appendices 11 and 12 show that with increased frequency of watering both shoot and root production significantly ($P \leq 0.05$) improved.

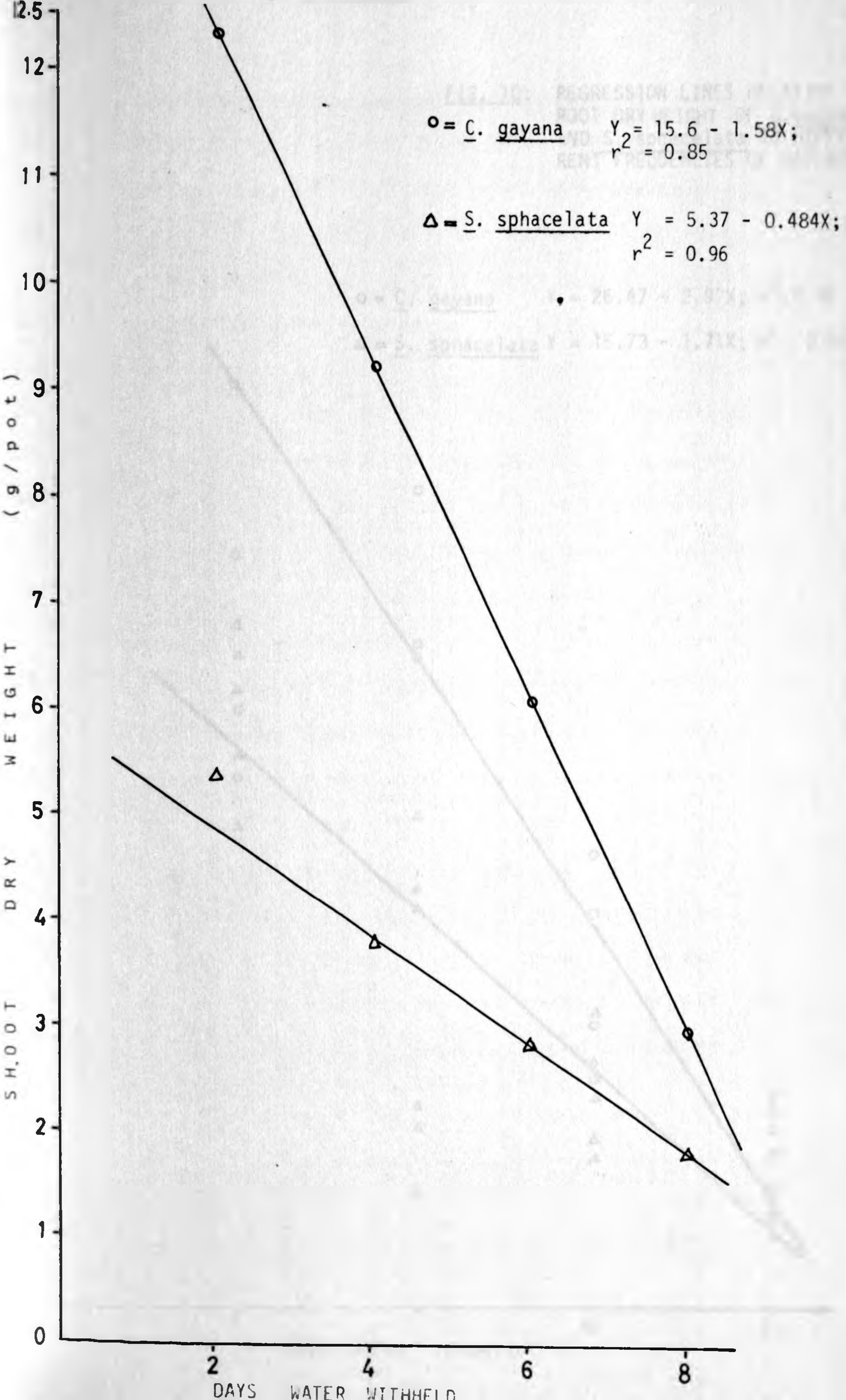
Figures 9 and 10 graphically represent these variations and they indicate a positive linear relation between the two variables measured. What this means in essence was that

TABLE XI: MEAN ROOT DRY WEIGHT OF *C. gayana* AND *S. sphacelata* AT DIFFERENT WATERING REGIMES

WATERING FREQUENCY (days)	ROOT DRY WEIGHT (gm/pot)	
	C. gayana	*S. sphacelata*
2	20.82±4.83*	13.69±1.19
4	15.37±2.16	7.24±2.72
6	6.27±2.25	4.67±1.34
8	4.03±0.90	3.12±1.32

*Means are followed by standard deviations.

FIG. 9: REGRESSION LINES RELATING SHOOT DRY WEIGHT OF *C. gayana* AND *S. sphacelata* TO DIFFERENT WATERING FREQUENCIES



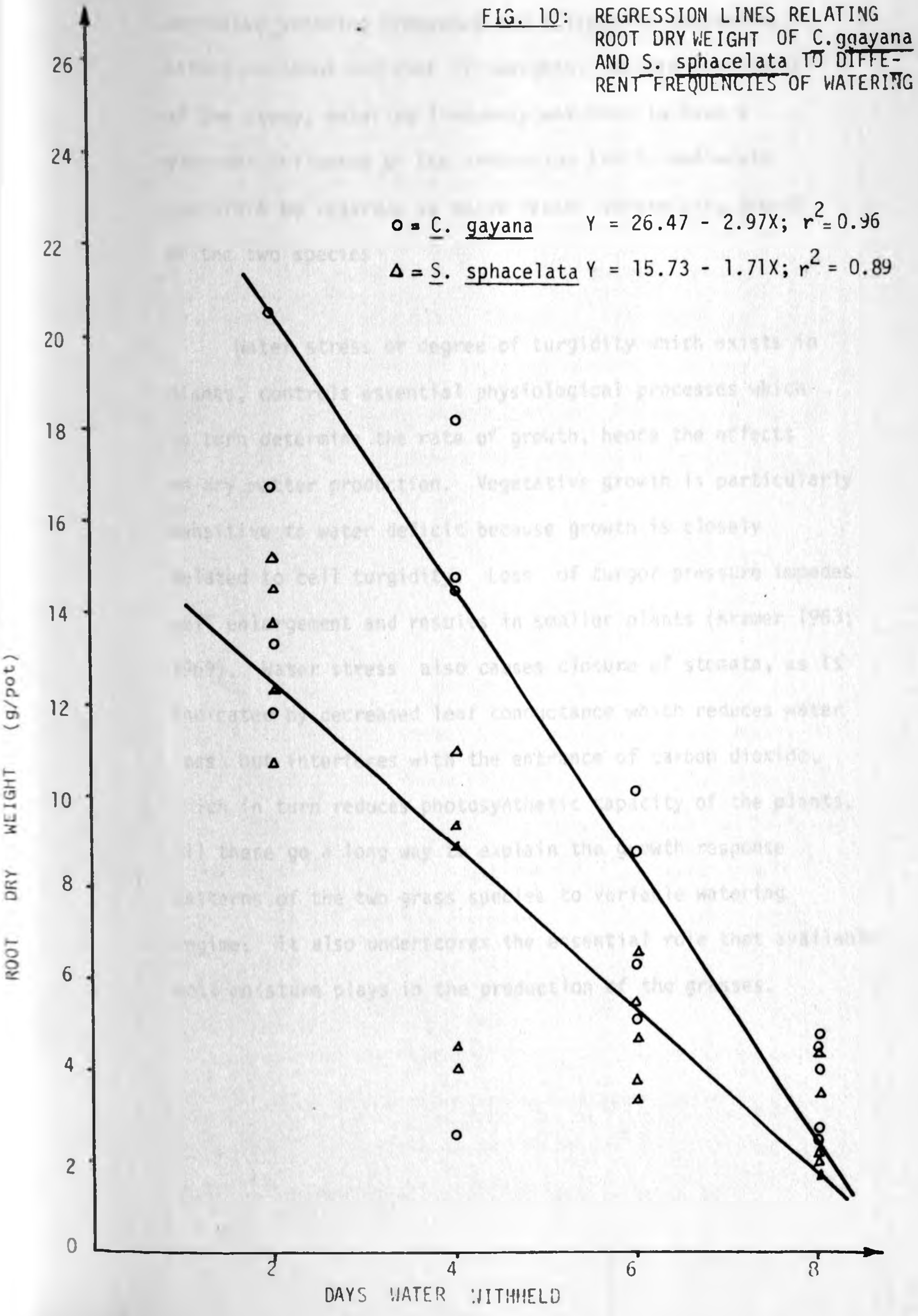


FIG. 10: REGRESSION LINES RELATING ROOT DRY WEIGHT OF C.ggayana AND S. sphacelata TO DIFFERENT FREQUENCIES OF WATERING

decreased watering frequency had a linearly depressing effect on shoot and root dry weights. Within the limits of the study, watering frequency was seen to have a dominant influence on the production traits and would therefore be regarded as major factor determining growth of the two species

Water stress or degree of turgidity which exists in plants, controls essential physiological processes which in turn determine the rate of growth, hence the effects on dry matter production. Vegetative growth is particularly sensitive to water deficit because growth is closely related to cell turgidity. Loss of turgor pressure impedes cell enlargement and results in smaller plants (Kramer 1963; 1969). Water stress also causes closure of stomata, as is indicated by decreased leaf conductance which reduces water loss but interferes with the entrance of carbon dioxide, which in turn reduces photosynthetic capacity of the plants. All these go a long way to explain the growth response patterns of the two grass species to variable watering regime. It also underscores the essential role that available soil moisture plays in the production of the grasses.

4.4 PHYSIOLOGICAL AND GROWTH RESPONSE OF *S. sphacelata* AND *C. gayana* TO MULCHING

Mulch plays an important role in conserving soil moisture for plants especially those that have high water demand like coffee, tea and vegetables or where a crop is grown in an area where the soil moisture availability is below its requirement. However it may introduce other problems e.g., it forms a suitable media for pathogen and pest breeding. The mulch material may also be a source of weed seeds or other forms of its propagative units.

In areas of limited moisture (semi-arid regions) any method that can conserve soil moisture is undoubtedly vital for production of vegetation or herbage that will serve as source of forage for livestock. Mulch which is shed in the form of straws, debris of leaves and stem during the dry spell represents one such soil moisture conserving method. By conserving moisture it is possible to extend the ecological amplitude of *C. gayana* as well as other pasture and range grasses, to regions of lower precipitation.

This study was selected to assess the advantage that mulching (as a moisture conserving method) confers on *C. gayana* and *S. sphacelata* in as far as dry matter production and maintaining desirable water status is concerned.

4.4.1 EFFECT OF MULCHING ON LEAF WATER POTENTIAL

The effect of mulching on the leaf water potential of *C. gayana* and *S. sphacelata* are given in Table XII. This together with appendix 13 show that mulch significantly ($P \leq 0.05$) elevates the leaf water potential of the two grasses. However no significant difference was detected between the species nor was there any interaction effect (Appendic 13).

The effect of mulch on leaf water potential could possibly have resulted from its influenced on soil water potential. Mulch reduces fluctuations of soil water potential, bringing about a gradual decrease in soil moisture. The influence of mulch on leaf potential is therefore achieved indirectly by dampening soil water potential changes.

4.4.2 EFFECT OF MULCH ON DRY MATTER PRODUCTION

The mulch treatment used in this study (straw mulch) had an insignificant effect on the production levels of both grass species in terms of shoot and root dry weights (Tables XIII, XIV and Appendic 14). This insensitive response of the plants biomass to mulching is likely to have resulted from some negative factors associated with the use of straw mulch. The straw mulch may have acted as a suitable media for pathogen and pest breeding. As a

TABLE XII: EFFECT OF MULCH ON LEAF WATER POTENTIAL (in bars) OF *C. gayana* AND *S. sphacelata*

TREATMENT	LEAF WATER POTENTIAL	
	Chloris gayana	*Setaria sphacelata*
MULCH	-11.91±1.76*	-12.38±1.35
NO MULCH	-14.75±1.66	-15.47±1.54

*Means are followed by standard deviations.

TABLE XIII: EFFECT OF MULCH ON THE ROOT DRY MATTER OF *C. gayana* AND *S. sphacelata*

TREATMENT	ROOT DRY WEIGHT[1]	
	C. gayana	*S. sphacelata*
MULCH	14.95±1.84*	15.47±1.09
NO MULCH	12.38±1.69	11.91±1.92

[1] Dry weights are measured in gm/pot.

*Means are followed by standard deviations.

TABLE XIV: EFFECT OF MULCH ON THE SHOOT DRY WEIGHT OF *C. gayana* AND *S. sphacelata*

TREATMENT	SHOOT DRY WEIGHT (g/pot)	
	C. gayana	S. sphacelata
MULCH	4.39±1.40*	4.22±1.08
NO MULCH	3.60±1.17	3.88±1.37

*Means are followed by standard deviations.

matter of fact, in this study the mulch plots were infested with aphids and white flies. These were being bred in a nearby experimental plot. Significant damage may have been inflicted on the grasses' growth by the time control measures were effected. Under the conditions of this study it is difficult to make inferences concerning the relative importance of the desirable and undesirable (mentioned above) impacts of mulch. The former include benefits resulting from lowered soil temperature, greater conservation of soil moisture which translates into favourable internal water status (Lal 1974).

SUMMARY AND CONCLUSIONS

The present study was aimed at investigating the effect of limiting moisture conditions on germination, water status and biomass production of two commonly used pasture grasses namely C. gayana and S. sphacelata so as to evaluate their drought tolerance responses.

The study showed that increased moisture stress delayed germination, reduced its rate as well as 24 day total germination of C. gayana and S. sphacelata. The study further demonstrated that within the limits of moisture stress (as expressed in solute concentration) used, the functional relationship was in the main, linear. This was particularly true for the response of total germination percentage of the two grasses to increasing water stress.

Analysis of the germination data also showed that there was a difference in the germination percentage of the two species, that of C. gayana being generally lower than that of S. sphacelata. However further tests proved that C. gayana showed a higher tolerance to increasing water stress than Setaria sphacelata during germination. This means that C. gayana can perform much better in areas of limiting and fluctuating soil moisture level of upto -12 bars of soil water potentials, optimal germination occurring around -4 bars.

Germination percentage was also found to increase with days after sowing. Germination percentage progressed in a sigmoid fashion, where there was an increasing rate of germination initially (exponential) and finally levelling off by twentieth day after sowing.

Differential watering regimes which create a corresponding range of soil moisture levels was found to have a significant ($P \leq 0.05$) effect on the leaf water potential, leaf conductance as well as dry shoot and root weights. Except for the leaf conductance and to a lesser extent root weights, C. gayana showed superior ability in maintaining higher tissue water content as well as greater shoot dry matter production, a feature that would make it more adaptable to arid and semi-arid conditions.

The mulch study showed that mulching had a significant ($P \leq 0.05$) effect on the leaf water potential of both grass species thereby increasing the internal water status which is advantageous in water-use efficiency. This effect of mulch is realised indirectly by maintaining desirable soil water potential. In this way mulch contributes to soil water conservation. However mulch treatment did not have any significant effect on both shoot and root dry matter production. This could be due to some negative growth factors associated with mulch, namely weeds and pests that breed in the mulch material. These coupled with heavy infestation of the mulch study plants with aphids and white flies may explain the conflicting effects that mulch had on leaf water potential and biomass production.

Since most of the microenvironmental conditions were roughly similar to those found in the field, there is no reason to doubt the extrapolability of the trends from this study to what happens in the field situation. However there is a need to undertake a more comprehensive study of soil-plant-moisture relationships by seasons over a longer period of time in the drier areas, particularly rangelands so as to be able to make sound recommendations as to where they could possibly be extended.

Through systematic studies of plant-water relationships of desirable pasture and range grasses, it should be possible to come up with a wide variety of species and ecotypes that possess adaptive features of drought tolerance which could be recommended for establishment in the extensive arid and semi arid regions of Kenya. This will also make it possible to identify grass species and ecotypes that could be used as a good source of germplasm which would then form the basis of pasture and range seeding programs. The role of plant-water relationship studies in elevating productivity of pasture-lands and range land cannot therefore be over-emphasised.

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APPENDICES

APPENDIX 1: ANOVA TABLE FOR EFFECT OF WATER STRESS ON 24-DAY TOTAL GERMINATION OF *C. gayana* AND *S. sphacelata*

Source of variation	DF	SS	MS	F cal.
Level	1	29571.04		
Treatment	11	6415.44	583.22	15.39*
B	5	5726.95	1145.39	30.23*
A	1	532.74	532.74	14.06*
A x B	5	155.75	31.15	0.82 ns
Total	48	7779.52		
Error	36	1364.08	37.87	

*Significant ($P \leq 0.05$)

ns - Not significant

B - osmotic potential

A - Species

APPENDIX 2: ANOVA TABLE FOR GERMINATION ACROSS TIME AT VARYING OSMOTIC POTENTIAL (*Chloris gayana*)

Source of variation	DF	SS	MS	F cal.
Level	1	67572.77		
Treatment	47	15598.03	331.87	17.79*
(T^S)	5	13837.43	2767.49	148.39*
Day (after planting)	7	1211.49	173.07	9.28*
Interaction	35	549.12	15.69	0.84 ns
Total	192	18283.73		
Error	144	2685.70	18.65	

*Significant $(P \leq 0.05)$

ns - not significant

Ts - osmotic potential

APPENDIX 3: ANOVA TABLE FOR GERMINATION ACROSS TIME AT VARYING OSMOTIC POTENTIAL (Setaria sphacelata)

Source of variation	DF	SS	MS	F cal.
Level	1	110053.13		
Treatment	47	28167.09	599.29	16.34*
(T^s)	5	22132.71	4426.54	120.68*
Day (after planting)	7	5182.98	740.98	20.19*
Interaction	35	851.40	24.33	0.66 ns
Total	192	33449.89		
Error	144	5282.80	36.68	

*Significant ($P \leq 0.05$)

ns - not significant

T^s - osmotic potential

APPENDIX 4: ANOVA TABLE FOR LEAF WATER POTENTIAL OF *C. gayana* AND *S. sphacelata* (DIFFERENTIAL WATERING STUDY)

Source of variation	DF	SS	MS	F cal
Level	1	15976.68		
Treatment	7	1849.88	264.27	70.47*
A	1	77.12	77.12	20.57*
B	3	1764	588	156.60*
Interaction	3	8.76	2.92	0.78 ns
Total	33	1939.89		
Error	24	90.01	3.75	

*Significant ($P \leq 0.05$)

ns - not significant

A - grass species

B - watering regimes

APPENDIX 5: ANOVA TABLE FOR LEAF WATER POTENTIAL AT THREE DIFFERENT TIMES OF THE DAY (6-10 a.m.; 12-2 p.m.; 4-6 p.m.) *C. gayana*

Source of variation	DF	SS	MS	F cal
Level	1	16131.13		
Treatment	11	4359.74	368.34	31.75*
T's	3	4155.89	1385.29	119.11*
A's	2	174.39	87.19	7.49*
Interaction	6	29.46	4.91	0.42 ns
Total	48	4778.57		
Error	36	418.83	11.63	

*Significant ($P \leq 0.05$)

ns - not significant

T's - watering regimes

A's - times of the day

APPENDIX 6: ANOVA TABLE FOR LEAF WATER POTENTIAL AT THREE DIFFERENT TIMES OF THE DAY (6-10 a.m.; 12-2 p.m.; 4-6 p.m.) *S. sphacelata*

Source of variation	DF	SS	MS	F cal
Level	1	12368.13		
Treatment	11	2237.56	203.42	4.67*
T's	3	2100.14	700.05	16.08*
A's	2	87.04	43.52	0.099 ns
Interaction	6	50.38	8.39	0.19 ns
Total	48	3804.87		
Error	36	1567.31	43.54	

*Significant ($P \leq 0.05$)

ns - not significant
T's - watering regimes
A's - times of the day

APPENDIX 7: ANOVA TABLE FOR LEAF CONDUCTANCE OF *C. gayana* AND *S. sphacelata* (DIFFERENTIAL WATERING STUDY)

Source of variation	DF	SS	MS	F cal
Level	1	0.644		
Treatment	7	0.107	0.015	25.86*
A	1	0.00014	0.0014	2.41 ns
B	3	0.103	0.034	58.62*
Interaction	3	0.0026	0.000871	1.50 ns
Total	32	0.121		
Error	24	0.014	0.00058	

*Significant ($P < 0.05$)

ns - not significant

A - grass species

B - watering regimes

APPENDIX 8: ANOVA TABLE FOR LEAF CONDUCTANCE WITH PARTITIONED MAIN TREATMENT EFFECTS

Source of variation	DF	SS	MS	F cal
Level	1	0.644		
Treatment	7	0.107		24.13*
A (spp.)	1	0.0014	0.0014	2.41 ns
B (watering regime)	3	0.103	0.034	58.62*
B_{linear}	1	0.102	0.102	175.86*
$B_{quard.}$	1	0.000013	0.000013	0.022 ns
Remainer	1	0.000987	0.000987	1.689 ns
Total	32	0.121		
Error	24	0.014	0.00058	

*Significant ($P < 0.05$)

ns - not significant

A - grass species

B - watering regime

APPENDIX 9: ANOVA TABLE FOR LEAF CONDUCTANCE AT THREE DIFFERENT TIMES OF THE DAY (6-10 am; 12-2 pm; 4-6 pm) *C. gayana*

Source of variation	DF	SS	MS	F cal
Level	1	1.82		
Treatment	11	0.38	0.035	6.60*
T's	3	0.26	0.086	16.23*
A's	2	0.03	0.015	2.83 ns
Interaction	6	0.09	0.015	2.83 ns
Total	48	0.57		
Error	36	0.19	0.0053	

*Significant ($P < 0.05$)
ns - not significant
T's - watering regimes
A's - times of the day

APPENDIX 10: ANOVA-TABLE FOR LEAF CONDUCTANCE AT THREE DIFFERENT TIMES OF THE DAY (6-10 am; 12-2 pm; 4-6 pm) *S. sphacelata*

Source of variation	DF	SS	MS	F cal
Level	1	0.905		
Treatment	11	0.175	0.016	4.57*
T's	3	0.095	0.032	9.14*
A's	2	0.057	0.029	8.28*
Interaction	6	0.023	0.0038	1.08 ns
Total	48	0.300		
Error	36	0.125	0.0035	

*Significant (P <0.05)
ns - not significant
T's - watering regimes
A's - times of the day

APPENDIX 11: ANOVA-TABLE FOR EFFECT OF DIFFERENTIAL WATERING REGIME ON SHOOT DRY MATTER PRODUCTION

Source of variation	DF	SS	MS	F cal
Level	32	2828.27		
Treatment	7	1158.24	165.46	4.16*
T's	3	917.41	305.80	7.69*
A's	1	157.98	1157.98	3.97*
Interaction	3	82.85	27.62	0.69 ns
Total	32	2112.10		
Error	24	953.86	39.74	

*Significant ($P < 0.05$)

ns - not significant

T's - watering regimes

A's - grass species

APPENDIX 12: ANOVA TABLE FOR EFFECT OF DIFFERENTIAL WATERING REGIME ON ROOT DRY MATTER PRODUCTION

Source of variation	DF	SS	MS	F cal
Level	1	2828.27		
Treatment	7	1158.24	165.46	4.16*
T's	3	917.41	305.80	7.69*
A's	1	157.98	157.98	3.97*
Interaction	3	82.85	27.62	0.69 ns
Total	32	2112.10		
Error	24	953.86	39.74	

*Significant ($P < 0.05$)

ns - not significant

T's - watering regime

A's - grass species

APPENDIX 13: ANOVA TABLE FOR EFFECT OF MULCH ON LEAF WATER POTENTIAL

Source of variation	DF	SS	MS	F cal
Level	1	2971.34		
Treatment	3	36.64	12.21	4.40*
Mulch	1	35.17	35.17	12.69*
Species	1	0.063	0.063	0.023 ns
Interaction	1	1.41	1.41	0.36 ns
Total	16	69.88		
Error	12	33.24	2.77	

*Significant ($P < 0.05$)

ns - not significant

APPENDIX 14: ANOVA TABLE FOR EFFECT OF MULCH ON SHOOT DRY WEIGHT (MULCH STUDY)

Source of variation	DF	SS	MS	F cal
Level	1	259.05		
Treatment	3	1.49	1.49	0.05 ns
Mulch	1	0.21	0.21	0.02 ns
Species	1	0.0091	0.0091	0.00099 ns
Interaction	1	1.27	1.27	0.14 ns
Total	16	111.49		
Error	110.0		9.16	

ns - not significant (P < 0.05)

APPENDIX 15: ANOVA TABLE FOR EFFECT OF MULCH ON ROOT DRY WEIGHT (MULCH STUDY)

Source of variation	DF	SS	MS	F cal
Level	1	658.89		
Treatment	3	20.93	6.98	0.43 ns
Mulch	1	15.96	15.96	0.98 ns
Species	1	4.93	4.93	0.30 ns
Interaction	1	0.04	0.04	0.0025 ns
Total	16	216.80		
Error	12	195.87	16.32	

ns - not significant (P < 0.05)

APPENDIX 16: TABLE OF EXPECTED MEANS OF LEAF WATER POTENTIAL (*C. gayana*)

Watering frequency (days without water)	Observed mean	General level	Expected mean
2	11.76	20.76	11.55
4	16.72	20.79	17.71
6	25.28	20.79	23.87
8	29.41	20.79	20.03

APPENDIX 17: TABLE OF EXPECTED MEANS OF LEAF WATER POTENTIAL (*S. sphacelata*)

Watering frequency (days without water)	Observed mean	General level	Expected mean
2	13.27	23.89	13.39
4	19.57	23.89	20.39
6	29.47	23.89	27.39
8	33.28	23.89	34.39