THE INFLUENCE OF SOME CLIMATIC FACTORS ON THE DISTRIBUTION AND WATER RELATIONS OF SOME C_4 TROPICAL GRASSES.

by

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DECLARATIONS

I, Michael Solomon Ndawula-Senyimba, hereby declare that this thesis is my original work which was conducted between 1972 and 1979 when I was a part-time student of the University of Nairobi. The material contained herein has not been presented for a degree award in any other University.

MSenyimba

Signature

I, the University supervisor, hereby declare that this thesis has been submitted for examination with my approval as University supervisor.

SKImbamba

Professor S.K. Imbamba
Supervisor

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ABSTRACT

Investigations were carried out in order to discover the patterns of distribution of C_3 and C_4 grasses along the altitudinal and soil moisture gradients in Kenya. Additionally, studies were conducted so as to evaluate the mechanisms which govern the distribution and water relations of C_4 grasses in the tropical environment characterized by intermittent soil moisture stress and high solar radiation.

These studies were conducted both in the field and in the laboratory. Sampling for distribution analysis was done in the grassland vegetation types along a North-East/South-West belt transect 20 Km wide and 360 Km long, running from the arid low altitude sites of Magadi through Mt. Kenya to Samburu Game Reserve. Most of the garden and laboratory studies were carried out at Chiromo campus of the University of Nairobi.

Distribution studies revealed that the geographical distribution of C_3 and C_4 grasses in Kenya was controlled by temperature which in turn was governed by altitude. All C_3 grass Tribes with exception of Ehrharteae were confined to alpine altitudes where the temperature is generally low. All the C_4 grass Tribes were found at medium and low altitudes where temperatures are generally uniformly high throughout the year. The few C_3 grass species which were found at non-alpine altitudes occurred in the understoreys of forests where the quantum yield of C_3 grasses possibly corresponded with low temperatures under

conditions of low irradiance. These findings supported the view that the distribution of C_4 plants is controlled by temperatures lower than 10°C.

At medium and low altitude, where ambient temperature is generally uniformly high, C_4 grass Tribes were distributed in a continuum manner along the available soil moisture gradient. All C_4 Tribes formed two distinct dispersion patterns. Tribes such as Chlorideae, Eragrostideae, Sporoboleae, Aristideae and Zoysieae were most common at low available soil moisture indices and absent at indices above 50. In contrast, the C_4 members of Paniceae and Andropogoneae attained their highest development at the intermediate soil moisture indices, of 40 to 60. The distribution of C_4 grass Tribes in Kenya agreed with the view that interactions between low soil moisture, high temperature and high available irradiance favour the abundance of C_4 plants.

The C_4 grasses such as Leptochloa obtusiflora and Themeda triandra normally found in arid environments were characterized by low leaf water potential, high diffusive leaf resistance and high stomatal frequency. These species exhibited higher transpiration ratios than C_4 species normally found in mesophytic habitats. The high leaf resistance of T. triandra decreased with increasing irradiance to a minimum at 1500μ E m.$^{-2}$ sec.$^{-1}$ while that of Panicum maximum leveled off at 400μ E m.$^{-2}$ sec.$^{-1}$. These results led to the view that the water relations of C_4 grasses adapted to arid conditions, is closely related to their leaf water potential which is influenced by light intensity and stomatal frequency. The light controlled leaf resistance might have a pronounced bearing on the distribution of T. triandra in well illuminated sites.

These findings emphasize the importance of C_4 plants in the tropics and give further support to the view that a concurrent evolution might have taken place in grazing mammals and the Gramineae family. Intensive grazing pressure would maintain an open canopy thereby providing strong selection pressure in favour of the C_4 syndrome. The distribution of C_4 grasses is of special importance to Kenya because the highest diversification of these grasses is between moisture indices 30 and 60 the zone in which arable agriculture and animal production are practised.

CHAPTER I

THE DISTRIBUTION OF C_3 AND C_4 GRASSES ALONG ALTITUDINAL AND MOISTURE GRADIENTS IN KENYA.

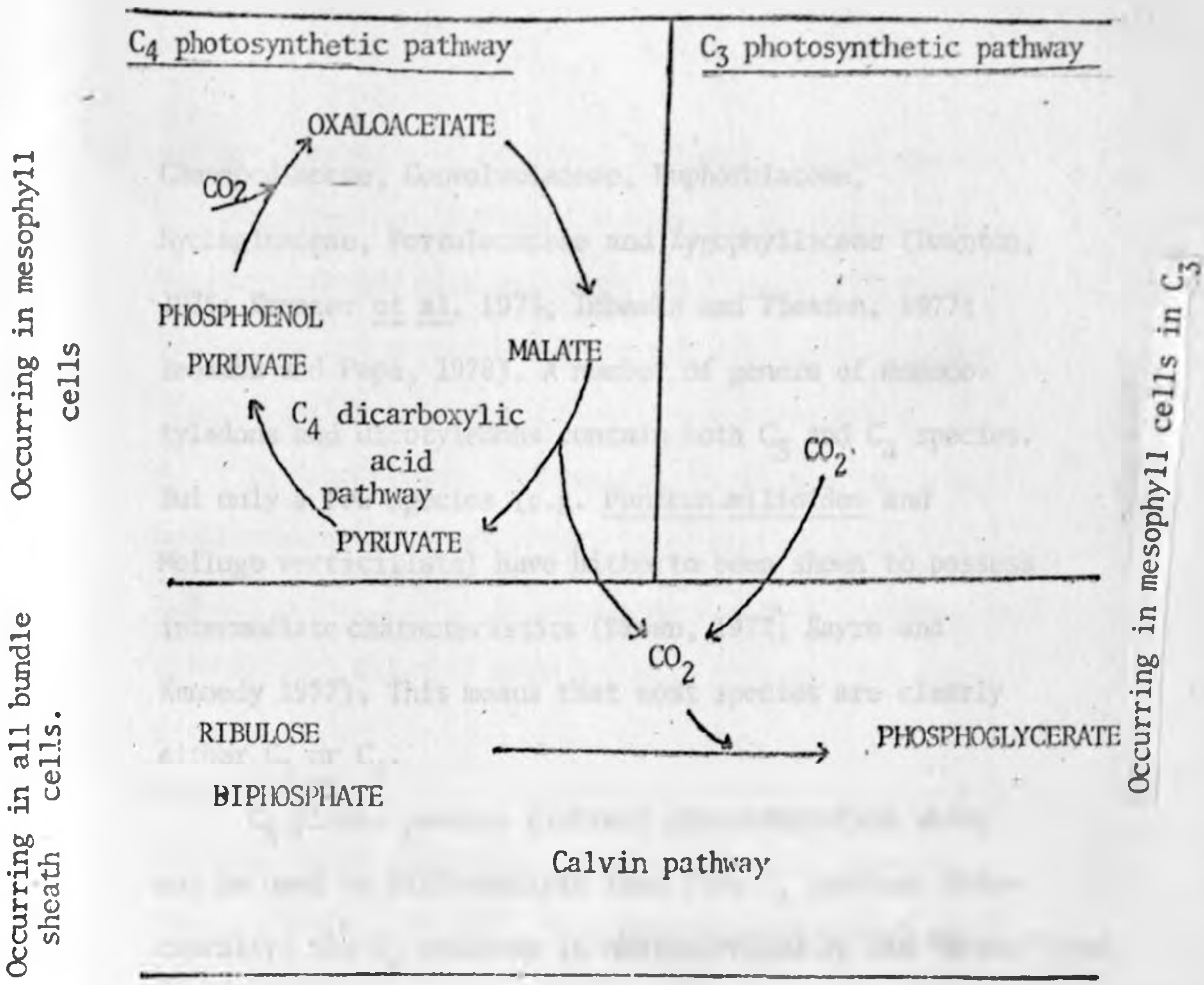
GENERAL INTRODUCTION

A plant like all other living things is subjected, in its environment, to a large number of varying external factors which influence its behaviour, performance and continued existence. The response of a plant to these numerous environmental factors results in growth, distribution, productivity and adaptability to the prevailing conditions. The internal factors on the other hand control the extent to which a plant type responds to the given environmental factors.

It is now well established, that on the basis of their photosynthetic mechanisms, green plants are divisible into three distinct groups. The C_4 grasses, on which this study is based, belong to one of these three groups. Since the late 1940's it was believed that all green plants fixed carbon dioxide through what is known as the Calvin pathway of photosynthesis. By means of radio active C^{14}, Calvin and his co-workers demonstrated that the major initial product of carbon fixation during photosynthesis was the C_3 compound called phosphoglyceric acid (Calvin and Benson, 1948; Calvin, 1949; Bassham and Calvin, 1957; Calvin and Bassham, 1962). In this process carbon dioxide is assimilated reductively by the enzyme ribulose <u>bis</u> phosphate carboxylase and metabolised through the Calvin cycle to produce the first stable three-carbon compound phosphoglyceric acid. It is from this phosphoglyceric acid, that the plants which exhibit only the Calvin pathway of carbon fixation derive their name of "C_3 plants."

In the mid 1960's Kortschak and co-workers (Kortschak et al.; 1965) found that in sugarcane leaves most of the radioactive carbon from $C^{14}O_2$ was found in C_4 compounds such as malate and aspartate when the fixation time was reduced to 4 seconds. They compared the $C^{14}O_2$ fixation in sugarcane to that in soybean leaves and found that in soybean the radioactive carbon was present in phosphoglyceric acid. This suggested that there were biochemical differences in the photosynthetic processes of the two plants. The work was extended by Hatch and Slack (1966) who found that the new pathway involved the production of phosphoenol pyruvate which acted as the CO_2 acceptor. Phosphoenol pyruvate is carboxylated by CO_2 in the presence of phosphoenol pyruvate carboxylase in the mesophyll to produce oxaloacetate. Through a reduction reaction with NADPH, Oxaloacetate is converted either to malate or aspartate.

It is suggested that through the action of the "malic" enzyme, malate is oxidised to pyruvate and carbon dioxide (Mac Mammon and Crawford, 1971). The CO_2 thus produced is then assimilated reductively in the bundle sheath by ribulose biphosphate carboxylase and metabolished through the well known Calvin pathway similar to that followed by C_3 plants.



The plants which exhibit photosynthetic carbon fixation resulting in the formation of four-carbon atom compounds are the "C_4 plants" and the pathway involved is the "C_4-dicarboxylic acid pathway". Although C_3 plants do not possess the C_4 pathway, C_4 plants possess the C_3 pathway as well.

The C_4 pathway appears to have evolved more recently probably in response to increasing atmospheric O_2 and decreasing CO_2 concentration (Smith, 1976). The C_4 syndrome is most common in the Gramineae family where about 40% of the species are C_4 plants. The syndrome is also present in the Cyperaceae and in some dicotyledonous families such as Acanthaceae, Aizoaceae, Amaranthaceae, Asteraceae, Boraginaceae, Capparaceae, Caryophyllaceae, Chenopodiaceae, Convolvulaceae, Euphorbiaceae, Nyctaginaceae, Portulacaceae and Zygophyllaceae (Downton, 1975; Krenzer et al. 1975; Imbamba and Tieszen, 1977; Imbamba and Papa, 1978). A number of genera of monocotyledons and dicotyledons contain both C_3 and C_4 species. But only a few species (e.g. Panicum milioides and Mollugo verticillata) have hitherto been shown to possess intermediate characteristics (Brown, 1977; Sayre and Kennedy 1977). This means that most species are clearly either C_3 or C_4.

C_4 plants possess distinct characteristics which may be used to differentiate them from C_3 species. Structurally, the C_4 syndrome is characterized by the "Kranz" type of leaf anatomy in which the vascular bundle is usually surrounded by thick-walled bundle sheath cells (Laetsch, 1974). The bundle sheath cells are chlorenchymatous and they are responsible for the C_4 dicarboxylic acid carbon fixation. It is now clear (Coombs, 1978) that the C_4 plants can be further subdivided on the basis of the nature of the enzyme which dicarboxylate the major C_4 acid formed, namely malate and aspartate. The enzymes involved are NADP-malic enzyme, NAD-malic enzyme and PEP carboxykinase. These groups can be distinguished on the basis of their anatomy and chloroplast structure or position in the bundle sheath cells as follows:

1. In monocotyledons; NADP-malic enzyme species are characterized by bundle sheath chloroplasts centrifugally

arranged having reduced grana. NAD-malic enzyme species are characterized by bundle sheath chloroplasts centripetally arranged with well-developed grana. PEP-carboxykinase species posses bundle sheath chloroplasts being centrifugally arranged with well-developed grana.

2. In dicotyledons, NADP-malic enzyme species possess bundle sheath chloroplasts arranged centripetally having reduced grana. NAD-malic enzyme species have bundle sheath chloroplasts arranged centripetally with well-developed grana.

Additionally, Hattersley and Watson (1975) observed 2 to 4 chlorenchymatous mesophyll cells intervening between bundle sheath cells in C_4 species, but more than 4 cells in C_3 species.

Physiologically, C_4 plants exhibit a higher photosynthetic capacity than C_3 plants (Black, 1971). Their net photosynthetic rate hardly reaches a light saturation point. Of greater ecological interest is the fact that C_4 plants possess higher temperature optima for saturation of photosynthesis (30 to 45°C) than C_3 species (20 to 25°C). This is associated with the ability of C_4 plants to take up CO_2 at low CO_2 concentration. Photorespiration is not easily detected in C_4 as it is in C_3 plants.

A carbon dioxide assimilation pathway closely related to the C_4- dicarboxylic acid pathway is the crassulacean acid metabolism (CAM). This type of metabolism was first observed by Heyne in 1815 and the organic acid involved were quantified in 1933 by Bennet-Clark (Zelitch, 1971 pp. 121). In this type of CO_2 fixation process, the CO_2 required is taken-up in the dark and fixed by means of phosphoenol pyruvate carboxylase reaction in the same way as in the C_4 plants. The first stable product is malate. Bradbeer et al (1958) found that although the C_4-dicarboxylic acid pathway is involved in the CAM plants, the C_3 pathway is also included and utilizes the CO_2 produced during the formation of pyruvate. The other product of the CAM CO_2 fixation in addition to malic acid is isocitric acid, an important intermediate in the tricarboxylic acid cycle (Vickery and Wilson, 1958).

The reducing power used to provide ATP and the CO_2 acceptor in the dark is stored in the form of starch in the light (Walker, 1966). It is argued that since species with the CAM CO_2 assimilation are plants adapted to arid conditions, fixation of CO_2 in the dark might enhance species survival under water stress. This metabolism is associated with succulent plants whose stomata are usually closed in the light and open in the dark in order to conserve water (Nishida, 1963). CAM plants are not productively efficient. Their photosynthetic efficiency is lower than that of C_3 plants. It was suggested by Laetsch (1974) that although CAM plants lack the Kranz anatomy, they might be intermediate between C_3 and C_4 plants.

Both C_4 and CAM plants utilize the same enzymic systems in the fixation and dicarboxylation of the major C_4 acids namely malic and aspartic acids. Both C_4 and CAM plants possess the C_4-dicarboxylic acid process as an additional mechanism to the Calvin CO_2 fixation process. This means that the C_4 and CAM carbon fixation systems are adaptational processes which enable the plants concerned to survive under environment stress such as intermittent aridity (Moore, 1974).

The discovery of a wide range of physiological features connected with the productivity of C_4 plants (Black, 1971) stimulated interest in the study of C_4 plants as potential food producers in the tropics. It was suspected that since C_4 plants, especially grasses, dominate the tropics, their development might enhance increased food production in warm and arid parts of the world. C_4 grasses are of added importance in East Africa partly because the majority of the local cereal crops are C_4 plants and partly because the grass-dominated East African vegetation is composed of mainly C_4 grasses (Rattray, 1960).

According to Lind and Morrison (1974), the distribution of vegetation in East Africa is closely related to rainfall distribution patterns. Therefore an understanding of the behaviour of the dominant species such as C_4 grasses in the vegetation could lead to a more economic and sound utilization of the vegetation. One of the objectives of this study was to find out whether the distribution of C_4 grasses (as a group) is related to soil moisture availability.

For a long time there was an expressed wish in East Africa to obtain a reliable way of classifying the vegetation on the basis of its production potential based on available soil moisture. Additionally, such a classification needed to be based on criteria that could be observed directly (Pratt et al, 1966). The first attempts to meet those needs, were made by Thornthwaite (1948), who proposed a moisture index based on the balance between rainfall and evaporative demands of the site. The index proved promising at medium and low altitudes where low temperature does not limit plant growth. The system was based on the fact that the soil water available to plants is mainly controlled by the balance of water between the incoming rain and the evaporational losses. Therefore Thornthwaite built his index on purely climatic factors which could be assessed with no reference to the vegetation types.

The main set-back of the Thornthwaite system was that he estimated evaporative demands on the observations of temperature based on the correlation between mean monthly temperature and solar radiation (Dagg and Waweru, 1965). Under temperature conditions, where both daily mean temperature and daily radiation depend mainly on day-length, the correlation was reasonable. However, in the tropics with near constant day-length, daily temperature is not an adequate guide to radiation. Therefore although Thornthwaite's concepts were valid and useful they did not give an accurate estimation of available water in East Africa especially at high altitudes.

At the time Thornthwaite presented his index, also Penman proposed the equations for estimating site water balance using climatic data (Penman 1948). Both Thornthwaite and Penman based their estimates on the assumption that differences in the water use of different plant special have only a negligible bearing on the overall water balance of the plant community. The water status of the place was determined from the empirical climatic data. Compared to Thornthwaite's index, Penman's equation gave more accurate estimates of water availability in East Africa (Dagg and Waweru, 1965). Further, the equations provided a possibility of determing the day-to-day water requirements of a site on which irrigation programmes could be based (British Ministry of Agriculture, Fisheries and Food, 1954).

In order to broaden the applicability of Penman's methods in East Africa, Woodhead (1970) designed an available soil moisture index system. The index expresses plant exploitable mean rainfall as a percentage of the potential evaporation (E_o) from open water.

$$\text{Water available for evapotranspiration} = \text{Total rainfall} - \text{Total water surplus}$$

$$\therefore \text{Available water index} = \frac{\text{Total rainfall} - \text{Total water surplus}}{\text{Potential evaporation } (E_o)}$$

The system was intended to give an estimate of the exploitable rainfall after due allowances had been computed for evaporational losses and soil moisture storage. Woodhead correlated his index with the six ecological zones of East Africa which had been demarcated by Pratt *et al* (1966) to relate land use potential with vegetation appearance (physiognomy).

Although, Thornthwaite (1948) Penman (1948) and Woodhead (1970) simplified the process of determining site water potential, they did not correlate available soil moisture with easily observed vegetation criteria. The usefulness of all these systems was greatly reduced by lack of meteorological data in most parts of East Africa. The classification of Pratt *et al*. (1966) covered only Kenya and Uganda and Woodhead's maps were confined to Kenya. The work reported in this thesis is an attempt to correlate easily observed distribution patterns of C_4 grasses to available soil moisture with a hope of extending the applicability of Woodhead's moisture index to areas where adequate meteorological data are not available.

Physiological studies of C_4 grasses were undertaken in order to assess the mechanisms on which the survival of C_4 plants in arid conditions is based. It is suspected that C_4 plants originated from the tropics (Teeri and Stower 1976) and that the C_4 syndrome is adapted to arid conditions (Black, 1971; Laetsch, 1974; Moore 1974). Only C_4 grasses were studied because the Gramineae family is the most abundant and wide spread plant family in East Africa. Secondly the Gramineae family was chosen because it contains the largest number of C_4 species in the plant Kingdom. Ratlry (1960) pointed out that the grass component of a vegetation is the least affected by landuse and other environmental changes. Therefore, grasses can give a more reliable index of site potential than any other vegetation plant components.

The objectives of this work may, therefore, be summarised as follows:

(a) to examine the relationship between C_3 and C_4 grasses and to correlate their distribution to available soil moisture; and

(b) to establish the mechanisms used by C_4 grasses in order to adapt themselves to moisture, temperature and light conditions prevailing in Kenya.

It was hoped that the information thus obtained would increase our understanding of the C_4 plants and also enable workers to use C_4 grasses as indicators of available soil moisture.

LITERATURE REVIEW

The study of the distribution of plants is based on the fact that plants of a given type are usually dispersed following definable patterns. The presence or absence of a particular plant in a site is controlled by definable external and internal factors. The external factors include physical and biotic factors such as mineral salts, light, temperature, wind, precipitation and influence of other organisms. The internal factors include the physiological, biochemical and anatomical factors inherent in the plant (Greig-Smith, 1964; Odum, 1969). All these factors, though many and complex, influence the patterns of plant distribution. Such distribution patterns could be described as random or uniform or clump distribution.

The distribution of plants is generally discontinuous i.e. there are always gaps between individuals and clumps occupied by individuals. Depending on the width of the gaps, plant species have two levels of distribution namely: (a) geographic distribution and (b) ecological distribution. On the geographic basis species distribution is indicated on the map by dots or generalized boundary lines. Within these large areas, the given species may only occur here and there under favourable habitat conditions. On the ecological basis the distribution of a species is considered in terms of habitat potentials.

The environmental features of sites are used to delimit the distribution boundries of a species.

As it was emphasised by Lind and Morrison (1974), the vegetation of East Africa is made up of a wide range of vegetation types. But with exception of alpine vegetation, all other vegetation types are mainly distributed in relation to the available soil moisture. At one extreme where water is in the least supply one finds arid bushed grasslands and thickets and at the other extreme one finds closed rain forests and swamps.

Although East Africa is within the equatorial belt, the vegetation types are not all equatorial. The rains which are basically convectional and due to equatorial wind system, are greatly modified by relief and the presence or absence of large water bodies in the path of the wind. Due to these modifying factors, large parts of Kenya and Tanzania receive less than 760 mm of rain a year (Hickman and Dickins, 1960). Besides the insufficient rain, the overhead position of the sun results into a high evaporation demand throughout the year thus leaving limited amounts of water in the soil to support plant growth. Since available soil water is such an important factor (Walter, 1973), it is not surprising that plant distribution has to conform to it more than on any other factor.

It is known that most of the grasslands in East Africa are derived from woodlands and forests by frequent burning and grazing (Rattray,1960; Lind and Morrison,1974).

However, the floristic composition of particular grassland types is controlled by the competitive powers of the individual species within the limits set by local moisture and light conditions. Walter (1973) pointed out that the natural limit of distribution of a particular species is reached when, as a result of changing physical environmental factors, its ability to compete is so much reduced that it can be ousted by other species. In this case a study of the dispersion of conspicuous and widely dispersed genera would reveal useful information about the environmental factors which govern their distribution.

Generally, East African rainfall increases as one moves from lowland to the alpine forest belt. Then from the alpine forest upwards the amount of rainfall decreases gradually (Trapnell and Griffiths, 1960; Walter, 1971). However, where the temperature is above the freezing point of water, the amount of soil moisture continues to rise with altitude due to melting snow and low evaporation. On Mt. Kenya rainfall increases with altitude up to between 2,700 and 3050 metres and decreases up to the summit where it is estimated to be about 760 mm per year (Hedberg, 1964; Lind and Morrison, 1974). The influence of altitude on rainfall and temperature greatly controls the distribution of grasses along the altitudinal gradient.

Although rainfall has a big influence on the amount of water available to plants, due to a number of reasons, total rainfall is not as important as soil water balance in controlling plant distribution in East Africa. As Gates (1962) pointed out, that the mean annual rainfall alone fails to show significant correlation with plant distribution because the water balance is variable even within a zone supposed to receive uniform rainfall. One cause of lack of correlation between mean rainfall and vegetation distribution is the very seasonal nature of tropical rains. Often large quantities of rain may fall in a short period of time leaving the rest of the year dry (Hickman and Dickins, 1960). Since the soil can not hold more water than its physical nature can allow it to hold at field capacity, the excess water received either percolates into the bed rock or it is lost as runoff. The other reason which causes lack of correlation between total rainfall and vegetation distribution is the variable nature of tropical rains. It is very common in East Africa for a place to receive an annual amount of rain which is very different from the average expected. For example Nairobi with an estimated annual average rainfall of about 890 mm, receives rain varying from 480 to 1520 mm (Lind and Morrison, 1974). This wide amplitude can lead to different vegetation types characterising places with the same annual average rainfall.

In order to obtain a way which can relate some aspect of the physical environment to site ecological potential, methods such as the evapotranspiration formulae of Penman (1948) and the available moisture index of Woodhead (1970) were designed.

Both these methods assess site potential by means of physical environmental factors and do not include soil or plant contributions to site production potential.

At low and medium altitude the influence of temperature on plant distribution in East Africa is not very pronounced (Lind and Morrison 1974). This is because the mean annual temperature of the low lying coastal belt of E. Africa is only two degrees higher than that of the inland plateaux. Temperatures in excess of 38°C are very rare and ground frost seldom occurs below 2460 m above sea level. Below alpine altitudes temperature influencesplant distribution only indirectly through its effects on the soil-plant-air water balance.

Since the whole of East Africa is located within the equatorial belt, there is no difference in the amount of light received in different places. Light intensity is always high throughout the year with only minor seasonal variations due to cloudiness especially at high altitudes. Generally speaking light intensity does not have any direct influence on the distribution of vegetation types. However, within a particular plant community, light variations help in the creation of specific micro-environment of plants and in so doing influence the competitive ability of individual species (Walter, 1973). Species such as <u>Themeda triandra</u> are known to favour well illuminated places created by moderate grazing and burning (Edwards, 1942; Ndawula-Senyimba 1972).

LOCATION OF STUDY SITES

Sampling sites were systematically located in a North-East/South-West belt transect of about 20 Km wide and 360 Km long. The area covered lies between 36°11' and 37°45' E (Appendix 1), running northwards from Magadi soda Lake, 2°S through the Eastern Kenya highlands and Mt. Kenya to north of Samburu Game Reserve 0°45' N. The belt ran across a number of contrasting vegetational and altitudinal types, depicting the characteristic contrasting altitudinal range of the Kenya vegetation (Edwards, 1949). Such a transect offered the best opportunity of studying the majority of the Kenya vegetation types in a single belt.

Sites located at the south most end of the transect were situated on the floor of the East African Rift Valley 610 m above sea level. The altitude continued to rise gradually as one moved North-East wards to the maximum of 4,000 m above sea level on Mt. Kenya. From Mt. Kenya the altitude dropped gradually to 910 m above sea level at the end of the transect. On the vegetational basis the areas sampled run from semi-desert thickets through bushed grasslands of the Rift Valley, then the open Acacia-Themeda grasslands of the Eastern highlands, then the Combretum - Hyperrhenia grasslands, then the Afro-Alpine vegetation of Mt. Kenya to semi-desert thickets of Samburu Game Reserve On its way, the transect had to cross at least twice each of the nine soil moistures index zones mapped by Woodhead (1970).

Since the aim of the study was to discover the relationship between available soil moisture and grass distribution, only general observations of other plant components of the vegetation were made. The area sampled consisted of 20 sites put into 12 blocks located in such a way that they represented various soil moisture levels according to Woodhead's moisture index (1970). Each site was often made up of two or three subsites situated in different places with in the block.

The first block, representing the moisture index 10 to 20, was the driest block. It was made up of sites from dry thickets near Lake Magadi. The vegetation of the area was characterized by thorny shrubs covering about 50% of the ground with gaps occupied by a sparse grass and forb cover greatly affected by soil erosion. The herb layer was dominated by annual plants both monocotyledons and dicotyledons. The dominant grass species was Tetrapogon spathaceus. Some of the shrubs and herbs found in the area included Acacia spp. Commiphora spp. Euphorbia sp, Jatropha sp. Boscia sp. Senservieria sp. and Balanites sp. This block graded gradually into semi-desert conditions.

Block two represented areas of moisture index 20 to 30. It consisted of sites and sub-sites from Ololkisalie north of Magadi and Samburu Game Reserve. The block included areas characterized by tall thickets and bush lands. The Bushlands consisted of areas covered by more than 50% shrubs and small trees growing closed together. The trees of mainly bushy type were branching from near the base with an average height of 3 to 9 metres. The ground had less bare ground than that in block one. The herb-layer was made up of perennial and annual grasses and forbs. Dominant grasses were Aristida adscensionis, Eragrostis cilianensis and Tragus berteronianus. Shrubs in the area included Acacia drepanolobium, Adansonia digitata and Commiphora sp.

Block three represented areas with a moisture index of 30 to 40. The vegetation type characteristic of this block is usually included among the Acacia- Themeda grasslands. Physiognomically the vegetation is characterized by open grasslands with dotted trees having flat tops. The block included sites from South Isiolo, North of Ololkisalie, Athi river plains and Ewaso-Kedong Valley in the Rift Valley. The floristic composition of this block varied possibly due to soil characteristics. Athi river plains which exhibited an open grassland type, its woody plant component was dominated by Acacia drepanolobium and Balanite aegyptica. The more bushy sites were dominated by shrubs such as Lippia javanica and Tarchonanthus sp. Dominant grasses were Themeda triandra, Chloris gayana, Dichanthium insculpta, Digitaria macroblephara, Pennisetum menzianum and Sporobolus spp.

Block four was made up of sites with moisture index 40 to 50. Representative sites in this block were located at Nanyuki, Naro Moru, north of Timau and Thika. The vegetation is characterized by a mixture of bush and scattered trees, a large number of which are broad leaved. Dominant trees included *Croton sp*. The grass cover was dominated by *Themeda triandra*, *Harpachene schimperi* *Sporobolus fimbriatus*, *Hyparrhenia lintonii*, *Setaria* sp. and *Loudetia kagerensis*.

Block five was made up of sites of moisture index 50 to 60. This block was extensively cultivated with very few less disturbed patches. A few relict patches often found in places difficult to cultivate, indicated that the characteristic vegetation was a woodland dominated by *Combretum* sp. *Albizzia* sp. and *Erythrina* sp. Heavily grazed areas had thick stands of *Lantana camara*. Sites included in this block were situated near Karatina, Gaturi near Muranga, Nairobi and Limuru near the escarpment. The grass herblayer was dominated by *Hyparrhenia* spp. *Brachiaria brizantha*, *Heteropogon contortus*, *Sporobolus pyramidalis* and *Digitaria scalarum*.

Block six represented areas with moisture index 60 to 70. Sites in this block were located near Timau and in the wooded grasslands boardering the alpine forests on Mt. Kenya about 2290 m above sea level. The vegetation of this block is very much affected by high altitude farming. On Mt. Kenya large parts of this block are covered by plantations of *Pinus* spp and *Cupressus* spp for soft wood production. Where there was not much disturbance, a grassland-forest mosaic characterised the vegetation. Forest trees were mainly of a broad-leaved deciduous nature.

The grass cover was dominated by species such as Exotheca abyssinica, Eleusine jaegeri, Andropogon amethystinus, Pennisetum clandestinum and Digitaria scalarum.

Block seven representing areas with moisture index 70 to 80 was located at above 2740 m above sea level just below the Meteorological station on Mt. Kenya. The vegetation was of the Montane forest belt. The dominant forest trees were Podocarpus spp. and Ocotea usambarensis. patches of bamboo were common here and there. The herblayer was composed of grasses and forbs spersely distributed. Dominant grasses were Pentaschistis borussica, Poa annua, Poa schimperiana and Pennisetum clandestinum.

Block eight represented sites with moisture index 80 to 90. Sites in this block were located at about 3050 m above sea level near the Meteorological station. The block was characterised by a high density of bamboo with patches of Podocarpus spp. and Hagenia abyssinica. Grasses were restricted to open patches and along elephant tracks. Dominant grasses in this block were Agrostis keniensis, Poa schimperiana and Poa annua.

The ninth block representing moisture index 90 to 100 was situated in the upper part of the Hagenia-Hypericum forest zone. The dominant trees were Hagenia abyssinica, Hypericum sp. and Podocarpus spp. The under story plants included Lobelia spp. tussock-forming Carex monostachya, Kniphofia sp. and grasses. Dominant grasses were Poa schimperiana Agrostis keniensis and Poa annua. The vegetation of this block graded gradually into the ericaceous moorland.

Block ten represented sites of moisture index 100 and possibly over. Sites used were situated in the lower parts of the high moorlands at about 3,510 m above sea level. Owing to low evaporation and poor drainage, the water which comes from rain together with that which comes from melting snow, gives rise to mires wherever water can collect. The vegetation was characterised by dwarf Juniperus procera, Lobelia sp. and large tussocks of Carex monostachya. Scattered bushes of Erica arborea and Stoebe kilimandscharica were also observed. Dominant grass species were Festuca pilgeri and Deschampsia flexuosa.

The eleventh block was also situated on the moorland with unclassified moisture index. The altitude was about 3,810 m above sea level. The block was characterised by a reduction in the woody shrubs, Lobelia sp. and large tussocks of Carex monostachya. The vegetation was of an open moorland type with short Senecio brassica scattered among the large tussocks of grasses. No Dendrosenecio of more than a metre tall was seen at this elevation although taller ones were seen at higher elevations. Dominant grasses were Festuca pilgeri and Poa leptoclada.

Block twelve was situated at about 4,000 m above sea level. The moisture level of the block was above 100 because the zone receive more water than what is required for plant growth. The vegetation of this block was sparsely distributed leaving large areas of bareground. The few plants which were found were of a small stature. Even the caespitose Festuca pilgeri could hardly exceed 30 cm tall. The woody shrub population at this level was more than what it was at the lower elevation. This block was located at a point overlooking the Teleki Hut above Northern Naro Moru river. From here the vegetation graded gradually into zones permanently covered by snow. The dominant grass was Festuca pilgeri.

All high altitude blocks were on Mt. Kenya and were situated within a West/East belt transect following the Naro Moru mountain route. Although one belt transect was used attempts were made to sample in as many places within the block as possible. Blocks seven to twelve were selected on the basis of increasing altitude and soil moisture. Changes in altitude were used to estimate changes in temperature according to Griffiths (1962).

Since the main objective of the study was to relate the distribution of C_3 and C_4 grasses to pre-fixed value of water balance of well drained soil, swampy habitats and river banks at non alpine altitudes, were not sampled. On the mountain especially on the moorland poorly drained habitats were sampled and put in special blocks (100a, 100b & 100c) to represent species which are distributed on the basis of temperature instead of soil water availability.

METHODS

A total of twenty sites were sampled in the whole 360 Km long belt-transect. The twenty sites were grouped into 12 blocks according to the soil moisture index of the places where the sites were located. Each block, with the exception of blocks 10, 11 and 12, represented a soil moisture index level following the index determined by Woodhead (1970). Sites 10, 11 and 12 were located on the alpine moorland where Woodhead's indeces could not apply because the water available in the soil was in excess of what the soil could hold at field capacity due to poor drainage. These three blocks were arranged on the altitudinal basis in order to demonstrate the effects of decreasing temperature on the distribution of C_3 and C_4 grasses when the influence of soil water stress is nil. No block was assigned to moisture index 0 to 10.

Sites within blocks were selected in such a way that each level of the available moisture was sampled at least in two different locations. Where vegetation disturbances limited the size of representative sites to small relict patches of vegetation, several sub-sites were combined to form one site. Each site was made up of ten line transects run randomly in different directions. Along each line transect ten metre-square quadrats were placed at regular intervals of ten paces measured along the line transect.

In each quadrat all the C_3 and C_4 grass species present were recorded. Initial identification of grass species was carried out by sight on the spot using the vegetative characters method proposed by Gwynne and Ndawula-Senyimba (1971). All grass species found were given numbers and representative samples collected and taken to the laboratory for further identification. Laboratory identification was carried out using floral keys compiled by Bogdan (1958), Harker and Napper (1961), Napper (1965) and Clayton (1970, 1974). Difficult species were identified by Miss C. Kabuye of the East African Herbarium, Nairobi.

Fresh leaf samples were collected from all species encountered in the field and preserved in Acetic acid-Formalin preservative for future use in anatomical differentiation between C_3 and C_4 grasses. In the laboratory handcut and freezing microtom-cut transverse sections of leaves were used to determine the presence of the Kranz anatomy which was used to distinguish C_4 from C_3 grasses (Black 1971).

The absolute occurrence percentage for each species was determined from the number of quadrats in which that species occurred, calculated as a percentage of the total number of quadrats thrown in the block. For better presentation of results it was decided to use Tribes instead of species since the former units were big enough to reduce the unnecessary variations which would have been created by using individual species.

Secondly, Tribes offered units which were distributed widely enough in order to show reasonable correlation with changing soil moisture. Very few species were found in more than two moisture blocks.

Since each Tribe contained a large number of species, the total absolute occurrence percentages of all species in the Tribe often exceeded a hundred percent.

$$\text{Specific Occurrence percentage} = \frac{a}{b} \times 100$$

where a is the number of the quadrats in which a particular species occurred and b is the total number of quadrats thrown in the block.

In order to avoid the ambiguity of reffering to percentages more than 100% when comparing the distribution of different Tribes, relative Occurrence percentages were used. Relative Occurrence percentage was defined as the total absolute occurrence percentages of all the species in the Tribe devided by the mean species number of all grasses per quadrat in the block. This was expressed as:

$$\text{Relative Occurrence of a Tribe} = \Sigma\left(\frac{100a}{b}\right) \Big/ n \ \%$$

where n is the mean number of grass species per quadrat in the block.

No temperature measurements were made directly in the field but the daily mean temperature values of each block were estimated from altitude values using the formulae suggested by Griffiths (1962). In his report on the temperature pattern of East Africa Griffiths (1962) pointed out that the mean annual maximum and minimum temperatures are very closely correlated with altitude. The mean maximum and minimum can be calculated using the regressions.

Maximum temperature T (^{o}F) = 93-3.0A

Minimum temperature T (^{o}F) = 76-3.8A

where A is the altitude in thousands of feet.

The daily average may be taken as half the sum of these two values.

Since the belt transect did not include the areas of Kenya which experience slightly different temperatures from those estimated by the formulae, no corrections were made on the temperature values obtained by calculation.

Biomass samples were collected from some of the communities included in the belt transect as well as other communities. These consisted of pooled harvests of grass component in the block. The samples were analysed in New Zealand by Troughton for carbon isotope ratio ($\delta\,^{13}C$) as described by Troughton and Card (1975). This ratio is operationally defined as $\delta\,^{13}C$ where

$$\delta^{13}C = \left[\frac{^{13}C/^{12}C \text{ sample}}{^{13}C/^{12}C \text{ standard}} - 1\right] \times 10^{3}$$

Sample ^{13}C: ^{12}C ratios were expressed as ppt. deviation from a standard reference.

RESULTS

Table I gives the distribution of C_3 and C_4 grasses expressed as absolute occurrence percentage of individual species. As this table indicates, a large number of species happened to be distributed only in one or two blocks. This meant that it could not be possible to illustrate clearly the influence of varying soil moisture on the distribution of such narrowly distributed species. The only species which were found in not less than three blocks were: Eragrostis tenuifolia, E. racemosa, Dactyloctenum aegyptium, Digitaria scalarum, Aristida adscensionis, Themeda triandra, Deschampsia flexuosa, Pentaschistis borussica, Pseudobromus silvaticus, Poa schemperiana, Poa annua and Festuca pilgeri. These were about 10% of the total number of species found. This led to the correlation of soil moisture variations with the distribution of Tribes instead of individual species.

TABLE I

The Distribution of individual C_3 and C_4 grass species expressed as absolute occurrence percentage at each soil moisture index level. The presence of Kranz anatomy indicates the presence of the C_4 pathway.   * P = Presence of Kranz anatomy. A = Absence of Kranz anatomy.

Species		Absolute percentage occurrence of species in each Moisture Index Block											
	*	10	20	30	40	50	60	70	80	90	100a	100b	100c
Enneapogon cenchroides (Roem & Schutt) C.E. Hubb.	P	8	36	36									
Eragrostis aspera (Jacq.) Nees	P	3	15			3							
E. cilianensis (All.) Lutati	P		42	1									
E. braunii Schweinf.	P		14	27	3	10							
E. tenuifolia (A.Rich) Steud.	P			10	19	4	10						
E. heteromera stapf.						3							
E. racemosa (Thunb) Steud.	P			14	5	3		26					
E. superba Peyr.	P				4	6	7						
E. blepharoglumis K.Schum.	P				1								

E. lehmanniana Nees	P	
E. olivacea K.Schum.	P	
E. curvula (Schrad) Nees	P	
E. kiwuensis Jedw.	P	
E. paniciformis (A.Br.) Steud.	P	
Harpachne Schimperi A. Rich	P	
Leptochloa obtusiflora Hochst.	P	
Eleusine africana Kennedy Obyrne	P	
Dactyloctenium aegyptium (L) Beauv.	P	13
Eleusine jaegeri Pilg.	P	
Dactyloctenium bogdanii Phillips	P	45

20	30	40	50	60	70	80	90	100a	100b	100c
		2								
			1							
2										
	1				6					
		3	1							
	7	38	3	2						
1	1									
			2							
12		1	3							
				7	6					
8										

		10	20
Tetrapogon tenellus (Roxb) Chiov.	P	3	3
T. spathaceus (Steud) Dur. & Schinz	P	58	40
Chloris gayana Kunth	P		3
C. roxburghiana Schult.	P		4
Cynodon dactylon Pers.	P		2
C. plectostachyus (K.Schum) Pilg.	P		
Eustachys paspaloides (Vahl) Lanza & Mattei	P		2
Microchloa kunthii Desv.	P		
Enteropogon macrostachyus (A.Rich) Benth	P		4
Sporobolus spicatus (Vahl) Kunth	P	28	20
S. marginatus A. Rich	P	25	30
S. angustifolius A. Rich	P		2
S. ioclados (Trin.)Nees	P		20

30	40	50	60	70	80	90	100a	100b	100c
5									
36	18								
9									
11	5	4							
1									
1									
2	5	2							
1									
10									

S. helvolus(Trin.) Dur. & Schinz	P	
S. pyramidalis Beauv.	P	
S. festivus A. Rich	P	
S. fimbriatus Nees	P	
S. angustifolius A. Rich	P	
S. stapfianus Gaud	P	
Aristida adscensionis L.	P	25
A. adoensis A. Rich	P	
Stipagrostis hirtigluma (Trin. & Rupr) de Winter	P	3
Tragus berteronianus Schutt	P	25
Loudetia flavida (Stapf.) C.E. Hubb.	P	
L. kagerensis (K.Schum) Hutch.	P	

20	30	40	50	60	70	80	90	100a	100b	100c
9										
	15	5	44							
	1									
	27	21								
	2									
	2	3	5							
44	42	10	1							
		9	2							
4										
42	6	2								
			5							
		4	10							

		10	20
Acritochaete volkensii Pilg.	P		
Cenchrus ciliaris L.	P	15	3
C. setigerus vahl	P	20	
Digitaria velutina (Forsk) Beauv.	P		3
D. scalarum (Schweinf.) Chiov.	P		
D. macroblephara (Hack) Stapf.	P		
D. diagonalis var. uniglumis (A.Rich) Pilg.	P		
Brachiaria scalaris (Mez.) Pilg.	P		
B. umbratitis Naper	P		14
B. deflexa (Schumach) Robyus	P		12

30	40	50	60	70	80	90	100a	100b	100c
				2					
2									
		3							
1	27	25	64						
31	22	3							
		3							
		8							
4									

		10	20
B. brizantha (A.Rich Stapf.	P		
Panicum maximum Jacq.	P		
P. atrosanguineum A. Rich	P		
P. trichocladum K. Schum.			
Pennisetum menzianum Leeke	P		1
P. clandestinum Chiov.	P		
Pennisetum stramineum Peter	P		
P. schimperi A. Rich	P		
P. catabasis Stapf & C.E. Hubb.	P		
Rhynchelytrum repens (Wild) C.E. Hubb.	P		
Setaria incrassata (Hochst) Hack	P		

30	40	50	60	70	80	90	100a	100b	100c
	4	17							
	2	21	4						
1									
	1								
16									
	5		31	50					
	1	[illegible]							
	1	11							
		8							
1	8	7							
			7						

		10	20
S. pallidifusca (Schumach) Stapf & C.E. Hubb.	P		
S. sphacelata Stapf & C.E. Hubb.	P		
S. Verticilata (L) Beauv.	P		
S. trinervia stapf & C.E. Hubb.	P		
Entolasia imbricata Stapf.	P		
Melinis minutiflora Beauv.	P		
Echinochloa haplochlada Stapf.	P		
Ehrharta erect var *abyssinica* (Hochst) Pilg.	A		
Dichanthium radicans (Lehm.) A. Camus	P		
D. insculpta (A. Rich) A. Camus	P		

30	40	50	60	70	80	90	100a	100b	100c
3		2							
8		21	43						
3	2	3							
5		4							
		1							
		1							
		1							
		1	21	8	10	9			
4									
8	6	10							

Chrysopogon aucheri (Boiss) Stapf.	P
Heteropogon contortus Roem & Schutt.	P
Ischaemum afrum (J.F. Gmel) Dandy	P
Trachypogon spicatus (L.f.) O. Ktze	P
Sehima nervosum (Wild) Stapf.	P
Andropogon dummeri Stapf.	P
A. amethystinus steud.	P
Hyparrhenia lintonii Stapf.	P
H. hirta (L.) Stapf.	P

20	30	40	50	60	70	80	90	100a	100b	100c
12	6									
1		7	43							
		1	1							
2										
	9									
			8							
				28						
	1	38	5							
2	12	11	5	2						

H. dissoluta (Stend) Hutch.	P
H. filipendula (Hochst) Stapf.	P
H. nyassae (Rendle) Stapf.	P
H. rufa (Nees) Stapf.	P
H. collina (Pilg.) Stapf.	P
H. cymbaria (L.) Stapf.	P
Cymbopogon excavatus (Hochst) Stapf.	P
Themeda triandra Farsk	P
Sorghum verticilliflorum (Steud) Stapf.	P
Exotheca abyssinica (A. Rich) Anderss	P

20	30	40	50	60	70	80	90	100a	100b	100c
		6	23							
			27							
			5							
			13							
		4	24	13						
			2	1						
		7	5							
		37	66	26	3					
			1	1						
					18					

		10	20
Phalaris arundinacea	A		
Agrostis volkensii Stapf	A		
A. quinqueseta (Steud) Hochst	A		
A. keniensis Pilg.	A		
Anthoxanthum nivale K. Schum	A		
Deschampsia flexuosa (L.) Trin	A		
Helictotrichon angustum C.E. Hubb.	A		
Pentaschistis borussica (K. Schum) Pilger	A		
Bromus unioloides H.B & K	A		

30	40	50	60	70	80	90	100a	100b	100c
				15					
							12	40	94
							10		8
			8	12	36	42			
							4		42
						3	32	16	14
				9					
			2	74	30	27	4		
			3						

		10	20
B. leptochados Nees	A		
B. cognatus Steud	A		
Pseudobromus silvaticus K. Schum	A		
Poa schimperiana A. Rich	A		
P. annua L.			
Streblochaete longiaristata (A. Rich) Pilger	A		
Festuca pilgeri St-Yves	A		

30	40	50	60	70	80	90	100a	100b	100c
		1	5						
			2	2	10	1			
			23	16	12	24	2		
			16	68	58	53			
			3	44	30	40	6		
					4	8	1		
					10	24	98	100	96

Results shown in Table II and Figure 1 illustrate the distribution pattern of C_3 and C_4 species pooled into Tribes. Relative Occurrence of each Tribe was plotted against the soil available moisture, altitude and temperature gradients. All the grass species encountered belonged to seventeen Tribes according to Napper (1965), ten of these Tribes were predominantly C_4 and seven were predominantly C_3 Tribes. As indicated by Figure 1, some of these Tribes were distributed over a wide range of available moisture gradient while others had restricted distribution ranges often represented by very few species. Of the Tribes which had a relatively wide range, ten were selected and presented in Table II. Eight of these Tribes are shown in Figure I. The seventeen Tribes encountered were: Zoysieae, Pappophoreae, Aristideae, Eragrostideae Chlorideae, Sporoboleae, Ehrharteae, Arundinelleae, Paniceae, Andropogoneae, Festuceae, Bromeae, Brachypodieae, Aveneae, Phalarideae, Agrostideae and Danthonieae.

As indicated by Figure I, the widely distributed Tribes encountered formed three distinct distribution groups along the altitude moisture gradient. These groups showed distinct dispersion patterns which differentiate the C_4 groups from C_3 groups. Tribes chlorideae, Eragrostideae Sporoboleae, Aristideae and Zoysieae were most common at low available soil moisture indices and absent at indices above 60. In contrast, the C_4 members of Paniceae,

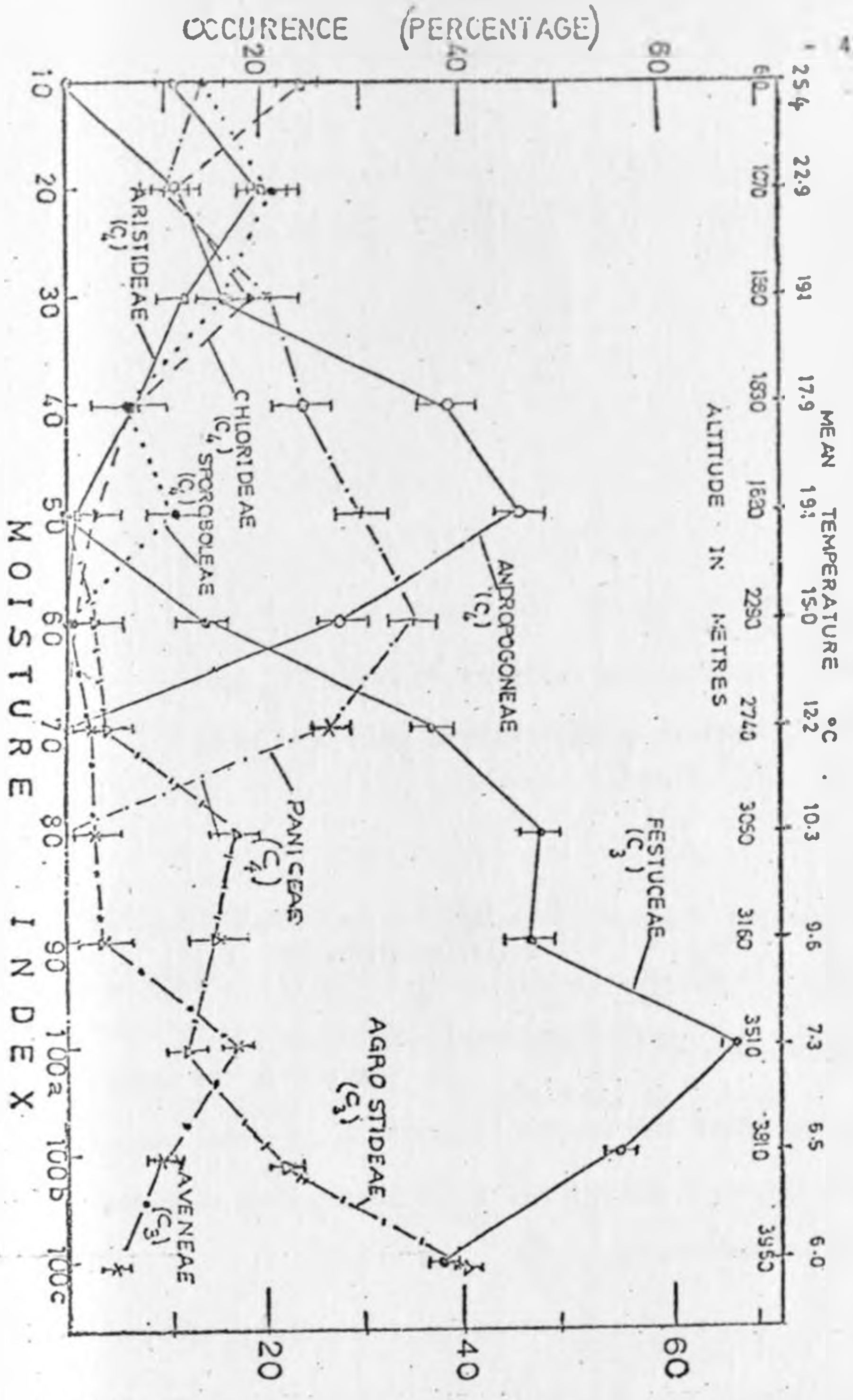


FIGURE I

Distribution curves of five C_4 and three C_3 grass Tribes plotted against soil moisture and temperature gradients in Kenya. The vertical lines indicate the confidence limits at 95%.

Site mean temperature was estimated according to the procedures suggested by Griffiths (1962).

TABLE II:

The relative occurrence of ten major Tribes of C_3 and C_4 grasses along moisture and altitudinal gradients based on Table I.

(i) Available moisture Index = $\dfrac{\text{Total rainfall - Total water surplus}}{\text{Potential evapotration } (E_o)} \times 100$

(ii) Relative Occurrence = $\left(\dfrac{100a}{b} \Big/ n\right)\%$ where a is the number of quadrats in which the species occurred, b the total number of quadrats thrown in a block and n the mean number of grass species per quadrat in the block.

TABLE II

MOIST. INDEX	ALT. (m)	ZOIZ. %	CHLOR. %	ERAGRO. %	SPOROB. %	ARIST. %	PAN. %	ANDROP. %	AGROST.	AVEN. %	FEST. %	OTHER %	MEAN sp.m^{-2}
		DISTRIBUTION BY TRIBES											
10	610	9.3	22.1	21.9	13.0	10.4	7.4	0				15.9	2.7
20	1070	6.8	15.1	20.0	20.8	12.5	8.9	6.2				9.5	3.9
30	1680	1.8	18.9	12.2	16.2	12.2	21.7	16.2				0.8	3.5
40	1830	0.6	6.8	14.2	6.4	7.0	24.0	32.8				8.2	4.0
50		0	2.9	6.3	11.6	0.5	31.1	46.7	0		0	0.9	4.6
60	2290		0.5	10.3	0	0	35.8	28.5	2.4	0	12.4	10.1	3.4
70	2740		0	9.3			21.8	0	4.2	2.5	37.5	24.7	3.4
80	3050			0			0		17.0	2.0	52.0	29.0	2.1
90	3160								16.0	5.9	50.4	27.7	2.5
100a	3510								12.8	19.6	65.3	2.3	1.6
100b	3810								22.2	8.9	55.6	13.3	1.8
100c	3960								39.2	5.4	37.7	17.7	2.6

and Andropogoneae attained their highest development at the intermediate indices, 40 to 70. The C_3 Tribes: Aveneae, Agrosteae and Festuceae occurred only at indices greater than 60 at high altitudes. The general pattern suggested by the major Tribes was in agreement with the trend indicated by the distribution of C_3 and C_4 grass specimens kept in the East African Herbarium (Ndawula-Senyimba et al; 1978). The transition between C_3 and C_4 groups was located in the forest zone at the foot of the alpine environment. This sharp transition between the distribution of C_3 and C_4 groups might have been due to sudden decreases in temperature caused by sharp rise in altitude. The last C_4 species encountered at high altitude were Eragrostis raccemosa, E. kiwensis, Eleusine jaegeri and Pannisetum clandestinum all these species with exception of P. clandestinum belong to Tribe Eragrosteae.

These results show clearly that the distribution of plants with the C_4 photosynthetic pathway is very closely related to available soil moisture which in turn is related to altitude. The relationship supports the view that the C_4 syndrome is adaptive to hot arid environments (Black, 1971; Laetsch, 1974; Winter et al, 1976; Tieszen et al, 1979). The distribution of C_3 Tribes which attained their peak at indices 90 to 100b was more correlated to decreasing temperature than increasing soil moisture. The absense of C_4 at alpine altitudes and the presence of C_3 species agreed with the suggestion of Teeri and Stowe (1976), that the deleterious effects of low temperature reduce the advantages of the C_4 syndrome in cooler habitats and possibly favours the presence of C_3 species.

The distribution of C_4 grass Tribes along the soil moisture gradient shown in Figure 1 agrees with the continum view of Curtis and McIntosh (1951). There was overlapping in the transitional zone between the arid and wet maxima to mark the point where the range of tolerance for the two groups are optimal. The gradual way soil moisture changes from one level to another prevented the existance of a sharp boundary between the arid and wet maxima. The widely dispersed Tribes such as Paniceae and Agrostideae contained large numbers of species having their individual optima at widely separated points.

Table III illustrates the distribution of the ten widely dispersed Tribes in terms of species abundance. Species abundance was expressed on the basis of the percentage of the number of species representing a Tribe in each moisture block to the total number of species found in the block. The data in this table agrees with that presented in Table II and Figure I. Tribes were represented by the largest number of species where their ranges of tolerance with respect to soil moisture and altitude were optimal.

TABLE III: The degree of species diversity in each of the ten major C_3 and C_4-grass Tribes along the moisture and temperature gradients expressed as percentages.

MOIST.	NO. OF	ABUNDANCE OF SPECIES												
INDEX	SP. sp.%	ZOIZ. sp.%	CHLO. sp.%	ERAGR. sp.%	SPOR. sp.%	ARIST. sp.%	PAN. sp.%	ANDRO. sp.%	AVEN. sp.%	FEST. sp.%	AGROS. sp.%	OTHER sp.%	MEAN m^{-2}	S.D.
10	13	7.7	15.4	23.1	15.4	15.4	15.4	0				7.6	2.7	1.0
20	26	3.8	7.7	19.2	19.2	7.7	19.2	19.2				4.0	3.9	1.5
30	41	2.4	19.5	19.5	19.5	14.6	4.9	19.2				0.4	3.5	1.2
40	45	2.2	6.7	22.3	4.4	6.7	31.0	26.7				0.0	4.0	1.7
50	64	0	6.3	14.3	4.8	4.8	32.0	31.7	0	0		6.1	4.6	1.5
60	25		4.0	20.0	0	0	12.0	20.0		16.0	8.0	20.0	3.4	1.1
70	14		0	21.0			14.3	0	6.3	21.4	8.0	29.0	3.4	2.2
80	8			0			0		8.3	37.5	17.3	36.9	2.1	0.9
90	11								8.3	45.5	19.0	27.2	2.5	1.1
100a	7								30.6	42.9	26.5	0.0	1.6	0.8
100b	5								28.0	20.0	32.0	20.0	1.8	0.8
100c	7								8.5	42.9	48.6	0.0	2.6	0.8

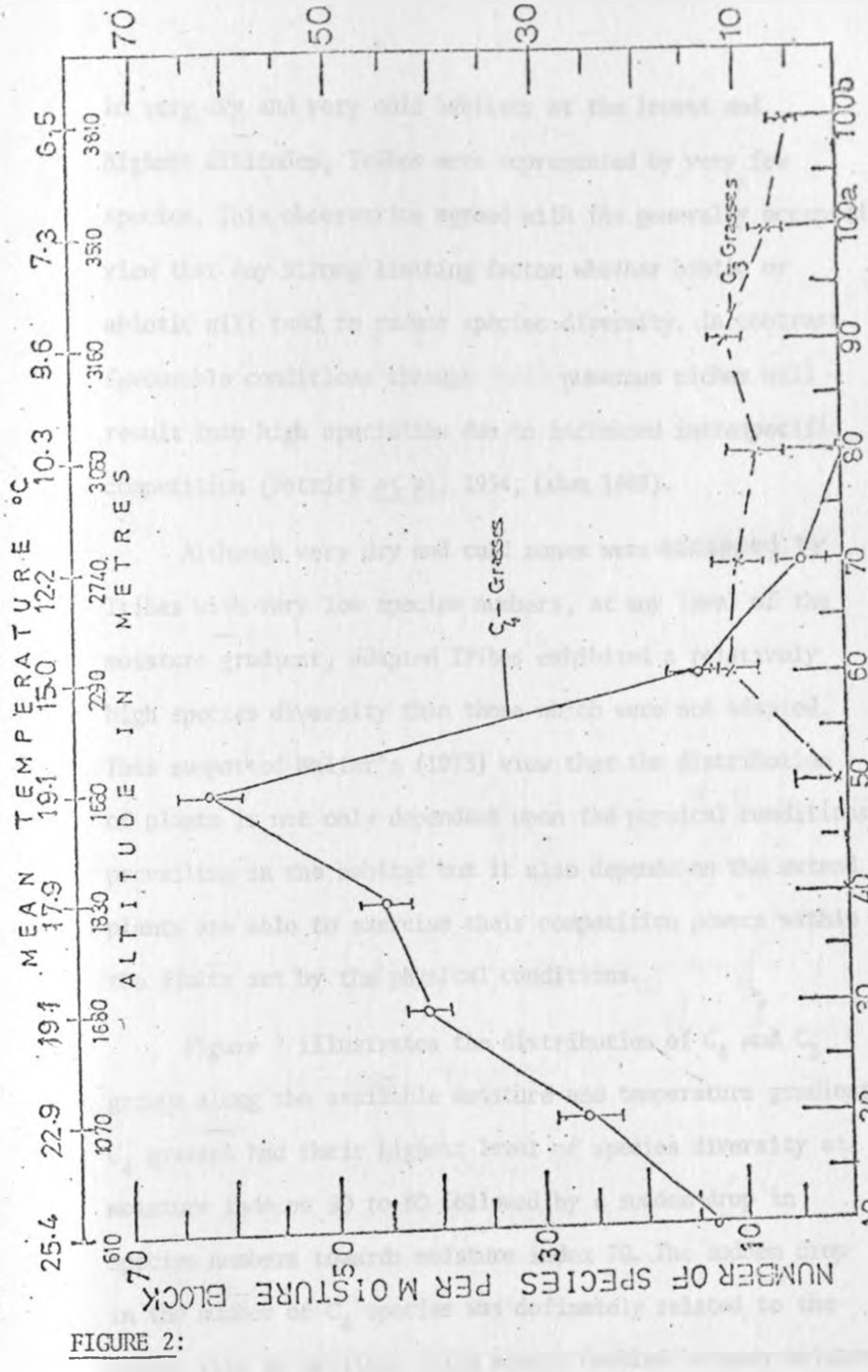


FIGURE 2:

The overall distribution of C_3 and C_4 grasses as groups plotted along soil moisture and temperature gradients in Kenya. The vertical lines indicate the confidence limits at 95%.

In very dry and very cold habitats at the lowest and highest altitudes, Tribes were represented by very few species. This observation agreed with the generally accepted view that any strong limiting factor whether biotic or abiotic will tend to reduce species diversity. In contrast favourable conditions through numerous niches will result into high speciation due to increased intraspecific competition (Patrick *et al*, 1954; Odum 1969).

Although very dry and cold zones were occupied by Tribes with very low species numbers, at any level of the moisture gradient, adapted Tribes exhibited a relatively high species diversity than those which were not adapted. This supported Walter's (1973) view that the distribution of plants is not only dependant upon the physical conditions prevailing in the habitat but it also depends on the extend plants are able to exercise their competitive powers within the limits set by the physical conditions.

Figure 2 illustrates the distribution of C_4 and C_3 groups along the available moisture and temperature gradients. C_4 grasses had their highest level of species diversity at moisture indeces 50 to 60 followed by a sudden drop in species numbers towards moisture index 70. The sudden drop in the number of C_4 species was definately related to the sudden rise in altitude which almost doubled between moisture indeces 60 and 80.

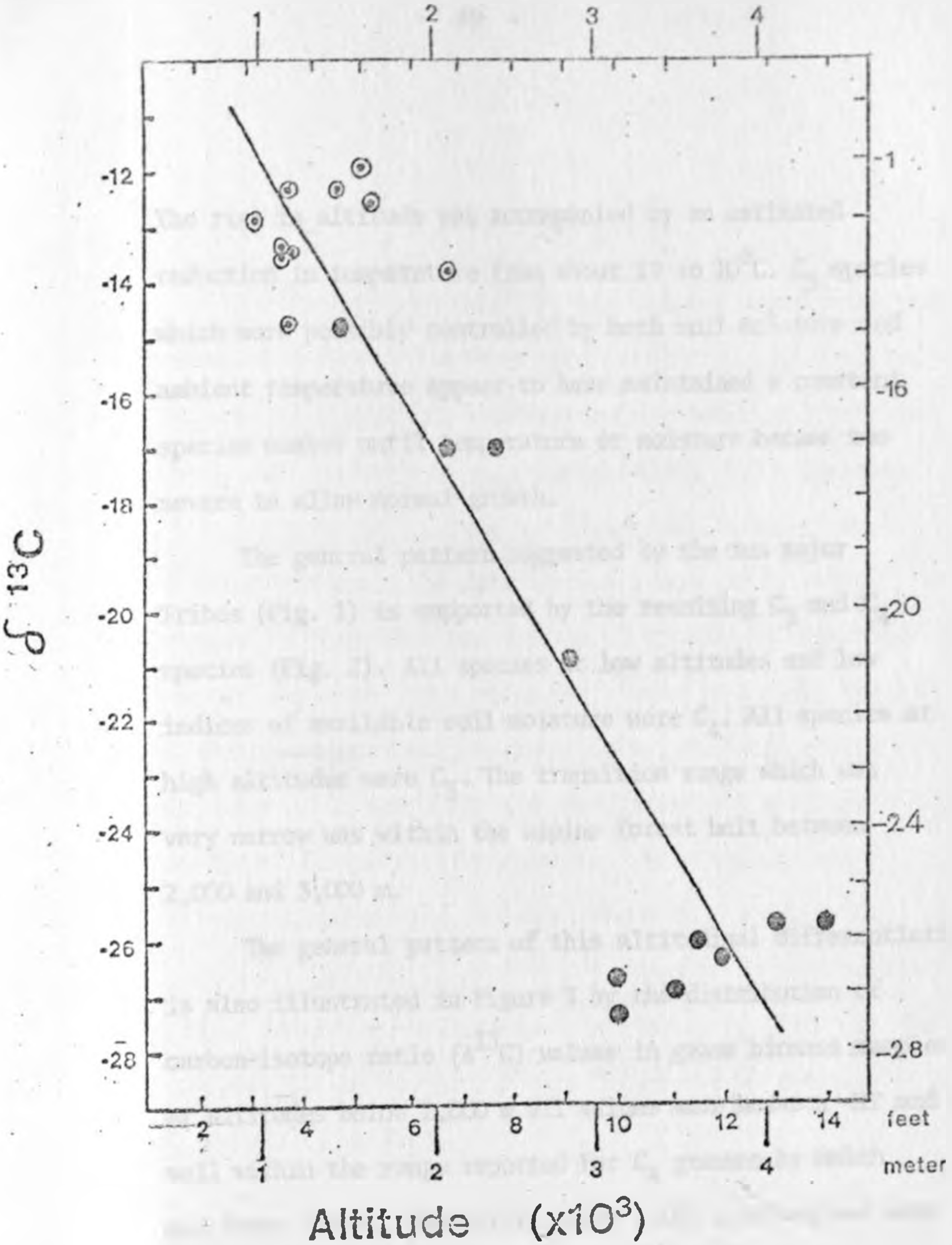


FIGURE 3:

A distribution curve of the carbon-isotope ratio ($\delta^{13}C$) values measured from the grass component of the vegetation along the altitudinal transect. ⊙ = samples which were predominantly C_4.and ● = samples which were predominantly C_3. The correlation coefficient with altitude is $r = 0.94$; $\delta^{13}C = 6.6 - 0.0016$ (feet). According to Troughton and Card (1975):

$$\delta^{13}C = \left[\frac{^{13}C/^{12}C \text{ sample}}{^{13}C/^{12}C \text{ standard}} - 1\right] \times 10^3$$

The rise in altitude was accompanied by an estimated reduction in temperature from about 19 to 10°C. C_3 species which were possibly controlled by both soil moisture and ambient temperature appear to have maintained a constant species number until temperature or moisture became too severe to allow normal growth.

The general pattern suggested by the ten major Tribes (Fig. 1) is supported by the remaining C_3 and C_4 species (Fig. 2). All species at low altitudes and low indices of available soil moisture were C_4. All species at high altitudes were C_3. The transition range which was very narrow was within the alpine forest belt between 2,000 and 3,000 m.

The general pattern of this altitudinal differentiation is also illustrated in Figure 3 by the distribution of carbon-isotope ratio ($\delta^{13}C$) values in grass biomass samples. At altitudes below 2,000 m all values were between -12 and -14 well within the range reported for C_4 grasses by Smith and Brown (1973). Similarly, above 3,000 m all values were around -26 to -27. The few values from intermediate altitudes suggest a contribution from both C_3 and C_4 species.

DISCUSSION

The results presented in this chapter support the view expressed by several authors that interactions between low moisture availability, high temperature and high irradiance favour the abundance of C_4 grasses (Black, 1973; Bjorkman, 1971; Laetsch, 1974; Teeri and Stowe, 1976). The clear difference between the distribution ranges of C_3 and C_4 grasses confirms that the ability of grasses to withstand low soil moisture and temperature stress is closely related to their photosynthetic systems. Open grasslands at low altitudes or at low indices of available soil moisture consist of C_4 species. In contrast, grasslands at high altitudes consist of C_3 species. These data support the hypothesis that the C_4 syndrome is adaptive to arid habitats. Similar results were obtained by Winter et al (1976) in the Gramineae of the Northern Sahara Desert and by Hofstra et al. (1972) in Java.

Although no direct experiment was carried out to differentiate the effects of temperature from those of soil moisture, the broad distributional pattern along the altitudinal gradient obtained was similar to that proposed by Teeri and Stowe (1976). These authors found that in North America the presence of C_4 grasses was highly correlated with the July minimum temperature. They indicated that few or no C_4 species were found where July minimum temperatures were below 8°C. Along the transect run on Mt. Kenya no C_4 species were found where the mean annual temperature was below 10°C. In contrast, C_3 species had their largest number of species at mean annual temperature below 10°C. Although low temperature may not be the only selective force operating on the C_3, C_4 systems as has been pointed out by Caldwell et al. (1977), it plays a major role in the distribution of C_3 grasses (Hartley 1961, 1973).

It is generally accepted that the C_4 syndrome concentrates CO_2 near the site of Ru BP carboxylation (Hatch, 1976) and that this is of selective advantage whenever internal CO_2 concentrations become low. These conditions could occur under high light intensities as well as during periods of water stress and increased stomatal resistance (Laetsch, 1974). At low altitudes in Kenya the environment is characterised by water stress, high irradiances and high temperatures; and the C_4 syndrome is adaptive to such conditions. The few C_3 species which occurred at low altitudes were found mainly in understoreys of closed forests and were from Tribes which more often consist of C_4 species. Under shade, irradiance would be low and leaf temperatures low. Ehleringer and Bjorkman (1977) and Ehleringer (1978) showed that at temperatures below 32°C the quantum yield for C_3 is higher than that of C_4 plants. Thus, with all other things equal, the C_3 plant should be at an advantage with respect to carbon balance in shaded environments and maximum leaf temperature below 30°C. This hypothesis is supported by results in this chapter.

Although the broad distributional patterns of C_3 and C_4 confirmed the trends one would predict on the basis of their physiological differences, not all C_4 species were equally adapted to arid conditions. C_4 Tribes such as Chlorideae, Zoysieae, Aristideae, Sporoboleae and Eragrostideae were most common at the more arid low altitudes. In contrast Tribes such as Paniceae and Andropogoneae were less common in very arid areas but were very common at the wetter end of the distributional range of C_4 grasses. These results supported Hartley's (1958a) and (1958b) findings that on a global scale Paniceae and Andropogoneae are best developed in hot moist climates. He further suggested that for the Paniceae rainfall is of primary importance and for the Andropogoneae mild temperatures are essential.

As regards the five C_4 Tribes found to be associated with arid habitats, Hartley and Slater (1960) indicated that on a global scale these Tribes are excluded from regions of low winter temperatures and that most of their member species are adapted to "erratic rainfall". The results presented here confirm these observations.

These results indicate that as far as grass distribution is concerned, it is only the distribution of C_4 grasses which is closely related to the available soil moisture index of Woodhead (1970).

However, this does not reduce the usefullness of Woodhead's indices because the distribution range of C_4 grasses in Kenya include all the usable land in Kenya from sea level to the alpine bamboo forest. Therefore, in this respect it can be concluded that the distribution of C_4 grasses can give a fair indication of the available soil moisture like the Woodhead's moisture index. Since Woodhead's available moisture maps covered only Kenya, C_4 grasses could be used to give a rough indication of the soil water status in places where maps do not exist.

CHAPTER II

THE GENERAL DESCRIPTION OF THE SELECTED GRASS SPECIES IN THE PHYSIOLOGICAL EXPERIMENTS

INTRODUCTION

Although it has been stated by several authors (Bjorkman, 1971, Black 1973, Laetsch, 1974, Teeri and Stowe 1976) and confirmed in the earlier part of this thesis that C_4 plants have adaptive features to conditions of high temperatures and aridity, the way these adaptive features operate is not fully known. It has been suggested that since C_4 plants have a low compensation point for CO_2, they can continue photosynthesis even when the stomata are almost closed due to water stress (Hatch 1976). This might be so in special cases but as it will be shown later, C_4 grasses adapted to semi-arid habitats have more stomata and they normally do not wilt or have their stomata closed earlier than the drought susceptible species.

As regards CAM plants, their morphology enables them to store large quantities of water in their tissues which protect the cells from getting dehydrated during the dry period. C_4 plants have no morphological similarity with CAM plants; externally they look exactly the same as C_3 plants. Often they have no structual features which are usually associated with sclerophyllous and stenohydric xerophytes (Walter, 1971). It seems that most of the adaptive features of C_4 plants especially grasses are intrinsic and physiological. Therefore, in order to assess the way some of these physiological feature of C_4 grasses operate under moisture and temperature stress, detailed physiological experiments were carried out.

The C_4 grass species used for the detailed experiments were selected partly because they are commonly associated with dry places and partly because they are among useful herbage species found in the semi-arid parts of Kenya. The grazing value of these species was based on the evaluations of workers such as Bogdan (1958); Bredon and Wilson 1963; McKay (1971); Dougall (1960); Dougall and Bogdan (1965), van Voorthuizen (1971); Olsen (1972); Wigg *et al*. (1973) Reid *et al*. (1973) and Karue (1974). Some species such as *Panicum maximum* which are usually found in wet places were used for comparison with semi-arid species.

The species selected for detailed physiological studies were grouped as follows:

A. Arid condition species:

Leptochloa obtusiflora
Chloris roxburghiana
Sporobolus marginatus

B. Semi-arid condition species:

Eragrostis superba
Pennisetum menzianum
Themeda triandra

C. High moisture condition species:

Panicum maximum
Cenchrus ciliaris (Biloera)
Eleusine coracana (Gulu E.)

Leptochloa obtusiflora Hochst, (App. IIA (i)) is a perennial tufted grass with branching culms 90-120 cm tall. It is a very branched perennial with little or no basal leaves in the mature stage. The bottom parts of the branches are semi-woody and brittle but the top leafy parts are easily masticated by most grazing animals. The plant belongs to Tribe Eragrostideae and it is characterized by non-spatheate panicles of a 5 to many similar awnless spikelets having one floret each (Clayton 1974).

The leaves are upto 1.5 cm wide and 35 cm long. They are glabrous, lanceolated and often having a constricted part at about 2/3 the length towards the tip. Leaves remain soft and very palatable throughout the growing period and they make the species one of the few tropical range grasses with a relatively high crude protein content (unpublished results obtained by the author at E.A.F.R.O. Muguga). Values as high as 19% and 7% crude protein were measured in green and dried up leaves respectively.

Ecologically, the species is widely spread in open thickets and arid grasslands on sandy and clay soils. (Bogdan, 1958; Napper 1965; Clayton 1974). L. obtusiflora is often found in small pockets associated with clumps of thickets.

It is not known why L. obtusiflora is not recommended for range or pasture reseeding. In 1949, it was included among the possible species by the pasture research division in Kenya (Edwards, 1949). Later, it was reported to be among the more promising pasture species but no further mention of it has every been made.

Chloris roxburghiana Schult; Synonym. C. myriostachya Hochst (Appendix IIA (ii)), is a member of Tribe Chlorideae. It is a tufted perennial about 60 cm high with culms branching above the ground at compound nodes. Its inflorescence is a panicle of about 10-15 cm long, with feathery white or purple racemes especially when it has just opened (Napper, 1965). This species has been described by Lind and Morrison (1974) and Cassady (1973) as one of the ephemeral grasses found growing with thorny shrubs and bush in semi-desert grasslands covering very large parts of North-East Kenya (Pratt et al. 1966). The species is often found growing in areas with rainfall between 250 and 500 mm associated with Chrysopogon aucheri, Aristida sp and Cenchrus ciliaris. It grows on sandy soil at altitudes ranging from sea level to about 1600 m a.s.l.

Rattray (1960) used C. roxburghiana to characterize extensive areas of semi-arid grasslands found in East Africa, Somalia, Ethiopia and Mozambique. The grassland vegetation characterized by this species is often associated with an open steppe type of vegetation found where temperature and water strees limit plant growth.

The species has soft hairy leaves which are palatable to animals. It was once used successfully for reseeding a denuded land in Kitui area (Bogdan, 1958).

Sporobolus marginatus. A. Rich, belongs to Tribe sporoboleae. It is a tufted perennial up to 45 cm high and sometimes it is found to be slightly stoloniferous. Panicles are loose with the lower most branches verticillate (i.e branches arising from one point). Panicle branches are spreading densely covered with spikelets. Leaves are smooth and about 0.5 cm wide and 15 cm long (Bogdan 1958). S. marginatus is found in dry grasslands on sandy soil and sometimes on slightly saline soil. Its leaves are generally soft and can provide feed for animals in semi-arid areas since it is moderately palatable (Appendix II B (i)).

This species is very variable and often it is made to include S. laetevirens coss and S. humifusus var cordofanus Auctt (Napper, 1965).

Themeda triandra Forsk (Red Oatgrass) is a member of Tribe Andropogoneae and the only species of the genus Themeda found in East Africa. This species is the most widely distributed species of the Tribe Andropogoneae in East Africa (Lind and Morrison 1974). It is an important species used to characterise a large number of grassland types forming the most productive range lands in Eastern tropical and sub-tropical Africa (Rattray 1960) (Appendix IIA (iv)).

Themeda triandra being adapted to a wide range of ecological types, is represented by a large number of ecotypes. The species can grow as tall as 1.5 metres and when it is fully grown it can produce a complete cover of the ground. Its inflorescence is a loose reddish spatheate panicle. The racemes are made up of a group of spikelets supported by spatheoles with one spirally twisted awn per raceme. Napper (1965) recognised two varieties of this species in East Africa; Var. burchechii which is the commonest and var. hispida differentiated only from the other variety by the presence of warted-based hairs found on the spatheoles and glumes of the involucral spikelets.

Karue (1974) reported that T. triandra had been labelled as a useless grass in rangelands despite its predominance in many areas of semi-arid lands. However, the species being dominant over most of ecological zone IV (Pratt et al. (1966) and having to support a large population of beef cattle, can not be just ignored. McKay (1971) believed that by means of herbage selectivity practised by cattle and other grazers T. triandra grasslands can be made to provide at least enough digestible protein required to maintain a mature beef cattle.

The species grows best in places which are free of bush often associated with frequent bush burning (Edwards, 1942 and 1949; Ndawula-Senyimba 1972). T. triandra favours exposed sites and it gradually dies out when burning and grazing are withdrawn altogether (Bogdan 1954, Van Rensburg 1952;

Ndawula-Senyimba 1972).

Leaves of T. triandra are soft only when they are young but they become rough and hard in the mature stage. Generally these leaves do not roll up even when they are dry.

Eragrostis superba Peys. (Masai Lovegrass) is a densely tufted perennial 30-100 cm high. It is a member of Tribe Eragrostideae having large purplish flat spikelets widely distributed on a loose panicle. Its stems are rather hard although palatable and its leaves are up to 1.5 cm wide and 45 cm long. They are smooth with a few long hairs which are often lost as the leaf matures. (Appendix II B (ii)).

The plant is associated with semi-arid bushed grasslands and it is found growing on sandy and other well drained soils. Rattray (1960) associates E. superba with T. triandra and Bothriochloa insculpta in grassland types on sandy soils experiencing heavy grazing. The species is also found in association with Cenchrus ciliaris on the wetter boarders of semi-deserts.

E. superba is of high grazing value in dry and medium rainfall areas and it is one of the recommended species for reseeding denuded grasslands (Bogdan 1958). As far as productivity is concerned E. superba was equated to Cenchrus ciliaris in leaf production by Taerum (1970) and was only exceeded by Panicum maximum. However, both P. maximum and E. superba were said to have the highest shoot/root ratio at Muguga. The main setback of this species is its low-seed germination percentage.

Pennisetum menzianum. Leeke (Bamboo grass) is a member of the Tribe Paniceae. It is a tufted perennial 120 cm high with hard wiry stems which are much branched in the upper parts. The species is shortly rhizomatous with usually greyish glabrous flat or folded leaf bades. The inflorescence is a compact terminal false spike with numerous spikelets supported by numerous bristles. The inflorescences and the young shoots are often bluish in colour (Appendix IIA (iii)).

The species is often found in very open semi-arid grasslands associated with scattered Acacia drepanolobium (Karue 1974), always favouring seasonally water logged black cotton soil (Ndawula-Senyimba 1972). P. menzianum is of low grazing value and have a very low digestible protein and plant of fibres (Karue 1974). However, since it is very abundant on a large part of ecological zone IV grasslands in Kenya its use can not be overlooked. Its leaves and new shoots are very palatable but after a short time the culms become wiry and unpalatable. If not burnt, the culms can remain alive for some years and new seasonal growth is produced by means of short branches which produce a few leaves and flowers.

Panicum maximum Jacq. (Guinea grass) belongs to Tribe Paniceae. It is bunched perennial grass up to 2.5 metres high with long flat roughly hairy leaf-blades upto 100 cm long. The inflorescence is an open panicle, 15-45 cm long with the lower most branches whorled (Appendix IIB (iii)).

The species is well represented all over the continent of Africa South of the Sahara (Rattray, 1960), but it reaches its best growth under moist and warm conditions on forest edges and grasslands derived from forest (McCosker and Teitzel, 1975). The species is highly ubiquitous and may be represented by very many ecotypes adapted to different environmental conditions. In general P. maximum seems to belong to communities of secondary succession and it will often die out as the community advances towards a climatic climax (unpublished observations). Because of this feature, P. maximum rarely dominates undisturbed grasslands with exception of riverbanks and damp ravines.

P. maximum is one of the high yielding grasses in the family Gramineae (Mac Ilroy, 1964; Vicente-Chandler et al. 1959) and it attains the highest productivity under high temperature and rainfall greater than 1300 mm (McCosker and Teitzel, 1975) on good soil. Studies on the nutritive value of P. maximum have been carried out in many parts of the tropics; in Cuba by Mahendranathan (1971) and Reyes, (1972), in Tanzania by Van Voorthuizen (1971) in Uganda by Olsen (1972) and Reid et al. (1973), in Kenya by Dougall (1960). All these studies generally indicate that the species is very nutritious. Its crude protein declines with age from about 19% to 9%. It is highly recommended for pasture in high rainfall areas.

This species does not form closed swards and it remains caespitose. Some ecotypes of it such as Makueni are found in arid areas although none of them would endure heavy grazing or cutting (Cassady, 1973). Its seeds are easily obtained but their germination ability is very low possibly because all the seeds on the same inflorescence do not mature at the same time.

Cenchrus ciliaris L.(African foxtail or Buffel grass) belongs to Tribes Paniceae. It is a tufted perennial with short stout rhizomes. The grass occurs in several distinct forms some adapted to arid conditions others adapted to wet habitats. The species grows up to 120 cm high with culms much branched bearing terminal inflorescences. The inflorescence is a false spike which is usually dense and purplish in colour when young. It is 2.5 to 15 cm long with spikelets subtended by numerous bristles (Appendix IIB (iv)).

C. ciliaris is a native of tropical Africa, India and Indonesia and is used in permanent pastures in South Africa and Australia. It remains green in the dry period but its stems soon become woody. Wigg et al. (1973) reported that since 1953 considerable areas of C. ciliaris have been established at the pasture Research Station, Kongwa providing a stable perennial pasture for beef production. The grass is fairly high yielding reported to produce as much as 5,440 Kg/ha when fertilized.

In natural conditions some ecotypes of C. ciliaris are found associated with Eragrostis superba in semi-arid grasslands (Rattray 1960).

Eleusine coracana (L) Gaertn; Gulu E(Finger millet) belongs to Tribe Eragrostideae and it is grown as an arable food crop in many parts of East Africa. It is an annual crop up to a metre tall, hardy and capable of growing in almost any type of soil. Sometimes it is found growing on roadsides as a weed (Langdale Brown et al. 1964; Bogdan, 1958). For high production, finger millet requires a moist climate where rains are not too heavy and temperature high. Millet areas have rainfall ranging between 760 and 1280 mm (Appendix IIc).

Finger millet has been subjected to breeding and agronomic research both in India and in East Africa and a number of cultivars such as Gulu E. have been released having various agronomic advantages. However, on the whole E. coracana is generally regarded as the "poor man's cereal" and it is not given priority as a world cereal of great importance. In Africa on the other hand finger millet is one of the most desirable indigenous cereals often preferred to others.

CHAPTER III

THE RELATIONSHIP BETWEEN LEAF WATER POTENTIAL, SOIL MOISTURE STRESS AND ADAPTATION TO ARID CONDITION OF C_4 GRASSES

LITERATURE REVIEW

Drought is one of the most serious problems responsible for frequent crop failure and animal starvation. In East Africa large parts of farmable land are made less productive because of lack of rain or because of rain which comes at wrong times.

Water shortage affects plants in a number of ways. Severe water stress may result into killing the crops altogether or stunting them in such a way that they do not produce any harvestable yield. However, for crop production, it is not the drought that kills completely the crops, which is the major cause of economic losses to the farmer. It is the water stress which goes on unnoticed inside the plants growing in areas with marginal rainfall, which is responsible for a larger part of the world crop shortages. This moderate water stress is not only responsible for reducing the yield but it is also responsible for lowering the quality of crops and in some cases making the plants toxic to animals and human beings (Jones, 1959 Gangstad, 1959).

As Ritchie (1974) pointed out, the growth of plants is directly controlled by the water deficit in the plant and only indirectly by soil water deficits. Therefore, this means that plant production losses may be experienced even when soil moisture stress is not considered severe.

The magnitude of this internal water stress is influenced by environmental factors such as sunshine and by plant factors such as tomatal characteristics (Raschke 1975).

The internal water stress of plants which is generally known as the water potential (Ψ) results directly from evaporational water losses through the stomata. The suction force thus created drives the transpiration stream which enables water absorption to take place. In this instance although soil water status influences the plant water potential, the magnitude of such potential will be greatly modified by the plant factors (Bange, 1953; Stanhill, 1965). The importance of plant factors on the plant internal water stress help to explain the difference between drought resistant and drought susceptible plants. It is possible that the C_4 grasses adapted to arid condition possess some physiological or structual mechanisms which enable them to maintain a favourable internal water stress when soil water is in short supply.

There are a number of ways by which plants maintain a high plant water potential against a low soil water potential. The mostly referred to method is by losing as little water as possible through transpiration. This is based on the fact that most of the water lost from the plant passes though the stomata. Kramer (1969) has pointed out that water lost through transpiration via the stomata is almost three times more than the water which evaporates from the bare soil.

Also Todd (1970) indicated that about one half to six-seventh of the water precipitated on the land returns to atmosphere through stomata by transpiration. In this case plants which either have very few stomata or keep their stomata closed when the evaporation demand is high would lose little water. Therefore, drought resistant plants in this group would be those plants which conserve the little water they have by restricting water loss through modified cuticular and stomatal structures which decrease transpiration (Pieniazek, 1944; Daubenmire 1965).

The second general method by which plants avoid severe internal water stress is by absorbing large quantities of water either through an extensive root system or by transpiring more freely than mesophytes so as to generate enough force to over come the low soil water potential (Maximov, 1929; Levitt 1972). In the latter case, the plant may have cells which are made in such a way that they may withstand very negative water potential levels without willing or causing stomatal closer.

Since reduction of water loss by either stomatal closure or by the techniques employed by succulent plants leads to impeded CO_2 uptake, productivity would be greatly reduced by water conservation. Such plants would reduce water loss at the expesne of productivity (Raschke, 1975).

C_4 grasses being generally known as highly efficient plants would not be expected to withstand arid condition by restricted transpiration which would result into impeded production. It is necessary to ascertain which mechanisms enable C_4 grasses to adapt themselves to arid conditions without losing their efficient photosynthetic productivity.

The objective of this part of the study was to discover the mechanisms which govern the water relations of C_4 grasses adapted to arid conditions and to find out how such mechanisms are related to the distribution and productivity of such plants in arid habitats.

METHODS

In order to examine the water relations of selected C_4 grasses, representative specimens were collected from their natural habitats and grown in semi-natural growing conditions for closer observations. L. obtusiflora, C. roxburghiana, S. marginatus, T. triandra, E. superba, P. menzianum, P. maximum, C. ciliaris and E. coracana, were planted both in the Botanical garden and in posts at the University of Nairobi. The first three species represented C_4 grasses which normally grow in arid conditions, the second group of three species represented the grasses normally found in places with intermediate rainfall and the last three species represented C_4 grasses found in warm and high rainfall areas.

All species except E. coracana were established vegetatively in the same plot and were left to grow for a year before measurements were made. E. coracana was grown separately from seeds and was normally used too months after planting. Potted specimens were grown in 20 cm-diameter plastic pots and were used one and half months after planting.

The leaf water potential (leaf Ψ) of all specimens was measured with a Pressure Chamber Model 600, obtained from the PMS Instrument Company, following the procedure first described by Scholander et al.(1965). All determinations of water potential done in the field were carried out using fully expanded leaves which were well illuminated during the growing period. Attempts were made to use leaves of approximately the same age determined by their position from the growing tip of the culm . For anyone determination, several leaves were taken from one plant and an average value taken. Diurnal variations in leaf Ψ were determined in the field on sunny days, at a pre-determined soil moisture level.

The effects of soil moisture stress on the leaf water potential was first determined in the natural grassland at Athi River on the formally East African Agriculture and Forestry Research Organization Ranch, 32 km East of Nairobi.

The place is estimated to receive about 700 mm of rain per year. The grass stands used had been planted for range-reseeding trials in 1971, four years before the time of this experiment. The second set of measurements were made on the grasses grown in the botanical garden at the University of Nairobi and the third set of measurements were made using potted plants. On the Athi River ranch, drought conditions developed naturally at the end of the long rains. Measurements of leaf ψ were taken periodically as the rainless period increased.

In the botanical garden, water stress conditions were developed artificially. A 6 x 10 metre-shade was erected over the grass plot and covered with a transparent polyethelene sheet gauge 400. The shade, whose use was to prevent rain from re-watering the plot, was at least 2 metres above the ground at the slopping ends. Only the roof of shade was covered with polyethelene, the sides were left uncovered to allow free air movement. Unrestricted air movement enabled the temperature and humidity conditions inside the shade to remain as near those outside as possible. Polyethelene reduced the light intensity inside the shade by approximately 1%.

The shaded plot was watered heavily at the beginning of the water stress trial at the beginning of May and no further watering was done for a period of two months.

The water content of the soil was determined gravimetrically using soil cores sampled at 20 cm depth. At each sampling time, several cores were taken, from various points in the plot, all the samples were mixed together and a sub-sample taken from the mixture to represent the block. Soil moisture measurements and leaf Ψ were made simultaneously each sampling time.

Diurnal measurements of leaf water potential were made on clear sunny days. Light intensity measurements were made concurrently, .using a LI-COR Model LI-185 light meter obtained from the Lambda Instrument Corporation.

Simulated water stress of potted specimens was obtained by first standing the pot containing the plant in a bucket of water for 5 minutes and then taking it out and leaving the excess water to drain out overnight. This type of watering ensured that all pots were watered to field capacity before the beginning of the gradual drying of the soil. No further rewatering was done until a level near the permanent wilting point was reached. All potted plants were kept under the polyethelene shade until they were required for water potential determinations. The plants to be used for various measurements during the day, were kept in the dark the night before in order to enable the leaf Ψ to be equated to the soil Ψ when measuring started.

Soil water content of each pot was measured gravimetrically.

The effect of soil ψ on the transpiration ratio or plant water requirement (Black et al, 1969; Shantz and Piemerisel 1927) was determined during the measuring of photosynthesis. The photosynthetic rates of intact leaves of potted plants were determined by a Beckman 215 Infra-red Gas Analyser. Transpiration rates were determined concurrently using a Dew-point hygrometer model 880 from the EG & G International which was connected to the gas analyser.

The stomatal density of some of the species collected from semi-arid and wet habitats was determined for both the adaxial and abaxial leaf surface. Stomatal counts were made under a watson microscope at high power magnification using impressions made with colourless cutex. In each case several impressions were made from leaves of different plants of the same species and an average number of about 30 counts taken per species.

RESULTS

Table IV gives the average leaf water potential (ψ) of C_4 grasses grown on the Athi River Ranch. The average values of leaf ψ were obtained from several determinations made on different grass tufts growing in the same area. Measurements were made at different times of the day at an average soil moisture level of 31%.

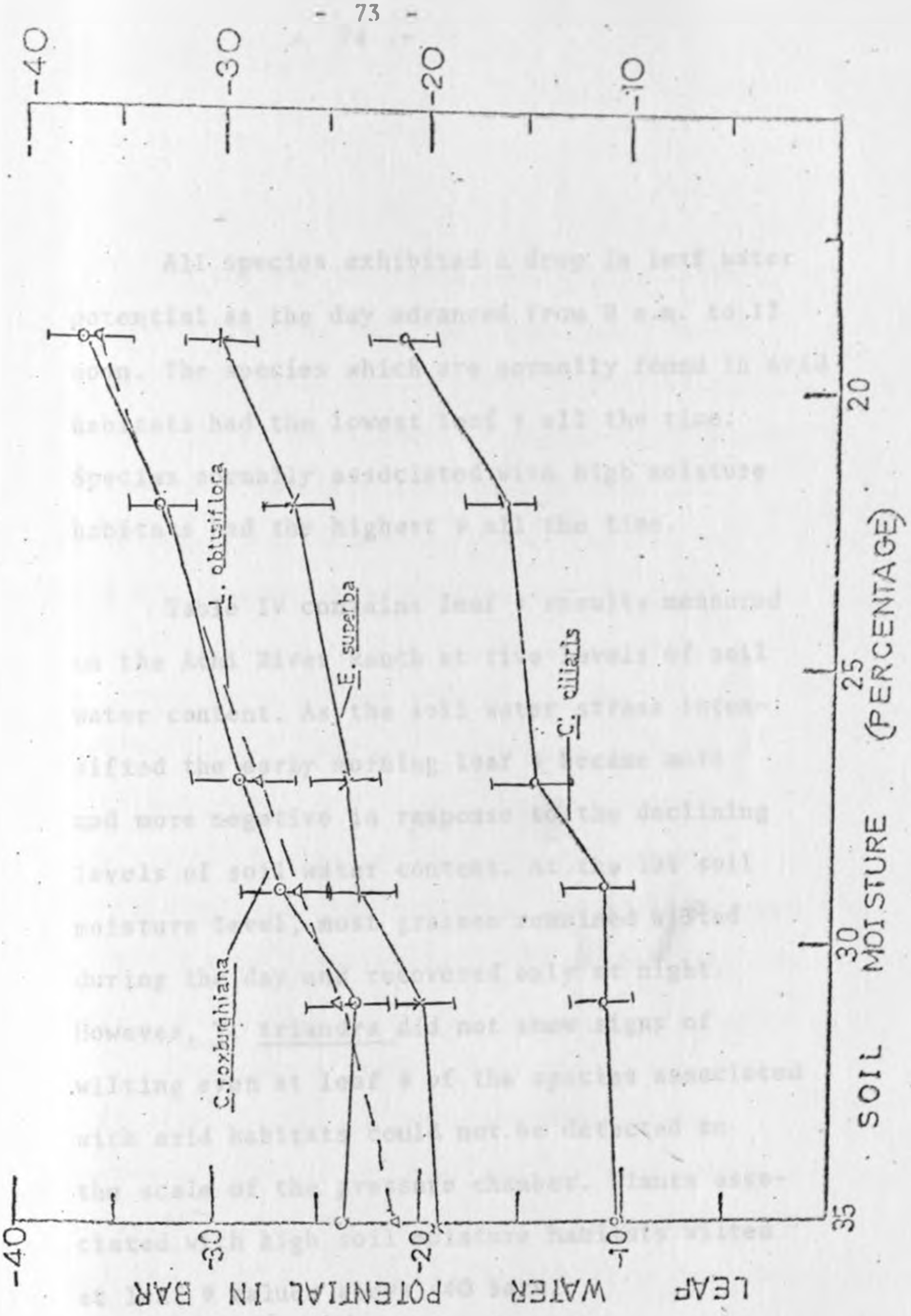


FIGURE 4:

Leaf water potential of C. roxburghiana, L. obtusiflora, E. superba and C. ciliaris expressed as a function of soil water stress measured in the field at light intensity between 2200 and 2400 µE m^{-2} $sec.^{-1}$. Each point is the average of several determinations made on at least three tufts of the same species.

All species exhibited a drop in leaf water potential as the day advanced from 9 a.m. to 12 noon. The species which are normally found in arid habitats had the lowest leaf ψ all the time. Species normally associated with high moisture habitats had the highest ψ all the time.

Table IV contains leaf ψ results measured on the Athi River Ranch at five levels of soil water content. As the soil water stress intensified the early morning leaf ψ became more and more negative in response to the declining levels of soil water content. At the 19% soil moisture level, most grasses remained wilted during the day and recovered only at night. However, T. triandra did not show signs of wilting even at leaf ψ of the species associated with arid habitats could not be detected on the scale of the pressure chamber. Plants associated with high soil moisture habitats wilted at leaf ψ values above -40 bars.

As the results contained in both Table IV indicated, the early morning leaf ψ was determined partly by the level of soil water and partly by the internal factors characteristic of each species. There was an apparent relationship between the type of habitat to which a species is associated and the level of leaf ψ it can attain at any given soil moisture level at any time of the day. *C. ciliaris* and *P. maximum,* which are associated with mesophytic conditions had less negative leaf ψ, but *T. triandra*, *L. obtusiflora* and *C. roxburghiana* from semi arid and arid environment had more negative leaf ψ throughout the day.

There was a gradual decrease in the leaf ψ of each species as the evaporative demand increased with the time of the day from 9.00 to 12.00 hours. The amplitude between the 9.00 and the 12.00 hours values decreased as the soil moisture stress increased.

TABLE IV: Leaf water potential in bars of C_4-grasses adapted to different soil moisture regimes measured in the field at different soil moisture potential and times of the day. All measurements were taken on sunny days using well illuminated leaves. Each figure is an average of not less than three determinations made on each of at least three different tufts.

TIME OF THE DAY	9 00 hrs				10 00 hrs					12.00 hrs				
SOIL MOISTURE %	31	27	22	19	31	29	27	22	19	31	29	27	22	19
C. ciliaris	-9	-11	-13	-18	-11	-11	-15	-16	-21	-23	-28	-25	-26	-33
P. maximum	-12	-16	120	-27	-18	-18	-20	-28	-32	-26	-28	-29	-32	-35
E. superba	-14	-17	-17	-37	-19	-20	-34	-27	-30	-24	-27	-26	-33	-35
P. menzianum	-16	-17	-14	-20	-20	-22	-26	-29	-30	-23	-34	-33	-36	-37
T. triandra	-16	-24	-27	-40	-23	-24	-27	-32	-35	-30	-33	-35	-38	-42
L obtusiflora	-17	-18	-23	-39	-24	-26	-28	-33	-36	-26	-32	-32	-40	-42
C. roxburghiana	-22	-26	-30	-36	-24	-27	-29	-33	-36	-35	-42			

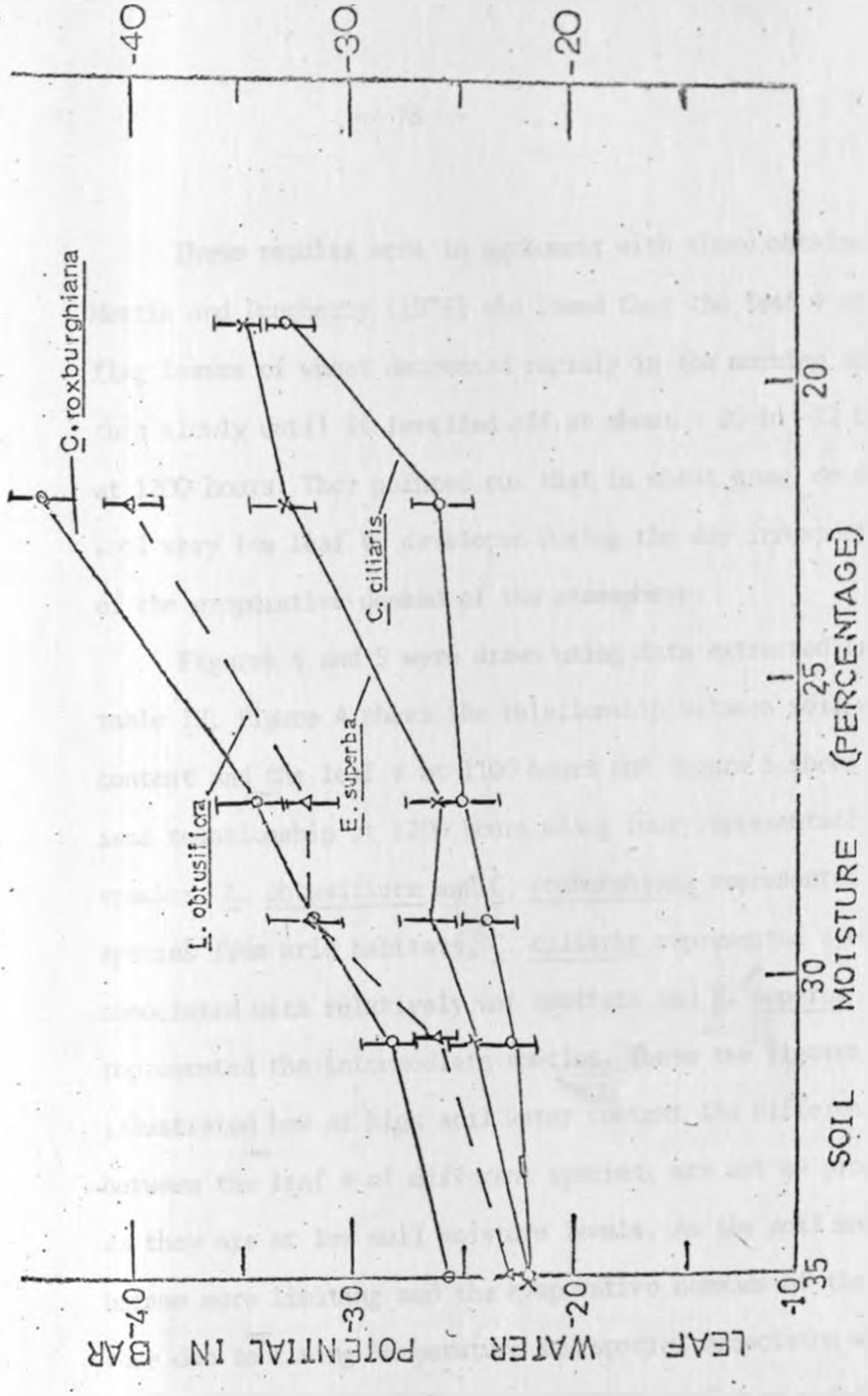


Figure 5:

Leaf water potential of C. roxburghiana, L. obtusiflora, E. superba and C. ciliaris measured in the field at Athi River at noon in relation to decreasing soil moisture. Light intensity was between 2400 and 2600 μE m^{-2} $sec.^{-1}$. Each point is an average of not less than three determination made on each of at least three tufts of the same species.

These results were in agreement with those obtained by Martin and Dougherty (1975) who found that the leaf ψ of the flag leaves of wheat decreased rapidly in the morning and then slowly until it levelled off at about - 20 to -22 bars at 1200 hours. They pointed out that in wheat grown on dry soil very low leaf ψ developed during the day irrespective of the evaporative demand of the atmosphere.

Figures 4 and 5 were drawn using data extracted from table IV. Figure 4 shows the relationship between soil water content and the leaf ψ at 1100 hours and figure 5 shows the same relationship at 1200 hours using four representative species. L. obtusiflora and C. roxburghiana represented species from arid habitats, C. ciliaris represented species associated with relatively wet habitats and E. superba represented the intermediate species. These two figures illustrated how at high soil water content the differences between the leaf ψ of different species, are not as pronounced as they are at low soil moisture levels. As the soil moisture became more limiting and the evaporative demands of the air rose due to rising temperature and species associated with arid conditions developed more negative leaf ψ at a faster rate than the species associated with relatively wetter places.

Even at noon when light intensity was high enough to enable the stomata of all species to be fully open, there were leaf ψ differences between different species.

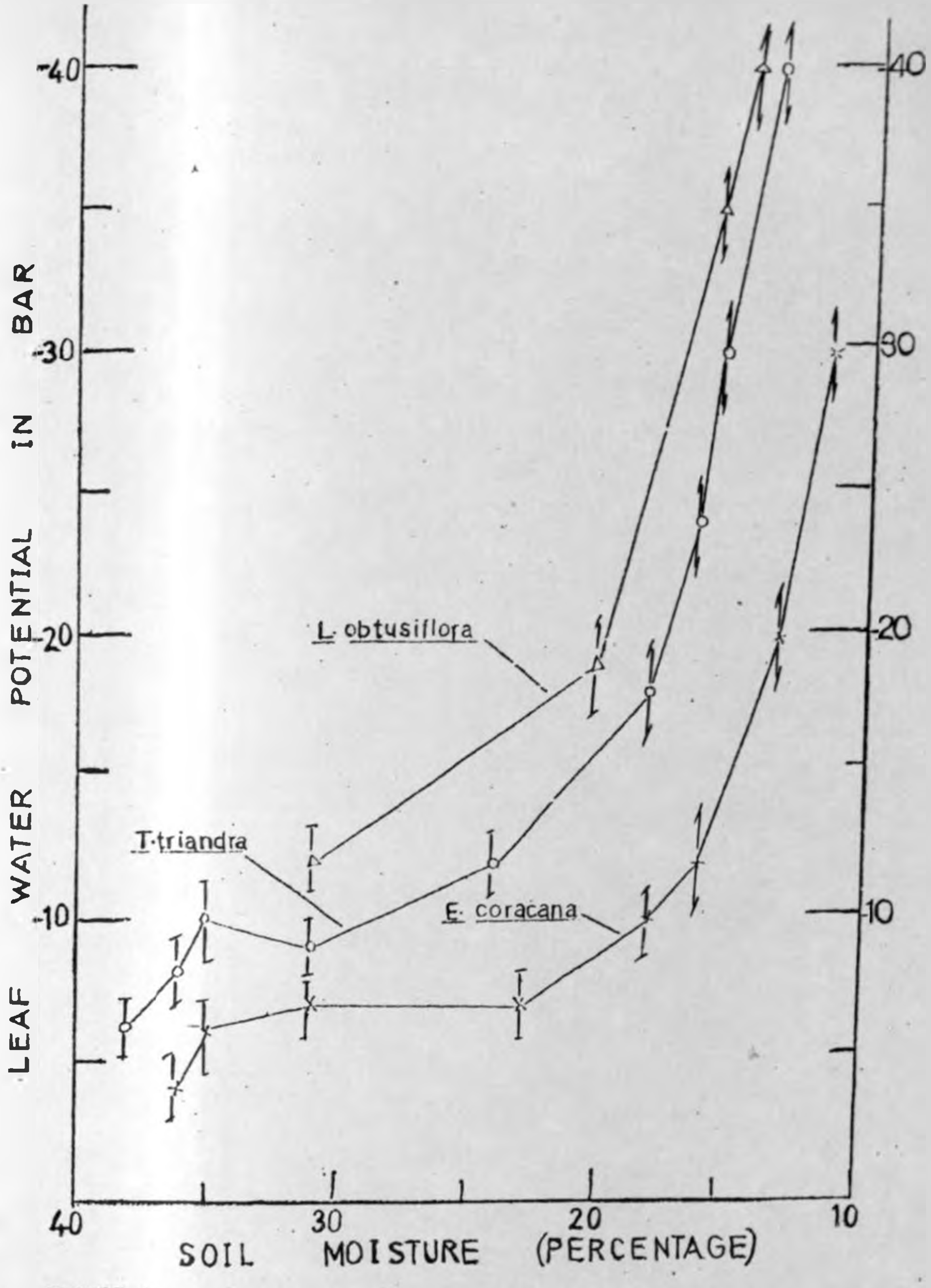


FIGURE 6:

Leaf water potential of L. obtusiflora, T. triandra and E. coracana measured at decreasing levels of soil moisture under artificial light of 1500 µE $m^{-2}sec.^{-1}$. Each point is the average of determinations made on three plants.

The distinctively low leaf water potential could not be attributed to any feature other than some internal characteristics possessed by species adapted to arid conditions. These results suggest that there might be a relationship between the distinctly more negative leaf water potential and adaptation to arid conditions in C_4 grasses.

Results presented in Figure6were measured using potted plants under artificial light. Potted plants were used in order to standardize the depth of root penetration. These results indicated that inspite of the fact that the pots used by all species were of the same size, L. obtusiflora and T. triandra had more negative leaf ψ than E. coracana irrespective of the soil moisture level. The results were consistent with those shown in figures 4 and 5 obtained under natural field conditions where differences in root depth might have existed.

Figure 7 illustrates the diurnal trend of leaf water potential of four C_4 grass species at 29% soil moisture level. These results demonstrate the influence of increasing light intensity and the concomitant decreasing atmospheric relative humidity on leaf ψ during the day. All the plants used were growing under the same environmental conditions.

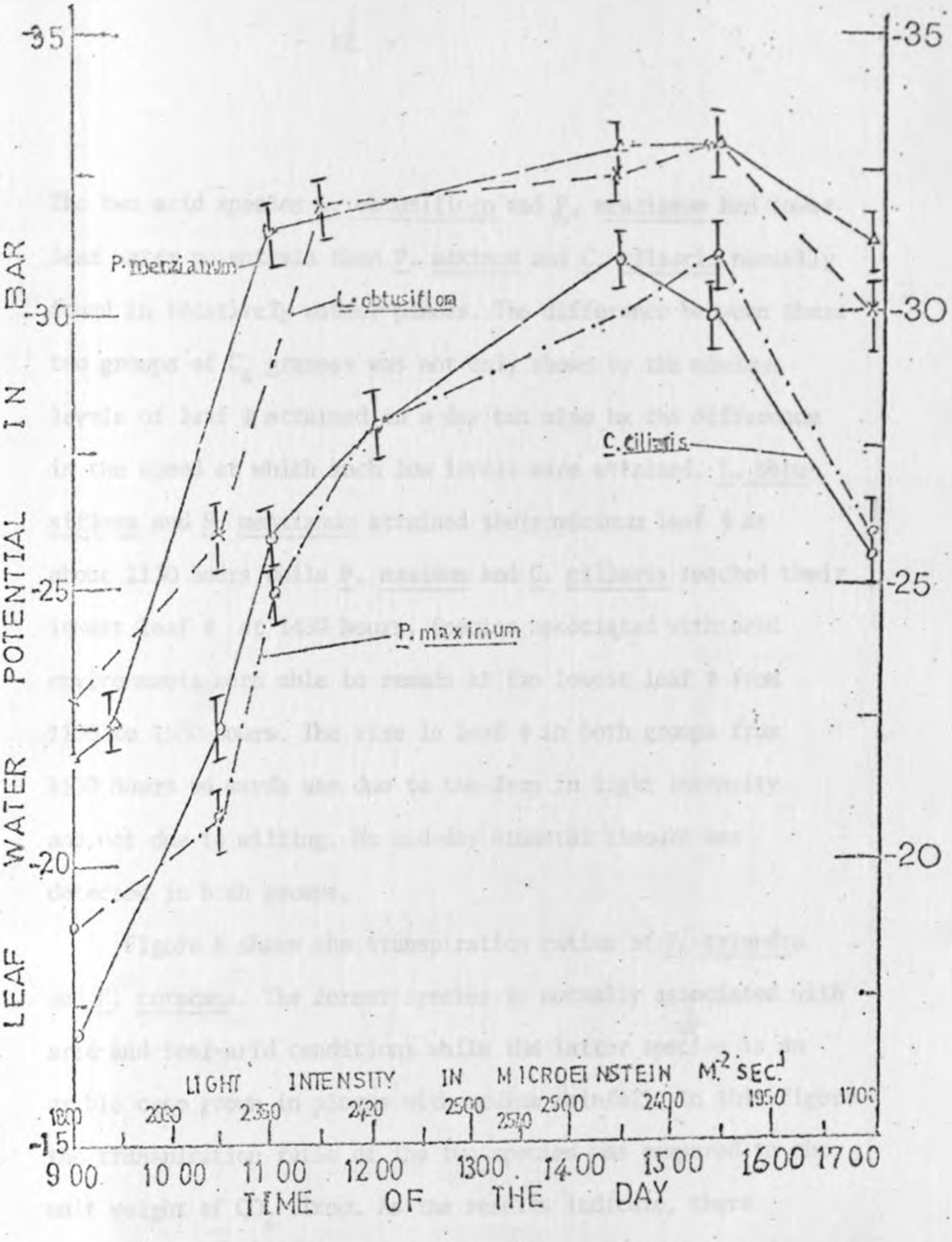


Figure 7:

Leaf water potential of P. menzianum, L. obtusiflora, C. ciliaris and P. maximum in relation to changing light intensity throughout the day and measured at 29% soil moisture. Each point is the average of not less than three determinations made on each of three tufts of the same species.

The two arid species L. obtusiflora and P. menzianum had lower leaf water potentials than P. maximum and C. ciliaris normally found in relatively wetter places. The difference between these two groups of C_4 grasses was not only shown by the minimum levels of leaf ψ attained in a day but also by the difference in the speed at which such low levels were attained. L. obtusiflora and P. menzianum attained their minimum leaf ψ at about 1130 hours while P. maximum and C. ciliaris reached their lowest leaf ψ at 1430 hours. Species associated with arid environments were able to remain at the lowest leaf ψ from 1130 to 1530 hours. The rise in leaf ψ in both groups from 1530 hours on wards was due to the drop in light intensity and not due to wilting. No mid-day stomatal closure was detected in both groups.

Figure 8 shows the transpiration ratios of T. triandra and E. coracana. The former species is normally associated with arid and semi-arid conditions while the latter species is an arable crop grown in places with medium rainfall. In this figure the transpiration ratio of the two species was compared to the unit weight of CO_2 fixed. As the results indicate, there was no marked difference between the water requirements of the two species at high leaf ψ. Differences appeared only at very low leaf water potentials. Both T. triandra and E. coracana exhibited sharp increases in their transpiration ratios at very low leaf ψ although the transpiration ratio of

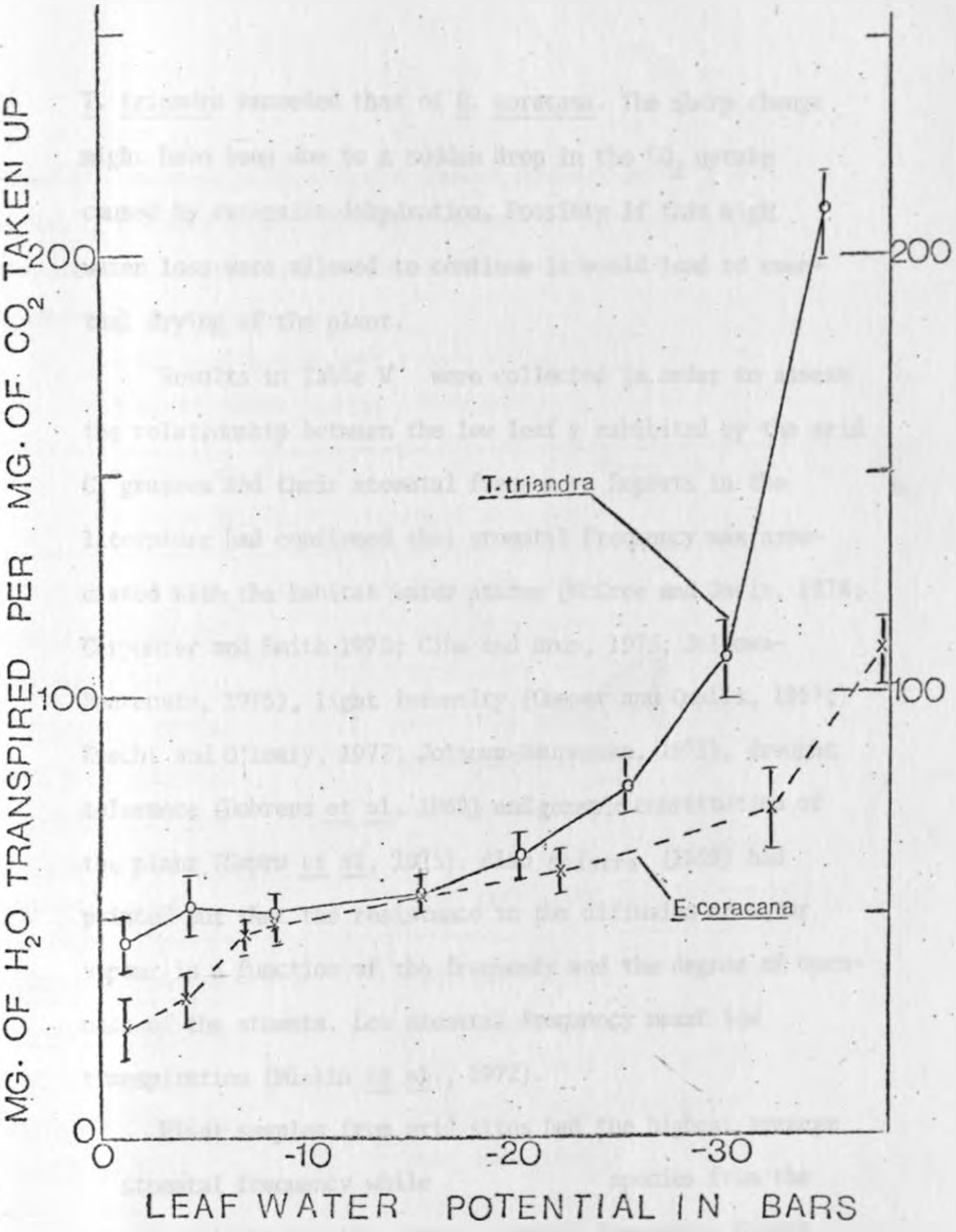


FIGURE 8:

The transpiration/photosynthesis ratio of T. triandra and E. coracana expressed as a function of the decreasing leaf water potential. Each point is the average of determinations made on three plants.

T. triandra exceeded that of E. coracana. The sharp change might have been due to a sudden drop in the CO_2 uptake caused by excessive dehydration. Possibly if this high water loss were allowed to continue it would lead to eventual drying of the plant.

Results in Table V were collected in order to assess the relationship between the low leaf ψ exhibited by the arid C_4 grasses and their stomatal frequency. Reports in the literature had confirmed that stomatal frequency was associated with the habitat water status (McCree and Davis, 1974; Carpenter and Smith 1975; Ciha and Brun, 1975; Jolsova-Baurenska, 1975), light intensity (Cooper and Qualls, 1967; Knecht and O'leary, 1972; Jolsova-Baurenska, 1975), drought tolerance (Dobrenz et al. 1969) and genetic constitution of the plant (Sapra et al, 1975). Also Gaastra (1959) had pointed out that the resistance to the diffusion of water vapour is a function of the frequency and the degree of openness of the stomata. Low stomatal frequency meant low transpiration (Miskin et al., 1972).

Plant samples from arid sites had the highest average stomatal frequency while species from the wetest habitats had the lowest stomatal frequency. Plants which are often found in a wide range of habitats had varying numbers of stomatal frequency depending on the nature of the habitat where the specimens were collected from. The results supported the findings of Shearman and Beard (1972) and Teare et al, (1971) who pointed out that species with more than one ecotypes have varying numbers of stomatal frequency.

TABLE V

Number of stomata per cm^2 expressed as stomatal frequency in various C_4 species adapted to different soil moisture regimes. Each figure is the average of several counts on not less than 10 epidermal impressions.

A = No. of stomata on lower surface per cm^2

B = No. of stomata on upper surface per cm^2

NATURAL HABITAT	SPECIES	A	B	$\frac{A+B}{2}$	Group Mean	SD	LSD
High rainfall vegetation	*Pennisetum purpureum*	9280	7670	8480			
	Pennisetum clandestinum	7220	9810	8520			
	Digitaria velutina	9370	4900	7140			
	Rhynchelytrum repens	12490	14630	13560	9591	92.9	
	Setaria verticillata	10890	10350	10620			
	Sporobolus filipens	13560	14370	13970			
	Cenchrus ciliaris (Biluera)	11150	6380	8770			
	Digitaria scalarum	9560	1780	5670			1,040
Semi-arid vegetation	*Digitaria macroblephere*	15940	9560	12750			
	Heteropogon centortus	10440	13380	11910			
	Eragrostis superba	11900	21360	19130			
	Sporobolus fimbriatus	19999	20520	20260	15648	106.7	
	Hyparrhenia hirta	19010	6020	12520			
	Chloris gayana	21590	18740	20170			
	Aristida acloensis	13920	16060	14990			
	Eragrostis branii	9820	21420	15620			
	Hyparrhenia filipendula	17850	9100	13480			2,119

TABLE V Cont.

NATURAL HABITAT	SPECIES	A	B	$\frac{A+B}{2}$	Group Mean	SD	LSD
Arid vegetation	Cynodon dactylon	24000	26770	25390			
	Leptochloa obtusiflora	22160	25550	23860			
	Chloris pycnothrix	27660	25880	26770			
	Chloris roxburghiana	35070	40010	37540			
	Sporobolus sp.	20240	25980	23110	27269	144.1	
	Harpachne schimperi	20260	33900	27080			
	Themeda triandra (Athi)	23110	27500	25510			
	Panicum maximum (Hakneni)	27170	29010	29090			2,580
Varying habitats	*P. maximum* (Chirono-moist)	19930	22000	20970			
	P. maximum (Kedong-semi-dry)		22310				
	P. maximum (Makueni-dry)	27170	29010	29090			
	T.*triandra* (Kenong-semi-dry)	14100	8920	11510			
	T. triandra (Athi-dry)	23110	27500	25310			

Available results indicated that there is a close relationship between increasing habitat aridity and increasing stomatal frequency. Even the species such as P. maximum and T. triandra, with more than one ecotypes, were represented, in arid habitats, by ecotypes having higher **stomatal** frequencies compared to the ecotypes of the same species found in moist habitats.

DISCUSSION

It is now well established that water moves from the soil through the plant to the atmosphere under the influence of a gradient in water potential (Ψ) existing within the plant (Meyer et al., 1960; Dainty, 1963; Koslowski, 1964; Kramer, 1969; Hsio, 1973; Bidwell, 1974). As water moves it encounters a number of resistances which impede its flow. The resistances include the viscosity of the transpiration solution, the permeability of various membranes traversed and the narrowness of passages within the conducting cells such as xylem vessels and stomata. If the plant system were regarded as a steady state system with a constant flow of water, then the drop in potential across such a system would be related to the magnitude of the resistance in the system.

Besides depending on the internal resistances, plant Ψ is greatly influenced by the soil Ψ and the atmospheric evaporative demands. All these factors combine to establish the potential difference between the leaf Ψ and the soil Ψ. As a result of this potential difference water will be drawn from the soil through the leaves to the atmosphere. If the soil has enough water to meet the transpirational demands of the plant, then the magnitude of the leaf water potential will remain at the level determined by the plant resistances and the evaporative demands.

If different plant species are subjected to similar soil water conditions and similar atmospheric evaporative demands, then any difference in leaf Ψ will be attributed to plant factors which modify the transpiration requirements of the plant. Therefore, on the basis of this argument it can be stated that the differences in leaf Ψ data in TableIV and Figure 4, with respect to different species grown under similar conditions, must have been due to differences in internal plant factors characteristic of each species. The view that different plants experience different plant Ψ levels under similar environmental conditions is supported by Ehleringer and Miller (1975). These workers reported that the leaf water potential of monocotyledons was more negative than that of dicotyledons when grown under the same conditions.

As Walter (1973) pointed out, it is the difference in response of different plant species to similar growing conditions which enables one species to tolerate a given environmental stress better than another species. Other than the difference in stomatal frequency which existed between arid and wet C_4 grasses (Tab. V), there were no other observable structural and anatomical differences between the two groups of grasses. It is most likely that the differences in leaf Ψ values were due to physiological and stomatal frequency modifications associated with C_4 grasses adapted to arid conditions. On the basis of the results obtained, it is certain that the very low leaf ψ attained at a relatively faster rate is an adaptive feature of arid C_4 grasses. These results are supported by Simmelsgaard (1976), who found that at the root medium of Osmotic potential ranging between 0 and -14 bars, the leaf ψ of drought hardened plants was more negative than that of the control.

From the results of the diurnal variation in leaf water potential at 29% soil moisture, it was noticed that C_4 grasses normally found in arid places attained their lowest leaf ψ levels faster than C_4 grasses normally found in wet places. Since there was an apparent relationship between light intensity and variations in leaf ψ in all species (Fig. 7), the fast drop of the leaf ψ of C_4 grasses associated with arid sites could be due to their faster stomatal response to light changes.

Although it could not be proved beyond doubt which factors were directly responsible for the very negative leaf ψ values, stomatal frequency might have had something to do with it. Turner (1970) commenting on the importance of stomata in regulating transpiration said that the regulation of transpiration by stomata depended on both the stomatal number and dimensions. Also Miskin and Rasmusson (1970) reported that the lines of barley which had a 25% decrease in stomatal frequency also had a 24% reduction in their transpiration rate. Results in Table V indicated that arid species associated with high stomatal frequency are also characterized by more negative leaf ψ (Fig. 7). Results showed later in Figs. 18 & 19 indicated that species having high stomatal frequency were also associated with high leaf and mesophyll resistances.

From the available results it could be concluded that the low leaf water potential and high stomatal frequency are very closely related to the adaptability of C_4 grasses to arid conditions. Such a more negative leaf ψ would exert a strong extraction force on soil moisture and enable the plant to obtain its water requirements from relatively dry soils. As results in Figures 5 and 8 indicate the differences between the species adapted to arid conditions and those normally found in moist habitats are more apparent under low soil water potential. This means that the C_4 grasses adapted to arid conditions will only exhibit their adaptive advantages under water stress conditions.

CHAPTER IV

THE INFLUENCE OF SOIL MOISTURE STRESS ON PHOTOSYNTHESIS AND LEAF DIFFUSIVE RESISTANCE OF C_4 GRASSES

LITERATURE REVIEW

One of the facts which make soil water stress measurements difficult to relate directly to plant growth responses is the manner in which water stress affects a wide range of plant metabolic processes. Water is involved in almost all biochemical processes of a plant and its reduction due to stress will transduce a multiplicity of primary and secondary growth responses (Slatyer, 1969; Weatherley, 1970; Hsiao, 1973). Although a great deal of research has been carried out on this subject, more information is still required in order to discover all the links between water variations and the number of growth connected with them. Information is still required on the physiological events underlying the morphogenetic effects of water stress at different stages of particular crop plants. It is also necessary to know at which level of stress do processes such as photosynthesis begin to be markedly impeded in specific plants especially those with the C_4 syndrome.

The objective of this part of the study was to assess the influence of soil moisture stress on the photosynthesis and leaf diffusive resistance of C_4 grasses adapted to arid habitats.

Past attempts to assess the effect of water stress on growth have tended to centre on carbon dioxide assimilation, stomatal movement and structural development (Kramer, 1973;

Slatyer and Bierhuzien, 1964b, Hiller and Greenway, 1968; Slatyer 1969; Troughton, 1969; Acevedo et al, 1971; Hsio 1973). As far as CO_2 assimilation is concerned, it is known that much of the reductions caused by water stress are due to the influence of stress on stomatal closure. Slatyer (1973) pointed out that in controlled experiments, short periods of water stress have no effect on the photosynthetic apparatus themselves until stress greater than that required to induce permanent wilting is imposed. However, Hsio (1973) pointed out that there was evidence that non stomatal effects of mild water stress on net CO_2 fixation did exist in some species such as cotton, tobacco and sunflower.

Generally, photosynthetic capacity decreases due to stomatal closure or due to the dehydration of the photosynthetic apparatus. When the stress becomes severe even negative values of photosynthesis may develop (Hsiao 1973). Slatyer (1969) confirmed that the key compounds in the photosynthetic reduction of CO_2 such as ATP, NADPH and PGA remain unaffected until severe stress sets in. Iljin (1957) observed that one of the commonly reported effects of water stress on carbohydrate metabolism is the increase of sucrose synthesis and an immediate suppression of polysacharide synthesis. It is to this increase in sucrose synthesis that Hiller and Greenway (1968) attributed the often reported reduction in starch levels due to water stress.

Although it is generally accepted that the major indirect influence of water stress on photosynthesis is on stomatal movement, Raschke (1975) pointed out that stomata are insensitive to reduction in plant water potential until a threshold is reached. He added that this threshold is between -7 and -18 bars depending on the type of plant species involved. In this case one would not expect the stress influence mediated through the activity of stomata to proceed uniformly from the very beginning of the stress to the end. One would expect an initial period of no response followed by a gradual increase in response when the threshold is passed. It is necessary to know whether C_4 grasses possess this kind of response.

There are conflicting reports about the relationship between photosynthesis and drought hardness. Henckel (1964) reported that pre-sowing hardening of plants caused the drought hardened plants to maintain a higher rate of photosynthesis than the control during water stress conditions. He attributed the increased photosynthetic rate to the higher hydrophilic nature of protoplamic colloids which have been subjected to drought hardening treatment. However, Collatz _et al_, (1976) working on _Eucalyptus socialis_ found no difference between the photosynthesis of the hardened and control under drought conditions. It would be interesting to find out whether the C_4 species naturally adapted to drought conditions possess the photosynthetic features which Henckel (1964) attributed to drought hardened seedlings.

Stomatal closure due to water stress does not only affect the uptake of CO_2 but it also influence the rate at which moisture diffuses out of the leaf. The ease with which water vapour and gaseous exchange will take place between the mesophyll cells and the atmosphere outside the leaf will depend on the magnitude of resistances along the diffusion passage. Generally, the total resistance (R_t) to water vapour diffusing from the leaf, is equal to the sum of all the resistances in the passage. Such resistances are cuticular resistance (R_c), mesophyll cell wall resistance (R_w), substomatal cavity resistance (R_i) and stomatal pore resistance (R_s). Since the water vapour which passes through the stomatal pores first evaporates from the walls of mesophyll cells, R_s is in series with R_w and R_i and it is in parallel with R_c (Cowan and Milthorpe 1968). Therefore the reciprocal of the total resistance in the leaf is represented by:

$$\frac{1}{R_t} = \frac{1}{R_c} + \frac{1}{R_s + R_w + R_i}.$$

For practical purposes it is only stomatal resistance which is measured in order to assess the effects of environment changes on the leaf resistance. This is due to the fact that of all the resistances in the leaf, it is the stomatal resistance which is most variable.

Variations in the stomatal resistance is responsible for most of the moisture loss control exercised by most leaves (Raschke 1975).

Various workers have tried to use artificial methods of increasing stomatal resistance as a way of reducing water loss. Various chemical compounds are used along these lines to serve as antitranspirants (Gale, 1961; Slatyer and Bierhuzen, 1964C; Angus and Bielorai, 1965; Zelitch, 1964). What antitranspirant compounds do is to increase the diffusive resistance and in so doing reduce the water loss. Generally, the way a plant resists excessive water loss determines its ability to survive under arid conditions. It was reported by Downes (1969) that under comparable conditions C_4 plants had stomatal diffusive resistances two or three times higher than C_3 plants. There is need to find out whether diffusive resistance varies within the C_4 group in relation to whether the species is adapted to aridity or not.

Variations in leaf resistance might enable a plant to retain as much water as possible while at the sametime being able to obtain enough CO_2 for photosynthesis. Cowan (1972) suggested that stomatal oscillations may affect favourably the ratio between CO_2 assimilation and transpiration thus optimizing the relationship between assimilation and growth.

METHODS

(i) Growth experiments

In order to evaluate the effects of soil water stress on the growth of some C_4 grasses, simulated drought conditions were created as follows: Six wooden boxes each 130cm long, 60 cm wide and 130 cm deep were constructed and placed in the green house at the EAAFRO Muguga Research Station. Each of these boxes was filled with garden soil and Bouyoucos moisture resistance blocks were inserted at 100, 75, 25 and 10 cm levels. Fairly uniform young seedlings of P. maximum, T. triandra and L. obtusiflora were transplanted into each of the six boxes. Each box contained nine seedlings three for each species.

To begin with all the boxes were thoroughly watered but afterwards only three boxes were watered regularly while the other three were not watered for a period of three months. The bottoms of the boxes were provided with holes to allow free drainage. Weekly growth measurements and soil moisture readings were recorded. Growth was determined by leaf counting and measuring, non-destructively by linear methods of Kemp (1960), area of fully expanded green leaves. Tillers and flowered culms were also recorded. To avoid leaf loss, all the dry leaves were counted and removed during sampling.

(ii) Photosynthesis

The specimens which were used in the determinations of carbon dioxide uptake were grown in pots at the University of Nairobi as described earlier in this thesis. To prevent the roots of the potted plants from growing out through the bottoms of the pots into the ground, the pots were placed on boards and then moved round regularly. The CO_2 uptake was determined in the laboratory by an open gas analysis system using a Beckman 215 infra-red gas analyser, following the procedure described by Tieszen (1973) and Imbamba and Tieszen (1977). One or two leaves of the potted plant whose CO_2 uptake had to be measured were first sampled for the determination of leaf water potential. Then another intact leaf of the same plant was inserted into the assimilation chamber for the CO_2 uptake measurements. Soil moisture content was determined gravimetrically using soil samples scooped from the pot at least 5 cm below the soil surface.

Leaf temperature was measured by means of a thermocouple placed on the lower surface of the leaf in the assimilation chamber and monitered by a Keithley 160B Digital multimeter. The millivolt readings were later converted into degrees centigrade. Light was provided by the incandescent lamps shone through a plastic water tank to reduce the heating effects (Appendix III). Further cooling was provided both by an electric fan and by circulating water round the assimilation chamber. Light intensity was measured in microeinstein per square metre per second ($\mu E\ m^{-2} sec.^{-1}$) with a

LI-COR light meter. Leaf area of the exposed part of the leaf was determined by tracing on a paper and then measuring the area of the tracing with an Allbrit planimeter.

(iii) Transpiration

Transpiration and photosynthetic rates were determined simultaneously by assessing the amount of water given off by the leaf in the assimilation chamber. This was achieved by passing into the assimilation chamber atmospheric air of known concentrations of water and CO_2. Then the out-going air was passed through a Model 880 Dew-point Hygrometer which determined the increase in the water content of the out-going air. The measurements thus obtained were used in the final computation of the actual transpiration rate per unit leaf area.

(iv) Leaf diffusive resistance

The leaf diffusive resistance was measured both in the laboratory and in the field under varying light intensity and soil moisture stress using a LI-COR water vapour Diffusive Resistance Porometer Model LT-60 Comprising of an electric hydrometric sensor first described by Willihan (1964) and improved by van Bavel et al (1965). Well illuminated and fully expanded leaves were used and readings for both the adaxial and abaxial surfaces were always taken at different spots on the same leaf. This precaution was necessary in order to avoid shading one spot for long periods which would lead to stomatal closure. Several leaves were always measured and an average value taken.

R E S U L T S

Figure 9 illustrates the increase in the number of leaves per plant plotted against soil moisture percentage in the case of stressed plants and against days after transplanting in the case of unstressed plants. There was a normal growth increase in the leaves of the unstressed plants until flowering started. L. obtusiflora and T. triandra produced more leaves per plant than P. maximum but since P. maximum had wider and longer leaves its leaf Area Index was much higher than those of the other two species. All the three species were affected by soil moisture stress and from Figure 9 it was not easy to tell which species was most affected. L. obtusiflora and P. maximum wilted at about the same time but T. triandra persisted longer although the difference in time was not very big.

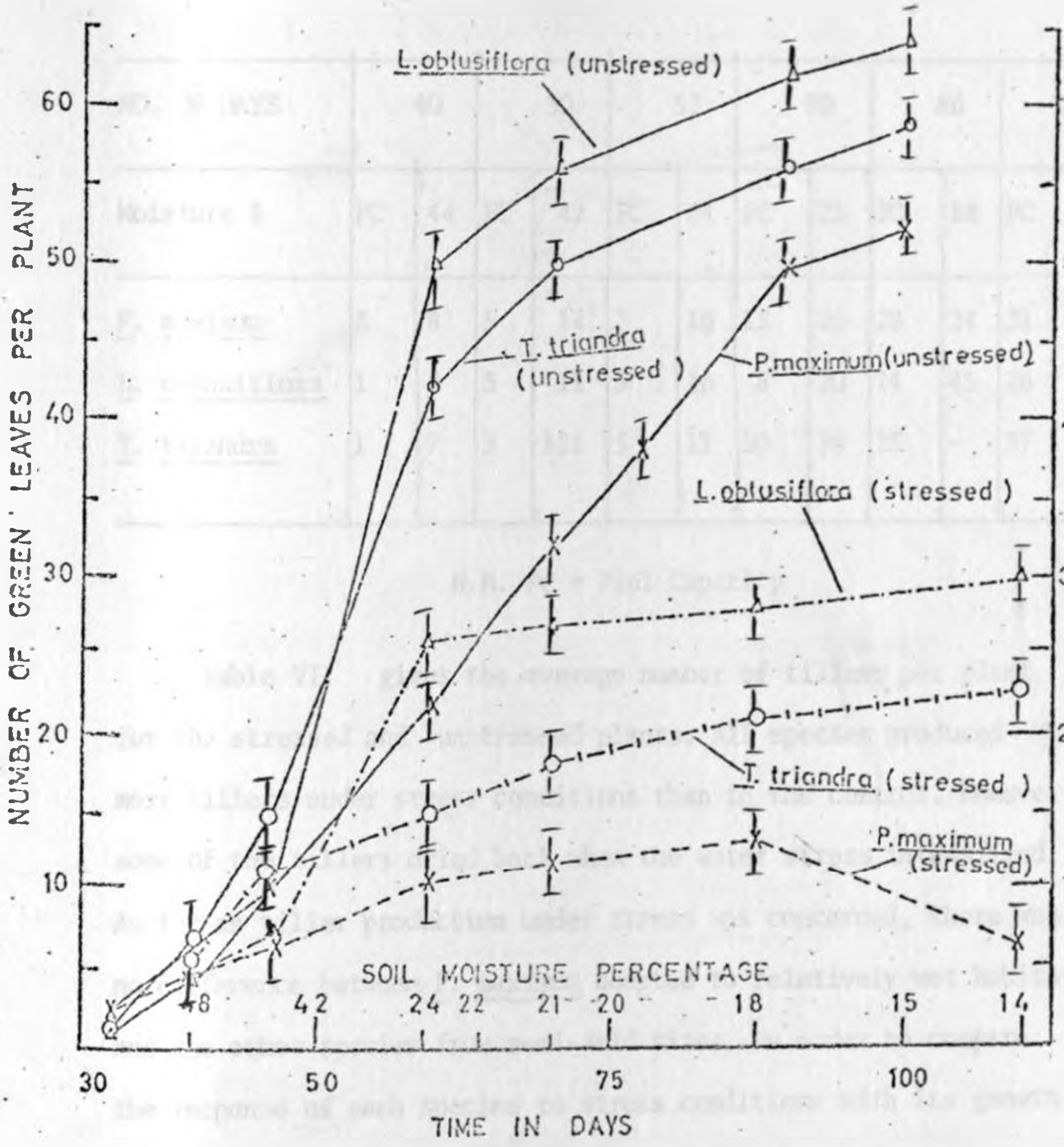


FIGURE 9:

Leaf production of L. obtusiflora, T. triandra and P. maximum grown under increasing soil moisture stress. Each point is an average of counts made on nine plants.

TABLE VI

Average number of tillers per plant recorded under increasing soil moisture stress. Nine plants per species were used for each average.

NO. OF DAYS	40		50		57		70		86		100	
Moisture %	FC	44	FC	42	FC	24	FC	21	FC	18	FC	15
P. maximum	3	8	5	14	7	16	15	26	28	24	31	24
L. obtusiflora	1	5	3	11	3	16	8	20	24	45	26	47
T. triandra	1	7	3	121	5	11	10	36	23	-	37	43

N.B. FC = Fiel Capacity

Table VI gives the average number of tillers per plant for the stressed and unstressed plants. All species produced more tillers under stress conditions than in the control. However, some of the tillers dried back when the water stress intensified. As far as tiller production under stress was concerned, there was no difference between *P. maximum* adapted to relatively wet habitats and the other species from semi-arid sites. In order to compare the response of each species to stress conditions with its growth under unstressed conditions, the leaves of each species understress were expressed as a percentage of the leaves of the control. Figure 10 illustrates the relative response of each species under water stress.

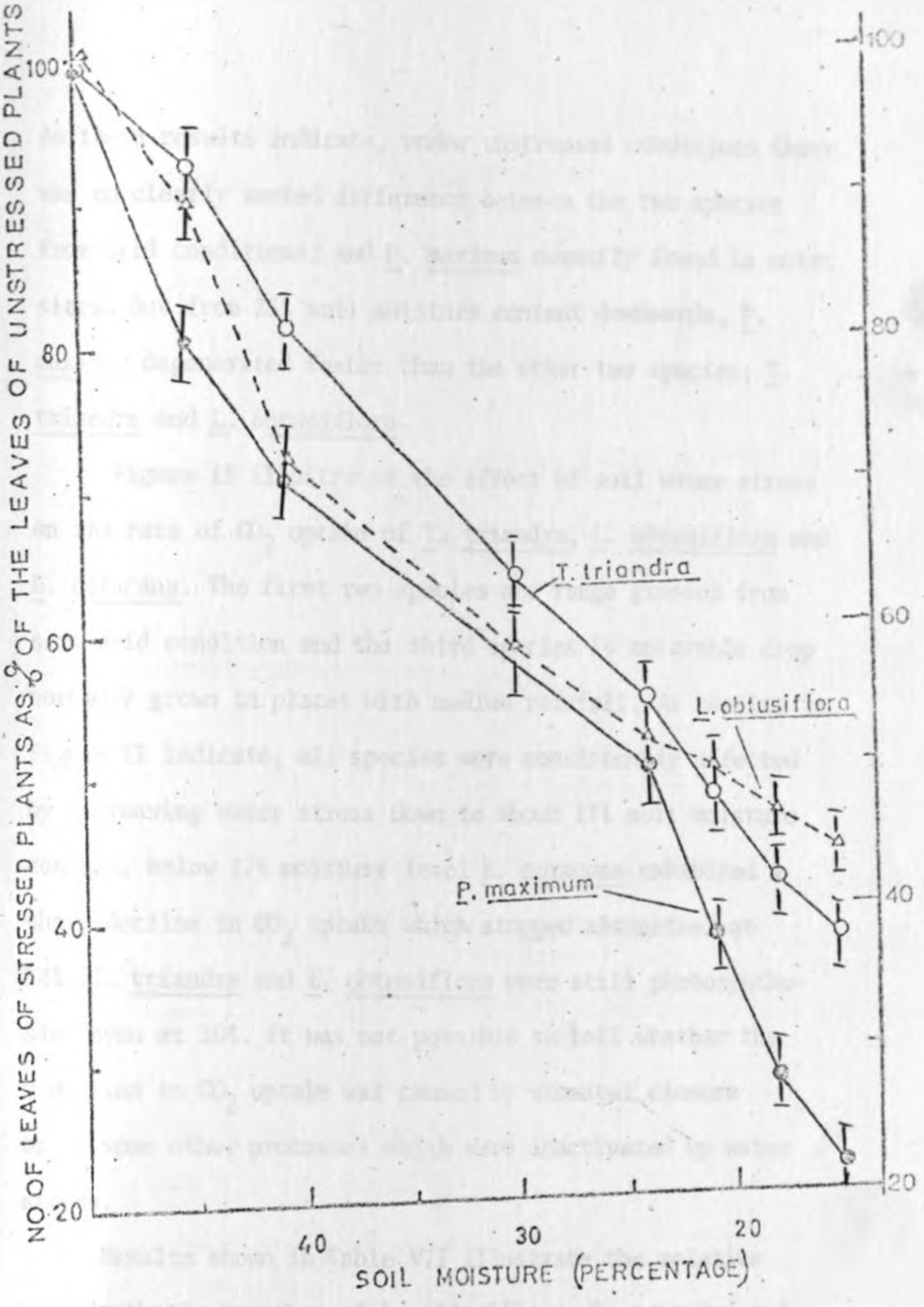


FIGURE 10:

Relative leaf number of L. obtusiflora, T. triandra and P. maximum under stress expressed as percentage of the leaves of plants of the same age growing under control condition. Each point is the average of leaf counts made on nine plants of the same species.

As these results indicate, under unstressed conditions there was no clearly marked difference between the two species from arid conditions; and P. maximum normally found in moist sites. But from 25% soil moisture content downwards, P. maximum degenerated faster than the other two species; T. triandra and L. obtusiflora.

Figure 11 illustrates the effect of soil water stress on the rate of CO_2 uptake of T. triandra, L. obtusiflora and E. coracana. The first two species are range grasses from semi-arid condition and the third species is an arable crop normally grown in places with medium rainfall. As results in Figure 11 indicate, all species were consistently affected by increasing water stress down to about 17% soil moisture content. Below 17% moisture level E. coracana exhibited a sharp decline in CO_2 uptake which stopped altogether at 14%. T. triandra and L. obtusiflora were still photosynthesing even at 10%. It was not possible to tell whether the reduction in CO_2 uptake was caused by stomatal closure or by some other processes which were inactivated by water stress.

Results shown in Table VII illustrate the relative photosynthetic response of L. obtusiflora, T. triandra and E. coracana expressed as percentage of CO_2 uptake at different soil moisture levels compared to the rates determined at 35% soil moisture content. Relative values were used in order to provide a way of comparing the responses of species with dissimilar photosynthetic rates.

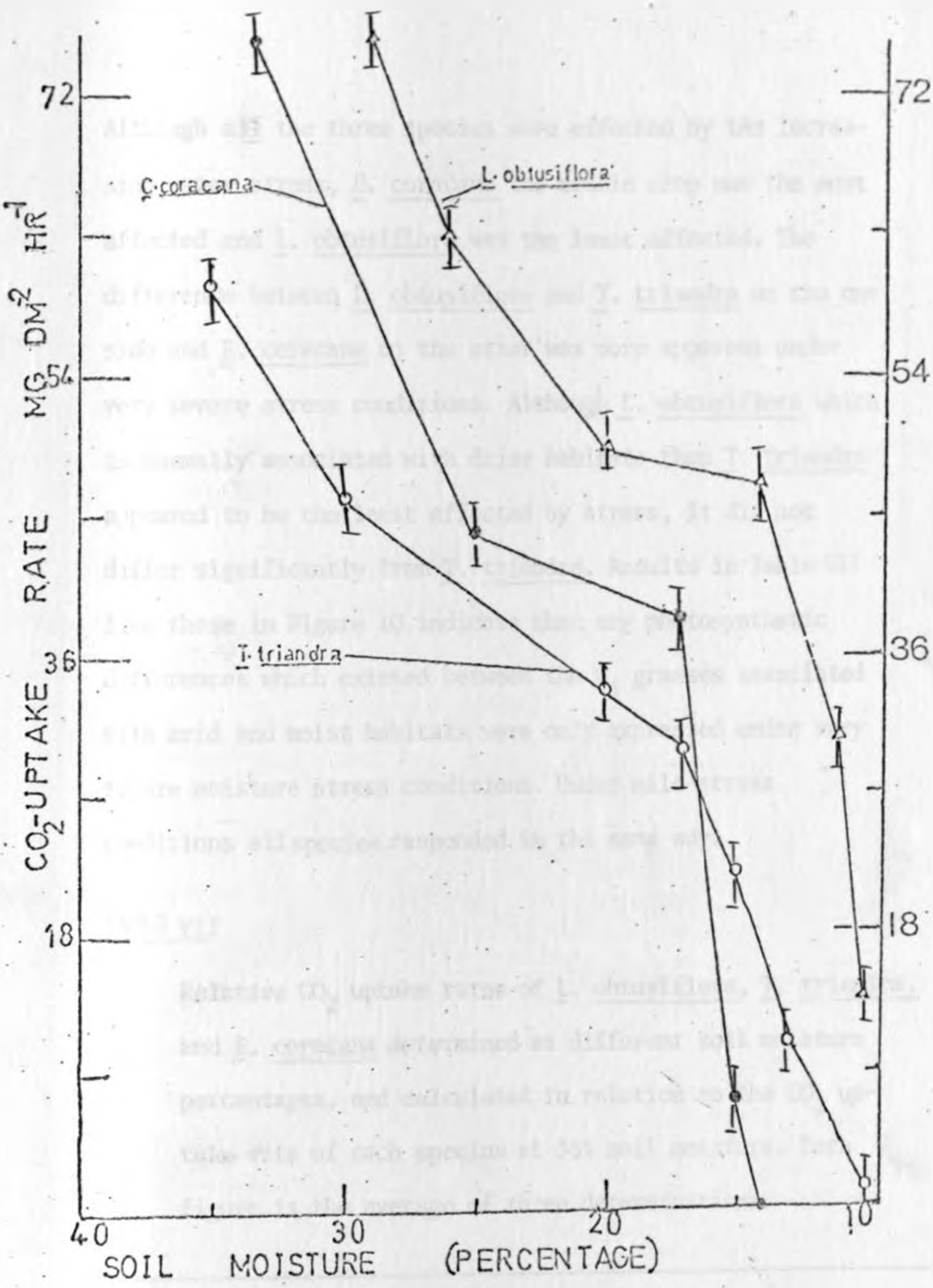


FIGURE 11:

CO_2 uptake rates in E. coracana, L. obtusiflora and T. triandra as a function of decreasing soil moisture. Each point is the everage of three determinations.

Although all the three species were effected by the increasing water stress, E. coracana the arable crop was the most affected and L. obtusiflora was the least affected. The difference between L. obtusiflora and T. triandra on the one side and E. coracana on the other was more apparent under very severe stress conditions. Although L. obtusiflora which is normally associated with drier habitats than T. triandra appeared to be the least affected by stress, it did not differ significantly from T. triandra. Results in Table VII like those in Figure 10 indicate that any photosynthetic differences which existed between the C_4 grasses associated with arid and moist habitats were only expressed under very severe moisture stress conditions. Under mild-stress conditions all species responded in the same way.

TABLE VII

Relative CO_2 uptake rates of L. obtusiflora, T. triandra, and E. coracana determined at different soil moisture percentages, and calculated in relation to the CO_2 uptake rate of each species at 35% soil moisture. Each figure is the average of three determinations.

SOIL MOISTURE %	35	30	25	20	17	15	12
L. obtusiflora	100	91	67	55	53	49	40
T. triandra	100	77	66	57	50	47	15
E. coracana	100	78	54	50	46	11	0

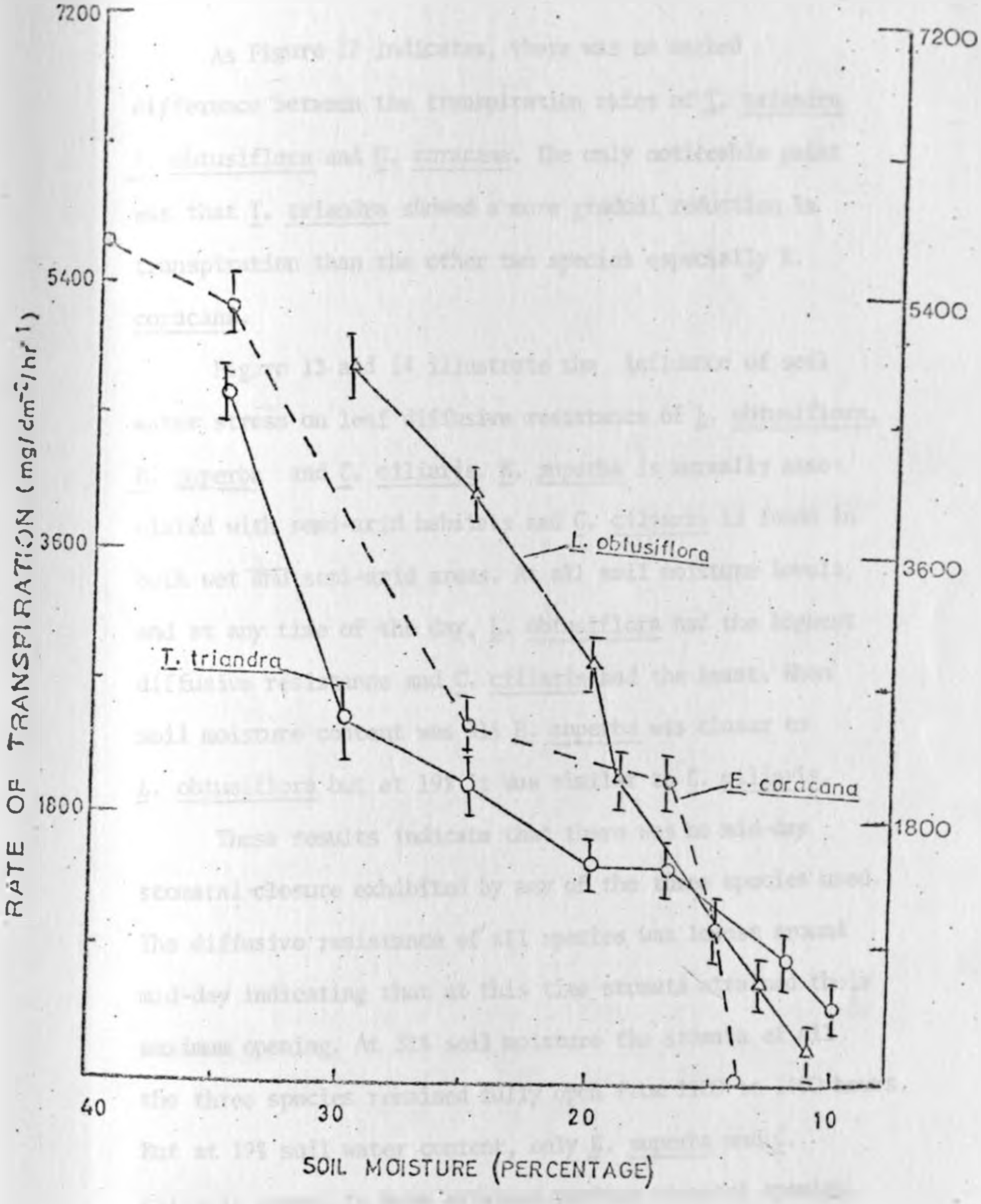


FIGURE 12:

The effect of decreasing soil moisture on the rate of transpiration of attached leaves of L. obtusiflora, T. triandra and E. coracana determined at 30°C. Each point is the average of three determinations.

As Figure 12 indicates, there was no marked difference between the transpiration rates of *T. triandra* *L. obtusiflora* and *E. coracana*. The only noticeable point was that *T. triandra* showed a more gradual reduction in transpiration than the other two species especially *E. coracana*.

Figure 13 and 14 illustrate the influence of soil water stress on leaf diffusive resistance of *L. obtusiflora*, *E. superba* and *C. ciliaris*. *E. superba* is normally associated with semi-arid habitats and *C. ciliaris* is found in both wet and semi-arid areas. At all soil moisture levels and at any time of the day, *L. obtusiflora* had the highest diffusive resistance and *C. ciliaris* had the least. When soil moisture content was 31% *E. superba* was closer to *L. obtusiflora* but at 19% it was similar to *C. ciliaris*.

These results indicate that there was no mid-day stomatal closure exhibited by any of the three species used. The diffusive resistance of all species was lowest around mid-day indicating that at this time stomata attained their maximum opening. At 31% soil moisture the stomata of all the three species remained fully open from 1100 to 1400 hours. But at 19% soil water content, only *E. superba* and *C. ciliaris* seemed to have attained maximum stomatal opening. At high soil moisture stress complete stomatal opening may not occur in species such as *L. obtusiflora* except at very high light intensity.

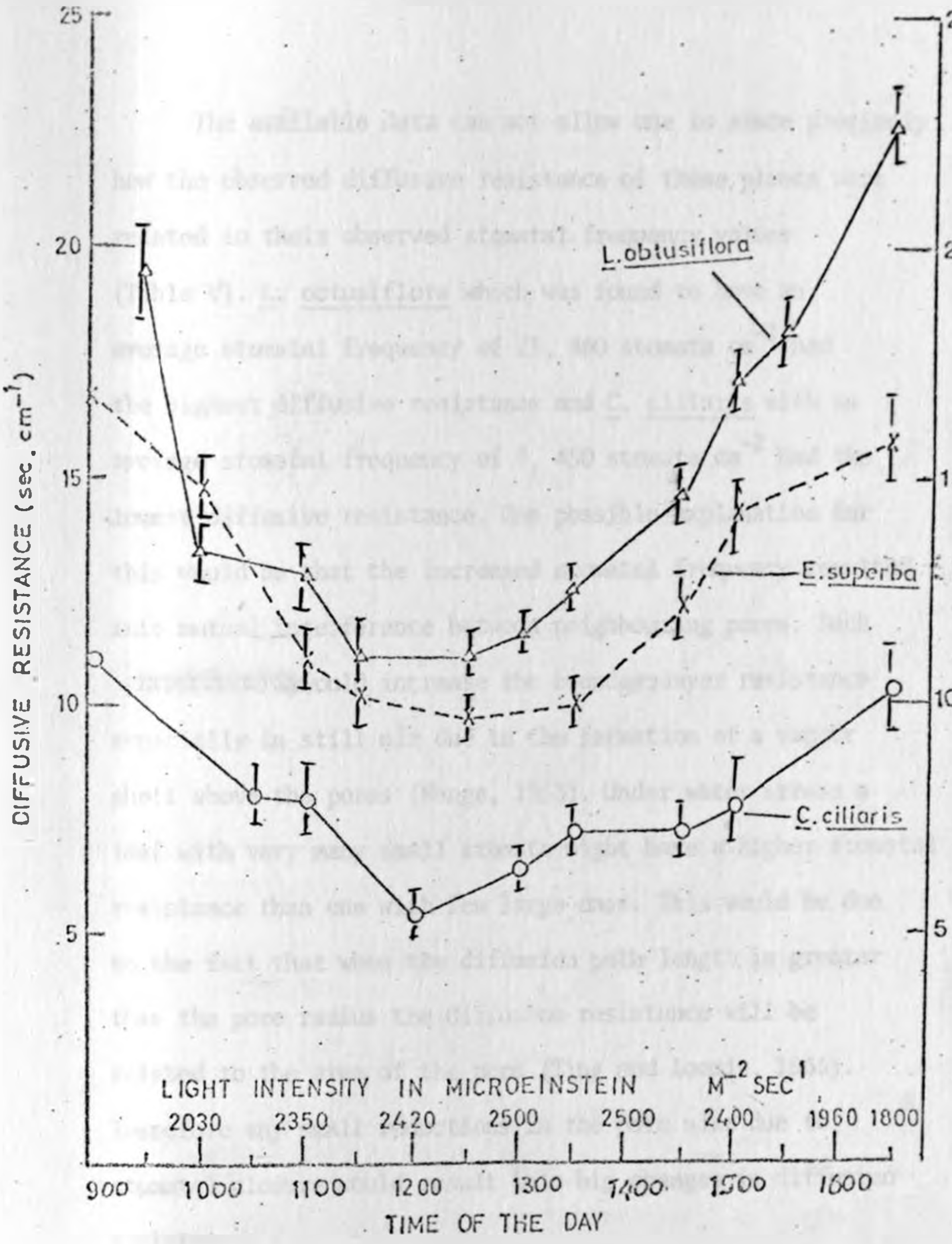


FIGURE 13:

The effect of light intensity on leaf diffusive resistance of L. obtusiflora, E. superba and C.ciliaris measured throughout the day at 31% soil moisture. Each point is the average of several determinations made on at least three tufts of the same species.

The available data can not allow one to state precisely how the observed diffusive resistance of these plants were related to their observed stomatal frequency values (Table V). *L. obtusiflora* which was found to have an average stomatal frequency of 23, 860 stomata cm^{-2} had the highest diffusive resistance and *C. ciliaris* with an average stomatal frequency of 8, 450 stomata cm^{-2} had the lowest diffusive resistance. One possible explanation for this would be that the increased stomatal frequency resulted into mutual interference between neighbouring pores. Such interference would increase the boundary layer resistance especially in still air due to the formation of a vapour shell above the pores (Bange, 1953). Under water stress a leaf with very many small stomata might have a higher stomatal resistance than one with few large ones. This would be due to the fact that when the diffusion path length is greater than the pore radius the diffusion resistance will be related to the area of the pore (Ting and Loomis, 1965). Therefore any small reductions in the pore size due to stomatal closure would result into big changes in diffusion resistance.

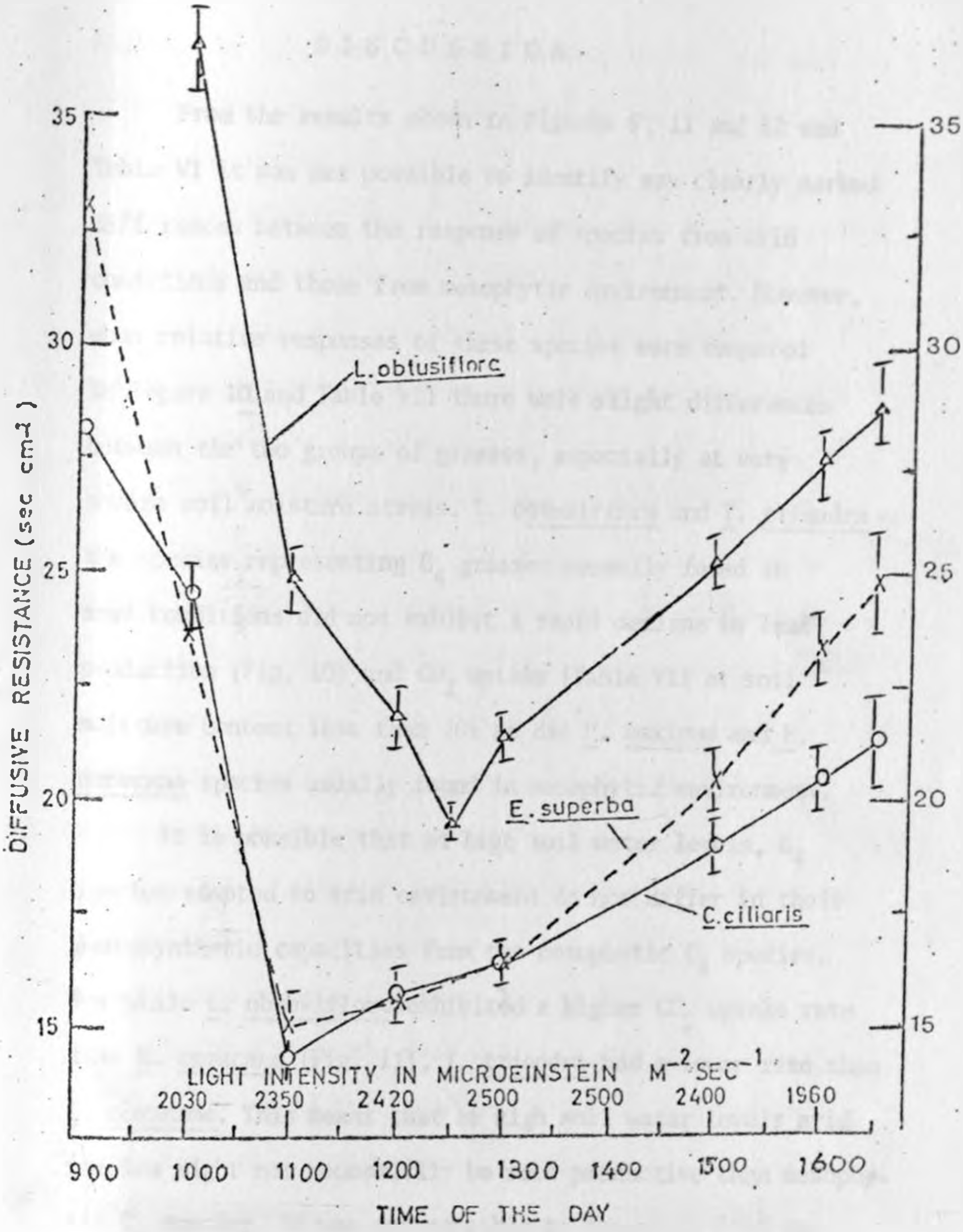


FIGURE 14:

The effect of light intensity on leaf diffusive resistance of L. obtusiflora, E. superba and C. ciliaris measured throughout the day at 19% soil moisture. Each point in the average of several determinations made on at least three tufts of the same species.

DISCUSSION

From the results shown in Figures 9, 11 and 12 and Table VI it was not possible to identify any clearly marked differences between the response of species from arid conditions and those from mesophytic environment. However, when relative responses of these species were compared in Figure 10 and Table VII there were slight differences between the two groups of grasses, especially at very severe soil moisture stress. *L. obtusiflora* and *T. triandra* the species representing C_4 grasses normally found in arid conditions did not exhibit a rapid decline in leaf production (Fig. 10) and CO_2 uptake (Table VII at soil moisture content less than 20% as did *P. maximum* and *E. coracana* species usually found in mesophytic environment.

It is possible that at high soil water levels, C_4 species adapted to arid environment do not differ in their photosynthetic capacities from the mesophytic C_4 species. For while *L. obtusiflora* exhibited a higher CO_2 uptake rate than *E. coracana* (Fig. 11), *T. triandra* had a lower rate than *E. coracana*. This means that at high soil water levels arid species might not necessarily be more productive than mesophytic C_4 species. It was not possible to ascertain from the available results whether the decline in CO_2 uptake and leaf production associated with the increasing soil moisture stress was due to stomatal closure or impeded CO_2 assimilation through other processes.

However, it is generally agreed (Hsiao, 1973), that much of the reduction in CO_2 assimilation during water stress is due to stomatal closure.

As results in Figure 12 indicate there was no apparent difference between the transpiration rates of species associated with arid environments and those found in mesophytic habitats until water stress became very severe. The sharp decline in the transpiration rate of *E. coracana* at soil moisture level of less than 17% might have been due to sudden stomatal closure. The results on transpiration agreed with those on leaf production and CO_2 uptake (Fig. 10 and Table VII). Also results in Figure 8 had indicated that at more negative leaf ψ the transpiration ratio of *T. triandra* was higher than that of *E. coracana*. It is possible that under severe water stress mesophytic species such as *E. coracana* cut down their waterloss by closing their stomata following leaf within, while arid species continue to lose water for a little longer through the partially opened stomata.

The results on the leaf diffusive resistance shown in Figure 13 and 14 indicated that both at low irradiance and at high soil moisture stress *L. obtusiflora* had a higher diffusive resistance than *C. ciliaris* species normally associated with mesophytic environment. These results were consistent with other results recorded earlier in figures 4, 5 and 6 on leaf water potential. It is known that leaf water potential is related to the degree of openness of the stomata.

Therefore the more opened are the stomata the lower the diffusive resistance and the more negative the leaf water potential. All these processes are related to light intensity which controls the openness of the stomata.

Although L. obtusiflora associated with very low leaf Ψ values seems to have the highest diffusive resistance throughout the day (Fig. 13, and 14), it is important to note that this species began the day with very high resistances. The responses in the diffusive resistances of these species which are comparable to diurnal changes in leaf Ψ and light intensity are best shown by the variations in the amplitude between the resistances at low irradiance and 900 or 1600 hrs and at high irradiance at 1200 hrs. L. obtusiflora exhibited wider differences between the mid-day and early morning values than C. ciliaris and E. superba. It is this big reduction in the diffusive resistance caused by irradiance which might be closely related to the more negative leaf Ψ associated with arid C_4 species.

At all levels of soil moisture, the level to which leaf diffusive resistance dropped in response to light intensity depended on the species type. For both species; L. obtusiflora and C. ciliaris, the duration the diffusive resistance remained at the lowest level around midday, depended on both species type and soil moisture stress. At 31% soil moisture, the leaf diffusive resistance of L. obtusiflora and C. ciliaris remained at minimum level for 1½ and 3 hours respectively.

At 19% soil moisture L. obtusiflora hardly leveled off while C. ciliaris remained at minimum values for at least an hour.

These results indicate that there is a direct relationship between the level of soil moisture stress and leaf diffusive resistance. As the soil moisture stress increased it became harder and harder to attain full stomatal opening even at high light intensity at midday. In his review of the plant response to water stress, Hsiao (1973) pointed out that the available evidence had demonstrated that there was a threshold level of water potential value above which leaf resistance and therefore stomatal openings remain unresponsive to changes in leaf water potential. Different plant species have different threshold values and there are species which do not exhibit this behaviour (Boyer, 1970; Fisher et al 1970). Since at 19% soil moisture level the diffusive resistance of both L.obtusiflora and C. ciliaris started rising while light intensity was still increasing (Fig. 14) it may be that stomatal closing started to occur as leaf water potential dropped below the threshold values. These results suggest that L. obtusiflora which is normally found in arid conditions, uses its high diffusive resistance to reduce its water loss when leaf Ψ becomes very negative due to the combined influence of light and soil water stress.

Although it was not possible to state conclusively the exact way in which high stomatal frequency, leaf water potential and high leaf diffusive resistance might be related to each other in order to enhance the adaptation of L. obtusiflora and T. triandra to arid conditions, it is known that some of these characteristics are associated with xeric plants. Carpenter and Smith (1975) pointed out that xeric plant species have more stomata per unit leaf surface area than mesophytic species. Also according to Miskin et al. (1972) higher stomatal frequency should result into higher transpiration rates and bigger reductions in leaf diffusive resistance when the stomata are fully opened. The available results agree with these findings.

The consistently high leaf diffusive resistances associated with species having high stomatal frequency could be attributed to mutual interference between neighbouring stomatal pores. The vapour shell formed above the crowded stomatal pores would interefere with the escaping vapour from the leaf especially when air movement and evaporative demand are low (Meidner and Mansfield 1968).

The results indicating that arid species namely; L. obtusiflora and T. triandra were associated with features such as higher stomatal frequency, more negative leaf ψ and higher leaf diffusive resistance than mesophytic species namely E. coracana, C. ciliaris and E. superba support the view that these features are closely related with the ability of these species to survive under arid conditions.

CHAPTER V

THE INFLUENCE OF LIGHT AND TEMPERATURE ON PHOTOSYNTHESIS AND WATER RELATIONS OF SELECTED GRASSES

LITERATURE REVIEW

The tropical environment in which C_4 grasses are most abundant is characterised by high light intensity, high ambient temperature and intermittent low soil moisture. Solar radiation controls directly the ambient temperature and indirectly influences soil moisture through its influence on rainfall and evapotranspiration. Therefore, in order to evaluate the nature of the water relations of C_4 grasses in the tropical environment, it is necessary to know the response of these plants to light and temperature variations.

Light controls plant water relations directly through its influence on stomatal movement (Bange, 1953; Meidner and Mansfield, 1968; Raschke, 1975) and indirectly through its influence on leaf and air temperature. Light controls general plant growth directly through its involvement in the CO_2 assimilation and indirectly by its effects on process such as endogenous rhythms, flowering and germination (Cumming and Wagner, 1968; Briggs and Rice, 1972).

Light affects photosynthesis both directly and indirectly. It provides the necessary energy quanta which set the complex processes of the light reaction into action (Hoch and Knox 1968; Zelitch, 1971). The energy which is absorbed by chlorophyll molecules is used in the splitting of one of the hydrogen bonds in the water molecule. The process is basically an oxidation-reduction reaction involving accepting and donating electrons.

The ATP thus produced is used in the CO_2 reduction processes leading to both the C_3 and the C_4 carbon compounds. Indirectly, light influences photosynthesis through its effects on stomatal movement which in turn results into the regulation of the gaseous exchange of a plant. Additionally, light influences photosynthesis indirectly by affecting leaf temperature thus in turn affecting the rate of the chemical reactions associated with photosynthesis.

Although a large amount of information is available on the influence of light on photosynthesis in general, there is still alot which can be learnt about the subject. Information is still needed about the way the photosynthetic efficiency in C_4 tropical grasses is related to their productivity. Is the presence of C_4 syndrome an advantage in biomass production or the basic photosynthetic differences between C_3 and C_4 plants are not exhibited in the final dry matter yield? It was suggested by Black (1971) that the C_4 syndrome might have production advantages in the tropics. It is also known that C_4 plants hardly reach a saturation point in increasing light intensity. However, Singh et al (1978) reported that although the leaf area and mean growth rate were higher in C_4 maize than in C_3 cowpea and sunflower the relative growth rate and net assimilation rate of C_3 crops were higher than those of C_4 crop. They concluded that C_4 plants are not better crops than C_3 on the account of their possession of C_4

CO_2-fixation pathway. They suggested that C_4 plants are able to perform better only under special environmental conditions such as high temperature and water stress; conditions which are normally not favourable for C_3 plants. It is necessary to find out whether the adaptive mechanism to water stress conditions are only operative under stress conditions or even when water is not limiting.

It is also known that light and leaf water content are the most important factors regulating stomatal apertures (Zelitch, 1971). In tropical grasslands, plants are usually subjected to severe water stress at high light intensity. It is not clear why the lack of an apparent light saturation point associated with C_4 grasses does not lead to excessive water loss and finally act as a disadvantage on the growth of these plants in the dry tropics. T. triandra, a grass characterizing a large number of semi-arid grassland types (Rattray, 1960) is reported to favour well illuminated sites and does not withstand shaded conditions (van Rensburg, 1952; Bogdan, 1954; Martin, 1966; Acocks, 1966; Bogdan and Kiner, 1967; Ndawula-Senyimba, 1972).

The influence of light on plant growth is closely related to the influence of temperature. Temperature affects plant growth both directly and indirectly. Temperature activates all the metabolic processes and also determines the upper and lower limits of heat energy suitable for proper growth.

Such limits are generally called cardinal temperatures and different plant types are characterised by different cardinal temperatures. C_3 plants have different cardinal temperatures from C_4 plants. C_3 plants have their optimum temperature for proper growth between 20-25°C (Evan et al., 1964; Mitchell, 1956; Tainton, 1967; Black, 1971). C_4 plants have their optimum temperature ranging between 30-40°C (Tainton, 1967; Black, 1971; Tieszen and Imbamba, 1977). C_3 species would exhibit some growth even below 5°C but C_4 plants would grow extremely slowly at temperature around 10-15°C. The maximum temperature which can be tolerated by C_3 plants is between 30 and 35°C while that for C_4 plants is above 50°C (Tieszen and Imbamba, 1977, Imbamba et al. 1977).

Indirectly, temperature influences plant growth by controlling vital processes such as water movement in the soil-plant-atmosphere continuum, photosynthesis, respiration, differentiation and breaking seed and bud dormancy. In the water relations of plants, temperature controls the vapour pressure gradient between the leaf and air. Also air temperature controls the vapour pressure of the evaporation surface in the mesophyll through its effects on leaf water potential (Kramer, 1969). Temperature controls the movement of stomata and generally stomatal opening follows, the temperature curve of CO_2 assimilation (Raschke, 1970).

Dark fixation of CO_2 is said to decrease in Agave americana with increasing night temperature as does stomatal aperture. Schulze et al. (1973) reported that the stomata of desert plants opened with increasing temperature as long as water stress did not interfere.

In many species, the temperature of brightly illuminated leaves is near air temperature if the latter is about 33°C. Below this temperature, leaves tend to be warmer than air and above this temperature leaves are cooler than air (Linacre, 1964). This peculiarity is partly due to the exponential increase in water vapour pressure with temperature, resulting in an increased negative feed back of transpiration and partly due to the increase in stomatal aperture with temperature (Drake et al., 1970). Leaf temperature is influenced by wind speed, relative humidity and transpiration. Etherington (1975) pointed out that by reducing the value of the boundary layer resistance, increasing wind speed tend to increase transpiration losses of water in the low wind speed range. If the leaf temperature is above air temperature due to radiant heating then increasing wind speed causes cooling and reduces the vapour pressure gradient between the leaf and air.

In their review paper on the biochemical basis for photosynthetic adaptation of plants to temperature regimes, McWilliam and Mison (1974), pointed out that the ability of thermophilic plants to sustain active photosynthesis at 35-50°C is associated with the presence of heat stable protein synthesizing mechanism. This meachanism is said to enable plants such as C_4 plants to replace enzymes lost by heat denaturation. The failure of these plants to maintain photosynthesis at temperatures below 10-12°C is suspected to be associated with a breakdown in the synthesis and function of macromolecules concerned with the formation of chlorophyll and enzymes involved in the carboxylation of CO_2. The C_4 plants adapted to temperate zones might possess some adaptive mechanisms which make them cold tolerant.

It is known that temperature does not only influence leaf water potential but it also controls stomatal conductance (Meidner and Mansfield, 1968). From simulated experiments, Haseba (1973) found that by promoting stomatal opening through the increase of insolation it was possible to increase transpiration.

The objective of this part of the study was to find out the way light intensity and temperature influenced the photosynthetic productivity and water relations of C_4 grasses adapted to arid habitats.

METHODS

The leaf water potential of selected species was measured with a pressure bomb as described earlier. Measurements were made using plants grown in pots and those grown in the botanical garden at Chiromo, University of Nairobi. Light intensity measurements both in the field and in the laboratory were made with a LI-COR Model L-185 light meter. Soil moisture was determined gravimetrically.

The rates of CO_2 uptake and transpiration were measured simultaneously using an infra-red gas analyser as decribed in the previous chapter. Total leaf resistance and mesophyll resistance were calculated from data obtained in the process of determining CO_2 uptake. The formulae used are described in Appendix VI. Total leaf resistance was computed on the assumption that water loss through transpiration is largely due to stomatal aparture changes. On the basis of this assumption transpiration resistance is equated approximately to total leaf resistance. Mesophyll resistance was computed by equating it to internal resistance to CO_2 uptake.

The influence of leaf temperature on CO_2 uptake and transpiration rates was measured using potted plants. Intact leaves of potted plants were inserted in the assimilation chamber of the infra-red gas analyser and the rates of CO_2 and transpiration determined at fixed temperature levels.

The required temperature was achieved and maintained by circulating cold or hot water through the water jacket of the assimilation chamber following the techniques described by Tieszen (1973). Soil moisture was kept as near field capacity as possible by watering the posts a day before the determinations.

The light intensity of the lamps used in the laboratory was varied by means of a rheostat inserted in the lamp circuit. Temperature effect measurements were made at maximum light intensity.

RESULTS

Results in Table VIII shows the diurnal variations in leaf water potential of L. obtusiflora, P. menzianum, E. superba, C. ciliaris and P. maximum at varying soil moisture levels. These results indicated that although species attain different levels of a leaf ψ at any given time, all species exhibited the same diurnal pattern related to the diurnal increase and decrease in light intensity. When soil water content was high, the leaf ψ of all species reached their lowest levels at about 1500 hrs and then started to rise again as light intensity decreased. When soil moisture became more and more limiting, the early morning starting point in leaf ψ dropped below the zero value.

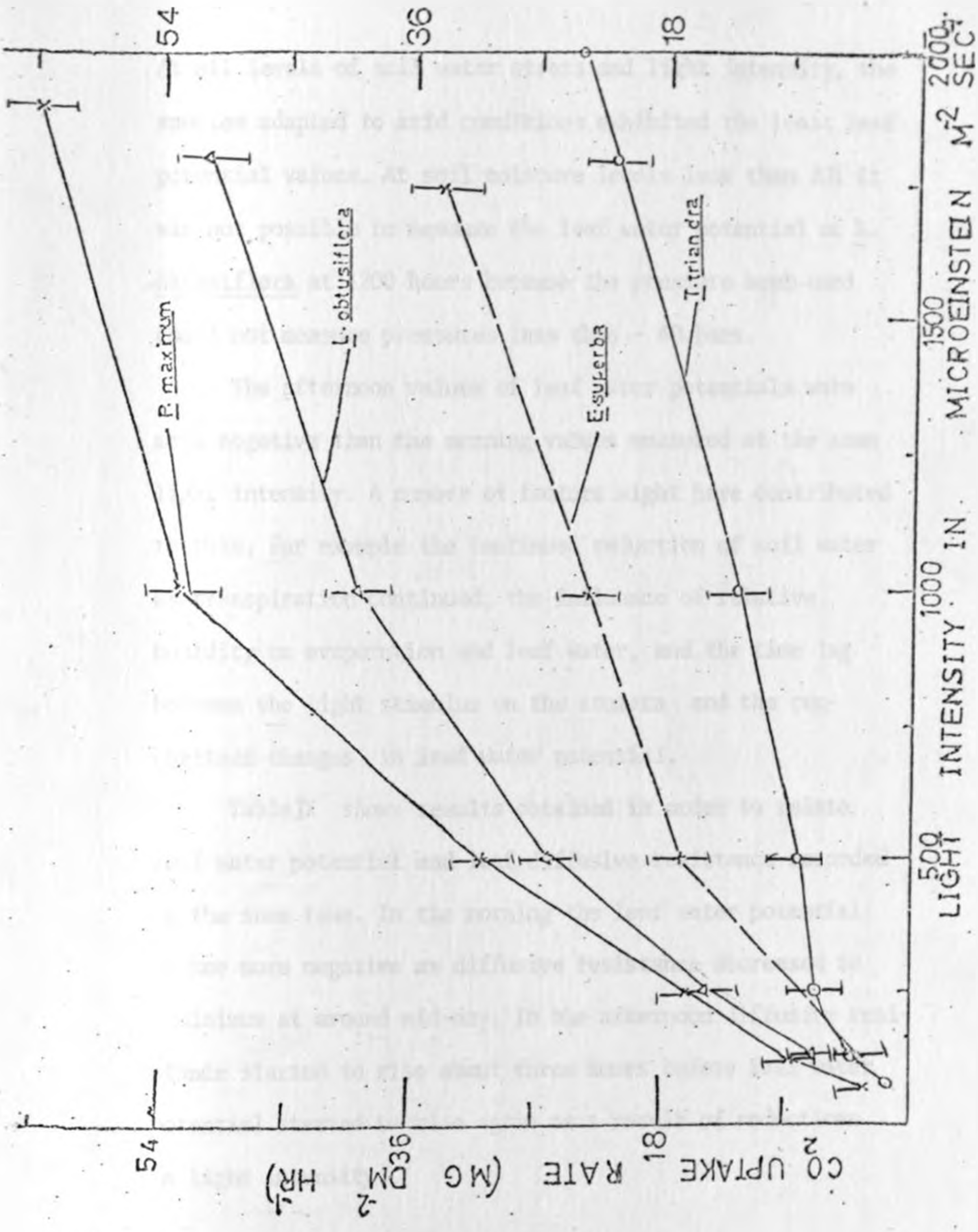


FIGURE 15:

Effects of light on the rate of CO_2 uptake in P. maximum L. obtusiflora, E. superba and T. triandra measured at field capacity and 30^0C. Each point is the average of three determinations.

At all levels of soil water stress and light intensity, the species adapted to arid conditions exhibited the least leaf potential values. At soil moisture levels less than 20% it was not possible to measure the leaf water potential of L. obtusiflora at 1200 hours because the pressure bomb used could not measure pressures less than - 40 bars.

The afternoon values of leaf water potentials were more negative than the morning values measured at the same light intensity. A number of factors might have contributed to this. For example the continued reduction of soil water as transpiration continued, the influence of relative humidity on evaporation and leaf water, and the time lag between the light stimulus on the stomata and the concomitant changes in leaf water potential.

Table IX shows results obtained in order to relate leaf water potential and leaf diffusive resistance recorded at the same time. In the morning the leaf water potential became more negative as diffusive resistance decreased to a minimum at around mid-day. In the afternoon diffusive resistance started to rise about three hours before leaf water potential started to rise again as a result of reductions in light intensity.

TABLE VIII

The effect of light and soil moisture stress on the leaf water potential (in bars) of five C_4 grasses on the same plot. Each figure is the average of three tussocks.

Soil moisture %	Light $\mu E.m^{-2}sec.^{-1}$	TIME hrs	*C. ciliaris*	*P. menzianum*	*E. superba*	*P. maximum*	*L. obtusiflora*
28.5	1650	9.00	-17.0	-22.0	-16.0	-19.0	-23.0
	2420	12.00	-28.0	-32.0	-31.0	-29.0	-32.0
27.0	1650	9.00	-18.0	-21.0	-19.0	-19.0	-26.0
	2300	10.30	-23.0	-25.0		-26.0	-28.0
	2420	12.00	-29.0	-33.0	-25.0	-30.0	-33.0
19.0	1650	9.00	-19.0	-24.0	-25.0		-30.0
	2300	10.30	-20.0	-30.0	-35.0	-32.0	-34.0
	2420	12.00	-33.0	-36.0	-38.0	-36.0	<-40.0

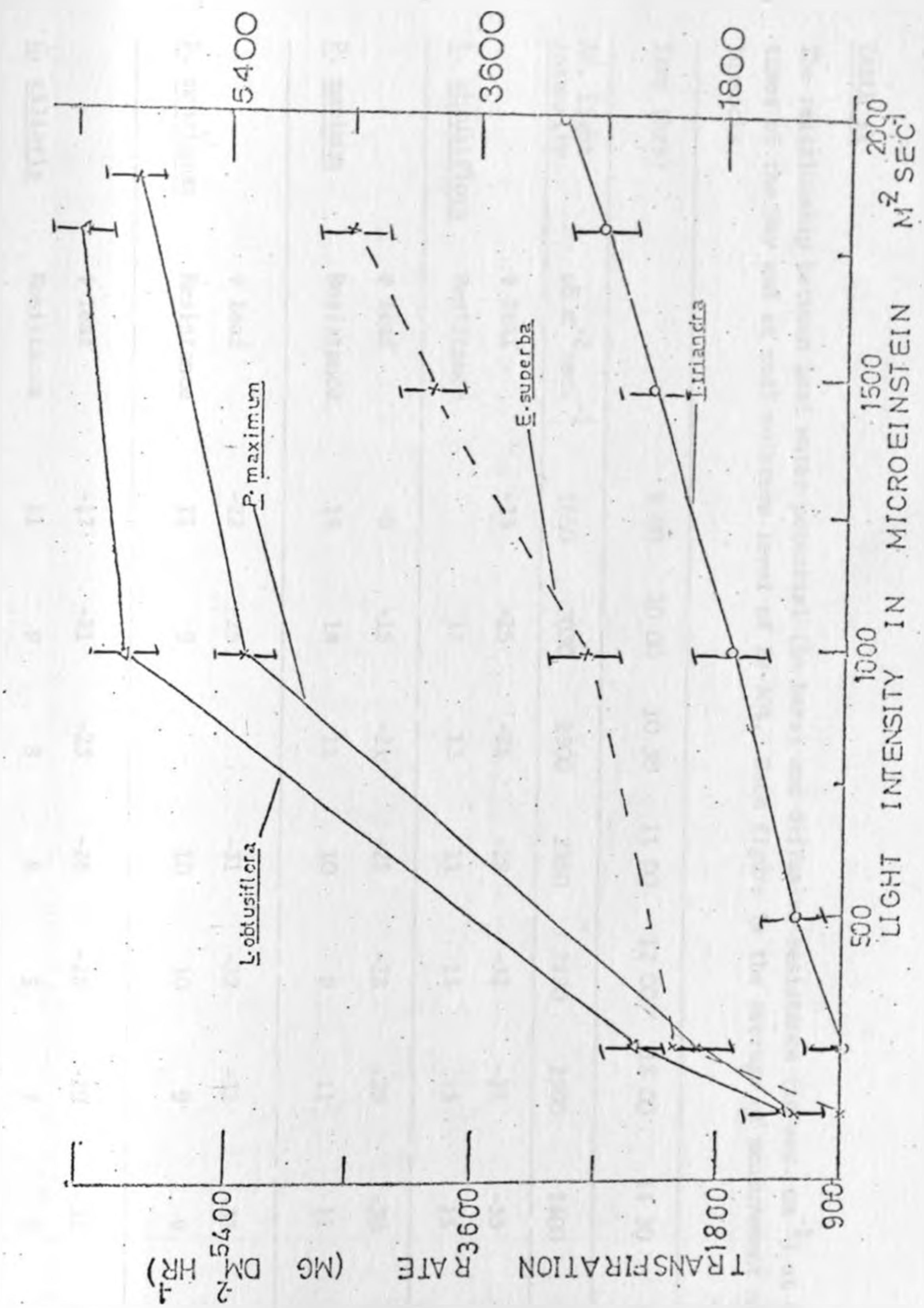


FIGURE 16:

The effect of light intensity on the rate of transpiration of intact leaves of L. obtusiflora, P. maximum, E. superba and T. triandra determined at 30°C and soil moisture at field capacity. Each pont is the average of three determinations.

TABLE IX

The relationship between leaf water potential (in bars) and diffusive resistance (in sec. cm^{-1}) at different times of the day and at soil moisture level of 29-30%. Each figure is the average of measurement made on three tussocks.

Time (hrs)		9 00	10 00	10 30	11 00	12 00	13 00	14 30	15 30	17 00
Av. Light intensity	μE m^{-2}sec.$^{-1}$	1650	2030	2300	2350	2420	2500	2400	2300	1700
	ψ leaf	-23	-25	-26	-29	-32	-32	-33	-34	-31
L. obtusiflora	Resistance		13	13	11	13	13	15	18	
	ψ leaf	-9	-15	-21	-25	-28	-29	-30	-31	-26
P. maximum	Resistance	14	14	11	10	9	11	11	13	19
	ψ leaf	-22	-26		-31	-32	-32	-33	-33	-30
P. menzianum	Resistance	11	9		10	10	9	9	11	14
	ψ leaf	-17	-21	-23	-26	-28	-29	-31	-30	-25
C. ciliaris	Resistance	11	9	8	8	5	7	7	8	10

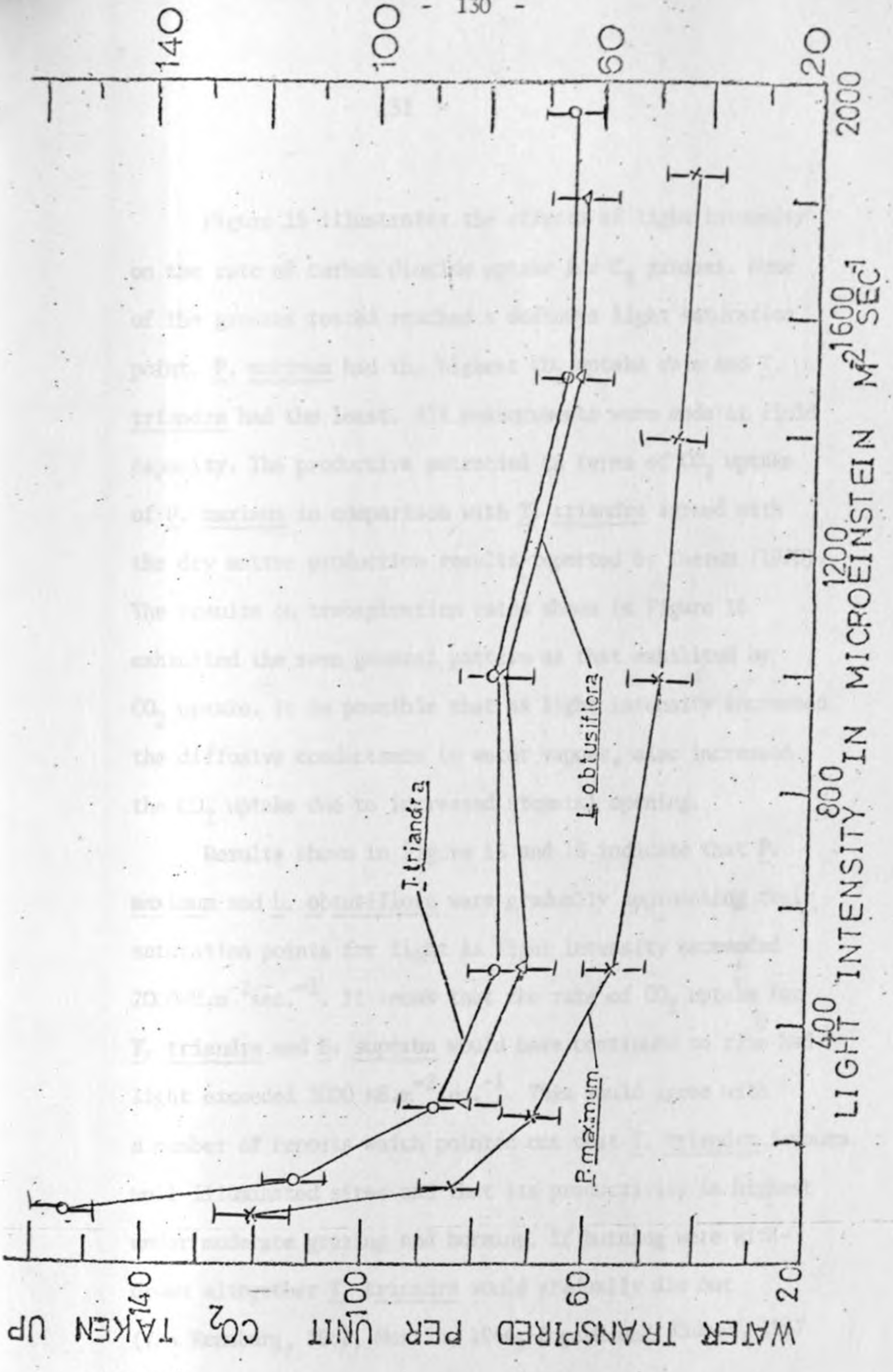


FIGURE 17:

The effect of light intensity on the transpiration ratio of T. triandra, L. obtusiflora and P. maximum measured at 30°C and field capacity. Each point is the average of three determinations.

Figure 15 illustrates the effects of light intensity on the rate of carbon dioxide uptake for C_4 grasses. None of the grasses tested reached a definate light saturation point. P. maximum had the highest CO_2 uptake rate and T. triandra had the least. All measurements were made at field capacity. The productive potential in terms of CO_2 uptake of P. maximum in comparison with T. triandra agreed with the dry matter production results reported by Taerum (1970). The results on transpiration rates shown in Figure 16 exhibited the same general pattern as that exhibited by CO_2 uptake. It is possible that as light intensity increased the diffusive conductance to water vapour, also increased the CO_2 uptake due to increased stomatal opening.

Results shown in Figure 15 and 16 indicate that P. maximum and L. obtusiflora were gradually approaching their saturation points for light as light intensity exceeeded 2000μE.m^{-2}sec.$^{-1}$. It seems that the rate of CO_2 uptake for T. triandra and E. superba would have continued to rise had light exceeded 2000 μE.m^{-2}sec.$^{-1}$. This would agree with a number of reports which pointed out that T. triandra favours well illuminated sites and that its productivity is highest under moderate grazing and burning. If burning were withdrawn altogether T. triandra would gradually die out (Van Rensburg, 1952, Martin, 1966; Bogdan and Kidner, 1967 Taerum, 1970, Ndawula-Senyimba, 1972).

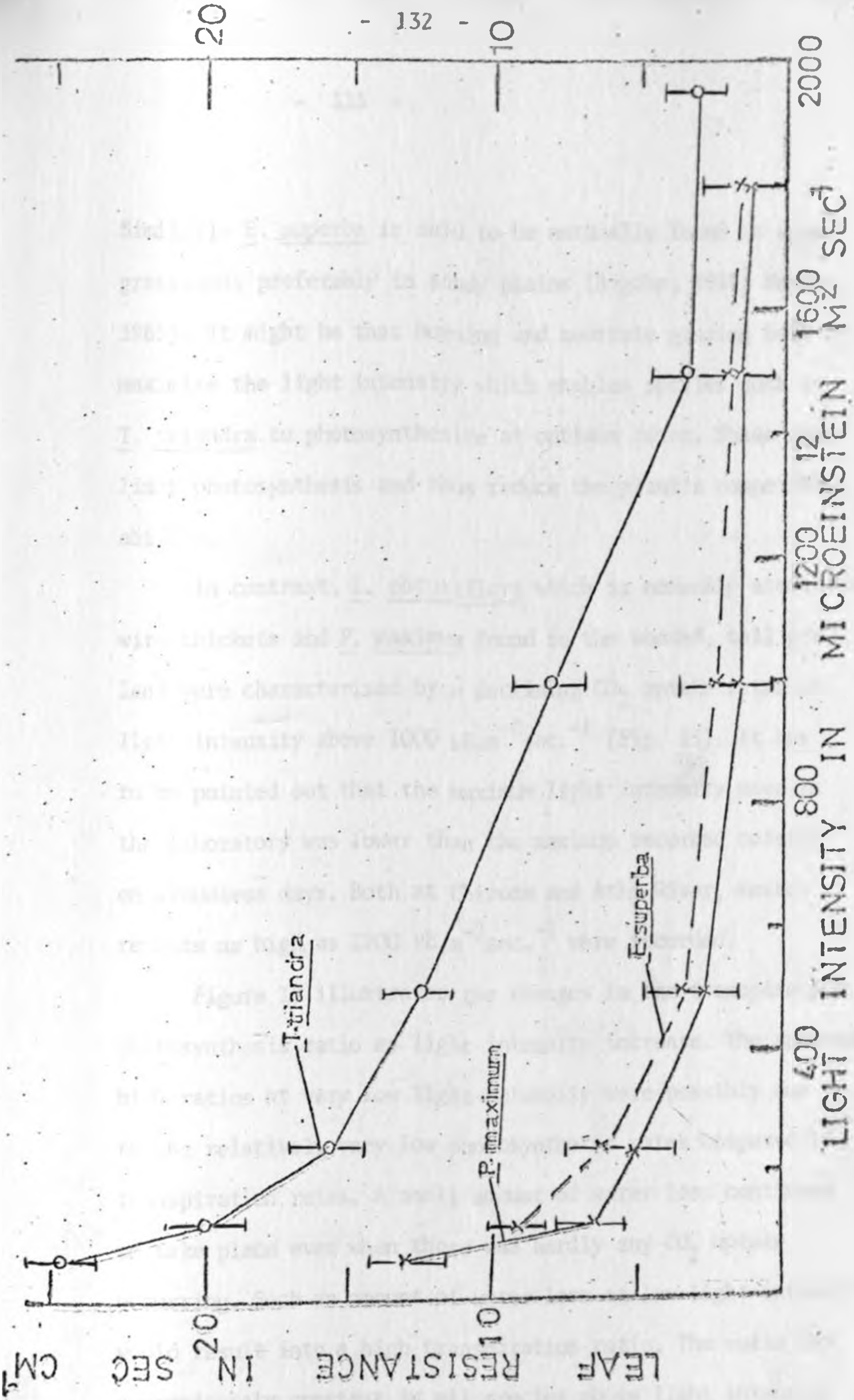


FIGURE 18:

The influence of light intensity on the leaf resistance of T. triandra, P. maximum and E. superba at field capacity and 30°C. Each point is the average of three determinations.

Similarly E. superba is said to be naturally found in open grasslands preferably in sandy plains (Bogdan, 1958; Napper, 1965). It might be that burning and moderate grazing help to maximize the light intensity which enables species such as T. triandra to photosynthesize at optimum rates. Shade would limit photosynthesis and thus reduce the plant's competitive ability.

In contrast, L. obtusiflora which is normally associated with thickets and P. maximum found in the wooded, tall grassland were characterized by a declining CO_2 uptake rates at light intensity above 1000 $\mu E.m^{-2} sec.^{-1}$ (Fig. 15). It has to be pointed out that the maximum light intensity used in the laboratory was lower than the maximum recorded outside on cloudless days. Both at Chiromo and Athi River, measurements as high as 2700 $\mu E\ m^{-2} sec.^{-1}$ were recorded.

Figure 17 illustrates the changes in the transpiration photosynthesis ratio as light intensity increase. The apparent high ratios at very low light intensity were possibly due to the relatively very low photosynthetic rates compared to transpiration rates. A small amount of water loss continued to take place even when there was hardly any CO_2 uptake occurring. Such an amount of water lost at low light intensity would result into a high transpiration ratio. The ratio was approximately constant in all species above light intensity 400 $\mu E\ m^{-2} sec.^{-1}$ implying that there were similar increases in both CO_2 uptake and transpiration as light intensity increased.

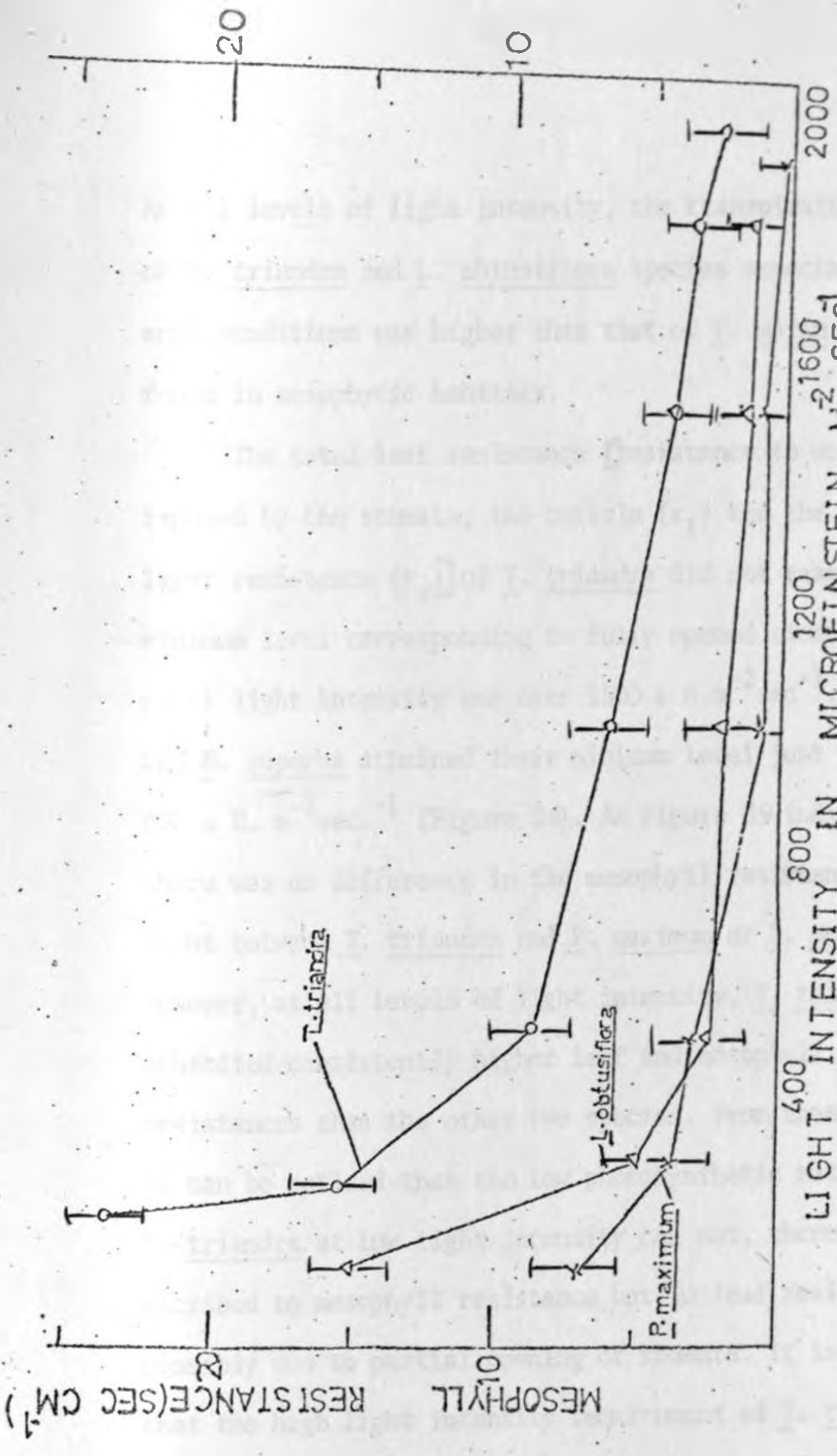


FIGURE 19:

The influence of light intensity on the mesophyll resistance of T. triandra, L. obtusiflora and P. maximum of field capacity and temperature 30°C. Each point is the average of three determinations.

At all levels of light intensity, the transpiration ratio of *T. triandra* and *L. obtusiflora* species associated with arid conditions was higher than that of *P. maximum* normally found in mesophytic habitats.

The total leaf resistance [resistance to water loss imposed by the stomata, the cuticle (r_1) and the boundary layer resistance (r_a)] of *T. triandra* did not reach the minimum level corresponding to fully opened stomata until light intensity was over 1500 µ E.m^{-2}sec^{-1}. *P. maximum* and *E. superba* attained their minimum level just above 400 µ E. m^{-2}sec.$^{-1}$ (Figure 18). As Figure 19 indicates there was no difference in the mesophyll resistance to light between *T. triandra* and *P. maximum* or *E. superba*. However, at all levels of light intensity, *T. triandra* exhibited consistently higher leaf and mesophyll resistances than the other two species. From these results it can be noticed that the low photosynthetic rates in *T. triandra* at low light intensity can not, therefore, be ascribed to mesophyll resistance but to leaf resistance possibly due to partial opening of stomata. It is possible that the high light intensity requirement of *T. triandra* is needed to reduce sufficiently leaf resistance. The consistently high leaf resistance of *T. triandra* agreed with transpiration values recorded in Figure 12 where it is shown to have a low transpiration rate.

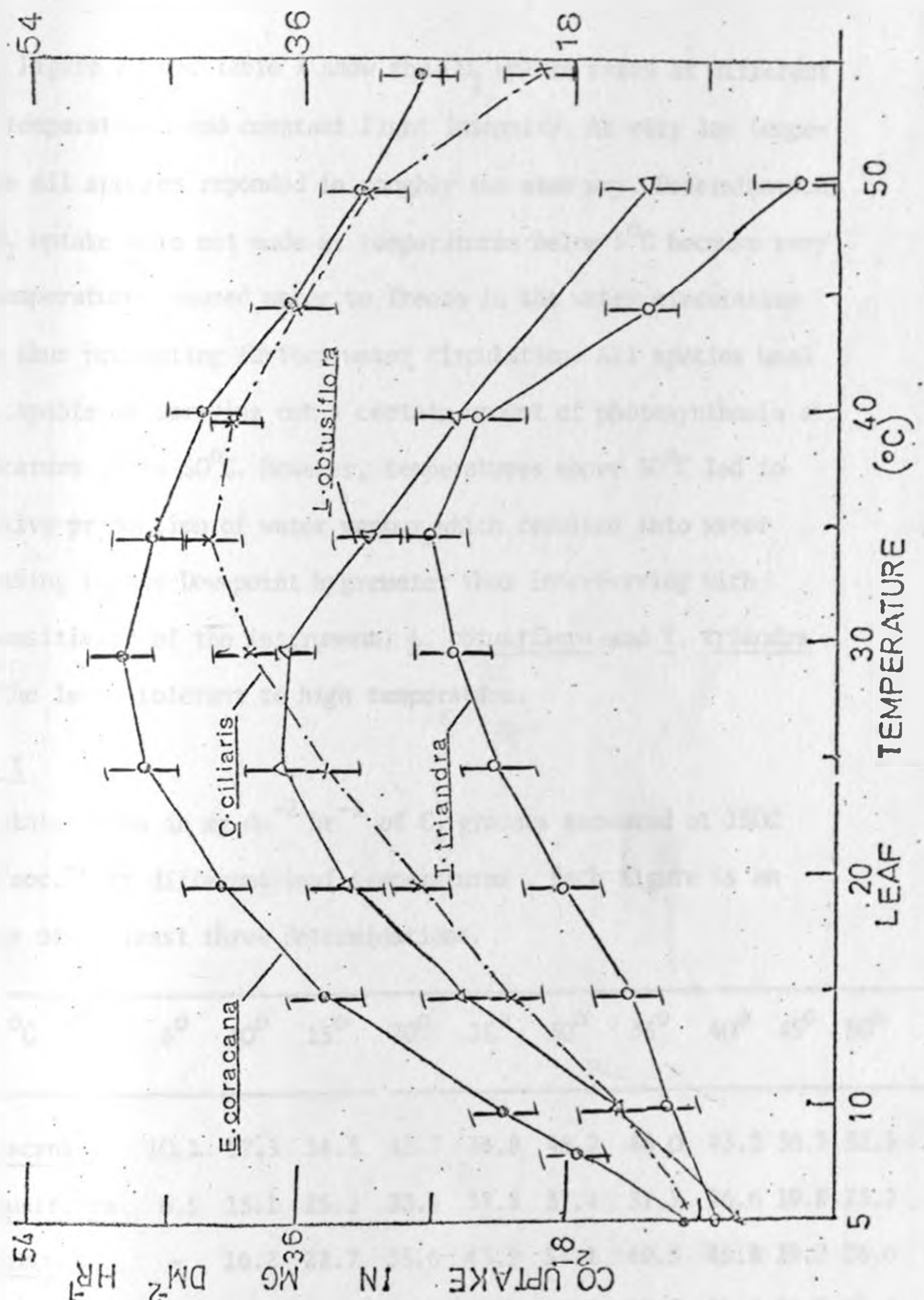


FIGURE 20:

The effect of leaf temperature on the rate of CO_2 uptake in E. coracana, C. ciliaris, L. obtusiflora and T. triandra at light intensity 1500 μ E $m^{-2}sec.^{-1}$ and soil at field capacity. Each point is the average of three determinations.

Figure 20 and Table X show the CO_2 uptake rates at different leaf temperatures and constant light intensity. At very low temperature all species reponded in roughly the same way. Determinations of CO_2 uptake were not made at temperatures below 5°C because very low temperatures caused water to freeze in the water circulation tubes thus preventing further water circulation. All species used were capable of carrying out a certain amount of photosynthesis at temperature above 50°C. However, temperatures above 50°C led to excessive production of water vapour which resulted into water condensing in the Dew-point hygrometer thus interferring with the sensitivity of the instrument. *L. obtusiflora* and *T. triandra* were the least tolerant to high temperature.

TABLE X

CO_2 uptake rates in mg.dm^{-2} hr^{-1} of C_4 grasses measured at 1500 µE m^{-2}sec.$^{-1}$ at different leaf temperatures . Each figure is an average of at least three determinations.

Temp. °C	5°	10°	15°	20°	25°	30°	35°	40°	45°	50°	55°
E. coracana	10.1	17.3	34.5	41.7	46.8	48.2	46.0	43.2	36.7	32.5	28.8
L. obtusiflora	6.5	15.1	25.2	33.5	37.8	37.4	31.7	26.6	19.8	13.7	-
P. maximum	-	16.2	27.7	35.6	43.2	51.1	49.3	46.8	39.2	26.6	19.8
E. superba	6.5	14.7	25.2	32.4	40.3	48.2	47.0	41.0	36.0	27.4	15.8
C. ciliaris	4.0	15.5	22.3	28.8	33.5	39.6	42.8	41.4	36.4	32.0	19.8
T. triandra	7.9	11.5	14.0	18.4	23.0	25.9	27.7	24.8	13.0	2.5	-

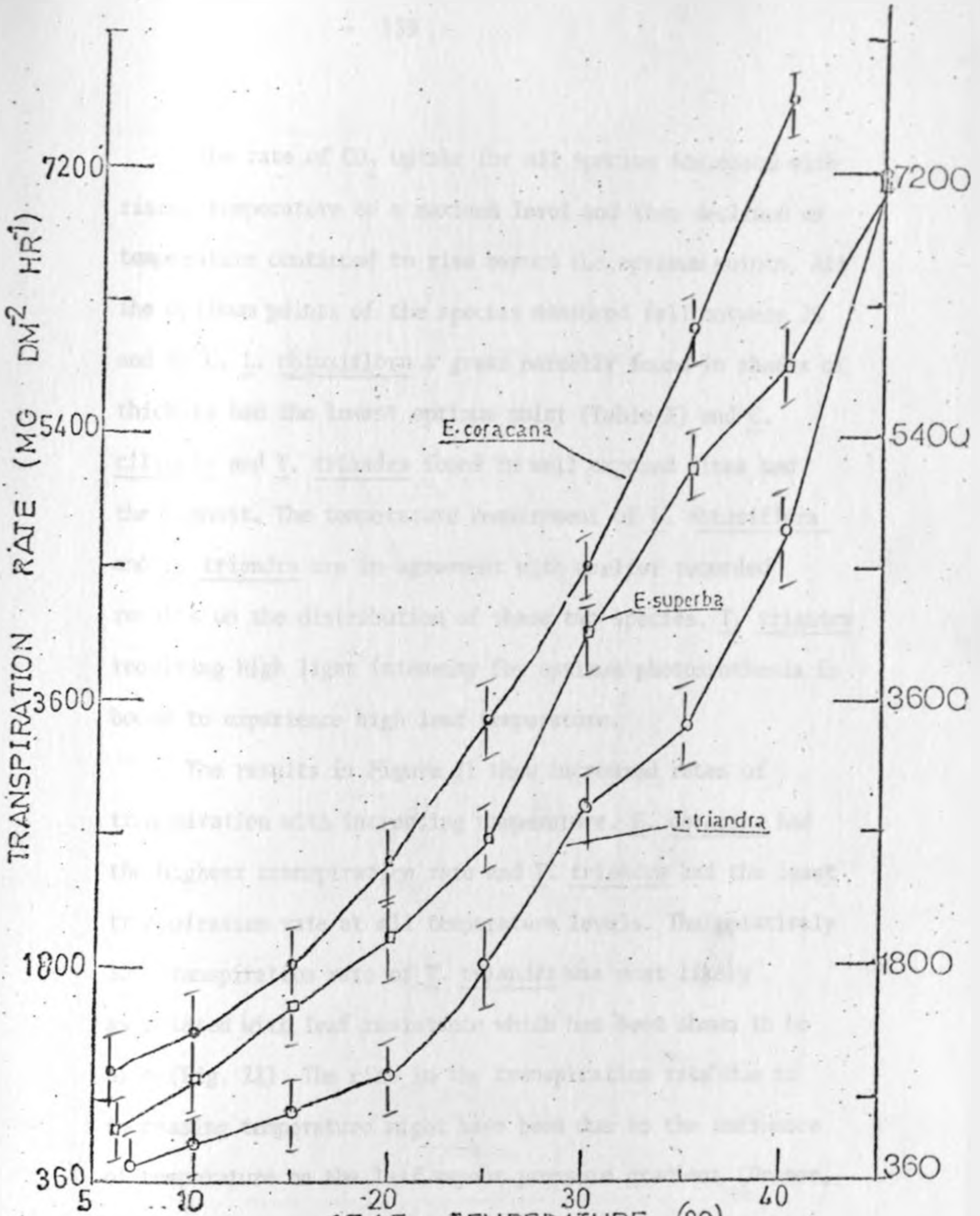


FIGURE 21

The effect of temperature on the rate of transpiration of E. coracana, E. superba and T. triandra measured at 15 µE m^{-2} sec.$^{-1}$ and soil moisture at field capacity. Each point is the average of three determinations.

The rate of CO_2 uptake for all species increased with rising temperature to a maximum level and then declined as temperature continued to rise beyond the optimum points. All the optimum points of the species measured fell between 25 and 35°C. L. obtusiflora a grass normally found in shades of thickets had the lowest optimum point (Table X) and C. ciliaris and T. triandra found in well exposed sites had the highest. The temperature requirement of L. obtusiflora and T. triandra are in agreement with earlier recorded results on the distribution of these two species. T. triandra requiring high light intensity for optimum photosynthesis is bound to experience high leaf temperature.

The results in Figure 21 show increased rates of transpiration with increasing temperature. E. coracana had the highest transpiration rate and T. triandra had the least transpiration rate at all temperature levels. The relatively low transpiration rate of T. triandra was most likely associated with leaf resistance which has been shown to be high (Fig. 22). The rise in the transpiration rate due to increasing temperature might have been due to the influence of temperature on the leaf vapour pressure gradient (Dramer, 1969).

Results shown in Figure 22 indicate that below 30°C, variations in temperature did not affect the leaf resistance of all the species measured. It should be pointed out that 30°C was the average optimum temperature for maximum photosynthesis in these species (Table X).

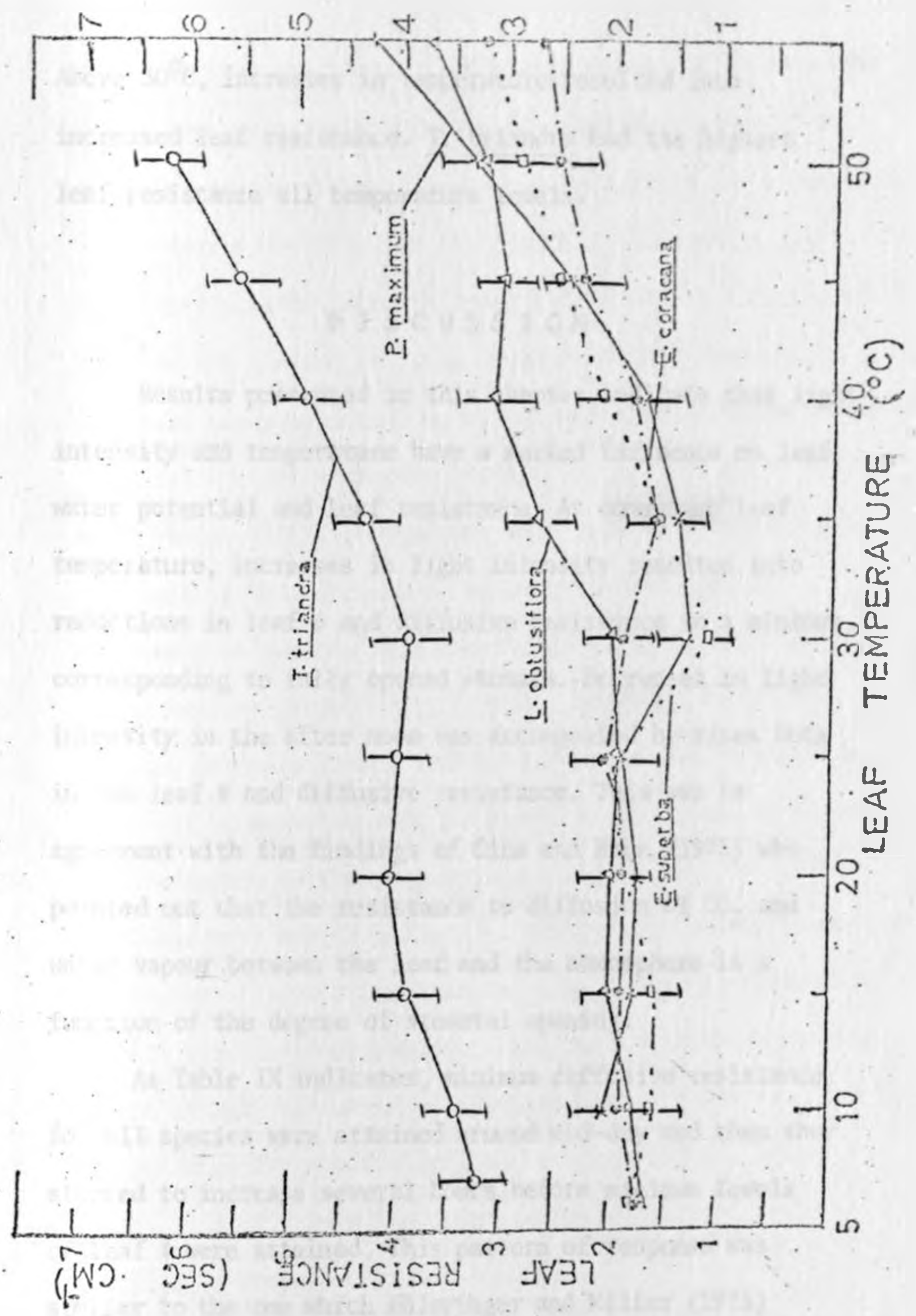


FIGURE 22:

The effect of leaf temperature on the leaf resistance of T. triandra, L. obtusiflora, P. maximum, E. superba and E. coracana measured at light intensity 1500 μ E. m^{-2} sec.$^{-1}$ and soil moisture at field capacity. Each point is the average of three determinations.

Above 30^{o}C, increases in temperature resulted into increased leaf resistance. T. triandra had the highest leaf resistance all temperature levels.

D I S C U S S I O N

Results presented in this chapter indicate that light intensity and temperature have a marked influence on leaf water potential and leaf resistance. At constant leaf temperature, increases in light intensity resulted into reductions in leaf ψ and diffusive resistance to a minimum corresponding to fully opened stomata. Decreases in light intensity in the after noon was accompanied by rises both in the leaf ψ and diffusive resistance. This was in agreement with the findings of Ciha and Brun (1975) who pointed out that the resistance to diffusion of CO_2 and water vapour between the leaf and the atmosphere is a function of the degree of stomatal opening.

As Table IX indicates, minimum diffusive resistance for all species were attained around mid-day and then they started to increase several hours before minimum levels of leaf ψ were attained. This pattern of response was similar to the one which Ehleringer and Miller (1975) reported. They pointed out that in Bistorta bistortoides, decreasing leaf ψ was later accompanied by big leaf resistances which helped to reduce water losses.

Also Kanemasu and Turner (1969) and Hansen (1974b) reported that there is a rapid increase in stomatal resistance as leaf Ψ decreases below a certain value. Since the reverse in the response of diffusive resistance to increasing light intensity occurred several hours before leaf Ψ started to rise in all species it could be assumed that there was a critical water potential level for each species below which stomatal control mechanism started to restrict water diffusion. Hsiao (1975) pointed out that generally stomata are insensitive to reduction in water potential until a threshold is passed. When the threshold is passed then the resistance triggered on by stomatal activity restricts further moisture losses through increased leaf resistance.

It is possible that increased light intensity through its influence on stomatal aperture led to increased water loss and more negative leaf Ψ. This suggestion is supported by the results on transpiration rates shown in Figure 18. In all species transpiration rates rose up with increasing light intensity. Increased stomatal aperture due to high light intensity would also lead to increased CO_2 uptake until a light saturation point characteristic of each species is reached.

Results on leaf resistance (stomatal and cuticular resistance plus boundary layer resistance) indicated that T. triandra normally associated with semi-arid open grasslands, had high leaf and mesophyll resistances

(Figures 18 and 19). This species was shown to require strong light intensity of over 1500 μ $E.m^{-2}sec.^{-1}$ to lower its leaf resistance to a constant minimum value which could probably correspond to optimum photosynthesis. Results on CO_2 uptake in Figure 15 had indicated how T. triandra continued to have increased CO_2 uptake with increasing light intensity. At 2000 $\mu E.m^{-2}sec.^{-1}$ curve for CO_2 uptake showed no indication of an approaching light saturation point. These results on both leaf resistance and photosynthesis in relation with light intensity support the view that strong light is required in order to reduce sufficiently the high leaf resistance and to promote maximum CO_2 uptake in T.triandra. This requirement will allow T. triandra to photosynthesize at optimum capacity only in sites devoid of shade. This view is supported by the findings of Van Rensburg (1952); Martin (1966); Bogdan and Kidner (1967) Taerum (1970); Ndawula-Senyimba (1972) that T. triandra favours well illuminated sites and that if burning or grazing are withdrawn altogether bush will increase and T. triandra will gradually die out.

The results on the transpiration ratio (Fig. 19) indicated that at constant temperature light influenced both transpiration and CO_2 uptake of a given species in the same proportion. Bierhuizen and Slatyer (1965) pointed out that transpiration ratio is strongly dependant on the evaporative demand at the leaf/air boundary.

T. triandra and L. obtusiflora normally assocated with arid conditions had higher transpiration ratios than P. maximum normally found in mesophytic habitats.

Whilst it is well established that C_4 plants have high optimal temperature for photosynthesis (Black, 1971; Imbamba and Tieszen, 1977) it is interesting to note that some C_4 plants have higher optimal points than others. The two species T. triandra and C. ciliaris whose maxima were at about 35°C are usually found in unshaded conditions in semi-arid environment. The high optimal temperature range of these species might be an adaptation to survival in habitats exposed to strong solar radiation. L. obtusiflora with an optimal point at about 25°C is normally found in shades of thickets. Results shown in Figure 22 indicate that temperatures above the optimal ranges of the species studied resulted into increasing leaf resistance. Increasing leaf resistance would lead to reduced productivity and thus confine the species within its required temperature range.

The available results did not indicate that in C_4 grasses resistance to water stress is accompanied by heat resistance. As a matter of fact species such as E. coracana P. maximum normally found in mesophytic conditions seemed to be more heat resistant than the species normally found in arid places (Table X). The relatively high optimal point associated with T. triandra might be related to the species distribution with respect to light and soil moisture level but not with respect to temperature directly.

From all the results presented in this section it can be concluded that the selected C_4 grasses normally found in arid environment are characterised by low leaf water potential values, high diffusive resistance, high leaf resistance, high mesophyll resistance and high stomatal frequency. For T. triandra found in well illuminated semi arid habitats, the strong solar radiation lowered the leaf water potential and in turn enhenced a strong suction force which might assist the plant to extract water from relatively dry soils. The high leaf resistance which is only lowered by very strong light and then raised again when excessively low leaf ψ is generated, could help to confine the species in sites which can guarantee maximum photosynthesis and controlled transpiration. All these characteristics seem to be adaptive features which could enable some C_4 grasses such as T. triandra and L. obtusiflora to adapt themselves to arid conditions. For the species forced to grow in habitat exposed to strong sunlight a high temperature optimum range for photosynthesis is inevitable.

GENERAL DISCUSSION

Results on the distribution of the Gramineae family in Kenya point out that tropical grasses are distributed differently according to their photosynthetic systems. Grasses with the C_4 -dicarboxylic acid photosynthetic system, occupied the low and medium altitude open grasslands characterized by low and medium available soil moisture indices and high temperature. In contrast, C_3 grasses were confined to alpine altitudes where temperatures are low. These results supported the hypothesis that the C_4 syndrome is adaptive to hot and arid tropical environments (Laetsch, 1974; Moore, 1974; Tieszen et al, 1979). Similar studies in the Gramineae of the North America (Teeri and Stowe, 1976), Northern Sahara Desert (Winter et al, 1976) and Java (Hofstra et al, 1972) are also consistent with this hypothesis. Although C_4 grasses were generally more adapted to arid conditions than C_3, some C_4 Tribes had their optimal distribution in relatively wet habitats.

Although no direct measurements were made in order to isolate the effect of temperature from that of soil moisture on the distribution of both C_3 and C_4 grasses, the broad distributional pattern along the altitudinal gradient obtained was similar to that proposed by Teeri and Stowe (1976) on temperature basis. The sharp change from predominantly C_4 to predominantly C_3 grasses between moisture indices 50 and 70 (Fig. 1) could only be accounted for on the basis of a sharp drop in temperature due to increase in altitude (Griffiths, 1962). Between these two points altitude rose by over 1000 metres with a concomitant drop in the daily mean temperature of 7°C. On the altitude basis according to Griffiths (1962), the mean minimum temperature for moisture index 70 is about 5°C. Teeri and Stowe (1976) found that in North America the presence of C_4 grasses was highly correlated with the July (Summer) minimum temperature. They indicated that few or no C_4 species were found where July minimum temperatures were below 8°C. The absence of C_4 grasses in Kenya in **habitats** with mean minimum temperatures 5°C and under is consistent with the findings of Teeri and Stowe (1976).

As an exception to the general distribution pattern of C_3 and C_4 along the moisture and temperature gradients, were a few C_3 species found at low altitudes. However, these were found mainly in the understoreys of closed forests and were from grass Tribes which more often consist of C_4 species. Under shaded conditions irradiances would be quite low and leaf temperatures would rarely exceed 32°C. Ehleringer and Bjorkman (1977) and Ehleringer (1978) showed that at temperatures below 32°C the quantum yield for C_3 is higher than that of C_4 plants. Thus with all other things being equal, the C_3 plant should be at an advantage with respect to carbon balance in shaded environments and maximum leaf temperature below 30°C. This hypothesis was supported by the reported presence of C_3 species in shaded conditions at low altitudes. The preference of C_4 grasses to unshaded conditions especially under arid conditions confirmed the findings of Teeri and Stowe (1976) that a greater proportion of C_4 grasses in North America, occurred in microsites characterized by low levels of shade.

From the results obtained in the laboratory on the physiological behaviour of the selected C_4 grasses, it was established that the distribution pattern of C_4 grasses along the altitudinal and soil moisture gradients is dependent on the internal physiological processes. As Walter 1973 pointed out it is the difference in response of different plant species to similar growing conditions which enables one species to tolerate a given environmental stress better than another species.

Available results indicated that the water relations of C_4 grasses adapted to arid conditions is very closely related to the stomatal characteristics of the plant and greatly influenced by the site light conditions. C_4 species normally associated with arid habitats, were characterized by more negative leaf water potential and higher stomatal frequency than mesophytic C_4 species. These results were consistent with the findings of Simmelsgaard (1976) who reported that at the root-medium of osmotic potential ranging between 0 and 14 bars, the leaf Ψ of drought hardened plants was more negative than that of the control. Turner (1970) commenting on the importance of stomata in regulating transpiration, pointed out that the regulation of transpiration by stomata depends on both the stomatal number and dimension. Also Miskin and Rasmusson (1972) reported that the lines of barley which had a 25% decrease in stomatal frequency were associated with a 24% reduction in their transpiration rate. Since both high stomatal frequency and more negative leaf Ψ are normally related to high transpiration rates and adaptability to aridity, then it is correct to assume that these two observed features of C_4 grasses are adaptive to arid conditions.

On the basis of the results reported in chapter III, it could be concluded that the existence of some C_4 grasses in arid habitats is greatly influenced by their characteristic more negative leaf Ψ and high stomatal frequency. Such a more negative leaf Ψ would be expected to exert a strong extraction force on soil moisture and enable the plants concerned to obtain their required water from the relatively dry soil. As results in Figures 5 and 8 indicate, differences between adapted and non-adapted species would only appear when the soil has become too dry for the non-adapted plants to obtain the water they require.

As results shown in Figures 13, and 14 indicate, species associated with arid conditions were characterized by higher diffusive resistance than those species normally found in mesophytic habitats. Although both the arid and the non-arid species showed increasing diffusive resistance with increasing soil moisture stress, the amplitudes between the low and high soil water stress were very different. C_4 species normally associated with arid habitats exhibited wider amplitudes than the non-arid C_4 species between mid-day and late afternoon. The bigger reduction in the diffusive resistance between the closed and fully opened stomata levels associated with arid species such as L. obtusiflora, were closely related to more negative leaf ψ of such species recorded in Figures 4, 5 and 6.

Diurnal variations in leaf diffusive resistance of L. obtusiflora and T. triandra support the view that the adaptive features of such species to arid conditions are closely linked with the mechanisms which control their leaf ψ and leaf diffusive resistance. Further results reported in chapter V indicated that light intensity and temperature had marked influence on leaf ψ and leaf resistance. At constant leaf temperature, increases in light intensity resulted into reduction in leaf ψ and diffusive resistance to levels corresponding to fully opened stomata. This meant that through its influence on the stomatal movement, light intensity controlled both the leaf ψ and diffusive resistance. This is in agreement with the findings of Ciha and Brun (1975) who pointed out that the resistance to diffusion of CO_2 and water vapour between the leaf and the atmosphere is a function of the degree of stomatal opening. Also Ehleringer and Miller (1975) reported that decreasing leaf ψ was accompanied by greater leaf resistances which in turn reduced water losses. This means that light intensity as a controller of stomatal opening has a big part to play in the water relations of C_4 grasses adapted to arid conditions.

Results on the leaf resistance and mesophyll resistance of T. triandra (Fig. 18 & 19), indicate that this species would require a strong light to lower sufficiently its resistances. This is supported by the findings of Van Rensburg (1952); Martin (1966); Bogdan and Kidner (1967); Taerum (1970) and Ndawula-Senyimba (1972) that T. triandra favours well illuminated sites and that if burning or grazing were withdrawn altogether bush will increase and T. triandra will disappear. Therefore, it is possible that increased light intensity in well illuminated sites assist to lower the relatively high diffusive resistances of arid species thus enabling them to maintain a more negative leaf ψ which is necessary for the absorption of water from the dry soil. The lack of light saturation in the photosynthetic system of species such as T. triandra (Fig. 16) would further strengthen the requirement of such species to well illuminated sites.

All these findings have led to the following conclusions:

(i) That the Gramineae families in Kenya are geographically distributed according to their photosynthetic systems along the altitudinal and available soil moisture gradients. All predominantly C_3 Tribes with exception of Ehrharteae were confined to alpine altitudes where temperatures are generally low. All the predominantly C_4 Tribes were confined to low altitudes where temperatures are approximately uniformly high and where available soil moisture is low

(ii) That at low altitude where the temperature is uniformly high, C_4 grass Tribes are distributed in a continuum manner along the available moisture gradient. Tribes such as Chlorideae, Eragrostideae, Sporoboleae, Aristideae and Zoysieae were most abundant at low available soil moisture indices and rare or absent at indices above 50. In contrast, the C_4 members of Paniceae and Adropogoneae attained their highest development at the intermediate soil moisture indices of 40 to 60.

(iii) That the adaptability of some C_4 grasses to arid conditions is greatly controlled by their internal leaf mechanisms influenced by light intensity. Strong irradiation, characteristic of the arid tropical grasslands, lowers the generally high diffusive and leaf resistances together with the leaf Ψ.

This process might enhance a strong enough water absorption force to draw water from a relatively dry soil. Also strong illumination maximizes the photosynthesis of species such as T. triandra which do not show signs of being light saturated. Such a requirement for high irradiation would favour the distribution of C_4 grasses, adapted to arid condition, into well illuminated sites.

These findings emphasize the importance of C_4 plants in the tropics and give further support to the view that a concurrent evolution might have taken place in grazing mammals and the Gramineae family. Intensive grazing pressure would maintain an open canopy thereby providing strong selective pressure in favour of the C_4 syndrome (Ndawula-Senyimba et al, 1978). The distribution of C_4 grasses is of special importance to Kenya because the highest diversification of these grasses occurs between indices 30 and 60, the zone in which arable agriculture and animal production are most practised. The distribution pattern of C_4 grasses along the available soil moisture gradient could be used as an indicator of available soil moisture during site potential evaluation in places where the relevant data for such evaluations is not available.

The distinct separation of C_3 grasses from C_4 grasses on an altitudinal basis is also of special importance in the further studies on the East African ecology and paleoecology.

As it was pointed out by Tieszen et al (1979), the differential fractionation of carbon isotopes could be used to predict the quantitative contribution of C_3 and C_4 species in animal feeds during range and pasture studies.

SUMMARY AND CONCLUSION

Investigations were carried out in order to discover the factors which control the distribution of C_3 and C_4 grasses in Kenya. Additionally, attempts were made to evaluate the mechanisms which govern the distribution, water relations, productivity and leaf diffusive resistance of C_4 grasses adapted to arid conditions and to relate these features to prevailing environmental factors such as soil water stress, high ambient temperature and light intensity characteristic of the tropics.

The study has revealed the following points:

1. That the overall geographical distribution of C_3 and C_4 grasses, as groups, in Kenya is controlled by temperature which in turn is governed by altitude. All C_3 grass Tribes with exception of Ehrharteas were confined to alpine altitudes where the temperature is generally low. All the C_4 grass Tribes were found at medium and low altitudes where temperatures are approximately uniformly high. These findings were supported by Teeri and Stowe (1976) who found that in North America the presence of C_4 grasses was highly correlated with the July minimum temperature. They pointed out that few or no C_4 species were found where July minimum temperatures were below 8°C.
2. That at medium and low altitude C_4 grass Tribes were distributed in a continuum manner along the available soil moisture gradient.

All C_4 tribes formed two distinct distribution peaks one at the dry end and another at the wet end of the available moisture gradient according to Woodhead's (1970) moisture index. The distribution of C_4 grass tribes in Kenya supported the view expressed by several authors that interactions between low soil moisture availability, high temperature and high irradiance favour the abundance of C_4 plants (Black, 1973; Bjorkman, 1971; Laetsch , 1974; Teeri and Stowe, 1976). Hartley (1958a, & b) and Hartley and Slater (1960) pointed out that on a global scale Paniceae and Andropogoneae are best developed in hot moist climates and Aristideae, Zoysieae, Pappophoneae, Eragrostideae and Chlorideae have most of their member species adapted to "erratic rainfall". C_3 Tribes were not distributed along available moisture gradient.

3. That the C_4 grasses such as *L. obtusiflora*, *T. triandra* and *P. menzianum*, representing the Tribes associated with arid environment, were found to possess comparatively more negative leaf water potential, high diffusive resistance, high leaf and mesophyll resistances, and high stomatal frequency. They were also characterised by higher transpiration rates and they exhibited a demand for stronger light intensity than the C_4 species associated with mesophytic conditions. The more negative leaf ψ associated with high stomatal frequency and a requirement for high illumination might be adaptive features for survival under arid and unshaded

conditions. The strongly negative leaf ψ would lead to extracting water from the relatively dry soil with a strong suction force. The possible existence of such a suction force was deduced from the high transpiration ratios found to be associated with the selected arid C_4 species. The high diffusive resistance might be used by these plants both to guard against excessive water loss when the leaf ψ become very low and to limit optimum photosynthetic productivity of plants such as T. triandra to well illuminated sites. The leaf resistance of this plant could only be reduced to a minimum in very strong light.

From all these results it was concluded that the overall distribution of C_3 and C_4 grass groups is controlled by temperature which is related to altitude. The individual C_4 Tribes are distributed in a continuum manner along the available soil moisture gradient in accordance with Woodhelad's (1970) available soil moisture index.

The available results lead to the conclusion that the adaptability of C_4 grasses to arid tropical conditions is closely related to their low leaf water potential and high leaf diffusive resistance. These two features which are greatly influenced by light intensity and stomatal frequency control the water relations of adapted C_4 grasses and give such grasses a competitive advantage over the arid susceptible species. As Walter (1973) pointed out it is the difference in response of different plant species to similar growing conditions which enables one species to tolerate a given environmental stress better than another species

Results on leaf resistance support the view that the association of T. triandra with unshaded semi-arid sites is related to the possession of a high leaf resistance which is gradually reduced by increasing light intensity. The light which is strong enough to lower sufficiently the leaf resistance and in so doing facilitate optimum photosynthesis, would be strong enough to lower leaf ψ so as to guarantee adequate water supply. In this way leaf resistance could influence the distribution of species such as T. triandra in illuminated semi-arid habitats.

These findings emphasize the importance of C_4 plants in the tropics and gives further support to the view that a concurrent evolution might have taken place in grazing mammals and the Gramineae family. Intesive grazing pressure would maintain an open canopy thereby providing strong selection pressure in favour of the C_4 syndrome. The distribution of C_4 grasses is of special importance to Kenya because the highest diversification of these grasses is between moisture indices 30 and 60 the zone in which arable agriculture and animal production are most practised.

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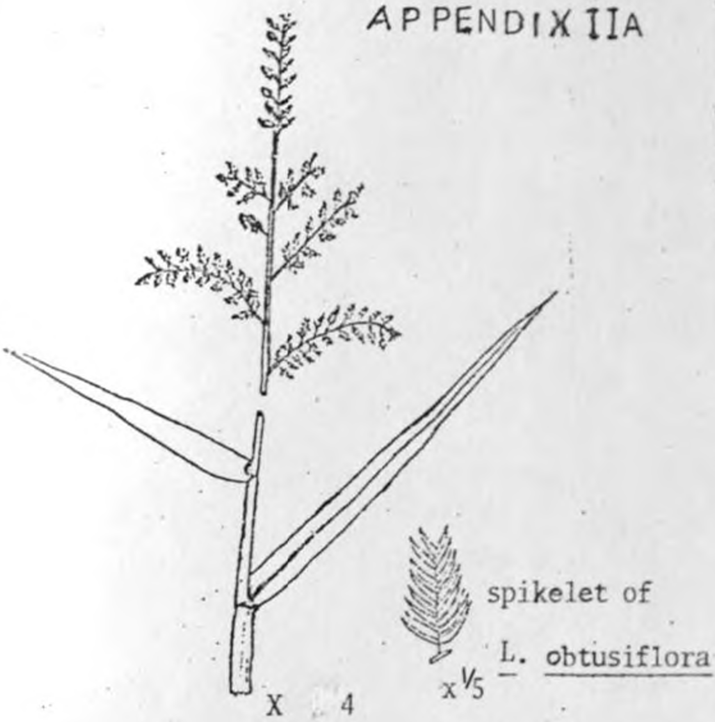
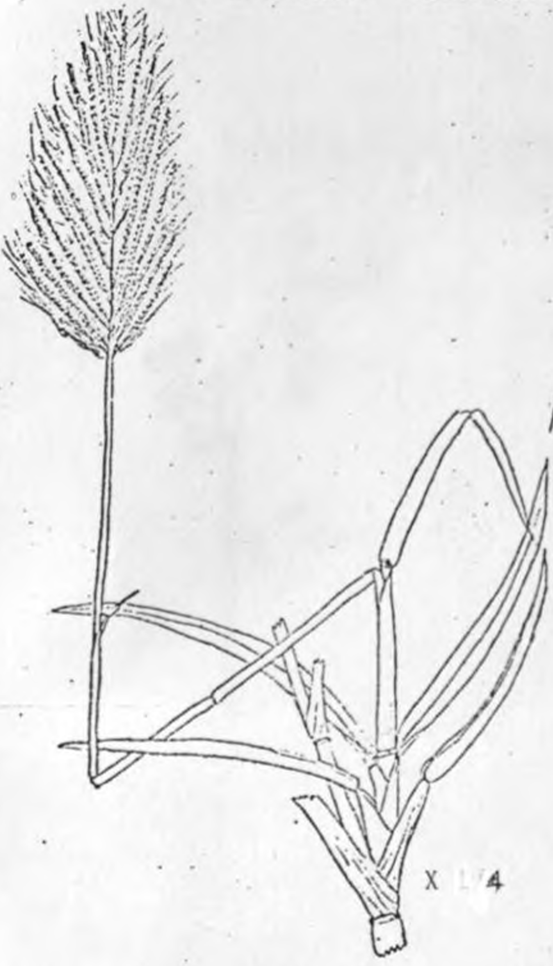
APPENDIX IIA



(i) Leptochloa obtusiflora

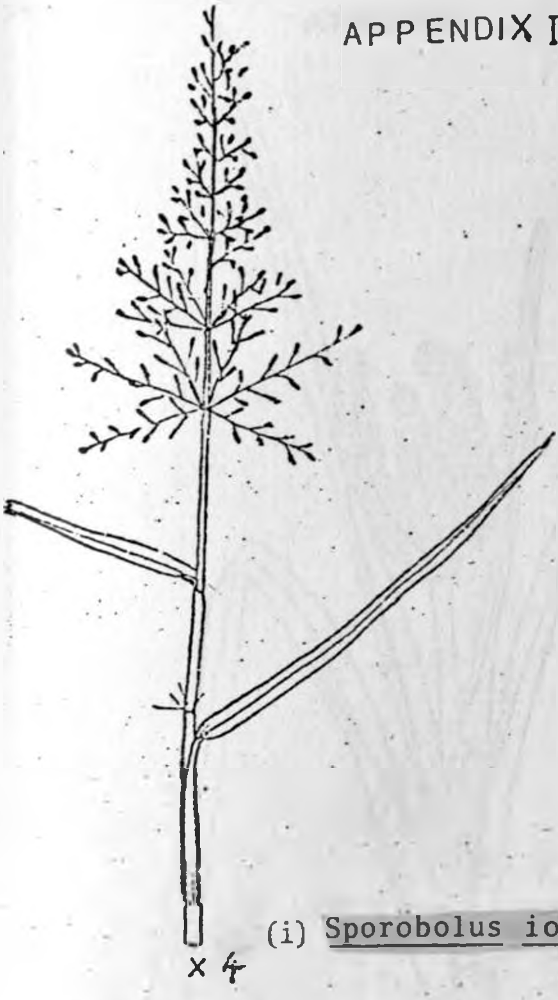
(iii) Pennisetum menzianum



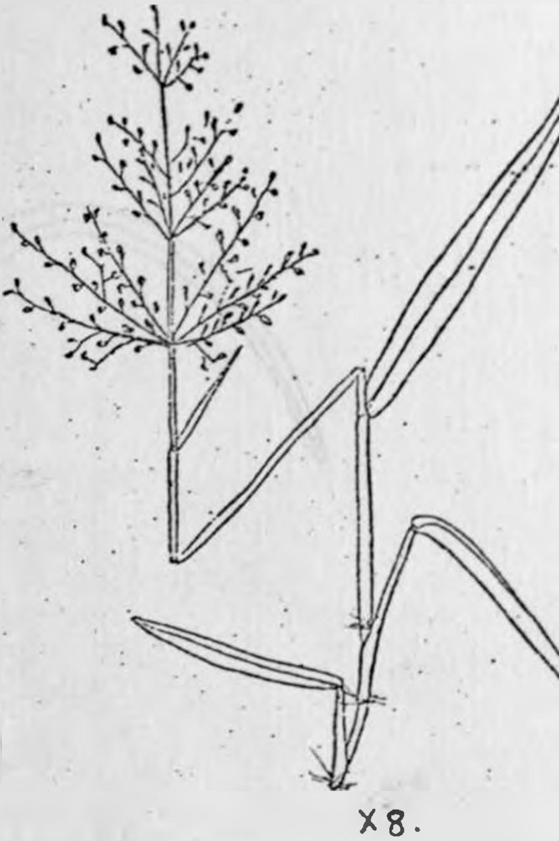
(ii) Chloris roxburghiana

(iv) Themeda triandra

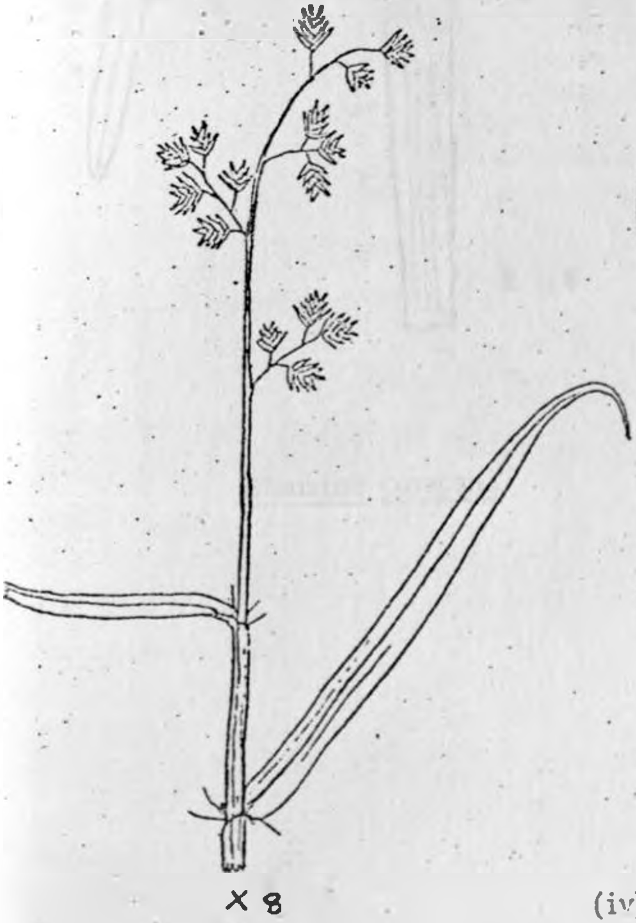
APPENDIX IIB



(i) Sporobolus ioclados



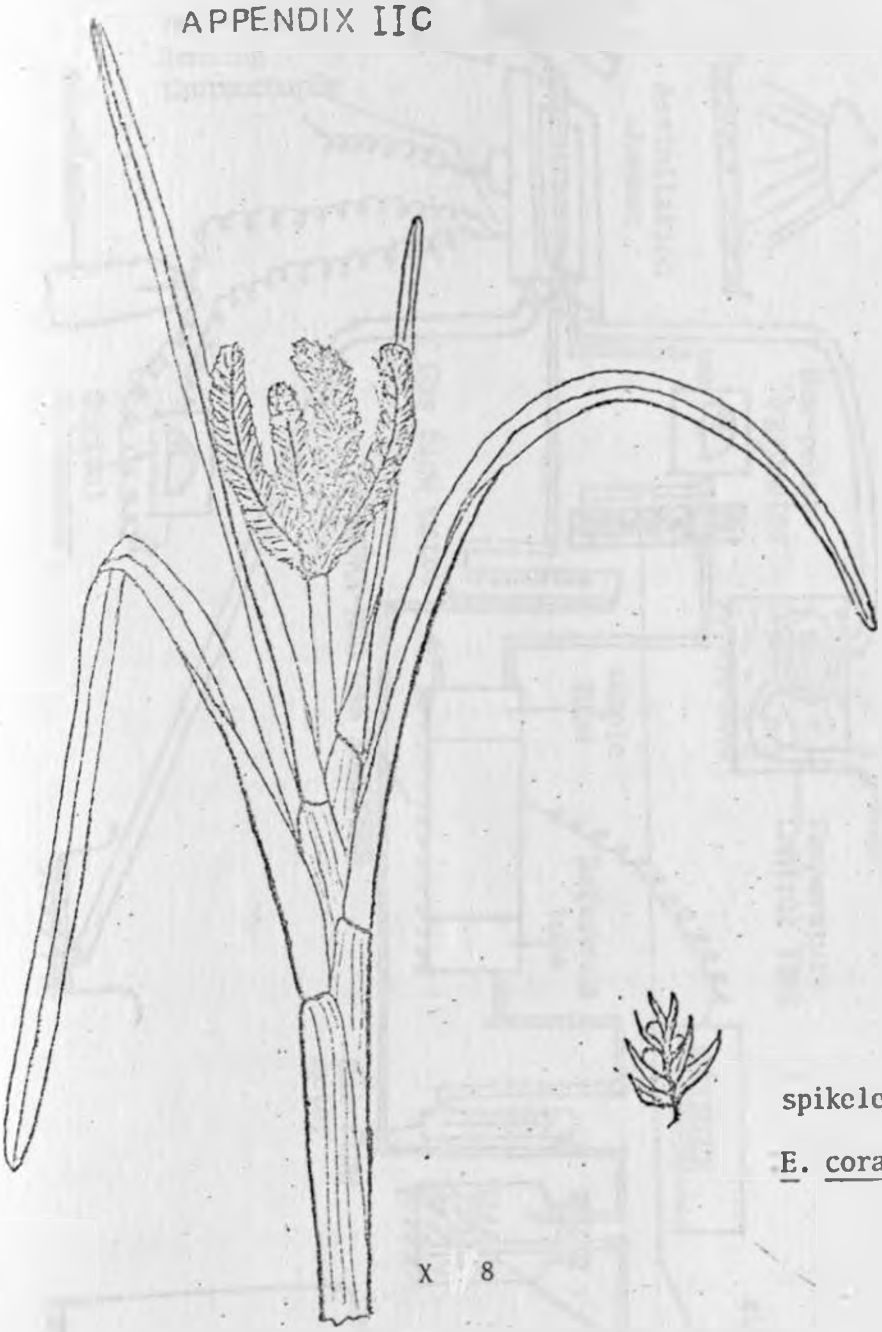
(iii) Panicum maximum



(ii) Eragrostis superba

(iv) Cenchrus ciliaris

APPENDIX IIC



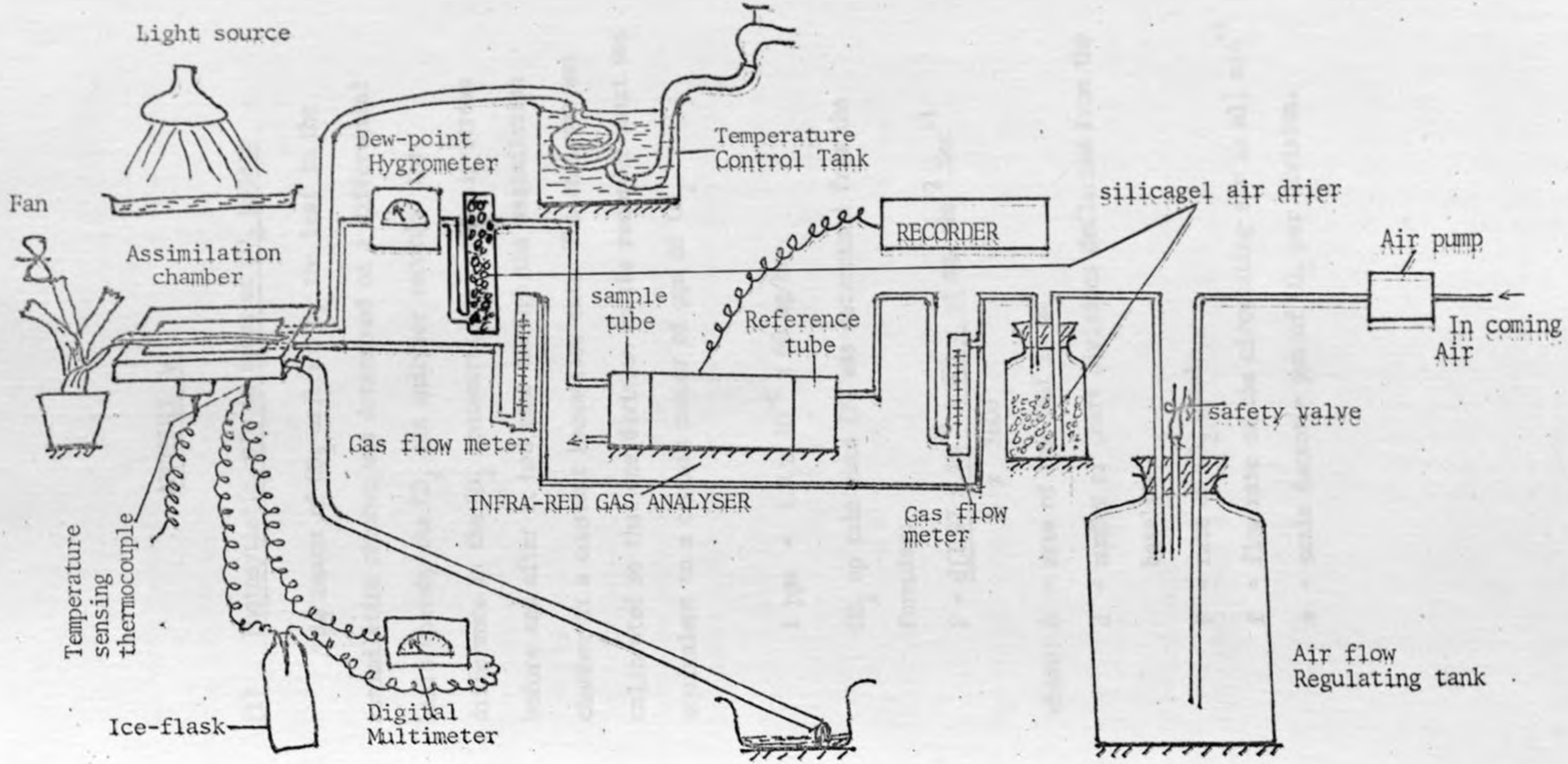
spikelet of

E. coracana

X 8

Eleusine coracana

APPENDIX III The open-system Infra-red Gas Analysis set-up



APPENDIX IV

(i) Photosythetic rate in terms of CO_2 uptake

The amount of CO_2 utilized by the leaf in the assimilation chamber was determined on a differential basis whereby the CO_2 gas analyser recorded the difference in the CO_2 concentration in the air stream before and after it had gone through the assimilation chamber at a constant known flow rate. The analyser was calibrated so that one division on the recorder chart was equivalent to a certain number of ppm of CO_2.

$$1 \text{ ppm} = 1.9 \times 10^{-6} \times 60 \text{ mg/hr}$$

CO_2 up take rate (F) was determined from the formular:

$$F = \frac{d(1.97 \times 10^{-6} \times 60) \times sf}{A \times 3600} \text{ mg. dm}^{-2}.\text{Sec}^{-1}$$

where: A = area of the leaf in dm^2

d = number of chart divisions deflected from the baseline.

F = rate of CO_2 uptake

f = flow rate of the circulating air in ml. min^{-1}

s = scale factor = ppm of CO_2 per division.

(ii) Transpiration rates determined together with photosynthesis

The water content of the air entering and leaving the assimilation chamber was determined using the Dew-point hygrometer and the rate of transpiration was calculated using the formula :

$$T = \frac{f(W_2 - W_1) \times 60}{A} \quad \text{mg.dm}^{-2}.\text{hr}^{-1}$$

where A = area of the leaf in dm^2

f = flow rate of the circulating air in ml. min^{-1}

T = transpiration rate

W_1= water vapour density of the incoming air (mg.cm^{-3})

W_2= water vapour density of the outgoing air (mg.cm^{-3})

The magnitude of the resistances to water loss from leaves, and CO_2 was calculated from the following formulae:

(a) Leaf resistance to water loss $R = r_a + r_s = \frac{(W_e - W_o)}{T}$ sec. cm^{-1}

(b) Mesophyll resistance to CO_2 exchange $M = r_t - 1.605\,R$ sec. cm^{-1}

where M = mesophyll resistance

R = leaf resistance in sec. cm^{-1}

r_t= total resistance to CO_2 uptake which is

$$= \frac{(CO_2 \text{ out} - CO_2 \text{ c.w.})}{F} \text{ sec. cm}^{-1}.$$

F = rate of CO_2 uptake in $mg.cm^{-2}.sec.^{-1}$

T = transpiration rate in $mg.cm^{-2}.sec^{-1}$)

W_e = water vapour density of the leaf ($mg.cm^{-3}$)

W_o = water vapour density of the air leaving the chamber ($mg.cm^{-3}$).