THE EFFECT OF WATER STRESS ON THE GROWTH AND PHYSIOLOGY OF COWPEAS (*VIGNA UNGUICULATA* (L.) WALP)

A Thesis

Presented to

The School of Graduate Studies

Addis Ababa University

In Partial Fulfilment

of the Requirements for the Degree

Master of Science in Biology

by

Masresha Fetene

June 1985.

ADDIS ABABA UNIVERSITY
School of Graduate Studies

"The effect of water stress on the growth and physiology of cowpea (Vinga unguiculata, (L) Walp)"

by

Masresha Fetene
Faculty of Science

Approved by Board of Examiners

Dr. J.C. Tothill
External Examiner

Dr. Amha Belay
Internal Examiner

Dr. Daniel C. Adjei-Twum
Research Advisor

Dr. Berhanu A. Gashe
Chairman

ACKNOWLEDGMENTS

I wish to express my sincere thanks to Dr. Shibru Tedla without whose initiative, encouragement and abundant support this work would not have been possible.

I deeply appreciate the excellent guidance, inspiration and unreserved support and cooperation during the conduct of the experiment and the preparation of this manuscript from my adviror, Dr. Daniel C. Adjei-Twum.

I am deeply grateful to Ato Legesse Negash for his inspiration and valuable suggestions, and for student Selome Bekele for her immense interest in this work and assistance in the statistical computations.

To the Management of the Institute of Agricultural Research (IAR) for allowing me to use their facilities at Nazareth, to the staff of the Crop Physiology Section of the IAR at Nazareth, and to all others who contributed in some way to the completion of this work, I owe them my sincere appreciation and thanks.

Finally, I would like to extend my acknowledgment to the Department of Biology, Addis Ababa University, for sponsering my studies and to the Swedish Agency for Research Cooperation with the Developing Countries (SAREC) for financial support.

ABSTRACT

Effect of water stress on growth, physiology, biochemical contents and seed yield of cowpea (Vigna unguiculata (L.) Walp CV.Black Eye Bean) grown at -5.0,-10.0,-12.5 and -15.0 bars leaf water potential were studied to examine the possible mechanismsof cowpea adaptation to drought. The experiment was conducted under greenhouse conditions and the treatments consisted of irrigating the soil to field capacity and allowing it to dry until the plants reached the above predetermined leaf water potential values.

Plant height, leaf area, dry matter, relative growth rates and net assimilation rates decreased as leaf water potential decreased. Stomatal resistance, on the other hand, increased as leaf water potential decreased. The heighest resistance was recorded in plants maintained at -15.0 bars leaf water potential. Nitrate reductase activity and nodule numbers decreased linearly with plant water deficit.

Water stress inhibited the accumulation of leaf chlorophyl starch and proteins, but it increased the amounts of amino acids, reducing sugars and soluble carbohydrates.

Seed yield was also reduced by water stress. Of all the components of seed yield, seed size, pod density and the number of seeds/pod were most affected. However, pod density was the most sensitive component of seed yield to water deficits.

It was concluded that the high drought resistance of the crop was mainly due to the plant's ability to avoid water loss by maintaining high stomatal resistance, reducing its total leaf area and by tolerating dehydration through osmoregulation.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

I N T R O D U C T I O N

Among the different environments encountered by a plant during its life cycle, drought is probably the most inhibitory and unpredictable factor (Boyer, 1976). Perhaps, there is no other factor that limits grain production so extensively as drought does (Boyer and McPherson, 1975). Its injury occurs when various combinations of the physical factors of the environemnt produce an internal water stress sufficient to delay or prevent crop establishment, weaken or destroy established crops, or alter the physiological and biochemical processes in plants (Larson, 1975).

Terrestrial plants rarely grow in a natural environment free from water stress for a period of more than a few days (Hsiao et al., 1976). In arid and semi - arid areas, there is no problem more ubiquitous than water stress (Hsiao et al., 1970). In such areas, agricultural production may be reduced virtually to zero during a prolonged period without water (Boyer, 1976). In a wide belt across some parts of South Asia, India, Africa, the Middle East, and in other areas, from Northern Argentina and North - East Brazil to Mexico, food production for millions of people is limited primarily by the erratic nature of the rainfall (Gupta, 1975). In Ethiopia alone, an estimated number of seven million people were severely affected by droughts in 1984/85 (RRC Bulletin, 1985). Thus, in a world that is globally threatened by droughts and the horrors of famine,

water is the most important of our natural resources which is invariably in short supply (Slatyer, 1967).

Having evolved in a medium of water, life of all forms including that of plants is inextricably dependent on water for the function and survival of all living organisms (Hsiao et al., 1976). The functions of water in general and the position it occupies in a plant complex, where it has a crucial role, is tremendous (Hsiao, 1973). Although a considerable amount of information on the functions of water has accumulated in the literature in recent times, most of the physiochemical bases of water in plants are little understood (Hsiao et al., 1976; Hsiao et al., 1977; Slavik, 1977). Whilst there have been some advances towards the understanding of water stress phenomena in plants recently (Kramer, 1974), the study and characterization of the behaviours of individual crops, under drought conditions, leaves much to be desired (Arnon, 1975).

It is therefore of great importance not only to characterize and quantify whole plant water stress phenomena (Kramer, 1974), but also to investigate and evaluate the various physiological consequences of water stress. This may facilitate the identification of the specific processes and control mechanisms of plant water responses (Albert and Thornber, 1977).

Thus, how plants are affected by water deficits and

what mechanisms enable them, nevertheless, to survive or even thrive are problems of prime significance in plant physiology with immediate practical implications to agricultural production (Hsiao et al., 1976).

The increasing realization that the occurrence of droughts is more or less inevitable, has led plant scientist to desperately look for crop plants which are better adapted to dryland conditions (Gupta, 1975). This has necessitated a close examination of the kind of resistances shown by such plants, including the anatomical, biochemical and physiologi mechanisms involved and the degree of tolerance.

As in most other cases, crop plants differ widely in their responses to water stress conditions. Not only are they different in the kind and degree of resistance they show, but also in the particular physiological and morphological mechanisms they employ to combat it. Thus, in the search for agriculturally productive crops, the identificati of drought resistant crops and the characterization of the specific adaptive traits for better management practices in general (Herbert and Baggerman, 1983), and breeding programmes to introduce the traits into more adapted genotypes in particular, has become of paramount importance (Keim et al., 1981). One such crop that has recently recieved the attenti of agriculturalists as a promising plant is cowpea (Kay, 1979; Turk et al., 1980; Allen and Obura, 1983).

Cowpea (Vigna unguiculata (L.) Walp) is a hot weather annual legume of arid, semi - arid and humid tropics which has been in cultivation since ancient times as food for human consumption (Irvine, 1974). It is grown throughout the sub-tropics and tropics both as a source of grains and green vegetables (Purseglove, 1968). According to Arnon (1972), it is the most important pulse crop grown in Africa, particularly in regions with low rainfall.

During the low rainfall years of the 1970's cowpeas produced seeds under rain-fed conditions in the Sudanian zone of Africa, when all other drought resistant crops like sorghum (Sorghum bicolor (L.) and pearl millet faile to produce grains (Turk et al., 1980). In experiments conducted by Hiler et al. (1972), cowpea produced seeds eve when it was maintained under so severe a water stress as -28 bars of leaf water potential which is normally lethal to many other crops.

Extreme drought resistance (Rachie and Roberts, 1974; Turke and Hall, 1980) is not the only attribute cowpea has in its favour. The crop is one of the few which combine drought resistance with high yielding potential (Turk et al. 1980; Ziska and Hall, 1983). Besides, cowpea can yield satisfactorily under a greater diversity of soil, climatic and cultural conditions than most other leguminous crops (Irvine, 1974; Allan and Obura, 1983), a fact that should

very well be borne in mind in countries such as Ethiopia, where there is much more diversity than uniformity and severe droughts occur with alarming frequency.

In connection with its wide adaptability, an interestin feature of cowpea is its capacity to grow on poor soils (Purseglove, 1968; Westphal, 1974). This is partly due to the fact that it is a legume. A leguminous crop can add upto 500 kg of fixed nitrogen to soil per hectar per annum (Purseglove, 1968). As a typical legume, the ability of cowpea to reduce atmospheric nitrogen to the utilizable form not only enables it to grow without any additional nitrogen fertilizer, but also gives it the capacity to add some nitro to the soil from which other crops could benefit. With the increasing prices for commercial nitrogen fertilizers for peasant farming, the role of cowpea in mixed farming systems in crop rotations and in general amelioration of soil conditions need greater exploitation.

Cowpea is also a crop that is relatively easy to cultiv (IAR 1970; Westphal, 1974). Owing to the ability of the crop to compete with grasses and other persistent weeds such as Imperata cylindrica in some systems of traditional agriculture, the crop could be planted without any previous land preparation (Arnon, 1972).

Among the several merits of the crop, the most importan

and widespread of its use is the utilization of the seed meal for various forms of human food (Irvine, 1974). Cowpea are now principally a subsistence crop for farmers in the semi-arid regions of Asia and Africa (Purseglove, 1976). Th seeds contain about 23% protein (Kay, 1979). Thus, they pla an important role in protein requirement in the human diet, particularly lysine supplementation in the diets of the people in those regions who are largely dependent upon cereals (Crabbe and Lawson, 1981).

In addition, cowpea is very popular as a pot-herb in some parts of tropical Africa (Purseglove, 1968; Irvine, 197 It is good fodder crop for hay (Westphal, 1974), and an exc- ellent cover or catch crop (Irvine, 1974).

In Ethiopia, which is considered to be the origin and the centre of diversity of cowpea (Steele, 1979), the crop is mainly grown in the drier regions of Hararge, Konso and probably Eriteria (Westphal, 1974). The crop can grow at altitudes as high as 2000 m. In the Konso area, they are usually grown together with other crops such as sorghum (Westphal, 1974). The seeds are ground into a powder form for the preparation of various meals. The Chako in South - West Ethiopia eat the leaves as spinach (Westphal, 1974).

Despite all the good attributes of cowpea, it has not

been studied much, in comparison with other crops (Allen and Obura, 1983). Several authors, notably Turk and Hall (1980), Turk et al. (1980) and Summerfield et al. (1976) have recomme that more studies on the specific adaptation traits of the crop be conducted. Based on the existance of conflicting results, Herbert and Baggerman (1983) and Shouse et al. (1981) also suggested that more investigations into the sensitivity of seed yield components of cowpea to droughts be conducted.

The present alarming drought condition in the country has necessitated the search for drought tolerant and widely adaptable crops to the country; and this has been the backgro and origin of this work. The studies being reported here, therefore, have the following specific objectives:

1. To study the growth and development of a cowpea cultivar, commonly grown in this country, under diff nt regimes of soil moisture;
2. To investigate the sensitivity of seed yield and its components in cowpea to water stress; and
3. To characterize the specific, morphological, physiological and biochemical mechanism involved in avoidance and/or tolerance of water stress in cowpeas.

REVIEW OF LITERATURE

A. The Role and Nature of Water in Plant Life.

Plant life takes place in aqueous medium. Deprived of water, plants wilt and die. Slatyer (1967) described water as the most important basis of life. Kramer (1966) called it the dynamic unifying entity. The amount of water which typical land plants consume is prodigious in quantity, vastl more than any of the other substances which enter them and s hundred times more than their water contents at maturity (Price, 1974).

The central position water occupies in life stems from its unique physical/chemical properties. It is an extremely good solvent for polar substances and particularly, for ions which have far-reaching consequences for life, since many biologically important substances are charged (Nobel, 1970). Water has relatively a high specific heat and thermal conductivity for a liquid. Both properties make it an ideal substance for the maintenance of temperature equ librum (Bidwell, 1979). It is relatively rather incompressible at high pressures under physiological conditions; and this property underlies its role in plant support (Nobe 1970). Water is relatively quite transparent to visible radiation, enabling sunlight to reach chloroplasts within the cells in leaves and in submerged plants in the oceans.

The physical structure of water involves hydrogen and dipole-dipole bondings which result in high internal pressures (tensile strength), and high surface tensions. Thus, water equilibria serve as important integrating forces in plant life (Crafts, 1968).

In the living plant, water occurs in many states and is involved in all physiological processes: water of hydration and imbibition in colloidal phases such as in cell walls, osmotic water in vacuoles and phloem conduits, and hydrostatic water in the xylem (Crafts, 1968). The source of oxygen involved in photosynthesis and the hydrogen used for carbon dioxide reduction is water. The phosphorylation that results in the generation of the important energy currency, ATP, is a dehydration process involving the extraction of the components of water from ADP plus phosphate (Nobel, 1970). Water is important for the structural integrity of cells, tissues, and organisms as a whole. It is the vital solvent with which mineral nutrients and other food substances are translocated. In fact, the functions of water in plant systems are so numerous; and according to Hsiao et al. (1976), any attempt to elaborate on them can only understate the case. Suffice it to say then, that, it is almost impossible to conceive of the properties of cells and whole plants without water and its unique properties.

Since droughts are the main causes of crop failures

and famine in most parts of the world, particularly in the third world countries, the physiological effects of water stress on crop plants have attracted considerable attention of scientists. Water stress can arise either from an insufficient presence of water in the plant environment or from its excessive presence. The former occurs as a result of water deficits or droughts while the latter occurs due to flooding of plants in excess of field capacity (Levitt, 1980). Flooding of plants in excess of field capacity causes leaching of mineral nutrients (Adjei - Twum, 1976) and essential intermediate metabolites from roots (Davidson et al., 1973). It also causes the replacement of air by water which results in poor aeration. Poor aeration causes oxygen deficiency in roots (Wample and Reid, 1975).

The effects of oxygen deficiency in plants have been studied by Wample and Reid (1975), Lambers(1976), Sojka et al., (1975) and Lambers et al. (1978) and there was a retardation of shoot development, as a result of oxygen deficiency in all cases. Boggie (1974) obtained a severely retarded growth in Picea sitchensis under low oxygen concentrations. Wignarajah et al. (1976) also reported a significant reduction in both shoot and root growth in barley. Lambers (1976) studied respiration under flooded conditions in Senecio and found that there was a 50% inhibition in the flood-resistant spp. (Senecio aquaticus) while respiration did

net occur in the flood - sensitive spp (S. jacobaea).

The most obvious injury of flooding in plant roots is the accumulation of toxic products of anaerobiosis that follows the stress imposed by oxygen deficiency (Levitt, 1980). Nevertheless, unlike the stress caused by water deficits, flooding does not bring about a direct water potential stress in plants (Levitt, 1980). Water deficit stress in soils, on the other hand, produces both primary and secondary effects (Hsiao, 1973) by directly affecting plant water potential (Hsiao, 1973; Kramer, 1974; Levitt, 1980).

Plant water relations is best explained by the concept of water potential. Water potenial (ψ) is the chemical potential of water which is defined as the partial molar Gibbs free energy of water at constant pressure and temperature (Oertile, 1971). The factors which affect the chemical potential of water in plants can be summarized into hydrostatic pressure or tension, collegative effects of solute and interactions with matrix of solids and macromolecules. Thus, pressure potential (ψ_p), osmotic potential (ψ_π) and matric potential constitute the components of water potential in plants (Hsiao, 1973), while gravitational potential (ψ_g) constitutes a fourth component of water potential in soils (Adjei-Twum, 1980).

Water flux through the soil - plant system tends to

occur along gradients of decreasing water potential (Kramer, 1969; Hsiao, 1973). The driving force, however, may not necessarily be the gradient of total water potential but a component potential (Slayter, 1967; Slavik, 1975). Among plant parts, leaves constitute the sink for liquid flow. The flux of water from the root-soil and plant -air interfaces is due to the replacement of the amount of water transpired. The driving force is, by and large, the overall differencess in water potential between absorbing root surfaces and transpiring aerial surfaces of plants (Slavik, 1975).

The theory of liquid flow requires that plant water potential be lower than that of the soil to facilitate water absorption by roots. Any decreases in the water potential of the soil is, therefore, accompanied by a corresponding decrease in the water potential of the plant. When this decrease in plants is below the level necessary for metabolic activities, water deficit stress sets in. Water deficit stress in plants, therefore, develops as a result of an imbalance between the supply furnished by the soil water and the requirements of the plant(Slayter, 1967; Hsiao, 1973; Slavik 1975).

However, a certain level of soil water stress will not necessarily be accompanied by an equivalent degree of plant water stress (Kramer, 1969; Levitt, 1980). According

to Arnon (1975) and Taylor and Klepper (1978), the water status of a plant depends on resistances to flow of water which vary with its water content; resistance to the flow within the roots and other tissues of the plant which depends on some physiological factors; and the resistance to the flow from the stomata into the atmosphere which varies with atmospheric condition.

The physiological processes in plants are primarily a function of their water status and are only indirectly affected by soil and atmospheric water stress (Kramer, 1969). That plant water potential is more dependent on the resistances of plant tissues to water flux, rather than on soild and atmospheric conditions, has been demonstrated by Janes (1970) and Stoker and Weatherley (1971). Begg and Turner (197), for example, found that abrupt changes in tobacco leaf water potential were as a result of higher local resistances between stem xylem and petiole xylem. Studies by Boyer (1968) showed that resistances in roots were twice as much as in stem and leaf tissues. Thus, in any meaningful study on the effects of water stress on the growth and development of plants, direct measurements of plant water status such as leaf water potential is recommended for valid and repeatable results (Kramer, 1969 ; Larson, 1975; Levitt, 1980).

B. Effect of Water Stress on Plant Growth

The growth of plants under water stress has been studied by several investigators (Kanemasu and Tanner, 1969

Boyer, 1970a; Taylor and Klepper, 1974; Brown and Tanner, 1983). Often, a reduction in growth is the first measureable effect of water stress (Hsiao, 1973; Kramer, 1974). In general, the extent of reduction depends on the degree of water stress and the species concerned (Gates, 1968). In cotton, for instance, growth inhibition may result from a very small reduction in water potential as from -1 to -3 bars (Taylor and Klepper, 1974). Brown and Tanner (1983) observed reduced shoot growth in Alfalfa when leaf water potential dropped below -10 bars. However, in some Acacia spp. growth may continue even if the water potential drops to a very low level of -50 bars (Hsiao, 1973).

The lowest possible plant water potential ever reported in cowpeas was -28 bars. This was under green house condition (Hiler et al., 1972). However, Clark and Hiler (1973) dete rmined water potential in lysimeters and reported that the lowest possible water potential in stressed cowpea plants, under field conditions, was above -15 bars. Similarly, Turk and Hall (1980) reported that pressure chamber measurements of xylem pressure potential in cowpea invariably remained above -18 bars.

Plant growth is a function of three stages: cell divisio cell enlargement and differentiation (Leopold, 1970). The degree of sensitivity of each stage to water stress varies considerably (Boyer, 1970; Slavik, 1975). Cell growth has

been quantitatively related to cell turgor; and cell turgor decreases with cell water potential (Boyer, 1968). Thus, it was the decrease in the turgor component of water potential which was responsible for the inhibition of cell enlargement (Lockhart, 1965). In cotton, cell enlargement was more sensitive to water stress than to any of the other stages of cell growth (Boyer, 1970a). Hsiao et al. (1970) observed a decrease in elongation of maize leaves with a very small reduction in leaf water potential

Cell division has also been found to be sensitive to water stress (Terry et al., 1971). This was due to a greater requirement of water, when cells were enlarging to several fold of their original size, during cell division (levitt, 1980). However, a study by Burstrom (1980) showed that cell division in pea stems was reduced at levels of stress that did not affect cell enlargement. Of the three stages of cell growth, cell differentiation was rather stimulated by water stress (Levitt, 1980).

Hiler et al. (1972) studied the effects of plant water deficit on the growth of cowpea and reported that plant height was progressively reduced with increasing water deficit Denmead and Shaw (1960) and Duncan (1975) showed that the height of maize plants, under water stress, was considerably influenced by the rate of stem elongation. Duncan (1975)

reported a 75% decline in the rate at wilting point. As the elongation of developing cells was inhibited under water stress (Duncan, 1975), the length of internodes were also reduced (Denmead and Shaw, 1960; Christiane, 1977); and this consequently resulted in shorter plants (Denmead and Shaw, 1960).

The effects of water deficits on cowpea leaf area have been studied under green house (Hiler et al., 1972) and field (Turk and Hall, 1980a) conditions. In both cases, substantial decreases in leaf area were observed with increasing water stress. According to Boyer and McPherson (1975), leaf enlargement in maize was most rapid when leaf water potentials were between -1.5 and -2.5 bars and they declined markedly, when leaf water potentials decreased further. Low leaf water potentials also influenced leaf production through their effects on leaf initiation in meristems and subsequent cell division (Boyer and McPherson, 1975). In studies by Boyer (1970b), leaf enlargement was severely inhibited when leaf water potential was about -2 bars and it practically ceased at values as high as -4 bars in sunflower, -8 bars in maize and -12 bars in soybeans. In alfalfa, the initial leaf water potential below which leaf area expansion stopped was -10 bars (Brown and Tanner, 1983). Thus, the reduction in leaf enlargement (expansion), as a result of reduced cell turgor following water stress, was the main cause of the reduction total leaf area. In cowpeas, the reduction in leaf area

represented an important mechanism of drought avoidance as it resulted in reductions in crop water use (Turk and Hall, 1980c; Turk and Shulze, 1980). It also resulted in less photosynthetic activity which was reflected in the reduction of total dry matter (Boyer, 1970a; Hiler et al., 1972; Duncan 1975; Turk and Hall, 1980a). However, a reduction in leaf area may occur as a consequence of increased senescence of leaves under water stress (Boyer, 1968; Sionit and Kramer, 1976; Turk and Hall 1980).

Dry matter accumulation in cowpea was also effected substantially by water stress imposed during all the various growth stages of the crop (Hiler et al., 1972). Boyer and McPherson (1975) reported a positive correlation between the rates of photosynthesis and dry matter accumulation. Their studies showed that the dry matter content of plants was reduced as photosynthetic rates declined in plants under water stress. Turk and Hall (1980a) also reported that soil moisture deficits during the vegetative and reproductive phases of field grown cowpeas resulted in significantly lower shoot dry matter.

The relationship between dry matter contents of roots and shoots of plants under water stress (i.e., root/shoot ratio) has been shown to be an important means of drought avoidance (Arnon, 1975; Levitt, 1980). In general, plants tend to

avoid droughts by accumulating larger amounts of dry matter in their roots than in their shoots (Arnon, 1975). Karmi et al. (1980) subjected soybean plants to water stress until their leaf water potentials reached -12 bars and reported that significant decreases in the dry matter contents of leaves, stems and petioles and an increase in root dry matter occurred. Silvius et al. (1977) investigated the effects of water stress on carbon assimilation ($^{14}CO_2$) and distribution in soybean plants at different stages of development and reported a relatively more accumulation of ^{14}C in roots than in aerial parts. Such alterations in ^{14}C distribution was found in plants with water potentials of between -15 and -20 bars. The growth of roots at the expense of shoots facilitates efficient water absorption by roots. It is also a function of the water potential gradient which is less steep in roots than in shoots (Christiane, 1977).

One growth parameter which has recently attracted the attention of researchers on soil-plant-water relationships is specific leaf weight (SLW) defined as leaf blade dry weight per unit leaf area (Silvius et al., 1977; Fischer and Turner 1978). In general, specific leaf weight increases under water stress conditions (Turk and Hall, 1980a). According to Fischer and Turner (1978), the specific leaf weight of desert shrubs is two to three-fold more than that of many herbaceous plants. However, SLW could also be affected by

planting density or changes in solar radiation levels (Turk and Hall 1980a). In a study to determine whether specific leaf weight could provide a measure of the long-term water status of cowpea plants, Turk and Hall (1980a) obtained positive correlations between SLW and cummulative xylem water potentials and between seed yield and SLW.

Water stress also caused some reductions in certain growth parameters such as relative growth rates (RGR) (Brown and Tanner, 1983) and net assimilation rates (NAR) (Lawler, 1970; Slavik, 1975). The RGR of plants is the rate of increase in plant material per unit time. NAR is the rate of increase in plant material per unit of assimilatory material per unit time (Radford, 1967). In general, water stress affects RGR through the same mechanisms with which it affects plant growth such as its effects on cell turgor, cell division, leaf area development and photosynthesis. However, the consequences of water stress were a reduction in plant growth (Levitt, 1980), due to decreases in growth promoting hormones such as cytokinins (Ilai and Vaadia, 1965) and increases in growth retardants (Levitt, 1980), and in ethylene (Pratt and Goeschl, 1969) and abscisic acid (Wright and Hiron, 1969; Loveys and Kriedmann, 1973; Quarrie and Jones, 1977) in particular.

Water stress affects NAR through its effects on

photosynthesis and respiration (Kanemasu and Tanner, 1969). Kanemasu and Tanner (1969) attributed a reduction in NAR, as leaf water potential decreased and stomatal resistance increased, to increased respiratory rates, due to higher ambient leaf and root temperatures as a result of reduced transpiration rates; and a decline in photosynthetic rates caused by a decreasing supply of Co_2 and impaired biochemical processes.

C. Effect of Water Stress on Some Metabolic Activities of Plants.

It has been reported by several workers that photosynthetic carbon assimilation is adversely affected by water stress (Boyer and Bowen, 1970; Boyer, 1971; Chen et al., 1971). Generally, both the light and dark reactions of the photosynthe processes are adversely affected by water stress. Plant water deficits inhibit the rate of photosynthesis by reducing CO_2 assimilation in the light as a result of stomatal closure (Gale and Hagan, 1966), by reducing total leaf area (Boyer, 1970a; Arnon, 1975) and by inhibition of Hill reaction (Boyer and Bowen, 1970; Boyer, 1960b).

Whilst working with isolated chloroplasts from water stressed pea and sunflower leaves, Boyer and Bowen (1970)

observed that oxygen evolution decreased linearly in proportion to leaf water potentials, when the latter was below -12 bars in both pea and sunflower. Boyer (1970) studied phctosynthesi in corn and soybeans at various leaf water potentials and reported that photosynthesis in soybeans was reduced at potentials less than -11 bars but the reduction in the rates of photosynthesis in corn occurred at -13.5 bars. He concluded that water deficits inhibited photosynthesis because it disrupted the integrity of chloroplast membranes and inhibited Hill reaction. Similar results were obtained by Alberte et al. (1977) who reported that pigment molecules were destroyed in water stressed plants. However, $NADP^+$ reduction during Hill reaction proceeded at decreased rates only when plant water deficits were very severe (Slavik, 1975).

According to Slavik (1975), the dark reactions of photosynthesis consist of two main processes: a) physical transfer of CO_2 from the plant's atmosphere to the carboxylation centres in the chloroplasts; and b) the various biochemical process of photosynthesis.

Under water stress, resistance to CO_2 influx, i.e., boundary layer diffusive resistance (transfer in the boundary

air layer adhering to the leaf surface), stomatal diffusive resistance (diffusion in air through the stomatal apertures) and mesophyll intercellular resistance (across the mesophyll intercellular spaces) have been shown to increase at different rates (Redshaw and Meidner, 1972; Pieters and Zima, 1975; Bunce, 1977). Of the three, however, stomatal diffusive resistance is the most obvious mechanism by which leaf water deficit affects photosynthetic CO_2 uptake in higher plants (Boyer, 1971; Levitt, 1980). Thus, it was primarily due to the resistance to CO_2 influx to the carboxylating centres in water-stressed plants that photosynthetic carbon assimilation was reduced (Levitt, 1980).

The sensitivity of stomata to water stress has been found to vary from one plant to another (Hsiao, 1973). The threshold level of water potential above which stomata remain open (or below which stomata close) is a measure of the resistance capacity of a plant. The threshold level of soybeans was found to be -10 to -12 bars (Boyer, 1970a), -7 to -9 for tomatoes (Hsiao, 1973). In some species of acacia, however, stomata remained open at a water potential of -50 bars (Kramer, 1974). The mechanism of stomatal action is largely dependent on the phenomenon of turgor pressure - a function of both the anatomy of guard cells and water potential gradients.

Stomatal resistance decreased as stomatal aperture increased, when the turgor pressure of the guard cells had sufficiently exceeded that of the neighbouring epidermal cells. Humble and Raschke (1971) and Schnable and Raschke (1980) reported that a light-induced increase in turgor of guard cells was primarily due to water uptake as a consequence of a decrease in osmotic potential caused by ATP - dependent intake of potassium ions. In the dark, the closure of stomata and a reduction in their resistances were attributed to some losses in the potassium ions (Humble and Raschke, 1971; Fischer and Hsiao, 1968).

The involvement of potassium ions in the regulation of stomatal aperture has been recently confirmed by Pemadasa (1979), Wilmer et al. (1983) and Pemadasa (1983). Besides potassium ions, changes in the concentration of starch, malate and chlorides in guard cells have also been implicated in the mechanism for the control of stomatal aperture (Raschke, 1975; Pemadasa, 1983).

Differences in the resistance of stomata on the adaxial and abaxial sides of leaves, under water stress, were reported by Raschke (1975). Normally, the abaxial side had a lower resistance than the adaxial (Kanemasu and Tanner, 1969). This observation has been supported by Pemadasa (1979) who reported that higher rates of starch hydrolysis and K^+ accumulation occurred in the abaxial than in the adaxial

guard cells.

Ever since the pioneering work of Wright and Hiron (1969), abscisic acid (ABA), a growth inhibitor, has been found by several investigators (Quarrie and Jones, 1979; Zeevart, 1980; Ackerson, 1980; Hall and McWha, 1981) to increase several fold in amount in tissues under water stress; and this resulted in the closure of the stomata of such plants. With regards to the mechanism of action of ABA, Dittrich and Raschke (1977) and MacRobbie (1981) showed that ABA induced the efflux of potassium ions and malate from guard cells to their surrounding epidermal cells. The efflux of potassium ions and malate increased the osmotic potential of guard cells from which water flowed, following water potential gradients. The overall effect of this was loss of turgor by guard cells and stomatal closure. Thus, reduced transpiration rates, due to the closure of stomata, were largely the result of increased synthesis of ABA in stressed plants (Milborrow and Noddle, 1970; Zeevart, 1980). However, since the path along which water escapes from a plant is also used by CO_2 to enter it; the same mechanism that the plant uses to avoid water loss, i.e. higher stomatal resistance, severely impairs photosynthetic rates.

A decline in the photosynthetic rates in water stressed plants was attributed to reduced activities of ribulose -1, 5-diphosphate carboxylase (O'Toole et al., 1976 and

1977) and glyceraldehyde -3-phosphate dehydrogenase (Lee and Stewart, 1971), due to some changes in the molecular configuration of the former and the oxidation of the sulfhydryl groups in the latter. However, the rates of ATP synthesis and reduction of 3-phosphoglyceric acid decreased only under very severe conditions of water stress (Slavik, 1975).

The respiratory rates in plants, under water stress, depend upon both the degree of the stress and the types of plant species (Brix, 1962). Koeppe et al. (1973) obtained maximum respiratory rates in maize seedlings at leaf water potential of -16 bars but Brix (1962) reported constant rates of respiration in tomato plants with leaf water potentials between 0 and -12 bars. The respiratory rates gradually decreased with leaf water potential, when the latter decreased further from -12 to -36 bars. In loblolly pines, however, there was a sharp drop in respiratory rates, when leaf water potential decreased to -12 bars followed by a rapid increase in respiratory rates to a maximum, as leaf water potential decreased further from -12 to -36 bars (Brix, 1962). According to Levitt(1980), a decline in respiratory rates in water stressed plants at zero cell turgor pressure was due to increased in enzyme and substrate concentrations as well as decreases in cell volume. However, inhibition of the activities of enzymes, decreased intercellular spaces, increased viscosity of cell contents and reduced rates of

gas exchanges in plant tissues with low water potentials led to decreased respiratory rates.

Translocation of photosynthetic products has been shown to be affected by water stress (Reid, 1974; Sheikholesslam and Currier, 1977). Phloem transport depended on gradients of hydrostatic pressure (Wareing and Patrik, 1975). Reduced translocation rates in water-stressed plants resulted from direct disturbances in phloem pressure gradients, due to a reduction in tissue water potentials (Sheikholeslam and Currier, 1977). However, Wardlow (1969), and Gallagher et al. (1976) reported that translocation per se was not a limiting factor in plants under water-stress. Reduced translocation at lower water potentials was attributed to limited source capacity because of a reduction in photosynthetic rates and smaller sink capacity, due to the adverse effect of growth inhibitiors (Wardlow, 1969).

Generally, most of the effects of water stress on the physiology of plants can be traced to the overall reduction in enzymatic activity (Arnon, 1975). This is a result of configurational changes in molecular structure due to dehydration (Darbyshire, 1974), on the one hand, and reduced protein synthesis (Barlow et al., 1977), on the other.

An enzyme that has consistently shown a decrease in activity with water stress is nitrate reductase (NR)

(Bardzik et al., 1971; Morilla et al., 1973). Morilla et al (1973) reported that NR activity in corn seedlings declined by 50% of the control plants as leaf water potential decreased to -2 bars. A decrease in NR activity was attributed to decreased rates of protein synthesis and increased rates of the degradation of enzymes. Similar results were obtained by Plaut (1974) in wheat seedlings. Nitrate reductase is an inducible enzyme (Afridi and Hewitt, 1964). Hence, lower translocation rates of nitrates from inactive pools to sites of activity in stressed plants was responsible for the reduction in the activity of the enzyme (Morilla et al., 1973).

Besides reduced nitrate reductase activity, water deficits in soils and plant tissues adversely influence nitroge metabolism in leguminous plants by inhibiting nodulation (Sprent, 1971b). Accoring to Sprent (1977a), the nitrogen-reducing activity of nodules ceased when the moisture content of detached soybean nodules decreased by 80% of their fresh weight, due to either an increased rate of destruction of enzymes or a reduction in the rates of protein synthesis.

Protein synthesis was shown to be adversely affected under water stress conditions (Barlow et al., 1977). Sugar beet leaves subjected to prolonged water stress contained smaller amounts of proteins than those found in normal leaves (Shah and Loomis, 1965). Similar results were obtained in soybeans by Fukutoku and Yamada (1982) who

reported a decrease of 83% in the tissues of stressed plants. Rapid changes in the levels of polyribosomes in Zea mays , in response to water stress, also resulted in reduced rates of protein synthesis (Hsiao, 1970). Deltour and Jaqmard (1984) reported that decreased rates of DNA synthesis occurre in stressed plants. Lower rates of protein-synthesis were also due to some losses in RNA as a result of increased RNase activity(Levitt, 1980). Soong and Hageman (1977) showed that leaf protein losses in stressed corn seedlings were due to some increases in the activity and concentration of proteol ytic enzymes. One group of cell organelles which is susceptib to such proteolytic activities, when subjected to water stress is that of chloroplasts (Soong and Hageman, 1977). Some 50% of the dry weight of chloroplasts is composed of various proteins (Bonner and Varner, 1965). Thus, the losses in the chlorophyll content of plant leaves in response to water stres as reported by Mohanty and Boyer (1976), Adjei-Twum (1976), an Soong and Hagemann (1977) were probably caused by enhanced catabolism and/or by the retardation of protein synthesis. Moreover, Alberte et al. (1977) reported that the synthesis of the light-harvesting chlorophyll a/b - protein was inhibited by, at least, 50% under mild leaf water stress (-8 bars) conditions.

Several investigators have studied the total free amino acid contents of plants under water stress (Soong and Hageman, 1977; Stewart et al., 1977 ; Stewart, 1980' Fukutoku and Yamada, 1982). In almost all cases, the total

free amino acids contents of stressed plants increased as a result of enhanced hydrolysis of proteins. According to Fukutoku and Yamada (1982), total free amino acids increase mainly due to the accumulation of proline. Among all the amino acids, proline is the most stable and resistant to oxidative acid hydrolysis and the least inhibitory of cell growth (Levitt, 1980). These properties might account for the observed significant rise in the concentration of this amino acid in plant tissues subjected to water stress (Barnett and Naylor, 1966). Stickler (1964) reported that proline was synthesized from glutamic acid in stressed shoots. However, stewart et al. (1977) reported that the conversion of proline to glutamic acid and, hence, to other soluble compounds, through proline oxidation, was inhibited in stressed barley leaves. Thus, according to Stewart et al. (1977), high levels of proline in stressed plants were maintained through the inhibition of proline oxidation. Besides its obvious role of reducing the osmotic potential of plant tissues which prevents dehydration, the synthesis of proline and other amino acids with smaller molecules could also have a role in decreasing the levels of the otherwise injurious NH_3 released during protein breakdown (Levitt, 1980).

Reductions in starch content followed by an accumulation of soluble carbohydrates in plants under water stress have been reported by several investigators (Naidu et al., 1967;

Barlow et al., 1976; Peterson et al., 1977; Fukutoku and Yamada, 1982). Fukutoku and Yamada (1982) reported that the starch content of soybean seedlings decreased with leaf water potential. It then became constant, when its level reached 35% of the amount in normal plants, but the content of soluble sugars nearly doubled. Accumulation of soluble carbohydrates is a mechanism of osmotic adjustment (Fereres et al., 1978). Increased solute concentration resulted in lower osmotic potentials which was essential for the avoidance of dehydration, under severe water stress conditions (Hodges and Lovio, 1969).

In lobolly pines subjected to droughts, Hodges and Lorio (1969) observed a marked increase in the concentration of reducing sugars, and total carbohydrates with an approximately equivalent decrease in starch. In addition to starch hydrolysis in stressed plants, an increase in soluble carbohydrates was also due to a decrease in plant growth (Hodges and Lorio, 1969).

D. The Effect of Water Stress on Seed Yield and Its Components.

It has long been known that the ultimate yield of a crop is determined by the interaction between its genetic constitution and the various environmental factors including soil moisture regimes. The effects of water stress on yield depend

on what proportion of the total dry matter is considered as useful material to be harvested (Arnon, 1975), when the yield consists of most or all of the aerial parts of the crop, as in the case of forage crops, for example, the effects of water stress on yield will be much the same as on total plant growth With fruits and seeds, on the other hand, the effect of water stress depends on the stage of growth at which the stress occurred (Arnon, 1975).

Although a number of physiological processes contribute towards grain formation in crops, photosynthesis and the translocation of photosynthates from sources to sinks, cell division and cell enlargement are the major processes involved (Boyer and McPherson, 1975). It has been recognised in a number of crops that the dry matter stored in seeds or grains mainly results from photosynthesis that occurs during and after anthesis (Arnon, 1975).

With respect to the effects of water stress on grain yield, many investigators have shown that the flowering and grain-filling stages are the most critical periods (May and Milthorpe, 1962; Talha and Osman 1975). Sionit and Kramer (1977) reported that seed yield in soybeans was considerably reduced when ewater stress was imposed during early seed-formation and grain-filling stages, due to a reduction in the number of flower primoridia (Arnon, 1975) and decreased photosynthetic activity (Shouse et al., 1981). On the contrary

Damptey and Aspinall (1976) reported that mild water stress promoted the development of inflorescence in Zea mays.

Reports on the effects of water stress on seed yield in cowpea are conflcting (Herbert and Baggerman, 1983). Hiler et al. (1972) imposed water stress at various phases of growth in cowpea and reported that imposing stress at the vegetative and pod-filling stages was less detrimental than at the flowering stage. However, Summerfield et al. (1976a) found the vegetative stage to be most sensitive. Turk et al., (1980) reported that the occurrence of droughts during both the flowering and pod-filling stages substantially reduced the yield in two seasons, however, droughts during the vegetative stage alone reduced yield in only one of the two years of experimentation. Similar results were obtained by Shouse et al. (1981) who reported that soil water deficits occurring at the vegetative stage had no significant effect on seed yield but water deficit at the flowering stage reduced seed yield by 44-45%. Shouse et al. (1981) also reported that occurrence of droughts during the pod filling stage of the crop reduced seed yield by 39%.

Herbert and Baggerman 1983) and Shouse et al. (1981) reported that, of all the components of seedyield, pod number per plant, seed number per pod and seed size were the most important regulators of seed yield in cowpea. However, the experimental results of Turk et al. (1980), Shouse et al.

(1981), and Herbert and Baggerman (1983) showed that pod number per plant (pod density) was the most sensitive component to water stress. Reduction in pod number in response to water stress has been described by Turk et al. (1980) as an ecological strategy of cowpea's response to stress to insure that viable seeds are produced for perpetuatio

A reduction in the number of seed primordia is responsible for reduced numbers of seed per pod. Reduced seed number per pod can result from water stress during flowering and pod - filling stages (Shouse et al., 1981; Turk et al, 1980).

Seed size reflects the relationship between sources and sinks of photosynthesis during the pod-filling stage. Smaller seeds result from limited source capacity due to higher pod densities or direct effects of water stress on photosynthesis and/or translocation (Shouse et al., 1981). A smaller number of seeds per pod and lower pod densities, due to water stress, result in limited sink capacity and a sink limitation which results in relatively bigger seeds (Shouse et al., 1981) One parameter which describes source-sink relationship is pod/seed weight ratio on per pod basis. This parameter is negatively correlated with the rate of translocation.

Besides the adverse effects of water stress per se, the yield of cowpea could also be reduced by high day time temperatures which are characteristic features of drought seasons (Shouse et al., 1981). Such excessively high

temperatures increased the rate of flower abscission in cowpea (Summerfield et al., 1976; Turk et al., 1981).

E. Some Adaptations of Plants to Water Stress.

Plants growing under conditions of frequent and often severe water stress may be adapted to survive in one of the following three ways: they may escape, avoid or tolerate droughts (Asana, 1965). Thus, following the terminology of Levitt (1965), Bewley (1979) divided xerophytes into: a) ephemeral annuals i.e. plants that complete their life cycles in arid habitats within brief periods when water is adequate b) drought avoiders i.e. plants with the ability to exclude droughts from their tissues by retarding the rates of water loss from their tissues and/or by increasing their ability to absorb water; and c) drought tolerants i.e. those plants which tolerate and survive water stress without conserving water in their tissues.

Unlike drought avoiders and drought tolerants, ephemerals (drought escapers) have no mechanisms for overcoming water stress. They rather escape droughts by shortening their life cycles (Levitt, 1965) and according to Arnon (1975) and Bewley (1979), such plants are not true drought resistants. Drought avoiders are equipped with some mechanisms which enable their tissues to maintain high level of turgidity and water potential when exposed to water stress (Keim and Kronstad,

1981). This is due mainly to some factors such as deeper roots systems, thicker cuticles and smaller cell volume which enable them to maintain the optimal water content for growth (Asana, 1965). Such maintainance of favourable water balance and turgidity is achieved manily by controlling transpirational water loss (Levitt, 1980). Stomatal control of transpiration is the most important mechanism for conserving water (Hsiao, 1973). As already described, the sensitivity of stomata varies widely from one plant to another and in general, the more drought adapted species have a better control over their stomata and could close them at relatively lower water potentials (Levitt, 1980).

It has long been known that stress avoiders have very low rates of cuticular transpiration. One way by which these plants increase their cuticular resistance is by increasing their surface lipids (Leek et al., 1977). The hydrophobic nature of lipids decreases the permeability of the cuticle of such plants to water; and this probably accounts for decreased cuticular transpiration (Hodgson, 1973). In addition to stomatal and cuticular resistance, other means stress avoiders employ to reduce water losses from their tissues are by reducing the surface area of their leaves and by rolling, folding and shedding of their leaves (Hall and Shulze, 1980).

Although the particular drought adaptation mechanism of cowpea is not clearly understood, it is suspected to be a drought avoider (Turk et al., 1980) primarily due to its ability to maintain high tissue water potential when under water stress. Moreover, reductions in leaf area (Hall and Schulze, 1980) and lower transpiration rates (Turk et al. 1980) are very common in cowpea plants subjected to water stress.

As it has already been mentioned, stomatal closure, as a means for increasing resistance to water loss, has serious limitations on photosynthesis. Some plants overcome this limitation by assimilating higher rates of CO_2 for a given size of stomatal aperture (Hatch and Slack, 1970). Thus, the rapid carbon dioxide fixation in many tropical grasses and some dicotyledons (C-4 plants), throught the C-4 decarboxylating pathway of photosynthesis (Hatch and Slack, 1969) is one mechanism used by plants to simulataneously increase photosynthetic efficiency and also avoid the adverse effects of water stress (Laetsch, 1968; Arnon, 1975). There is also another photosynthetic pathway in a number of succulent plants called crassulacean acid metabolism (CAM). This photosynthetic process reduces water loss in plant tissues without a concomitant reduction in photosynthesis. Large amounts of CO_2 are fixed into malic acid at night. During the day, the malic acid is decarboxylated to give pyruvic acid

and CO_2 and the latter is used for normal C_3 photosynthesis (Osmond, 1978). The CAM photosynthetic pathway is one mechanism used by some stress avoiders (Arnon, 1975).

Plants which tolerate water stress are those which resist dehydration or desication and survive severe conditions of water deficits (Bewley, 1979). Under these circumstances, plants are able to avoide dehydration only if they manage to accumulate sufficient amounts of solutes to decrease their osmotic potential to a level lower than that in their environment (Hodges and Lorio, 1969). One way throught which plants achieve this is by increasing the concentration of their contents of soluble substances such as reducing sugars, non-reducing sugars and total soluble carbohydrates (Hodges and Lorio, 1969; Peterson et al., 1977). Thus, the accumulation of relatively lower molecular organic compounds during water stress is one mechanism by which plants maintain a lower osmotic potential in their tissues and avoid dehydration.

One of the most severe consequences of water stress is the destruction of memberanes and macromolecules (Bewley, 1979). The integrity of enzymes, nucleic acids and other macro-molecules can be retained if some water remains associated with them to prevent the formation of unfavourable conformation (Bidwell, 1979). In plants tolerant to stress, normal conditions are again achieved by the production of

low molecular organic compounds. This facilitates the maintainance of bound water in plant tissues (Bewley, 1979).

The survival of either a drought avoiding or drought tolerant plant under arid conditions is the result of adaptive features that, at best, enable plants to grow, or at worst, allow them to survive. The study of these features not only facilitates the selection of breeding materials by plant breeders but it also increases our understanding of the physiological and/or structural buffers that enable plants to adjust to their environment (Arnon, 1975).

MATERIALS AND METHODS

A. Growing Conditions.

The experiments were conducted in the greenhouse at the Institute of Agricultural Researh Station (IAR) at Melkass, Nazareth, in the summer of 1983. During the experimental period, the temperature and humidity in the greenhouse were not controlled but were recoreded with a hygrothermograph.

The daily mean maximum and minimum teperatures were 40.5°C and 21°C respectively. The relative humidity ranged between 19.7 and 80%. The mean light intensity and the daily mean photosynthetic active radiation at 1200 in the greenhouse, during the growth period, as measured with Li- 188B integrating quantum radiometer/photometer (LI - Cor Incorporated. Lincoln, USA) were 300 watts m^{-2} and 685 ES^{-1} m^{-2}, respectively.

Cowpea (Vigna unguiculata (L.) Walp CV Black Eye bean seeds obtained from the pulse section of the Institute of Agricultural Research Station at Melkassa, Nazareth, were planted on June 3,1983 in black polyethelene pots (30 cm deep with internal diameter of 15 cm) containing 50 g of soil and sand 2:1 (v/v). Seven seeds were planted in each pot but the seedlings were thinned out to three per pot seven days after emergence.

B. Treatments and Experimental Design

Seedlings were watered adequately until 50% reached the trifoliate stages and then subjected to four leaf water potential treatments. Treatments consisted of irrigating the soil to field capacity and allowing it to dry until the plants reached a predetermined leaf water potentials of -5.0, -10.0, -12.5 and -15.0 bars. Leaf water potentials were monitored every other day between 1200 and 1400 h. The soil was re-watered to field capacity whenever each treatment reached its predetermined leaf water potential. This technique was considered to be superior to the use of soil moisture levels as treatments, since the water status of plants are more responsible for their physiological processes.

The treatments were in randonized complete block design with three replications. Each experimental plot consisted of 28 pots for the determination of the various parameters. In addition, there were other plants for monitoring leaf water potentials used as a guide for the watering treatments. All experimental plants were bordered by guard plants.

C. Determination of Leaf Water Potential Stomatal Resistance and Plant Growth

Except for plant height, leaf area and dry matter determinations, and unless otherwise indicated, all parameters were taken when the leaf water potentials in all treatments reached the predetermined values of leaf water potential and before rewatering.

1. Leaf Water Potential

Leaf water potential was estimated woth a pressure chambwr (Scholander et al., 1965)as described by Adjei-Twum (1976). The youngest leaves, fully expanded, healthy and well exposed to sunlight from three randomly selected plants earmarked for this purpose were removed from each plot, on each occassion, for determinations. The petiole was immediately placed through the aperture in the lid of the chamber with the cut end of the petiole projected to the outside. Pressure (with nitrogen gas) was applied until xylem sap appeared at the end of the petiole. The applied pressure was recorded as the negative potential of the xylem sap and a measure of the leaf water potential.

2. Stomatal Resistance

Stomatal resistance on the adaxial surface of the youngest and fully expanded leaves, which were optimally oriented to the sun, were used. The stomatal resistance was determined with a porometer (Lambda Instrument Corporation, USA) by the method described by Kanemasu et al. (1969). The measurements were taken from three leaflets randomly selected from separate plants in each plot.

3. Growth Parameters.

The effects of water stress on the changes in dry matter contents of plants, leaf area development and plant

height were studied at ten-day intervals. Net assimilation rates (NAR) and relative growth rates (RGR) were estimated during the period between the begining of the first drying cycle and the end of the second drying cycle in the treatment which recieved the severest water stress treatment.

i) Plant height

The height of plants from five randomly selected plants per plot was measured from the soil surface in the pot to the highest point on the tallest leaf at ten-day intervals from 25 until 65 days after sowing. The mean height per plant was then recorded.

ii) Leaf Area.

The leaf disc method as described by Adjei-Twum and Splittstorsser (1976) was used for the determination of leaf area. All leaves were removed from five randomly selected plants per plot and a 1.5 cm^2 disc was cut from a random sample of ten leaves. After drying the discs and the remaining leaves, the total leaf area was estimated from the known area of the discs, the dry weight of the discs and the total dry weight of leaves. Petioles were excluded.

iii) Dry Matter and Root/ Shoot Ratio.

Three randomly selected plants were removed from each plot and separated into shoots and roots, washed in tap

water to remove soil and debris, chopped into smaller pieces, dried overnight at 100°C and weighed. The data were expressed as dry weight per plant part and root/shoot ratio

iv) Specific Leaf Weight (SLW)

SLW was estimated from the following equation: specific leaf weight = $\frac{W}{L}$, where W and L are the dry weight and area of leaf laminae, respectively.

v) Relative Growth Rates (RGR)

RGR was estimated from the following equation.

$$RGR = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \quad g/\text{ unit time},$$

where W_1 is the estimated total dry weight at time t_1 and W_2 the corresponding dry weight at time t_2 (Radford, 1967)

vi) Net assimilation Rates (NAR)

NAR was estimated from the following equation:

$$NAR = \frac{W_2 - W_1}{L_2 - L_1} \times \frac{\log_e L_2 - \log_e L_1}{t_2 - t_1} \quad \text{g/unit leaf area/ unit time},$$

where W_1 and L_1 are the total dry weight and total leaf area, respectively at time t_1 , and W_2 and L_2 are the corresponding values at time t_2.

The data were reported as mg day $^{-1}$ and mg cm^{-2} day^{-1} for RGR and NAR respectively.

4. Nodules

Roots were carefully separated from soil and observed for effective nodules. Nodules separated from roots were dissected and those which contained a purplish tinge material wer considered as effective. The data was expressed as the numbe of nodules per plant.

D. Nitrate Reductase Assay

Nitrate reductase activity was determined by the *in vivo* method of Klepper *et al.* (1971) as modified by Harper and Hageman (1972) except that about 0.5 cm^2 leaf strips (Adjei-Twum, 1976) were used instead of discs.

The youngest and fully expanded leaves from three randomly selected plants in each treatment were composited into one sample and three determinations were performed from each sample. Fresh leaves (0.4 g) from each sample were transferre into 50 ml. Erlenmeyer flasks containing 10 ml incubation media (0.2 M KNO_3 in 1M potassium phosphate pH 7.5) and 0.02m "penetrating liquid" (0.4 ml 10% (v/v) in 100 ml distilled water). The samples were evacuated for 2 min. in a vacuum desciccator. Air was rapidly reintroduced and the procedure repeated. The samples were then incubated for 1 hr at 30°C in the dark in a shaking water bath. After

incubation, 0.2 ml aliquots were then analyzed for nitrite content at 540 nm. as described by Klepper (1971). Enzyme activity was expressed as μ Moles $N\bar{O}_2$ formed per gram fresh weight per hour and estimated from the following equation.

$$\mu MNO_2\bar{g}^{-1}hr^{-1} = \frac{1}{0.4}\frac{(OD_{70} \times 0.081 \times 9.8)}{0.4} - \frac{OD_{10} \times 0.081 \times 10)}{0.4}$$

where OD_{10} and OD_{70} were the optical densities after 10 and 70 min., respectively; and 0.4 and 0.081 were the weight of tissue used and the extinction coefficient of nitrite, respectively. Activity per plant was estimated by multiplying the activity per gram fresh weight by total leaf fresh weight.

E. Extraction of Biochemical Substances

1. Chlorophyll

The method of Arnon (1949) was used for the determination of chlorophyll. All the leaves of three randomly selected plants from each plot were removed and composited into one sample. Three aliquot samples of 5 g of fresh leaves from each plot were blended with 20-50 ml 80% acetone (v/v) in an HO_4 blender (Edmund Buhler, W. Germany at 20, 000 revolutions min^{-1} for five minutes. The slurry was twice strained with four layers of cheese cloth, filtered and the filtrate centrifuged for 20 minutes at 6,000 revolutions min^{-1}(in Labofuge 6000, Hereaus Christ model). The pellet was suspended in 10 ml 80% acetone (v/v), centrifuged and the second supernatant

2) Water - Ethanol Soluble Substances.

All the leaves of three randomly selected plants from each plot were cut into small pieces and boiled in 50 ml 80% ethanol (v/v) for eight minutes, homogenized with an HO_4 blender (Edmund Buhler, W.Germany) at 30,000 revolutions min^{-1} for two minutes. The homogenate was centrifuged (Labofuge 6000, Hereaus Christ Model) at 6000 revolutions min^{-1} for 20 minutes. While the supernatant was saved, the pellet was resuspended in 30 ml 80% ethanol and centrifuged. The two supernatants were combined and taken to a volume of 100 ml (Supernatant 1).

The ethanol - water insoluble fraction was used to extract either starch or proteins as required..

3) Starch

To solubilize starch in the ethanol - water insoluble fraction, 20 ml deionized water was added to the pellet and immersed in an ice bath. 13 ml of 52% $HClO_4$(v/v) was then added and the suspension continuously stirred for five minutes and occassionally, there-after, for 15 minutes. The suspension was then centrifuged and the pellet resuspended in 6.5 ml 52% $HClO_4$ in the same condition for 30 minutes and centrifuged. The two supernatants were combined and starch was determined from this supernatant following the same procedure as for total sugars.

4. Insoluble Proteins

Proteins were precipitated from the ethanol - water insoluble fraction by suspending the pellet in 20 ml 10% trichloroacetic acid (w/v) for 60 minutes. The suspension was centrifuged and the supernatant discarded. The precipitate was washed with 10 ml acidic methanol (1 ml 8M formic acid in 400 ml methanol) centrifuged and the supernatant discarded. Protein was then solubilized from the pellet with 30 ml 0.3 N KOH for 15 hr at 37°C. The KOH supernatant was diluted to 40 ml with 0.3 N KOH.

F. Determination Biochemical Substances

For all colorimetric determinations a Spectronic 20 spectrophotometer was used, and all readings were carried out at room temperature.

1. Chlorophyll

OD's of the chlorophyll extract were read at wave lengths of 645 and 663 nM with 80% acetone as the blank. The amount of chlorophyll was estimated using the following equation (Arnon, 1949).

Total Chlorophyll (μg/ml) = $20.2A_{645} + 8.02A_{663}$

Chlorophyll a (μg/ml) = $12.7A_{663} - 2.69A_{645}$

Chlorophyll b (μg/ml) = $22.9\ A_{645} - 4.68\ A_{663}$

chlorophyll content per plant was estimated by multiplying with the corresponding leaf fresh weight.

2. Total Soluble Carbohydrates

Total soluble carbohydrates were determined from Supernatant I (ethanol - water extract) with 0.1% anthrone reagent (w/v) by the method of Hassid and Neufeld (1964). Glucose was used as a standard, and OD's of samples were read at a wave length of 620 nm.

3. Amino Acids

Amino acids were determined from Supernatant I (ethanol - water extract) by the method of Yemm and Cocking (1955). Glycine was used as a standard and OD's of samples were read at a wavelength of 570 nm.

4. Proteins

Ethanol - water soluble proteins (Supernatant I) and Ethanol - water insoluble proteins (Supernatant II) were determined by the Biuret method as described by Gornall et al. (1949) with bovine serum albumin as a standard. OD's of samples were read at 550 nm.

5. Reducing Sugars

Reducing sugars were determined from the ethanol - water soluble extracts (Supernatant I) using the methods of Nelson (1964). Glucose was used as a standard and OD's of samples were read at 620 nm.

G. Determination of Seed Yield and Its Components

All flowers were tagged as they opened and the number which abscised were counted to determine the effect of water stress on flower abscission. At maturity, the pods were harvested and counted to estimate pod density. Their length were also measured. The pods were then dried at 60°C to constant weight. They were then shelled and seed yield/plant, seed yield/pod, seed size, and pod/seed ratio based on the dried materials were estimated for each plot.

RESULTS

A. Effects of Water Stress on Vegetative Growth

Plant height, leaf area and dry matter in vegetative parts sharply decreased as leaf water potential (LWP) decreased. There were significant differences in plant height among all levels of leaf water potential, except between those of plants grown at LWP of -12.5 and -15.0 bars (Figure 1A and Appendexs Tables 1A).

Leaf area of plants grown at -5.0 bars LWP attained a maximum value 35 days after emergence and declined thereafter. However, the leaf area of plants grown at -10.0 bars LWP increased throughout the experimental period, while that of plants grown at -12.5 bars was almost constant. Leaf area was at a maximum 25 days after emergence in the plants grown at -15.0 bars LWP but thereafter declined to a minimu by the end of the sampling period (Figure 1B). Except during the first and the last sampling occasions, leaf areas of plants grown at -5.0 bars LWP differed significantly from that of the other treatments (Table 2A).

The dry matter in the plants grown at -5 and -10 bars LWP increased throughout the experimental period. However,the dry matter contents of those grown at of -12.5 and -15.0 bars LWP fluctuated with time (Figure 1C). At all sampling occasions, except the first, the dry matter content of the plants grown at -5.0 bars LWP differed significantly

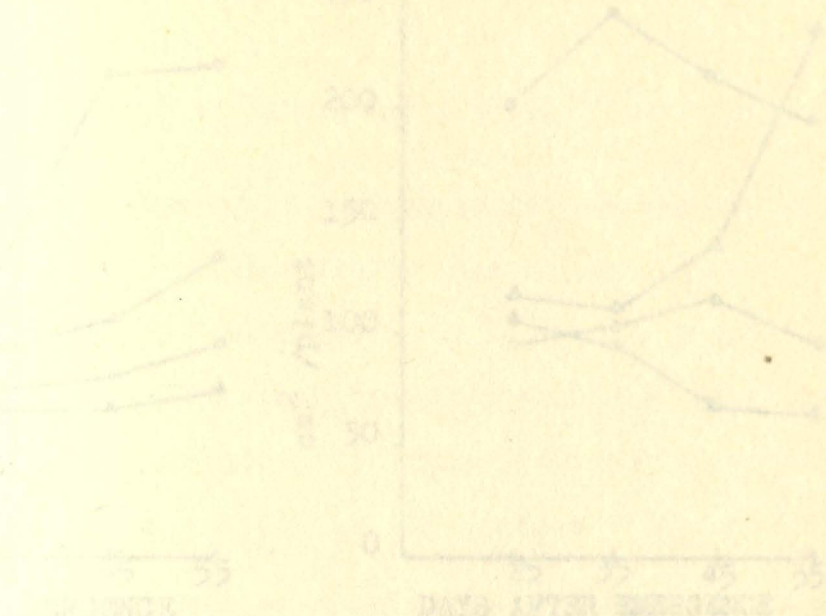
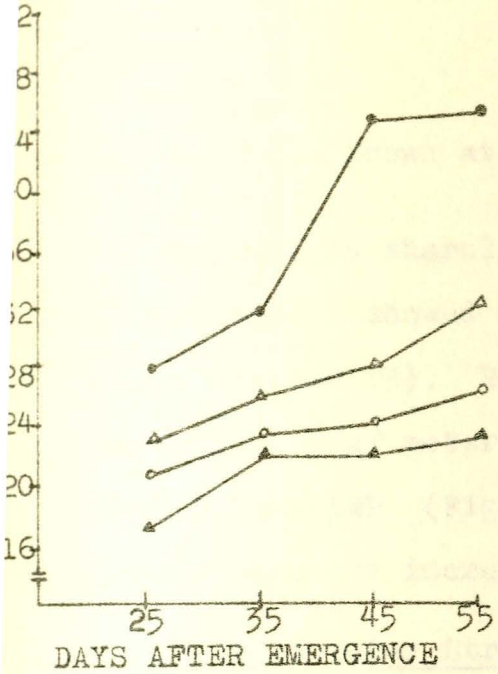
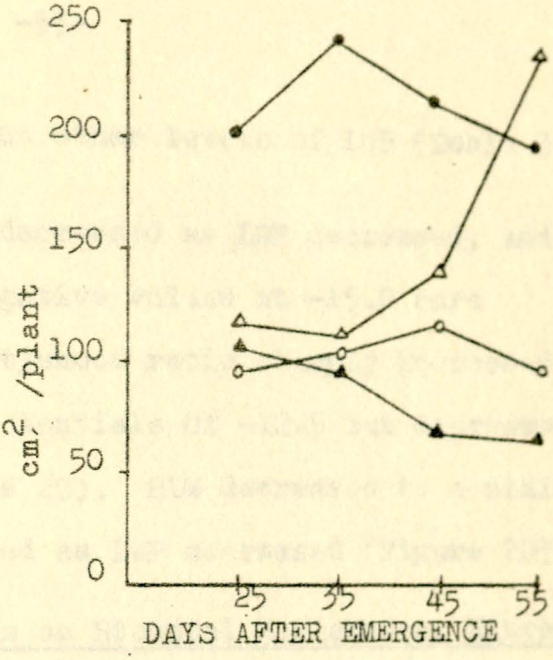


Figure 1. The relationship between leaf water pote ntial (•—• , -5.0; ▲—▲; -10.0; o—o ;-12.5; and ▲—▲ -15.0 bars) and plant height, leaf area and total dry matter in cowpea.

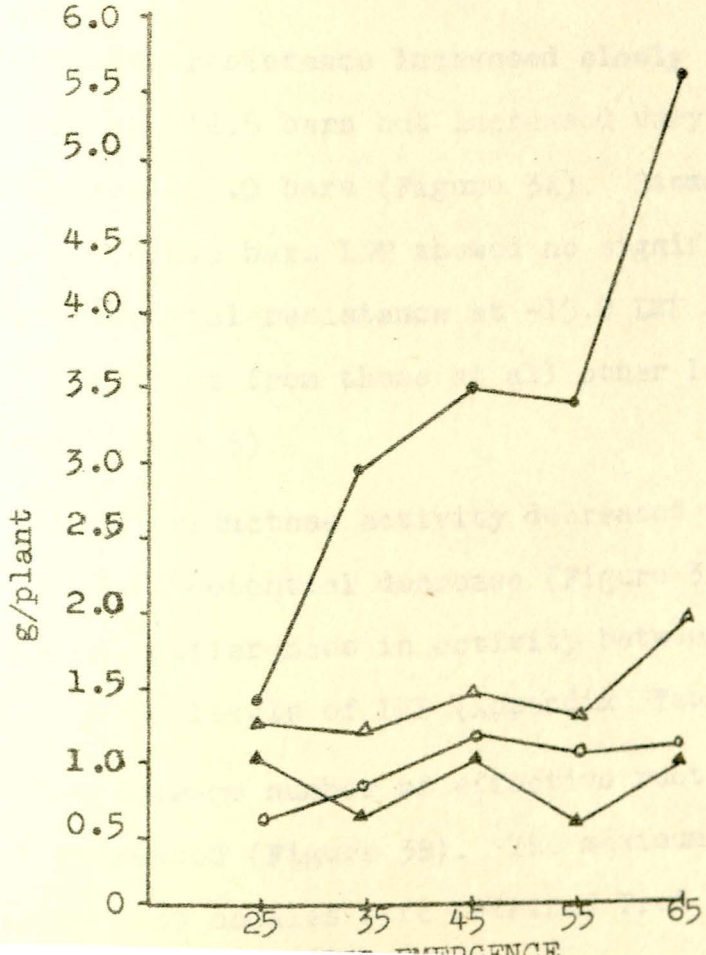
A. PLANT HEIGHT



B. LEAF AREA



C. DRY MATTER



that of those grown at the other levels of LWP (Table 3).

RGR and NAR sharply decreased as LWP decreased, and both parameters showed negative values at -15.0 bars (Figures 2A and 2B). Root/shoot ratio sharply increased to a maximum at leaf water potentials Of -12.5 but decreased at -15.0 bars LWP (Figure 2C). SLW decreased to a minimum at -10.0 bars but increased as LWP decreased (Figure 2D).

B. Effect of Water Stress on Stomatal Resistance, Nitrate Reductase Activity and Number of Effective Nodules.

Stomatal resistance increased slowly as LWP decreased from -5.0 to -12.5 bars but increased very sharply to a maximum when LWP was -15.0 bars (Figure 3A). Stomatal resistances at -5,-10 and -12.5 bars LWP showed no significant differences. However, stomatal resistance at -15.0 LWP bars was significantly different from those at all other levels of LWP (Appendix Table 5).

Nitrate reductase activity decreased very progressively as leaf water potential decrease (Figure 3A). There were significant differences in activity between LWP of -5 bars and all other levels of LWP (Appendix Table 5).

The average number of effective root nodules decreased as LWP decreased (Figure 3B). The maximum and minimum no. of effective root nodules were obtained from those grown at

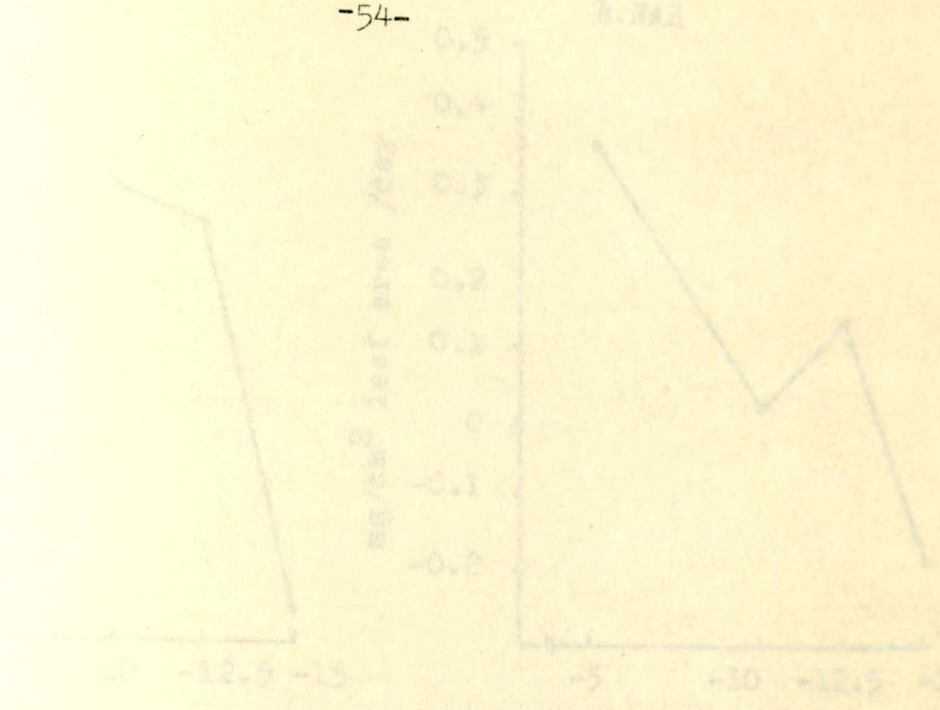
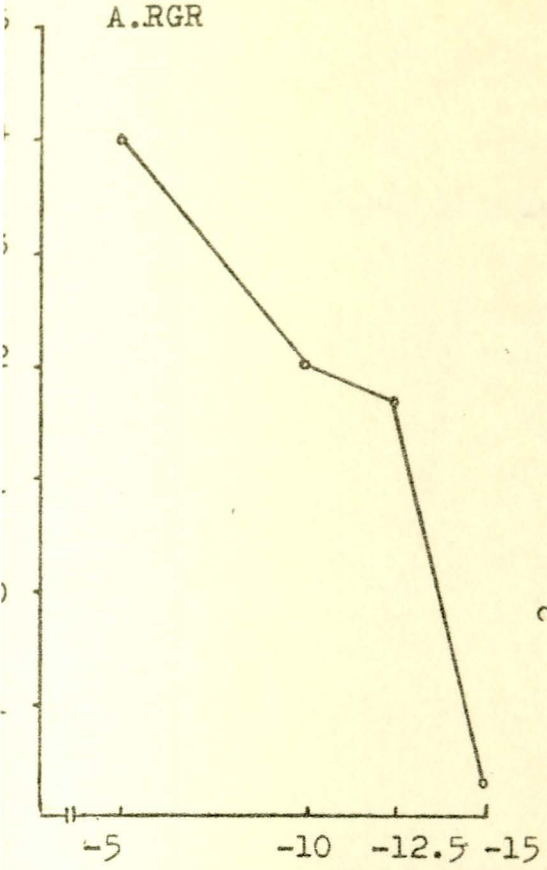
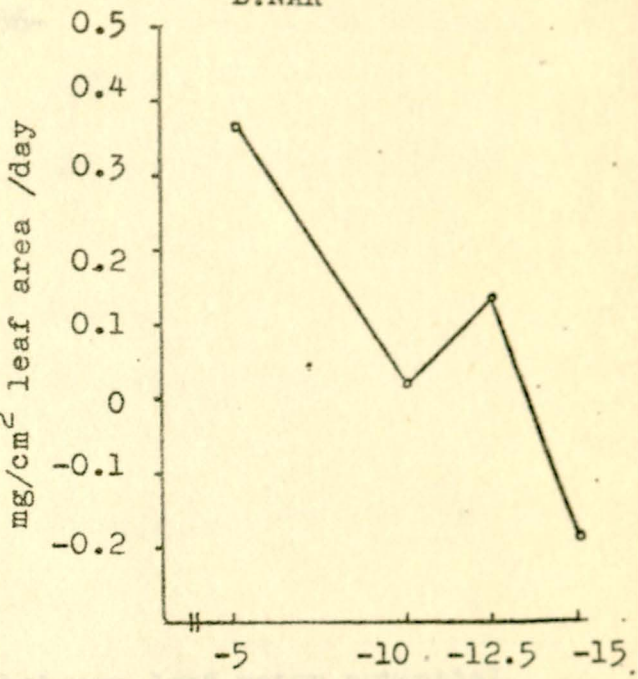


Figure 2. The relationship between leaf water potential and relative growth rates (RGR), net assimilation rate (NAR), root/shoot ratio and specific leaf weight (SLW).

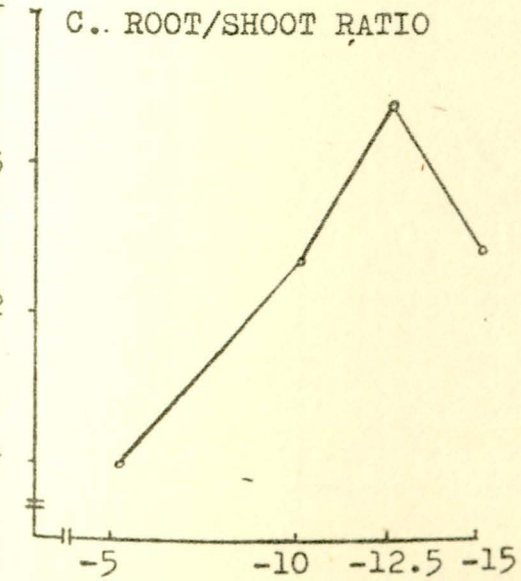
A.RGR



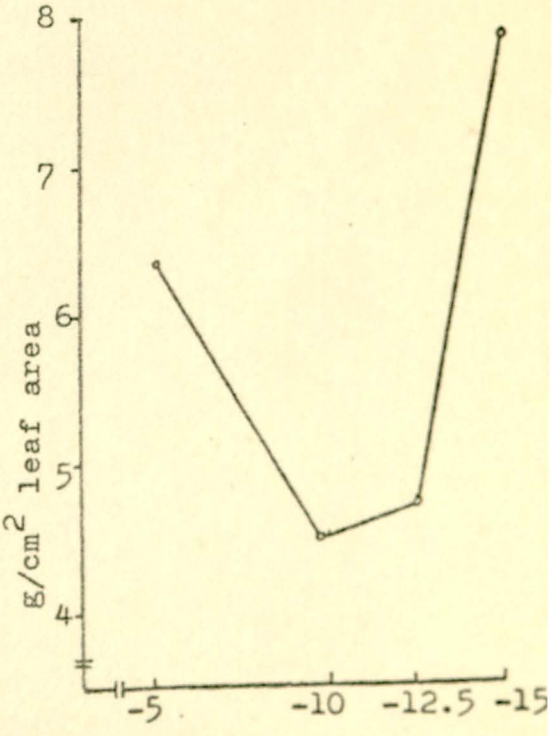
B.NAR



C.. ROOT/SHOOT RATIO



D. SLW



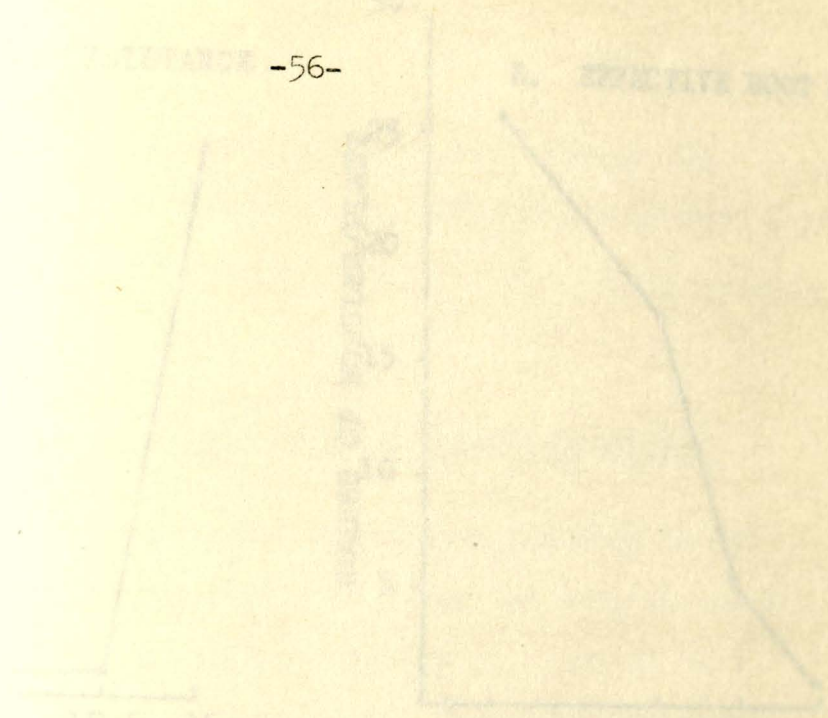
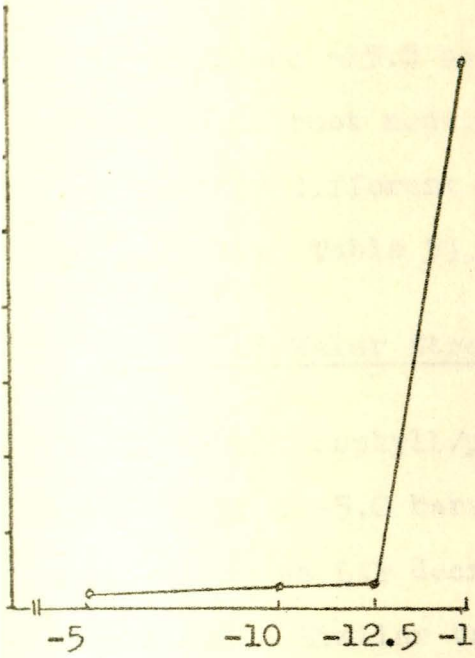


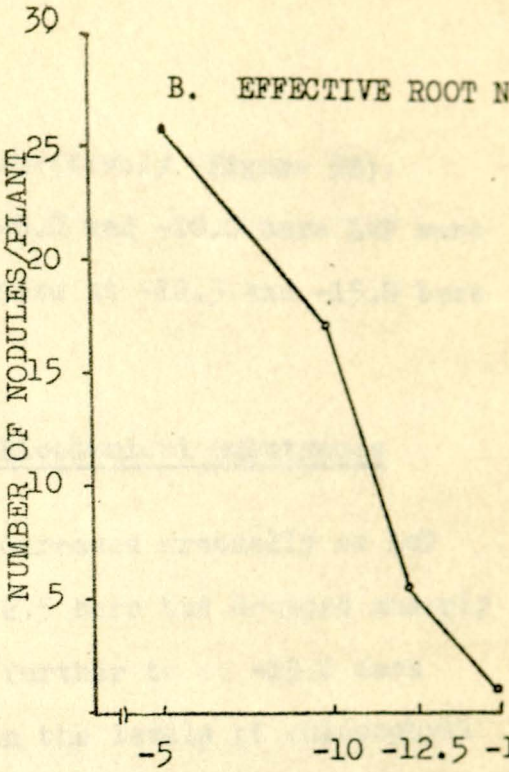
Figure 3. The relationship between leaf water potential and stomatal resistance, number of effective root nodules and nitrate reductase activity.

A. STOMATAL RESISTANCE



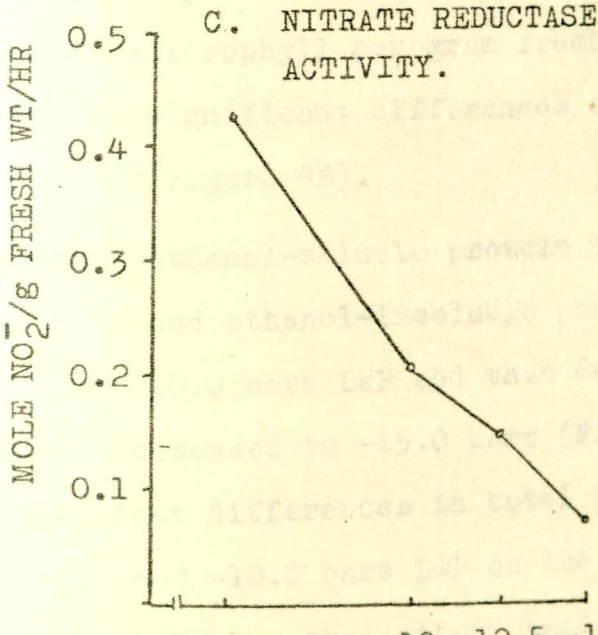
LEAF WATER POTENTIAL(BARS)

B. EFFECTIVE ROOT NODULE



LEAF WATER POTENTIAL (BARS)

C. NITRATE REDUCTASE ACTIVITY.



LEAF WATER POTENTIAL (BARS)

LWP of -5.0 and -15.0 bars, respectively (Figure 3B). The number of root nodules at -5.0 and -10.0 bars LWP were significantly different from those at -12.5 and -15.0 bars LWP (Appendix Table 5).

C. Effect of Water Stress on Biochemical Substances

Total chlorophyll/plant decreased gradually as LWP decreased from -5.0 bars to -12.5 bars but dropped sharply to a minimum as LWP decreased further to -15.0 bars (Figure 4A). Similar trends in the levels of chlorophyll a and chlorophyll b were observed. Total chlorophyll, chlorophyll a and chlorophyll b levels at -15.0 bars LWP showed significant differences between those at all other LWP levels, except at -12.5 bars. Although the amount of all types of chlorophyll per gram fresh tissue decreased LWP, there were no significant differences among them (Appendix Table 6 and Figure 4B).

Whereas ethanol-soluble protein decreased with LWP, total protein and ethanol-insoluble protein increased to a maximum at -10.0 bars LWP and then decreased sharply as LWP further decreased to -15.0 bars (Figure 5E). There were significant differences in total insoluble proteins between -5.0 and -10.0 bars LWP on the one hand and -12.5 and -15.0 bars LWP on the other hand. There were no

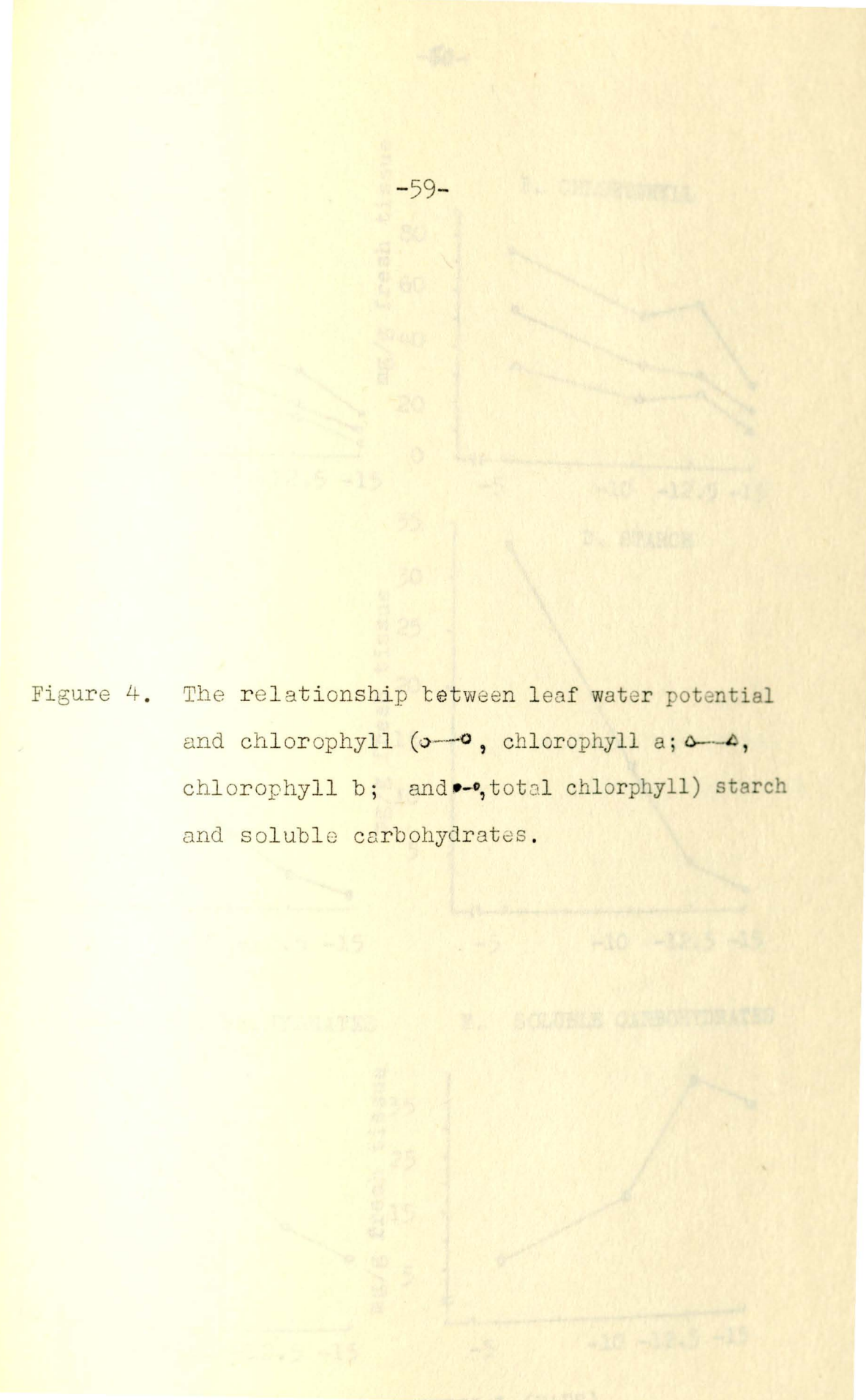
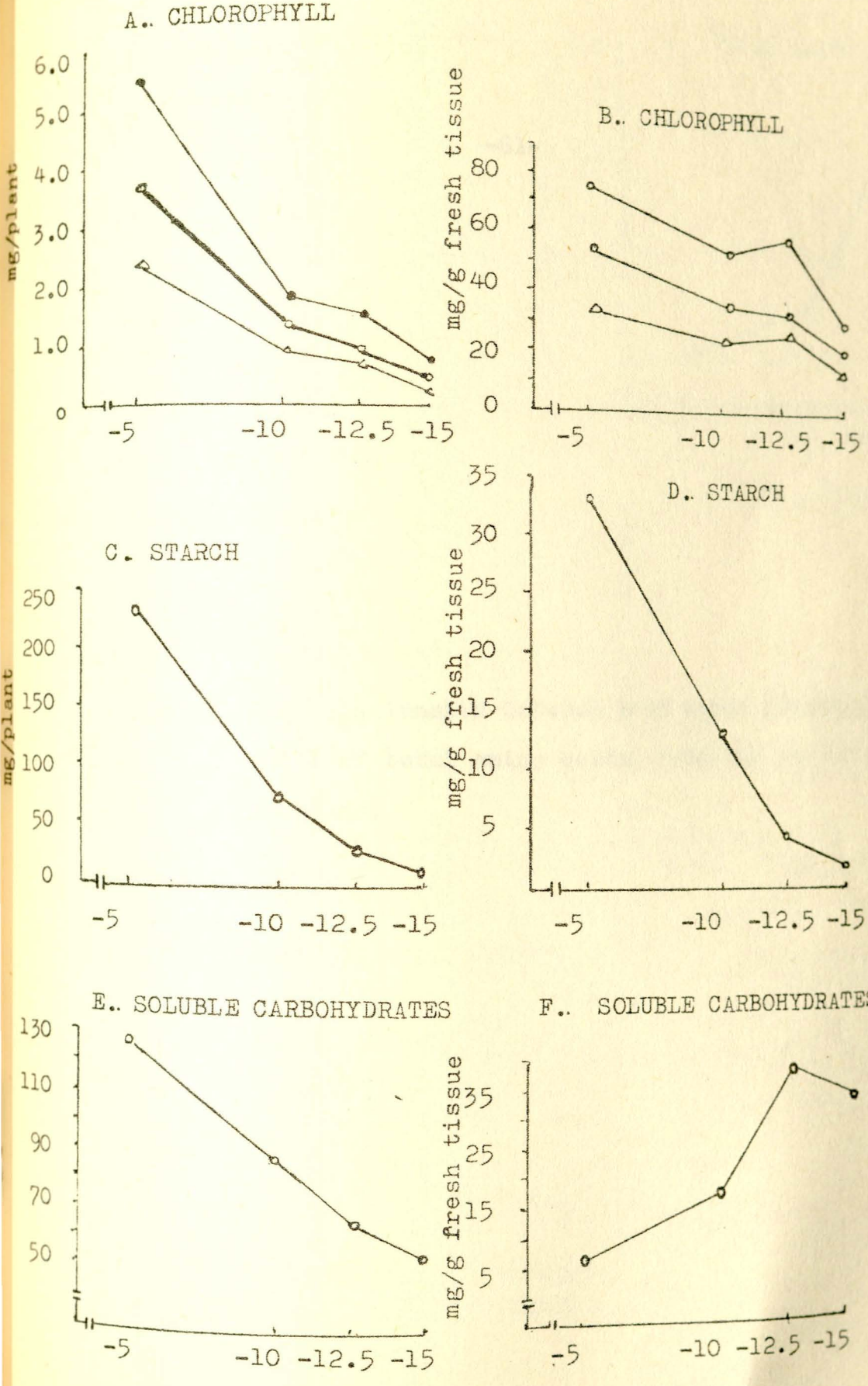


Figure 4. The relationship between leaf water potential and chlorophyll (o—o, chlorophyll a; Δ—Δ, chlorophyll b; and •-•, total chlorphyll) starch and soluble carbohydrates.


A.. CHLOROPHYLL
mg/plant
6.0
5.0
4.0
3.0
2.0
1.0
0
-5
-10
-12.5
-15
B.. CHLOROPHYLL
mg/g fresh tissue
80
60
40
20
0
C. STARCH
mg/plant
250
200
150
100
50
0
D.. STARCH
mg/g fresh tissue
35
30
25
20
15
10
5
E.. SOLUBLE CARBOHYDRATES
130
110
90
70
50
F.. SOLUBLE CARBOHYDRATES
LEAF WATER POTENTIAL (BARS)

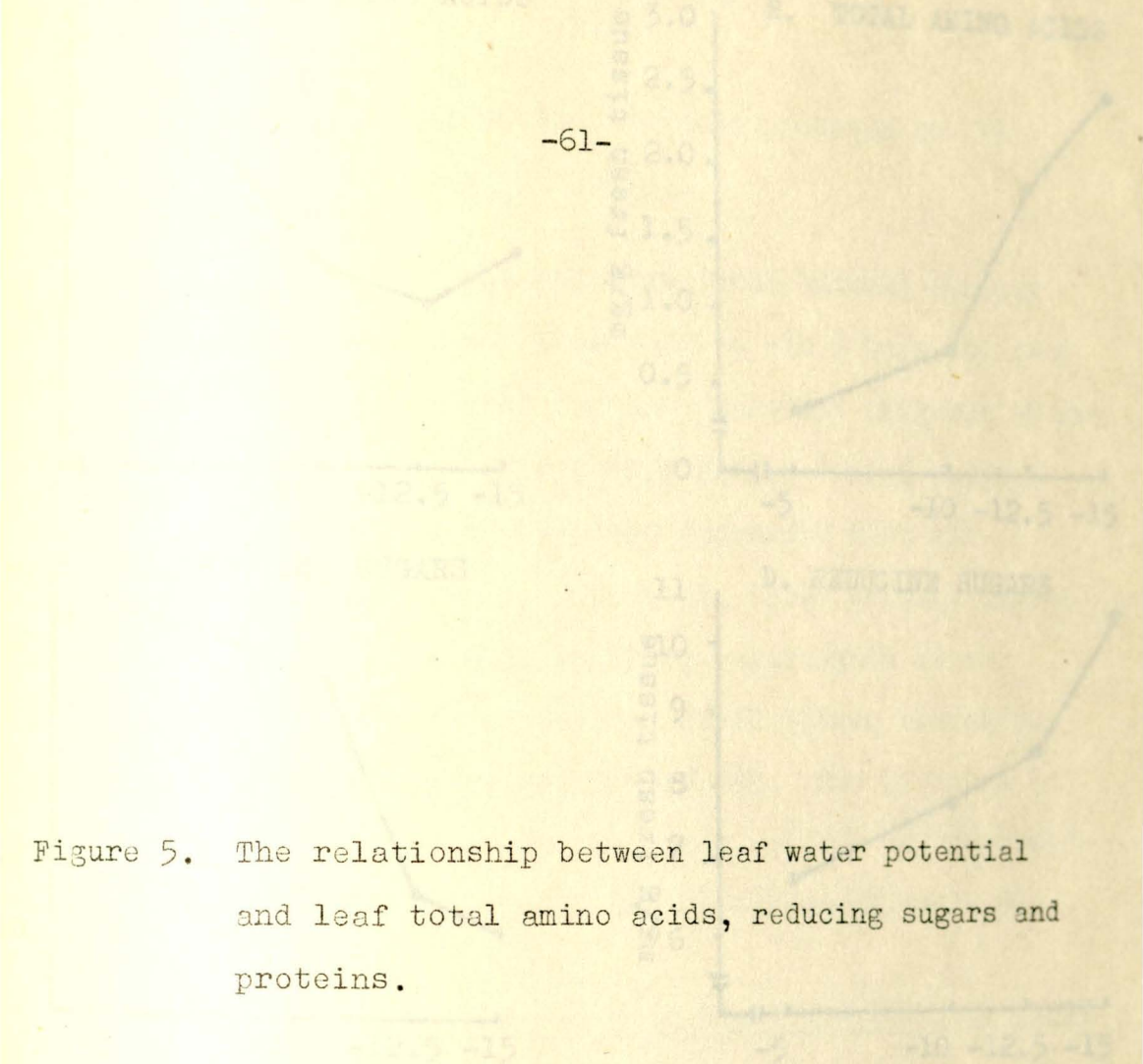
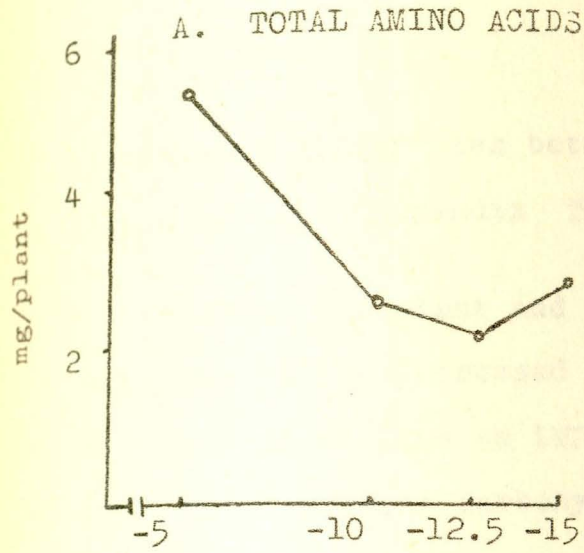
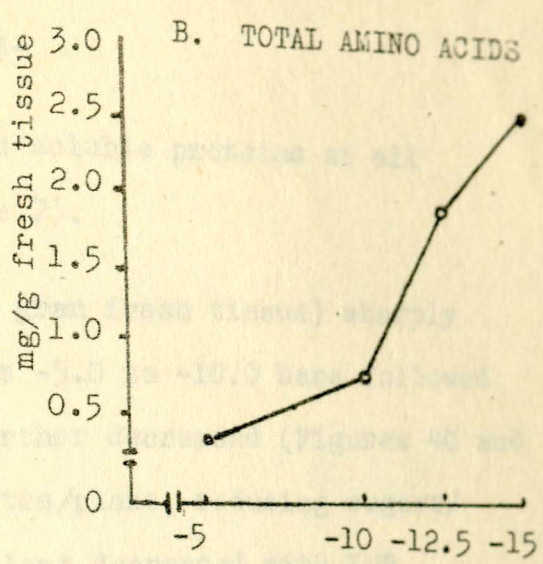
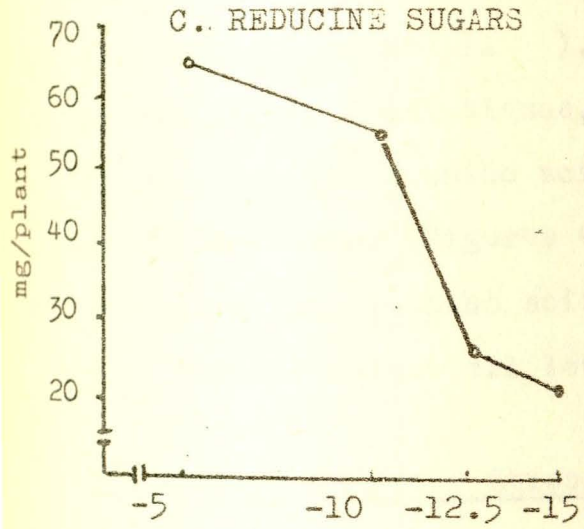
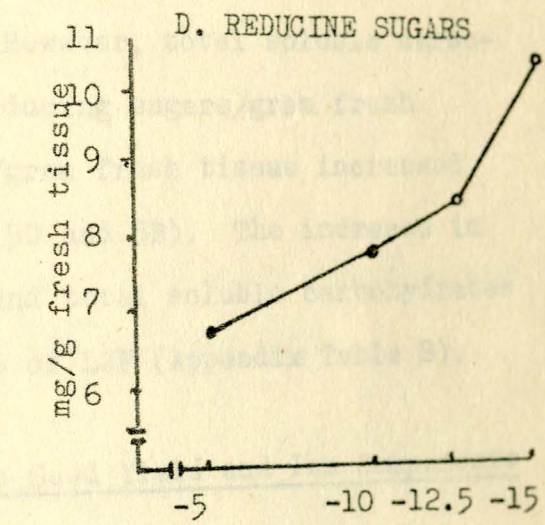


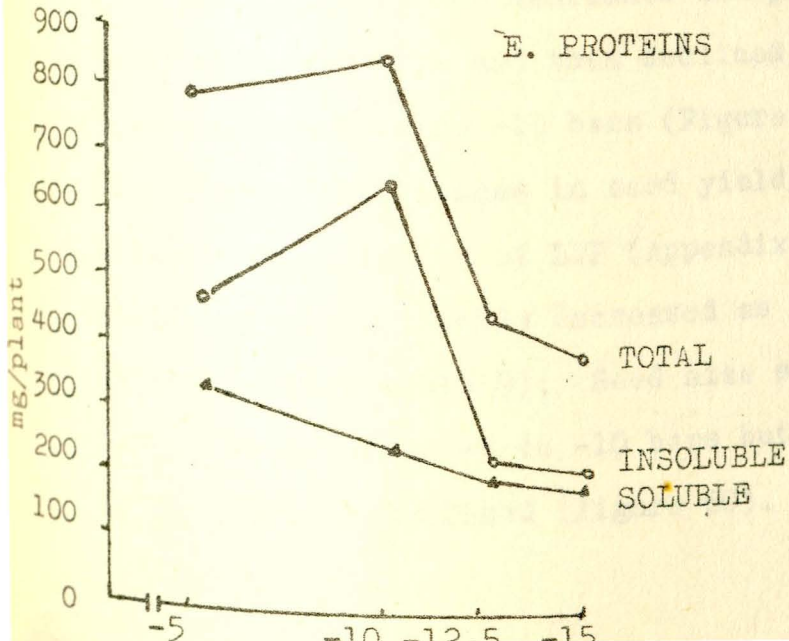
Figure 5. The relationship between leaf water potential and leaf total amino acids, reducing sugars and proteins.


A. TOTAL AMINO ACIDS
mg/plant
6
4
2
-5
-10
-12.5
-15


B. TOTAL AMINO ACIDS
mg/g fresh tissue
3.0
2.5
2.0
1.5
1.0
0.5
0
-5
-10
-12.5
-15


C. REDUCINE SUGARS
mg/plant
70
60
50
40
30
20
-5
-10
-12.5
-15


D. REDUCINE SUGARS
mg/g fresh tissue
11
10
9
8
7
6
-5
-10
-12.5
-15


E. PROTEINS
mg/plant
900
800
700
600
500
400
300
200
100
0
TOTAL
INSOLUBLE
SOLUBLE
-5
-10
-12.5
-15

significant differences between soluble proteins at all levels of LWP (Appendix Table 7).

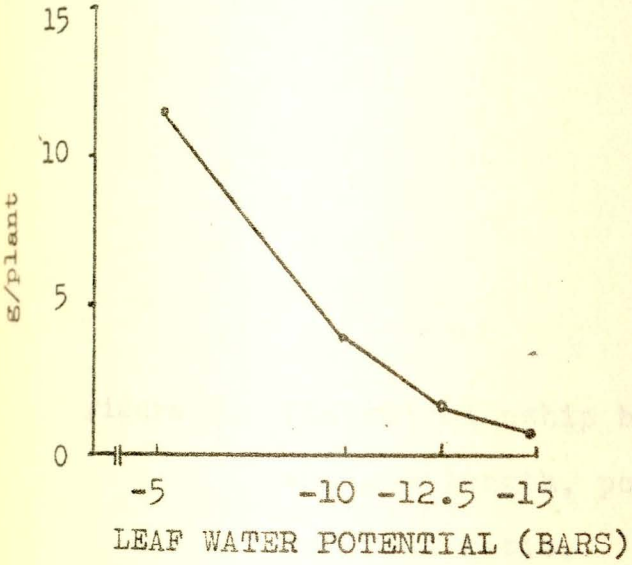
Starch (per plant and per gram fresh tissue) sharply decreased as LWP decreased from -5.0 to -10.0 bars followed by a gradual decline as LWP further decreased (Figures 4C and 4D). Total soluble carbohydrates/plant, reducing sugars/plant, and total amino acids/plant decreased with LWP (Figures 4E, 5C and 5A). However, total soluble carbohydrates/gram fresh tissue, reducing sugars/gram fresh tissue, and total amino acids/gram fresh tissue increased as LWP decreased (Figures 4F, 5D and 5B). The increase in concentration of amino acids and total soluble carbohydrates were significant at all levels of LWP (Appendix Table 8).

D. Effects of Water Stress on Seed Yield and Its Components

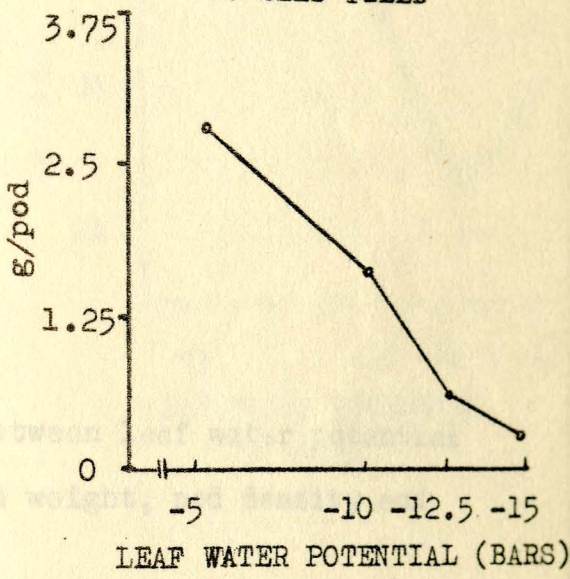
Seed yield/plant decreased sharply as LWP decreased from -5 to -10 bars and then declined fairly slowly as LWP further decreased to -15 bars (Figure 6A). There were significant differences in seed yield/plant between -5 bars and all other levels of LWP (Appendix Table 9). Seed yield/pod significantly decreased as LWP decreased Figure 6B and Appenix Table 9). Seed size slightly decreased as LWP decreased from -5 to -10 bars but increased remarkably as LWP further declined (Figure 6C). Pod/seed ratio showed

Figure 6. The relationship between leaf water potential and seed yield, seed number and seed size.

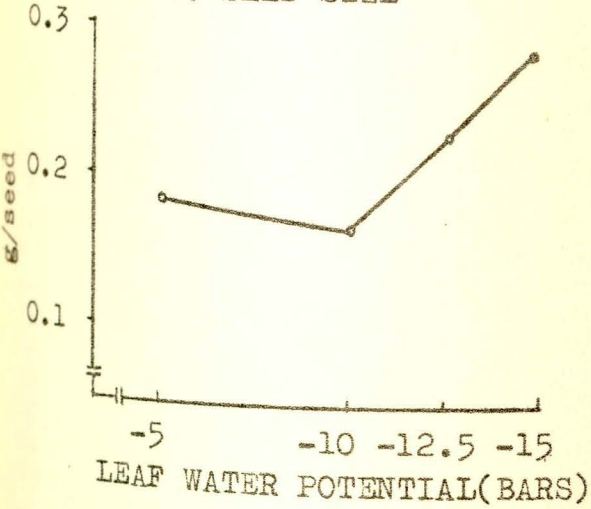
A- SEED YIELD



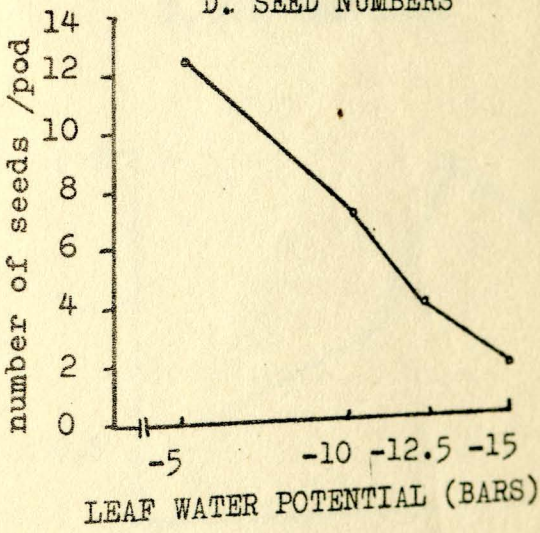
B.. SEED YIELD



C. SEED SIZE



D. SEED NUMBERS



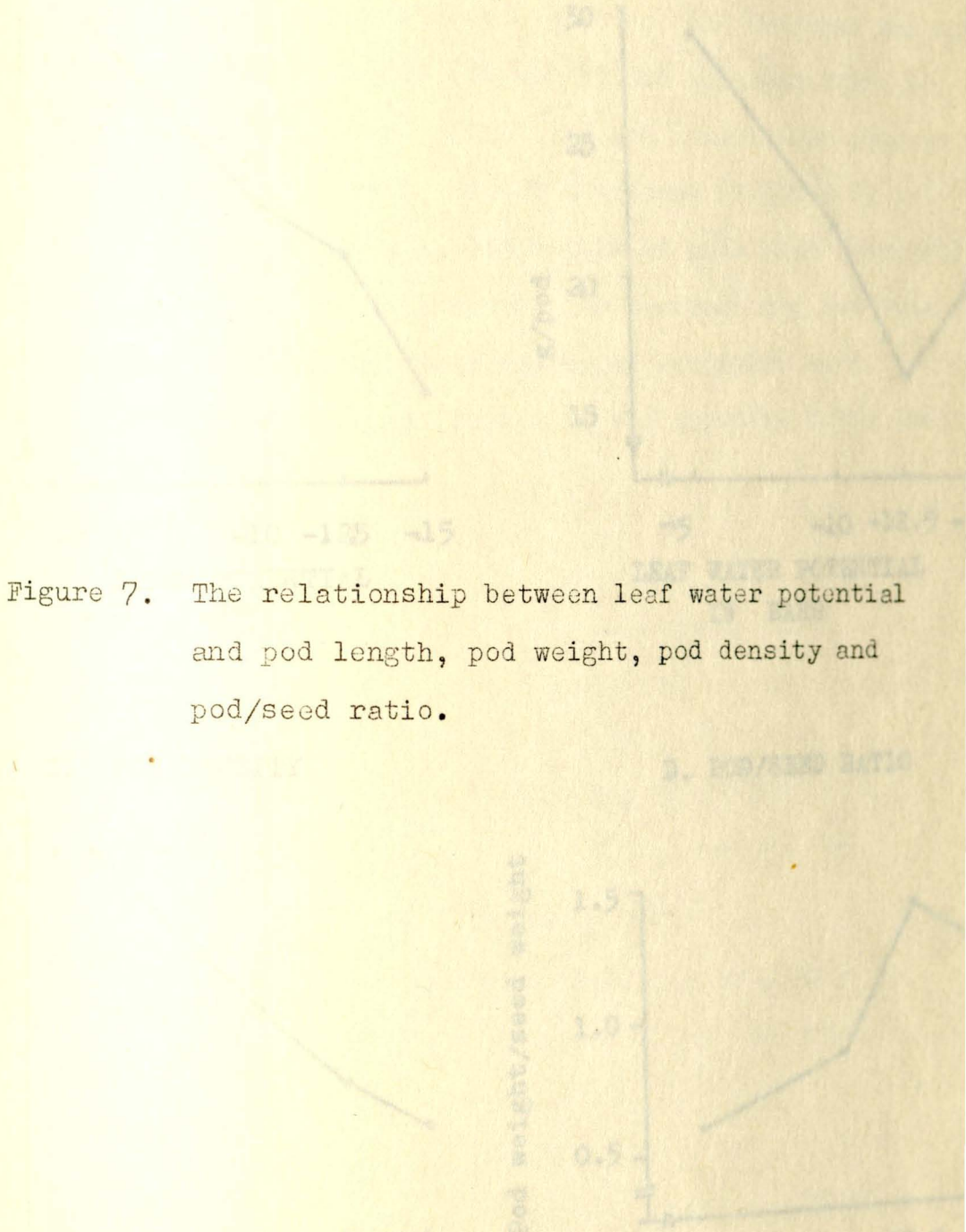
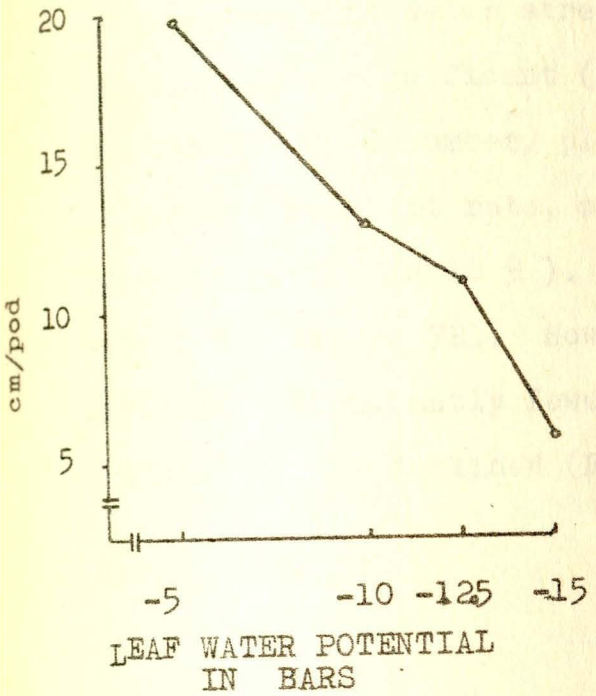
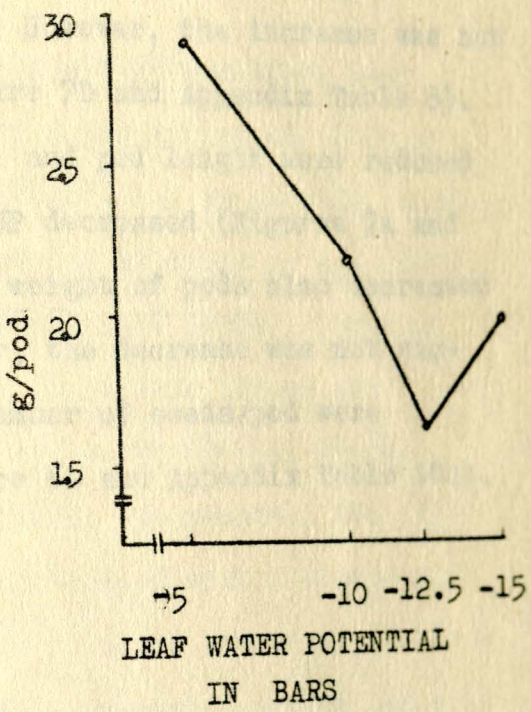


Figure 7. The relationship between leaf water potential and pod length, pod weight, pod density and pod/seed ratio.

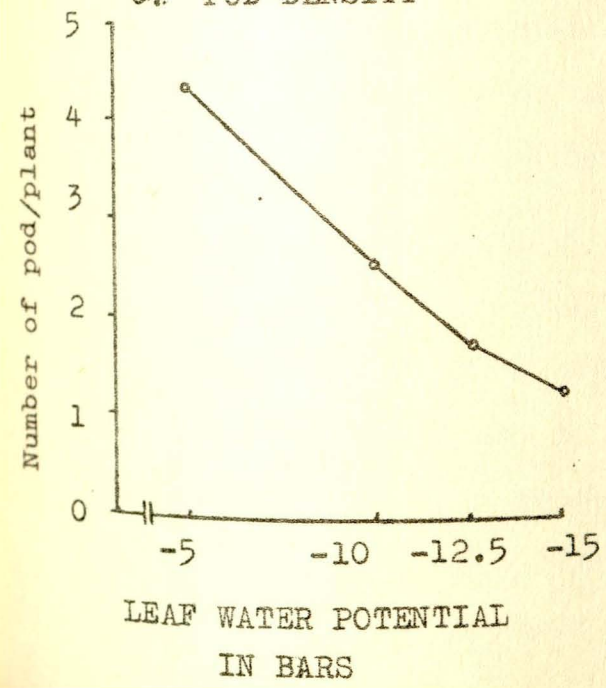
A.. POD LENGTH



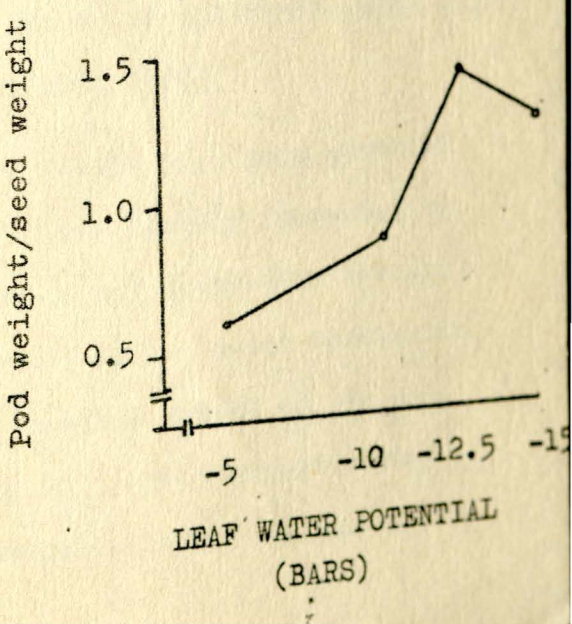
B.. POD WEIGHT



C.. POD DENSITY



D.. POD/SEED RATIO



an increase with water stress. However, the increase was not statistically significant (Figure 7D and Appendix Table 8). Pod density (pod number/ plant) and pod length were reduced at about a constant rate, as LWP decreased (Figures 7A and 7C and Appendix Table 9). Dry weight of pods also decreased with LWP (Figure 7B). However, the decrease was not significant. Signifantly fewer number of seeds/pod were produced as LWP declined (Figure 6D and Appendix Table 10A).

DISCUSSION

A. Plant Growth

The decline in vegetative growth (dry matter, leaf area and plant height) with leaf water potential (LWP) as observed in the present study (Figure 1A, 1B and 1C), closely resembles those described in cowpeas by Hiler et al. (1970), Hall and Shulze (1980) and Turk and Hall (1980). Similar results have also been reported in alfalfa (Brown and Tanner, 1983), soybeans (Boyer, 1970a) and maize (Boyer, 1970b; Acevedo et al., 1971; Duncan, 1975). In general, the influence of water stress on growth was associated with a decrease in the pressure potential component of water potential (Lockart, 1975; Boyer, 1970; Slavik, 1975). Extension growth has been shown to be very sensitive to water stress (Denmead and Shaw, 1960; Hsiao et al., 1970; Duncan, 1975). For instance, the rate of stem elongation in maize declined by 75% at wilting point (Duncan, 1975) and the length of internodes also reduced following water stress (Christiane, 1977).

In the present study, the height of plants grown at the leaf water potential of -5 bars rapidly increased to a maximum 45 days after emergence and thereafter remained almost constant. However, plants in the other treatments grew less rapidly and reached maximum height at the end of the sampling period (Figure 1A). This suggests that soil moisture had the most favorable effect on the

height of plants grown at -5 bars LWP but the other treatment had detrimental effects on plant height, as a consequence of water deficit .

Leaf area reduction in response to water stress, as observed in the present study (Figure 1B), is consistent with those reported in maize by Boyer and McPherson (1975), in soybean by Sionit and Kramer (1977) and in cowpea by Turk and Hall (1980). Although leaf numbers were not determined in the present study, it is more than likely that decreases in leaf numbers were more responsible for leaf area reduction in the stressed plants. Leaf abscission was observed in the plants grown at lower LWP. Moreover, Turk and Hall (1980) reported that decreases in leaf numbers due to leaf abscission were the main causes of leaf area reduction in water deficient cowpeas.

In the present study, while the leaf area of plants remained constant at -5 bars LWP and was significantly higher than those in the other treatments, the leaf area of plants grown at -15 bars LWP progressively declined at every sampling occasion (Figure 1B and Appendix Table 2A). This shows that water stress severely inhibited leaf area expansion. A reduction in leaf area provided a mechanism for reducing water losses from the major transpiring surfaces (leaves) at the expense of dry matter production. This ultimately delayed or prevented the development of a more

severe stress (Begg and Turner, 1976). Thus the data reported here agree with the observation made by Turk and Hall (1980) and Hall and Shulze (1980) that, in cowpeas, the reduction in leaf area represents an important mechanism of drought avoidance.

The relationship between RGR, NAR, and LWP in the present study (Figures 2A and 2B) is consistent with what has been reported in snapbeans (Kanemasu and Tanner, 1969) and maize, bean and cotton (Lawlor, 1970). Boyer 1970b studied the water relations of maize and soybeans and reported an increase in stomatal resistance whilst CO_2 assimilation apparently decreased at lower LWP. According to Kanemasu and Tanner (1969), stomatal resistance was inversely related to RGR. They, therefore, attributed lower NAR and RGR to lower photosynthetic rates , due to limited CO_2 supply and impaired biochemical processes on one hand, and to higher ambient leaf and root temperatures, as a result of reduced transpiratic rates on the other hand. The negative values of RGR and NAR at -15 bars of leaf water potential (Figures 2A and 2B) indicate that net photosynthetic activity ceased and the plants had to utilize their stored products for respiration.

An increase in root/shoot ratio was associated with water stress in the present study (Figure 2C). Similar results have been reported by several investigators

(Bhan et al., 1973; Ashenden et al., 1975; Pereira and Kozlowski, 1976; Silvius et al., 1977; and Karami et al., 1980). Working with the distribution of radioactive $^{14}CO_2$ in soybeans, Silvius et al. (1977) observed relatively more ^{14}C in roots than in shoots between -11 to -20 bars LWP The preferential development of the root over the shoot is an adaptive mechanism which facilitates efficent water absorption (Begg and Turner, 1976) and growth modification that favours an efficient use of the limited supply of fixed carbon (Silvius et al., 1977). Positive correlations between root/shoot ratio and a high degree of drought avoidar were observed in Eucalyptus spp. (Pereira and Kozlowski, 1976) and sorghum (Bhan et al., 1973). Similarly, increased root growth at the expense of the shoot as indicated by the high root/shoot ratio of the stressed treatments (Figure 2C), might also be a mechanism of drought avoidance in cowpeas.

Turk and Hall (1980a) reported positive correlations between SLW and cumulative xylem water potentials in field-grown cowpeas. In the present study, SLW showed a decreasing trend at relatively higher leaf water potentials but increase as leaf water potential further decreased (Figure 2D). Highe values of SLW will result if dry matter accumulation is less adversely affected than leaf area expansion. In the present study, the differences among SLW were not statistically significant (Appendix Table 4). This could be attributed

to the simultaneous and comparable reduction in leaf area and dry matter accumulation as LWP decreased (Figure 1B and 1

B. Stomatal Resistance, Nitrate reductase Activity and Nodulation

The observation that stomatal resistance increased with stress in leaves (Figure 3a) is consistent with those made by Raschke (1970) and Jordan and Ritchie (1971). There was a threshold level of water potential above which stomatal resistance remained constant in the present study. This threshold was -12.5 bars (Figure 3A). Similar results were reported by Boyer (1970) who obtained a threshold of -10 to -12 bars in soybeans.

Since CO_2 primarily enters the plant through the stomata, a high stomatal resistance affects photosynthesis by limiting CO_2 assimilation in light (Slavik, 1975). Such mutual function interdependence between photosynthesis and stomata explains the low dry matter content of the plants meintained at -15 bars of LWP which also had the highest stomatal resistance in the present study (Figures 1C and 3A).

The decrease in nitrate reductase activity (NRA) with decreasing LWP reported in the present study(Figure 3B) agrees with the observations made by Bardzik et al., (1971), Morilla et al. (1973), Plaut (1974), and Adjei-Twum (1976).

Nitrate reductase is an inducible enyzme (Afridi and Hewitt, 1964) which reduces nitrate to nitrite using nicotin-amide adenine dinucleotide (NADH) as an electron source (Devlin and Witham, 1983). Any decrease in activity, therefore, could be cause by a reduction in the electron source, a shortage of the inducer, or by reduced enzyme concentration through reduced synthesis or increased enzyme degradation. Whilst a reduction in respiratory rates, at low leaf water potential could limit NADH formation, the inducer (nitrate) could have also been limiting as a result of a reduction in ion uptake and low availability of soil nitrogen following water stress (Smith et al., 1973; Duham and Nye, 1974; Erlandson, 1975 Adjei-Twum, 1976). Moreover, Plant (1974) showed that NRA could be reduced by increased denaturation of the enzyme.

Although the rate of N_2 fixation in root nodules was not studied in the experiments being reported here, it is evident that water stress reduced the number of effective nodules in cowpeas (Figure 3C). A reduction in nodule number could have resulted from the inhibitory effects of water deficits on the rate of nodule initiation, or on the further development of existing nodules. Gallacher and Sprent (1978) reported that water stress resulted in reduced rates of nodule initiation and consequentley in low N_2 fixation. Sprent (1971a) suggested that dehydration of nodules and consequent enzyme denaturation in water deficien

plants caused a decline in N_2 fixation, but Huang et al. (1975 attributed it to reduced rates of the supply of photosynthates from wilted leaves. In any case, a reduction in effective nodules was one important mechanism through which water stress affected nitrogen metabolism in legumes (Gallacher and Sprent, 1978).

C. Biochemical Substances

The observation that all types of chlorphyll (per plant and per gram fresh tissue) decreased with leaf water potential (Figures 4A and 4B) is consistent with the results of Adjei-Twum and Splittstoesser (1976), Soong and Hageman (1977), and Bengston et al. (1978). Duysen and Freeman (1974) reported that the critical leaf water potential for the inhibition of chlorophyll synthesis in wheat seedlings was -9 to -14 bars. Alberte et al. (1977), on the other hand, attributed the reduction in chlorophyll content of leaves by water stress to denaturation of the protein component of chlorophylls. Wate stress hastened the senscence of leaves and the loss of a considerable amount of chlorophyll occurred in the process (Wardle and Short, 1983). Stillwell and Tien (1977) showed that photooxidation of chlorophylls in plants was inhibited by cartenoids present in the chloroplasts. However, Duysen and Freeman (1974) reported that the accumulation of carotenoi

was impaired following water stress. Thus, photoxidation could well be one of the means of chlorophyll destruction in water deficient plants.

Ethanol-water soluble proteins linearly decreased with leaf water potential. Although there was an unacountable rise in levels at -10.0 bars of leaf water potential both ethanol water insoluble and total protein generally decreased with leaf water potential (Figure SE). Except the unaccountabl rise in insoluble and total proteins, similar results were obtained by Shah and Loomis (1965) in sugerbeet, Adjei-Twum (1976) and Fukutoku and Yamada (1982) in soybeans and Soong and Hageman (1977) who reported decreases in protein as the LWP of maize declined. Low protein content is a result of either decreased rate of protein synthesis, an increased rate of destruction or both. Bewley et al. (1983) reported that maize seedlings exhibited reduced protein synthesis when subjected to water stress. Hsiao (1970), Dhindsa and Cleland (1975) and Bewley et al. (1983) associated reduced protein synthesis to a decline in polyribosome levels. Reduced DNA synthesis occurred in stressed plants (Deltour and Jacqmard, 1974) and increased RNase was observed following stress (Levitt, 1980). Soong and Hageman (1977) reported that, in water deficient plants, the loss of protein, carboxype-ptidase, aminopeptidases and chlorophyll was similar to the

loss of water from tissue. Feller et al. (1977) observed faster rates of increase in caseolytic activities concurrently with rapid loss of protein from leaves. They suggested that caseolytic enzymes might initiate rapid hydrolysis of leaf protein. Thus, a reduction in leaf protein as observed in the present study (Figure 5E) might have resulted from increased proteolytic activities and reduced protein synthesis.

It was noted that starch/plant and starch/g. fresh tissue decreased remarkably as leaf water potential decreased (Figures 4B and 4C). Similar results were obtained by Hodges and Lorio (1969), Naidu et al. (1967) and Barlow et al. (1976) who observed an apparent disappearance of starch in stressed plants. Plants normally utilize their stored products, such as starch, as substrates for respiration whenever there is considerable reduction in net photosynthetic activity. Consequently, one would expect a rapid hydrolyzation of starch into soluble carbohydrates in plants under water stress as reported by Hodges and Lorio (1969).

In this study total soluble carbohydrates per plant decreased but the amount per gram fresh tissue (i.e. concentration) increased as water deficits in plants increased(Figure (4E and 4F). This observation is consistent with the data obtained by Peterson et al. (1977), Fukutoku and Yamada

(1982), Soong and Hageman (1977) and Stewart (1980) . Hodges and Lorio (1969) found that the soluble carbohydrate content of plants decreased as water deficits increased due to reduced photosynthetic activity. An increase in the concentration of carbohydrates and other low molecular weight organic compounds in stressed plant cells could be the result of excessive water loss accompanied by cell volume reduction (Begg and Turner, 1976). Nevertheless, many investigators have reported actual increases in amounts of soluble carbohydrates following water stress (Soong and Hageman, 1977; Stewart et al. 1977; and Fukutoku and Yamada 1982). This was attributed to either accelerated starch hydrolysis (Maranville and Paulsen, 1970) or to a decrease in the translocation of assimilates from sources to sinks (Fanjul and Rosher, 1984).

The concentration of total free amino acids increasing in plants subjected to water stress as the consequences of enhanced hydrolysis of proteins has been reported by Soong and Hageman, (1977) Stewart et al. (1977) and Stewart,(1980), a reduction in protein synthesis by Stewart (1973) or de nuvo synthesis of certain amino acids related to drought avoidance by Stewart, (1980). The levels of individual amino acids was not determined in the present study. However, several workers have reported that an increase in total free amino acids content of stressed plants was mainly due to the accumulation

of proline (Saunier et al., 1968; Stewart et al., 1977; Fukutoh and Yamada, 1982).

According to Ilahi and Dorffling (1982), the accumulation of soluble charbohydrates and low molecular weight amino acids such as proline can have a protective function for enzymes by binding water to proteins and maintaining their hydration. In addition, Douglas and Paleg (1981) showed that such osmotically active metabolites exert favorable effects on enyme substrate or enzyme cofactor complex formations which protect enzymes from conformational disturbances.

Nevertheless, the most important role of solute accumulation in plants under stress is osmoregulation. The process of osmoregulation is the accumulation of solutes in cells beyond the increase in concentration caused by the loss of water (Parsons and Howe, 1984). Lowering cell osmotic potential by increased solute concentration permits turgor to remain more positive as a result of which cell growth can continue and root cells can penetrate into greater soil volume. Besides, lowering water potential through osmotic adjustment is an efficient way of avoiding dehydration through the loss of water to the plants' environment (Levitt, 1980).

On relative terms, stressed cowpea plants had the tendency to maintain higher leaf water potential (Girma and

Krieg, 1984) and turgor (Ludlow, 1982) but the osmotic potentials and the rate of their osmotic adjustment were comparatively lower. These attributes were due to the effecient stomatal control of water loss in cowpea (Ludlow, 1982; Girma and Krieg, 1984). Although osmotic potential was not determine in the present study, the presence of significantly higher concentrations of soluble carbohydrates and amino acids in stressed plants (Figures 4F and 5B and Appendix Table 8) might have resulted in a higher osmotic potential. Thus, the results being reported here show that osmotic adjustment might also be one of the mechanims of drought resistance in cowpeas.

E. Seed Yield and Its Components

The pattern of seed yield in relation to leaf water potential reported in this study (Figure 6A and 6B). was similar to those observed by Adjei-Twum and Splitstoesser (1976), Turk et al. (1980) and Shouse et al. (1981) in which seed yield was positively correlated with total dry matter in vegetative parts and leaf area at anthesis and the grain filling stages. It has long been recognized that a reduction in the photosynthetic process leads to a reduction in seed yield (Boyer and McPherson, 1975; Begg and Turner, 1976; Aggarwal and Sinha, 1984).

In the present study a marked abscission of flowers was observed at -12.5 and -15.0 bars LWP and this resulted in considerably low pod density. In fact pod density at -5.0 bars leaf water potential was approximately four times as much as in the -15.0 bars LWP (Figure 7C). Turk et al. (1980) Shouse et al. (1981) reported that whereas drought in the vegetative phase did not significantly affect seed yield in cow peas, drought in the flowering and pod-filling stages reduced it considerably. This is to be expected, since drought at flowering stage caused abscission of flowers and lowered pod density (Turk et al. 1980). In addition, water stress at flowering stage impaired anther development and the process of meiosis (Henckel, 1964).

Pod length was significantly reduced as LWP decreased (Figure 7A and Appendix Table 10). The reduction in pod length resulted from the effects of water stress on extension growth. In the present study, dry weight of individual pod exclusive of seeds showed no significant differences at the various leaf water potentials studied. This indicates that the plants with lower levels of water potential were able to supply their pods with almost the same amount of dry matter as in the well watered treatments, due to lower pod density. Pod/seed ratio remained almost constant as leaf water potential decreased (Figure 7D). This indicates that translocation rates of substances from pods to seeds were not limited by water stress.

According to Shouse et al. (1981) and Herbert and Baggerman (1983), pod density, seed number/pod and seed size were the most important factors which regulated seed yield in cowpeas. With regards to the relationship between leaf water potential and seed yield and its components, the treatme caused larger variations among the number of seeds/pod, seed size and pod density in the present study (Figures 6C ,6D and 7C). This is in agreement with Turk et al. (1980, Shouse et al. (1981) and Herbert and Baggerman (1983) who reported that the pod density was the most sensitive component of seed yield in stressed cowpea plants. In the present study seed number/pod was the most significantly reduced component of seed yield, as leaf water potential decreased (Figure 6D and Appendix Table 10). Lower pod density resulted from a reduction in the number of seed primordia which Henckel (1984) suggested was caused by the inhibitory effects of water stress on reproductive processes such as another development and fertilization.

Adjei-Twum (1976) reported that soybean plants regulated by physiological abortion, the number of seeds they could fill during the stress period when irrigation water was applied in cycles as in the present study. Fewer but larger seeds were, therefore, produced in the treatments subjected to water stress but more seeds of normal sizes were produced

in the treatments which recieved adequate water(Figure 6C). Thus, the significantly low seed number/pod in the plants subjected to stress in the present study (Appendix Table 10) might also be an adaptive response of cowpea to low levels of assimilate accumulation.

One consequence of the reduction in seed number/pod was an increase in seed size (Figure 6D). If the number of seeds/pod is reduced, the share of the assimilates of individual seeds increase (Turk et al., 1980) Shouse et al., 1981). In this respect Boyer and McPherson (1975) reported an increase in the size of maize seeds when the plants were subjected to desication. Similar results were also reported by Arnon (1975) in linseed. It seems apparent that the production of larger seeds in response to water stress, or other adverse environmental conditions, could be an adaptive trait in some plants, such as cowpea, which helps them to avoid going into extinction by producing relatively larger and more viable seeds.

SUMMARY AND RECOMMENDATIONS

The results of studies on the water relations of cowpea CV.Black Eyebean showed that drought resistance was mainly due to several mechanism that regulated plant water loss. Transpirational water loss was minimized by total leaf area reduction and maintenance of high stomatal resistance. Greater root growth, an indication of higher efficiency in water absorption, was observed in stressed plants. Higher concentrations of amino acids, soluble carbohydrates and reducing sugars in water deficient plants indicated that osmoregulation might be an important mechanism for drought tolerance in cowpeas. It was observed that under drought, cowpeas produced a fewer number of seeds/pod but the seeds were larger than normal. This characteristic of cowpea is believed to be an advantage to the plant because it enables it to survive under adverse conditions of droughts.

It is recommended that the use of important drought adaptive traits such as high stomatal resistance, better root growth and higher solute accumulation be included in the criteria for selecting drought resistant cowpea cultivars. Breeding experiments to produce strains that will possess these desirable traits and yield characteristics are recommend Further research to determine the effects of planned water deficits at different stages of plant growth so as to more clearily establish their practical value for cowpea production, is required.

APPENDIX

Table 1A Changes in Height with age of Cowpea Plants as Influenced by Leaf Water Potential

Leaf Water Potential (Bars)	Plant height (cm)			
	85	35	45	55
-5	27.66a	31.36 a	44.00a	44.30a
-10	22.64_{b}	25.53_{b}	27.30_{b}	31.30_{b}
-12.5	20.36_{c}	22.88_{bc}	23.60_{bc}	26.00_{c}
-15	17.70_{c}	21.03_{c}	21.60_{c}	23.00_{c}

* Means within the same column followed by the same letter are not significantly different at the 5% level of probability as determined by Duncen's Multiple RangesTest.

Table 2 Changes in Lean Area with Age as Influenced by Leaf Water Potential

Leaf Water Potential (Bars)	Leaf area (cm^2/ plant). Days after emergence			
	25	35	45	55
-5	201.22_a	247.00_a	214.53_a	199.66_a
-10	113.72_b	108.41_b	135.98_b	234.61_a
-12.5	91.33_b	101.58_b	112.26_b	93.69_b
-15	105.79_b	95.47_b	61.31_c	59.59_b

* Means within the same column followed by the same letter are not significantly different at 5% level of probability as determined by Duncan's Multiple Range Test.

Table 3 Changes in dry matter contents of cowpea seedlings with age as influenced by leat water potential

Leaf Water Potential (Bars)	Dry Matter (g/plant) Days after emergence				
	25	35	45	55	65
-5	1.33 $_{a}$	2.90 $_{a}$	3.47 $_{a}$	3.27 $_{a}$	5.63 $_{a}$
-10	1.13 $_{a}$	1.10 $_{b}$	1.30 $_{b}$	1.26 $_{b}$	1.90 $_{b}$
-12.5 $_{c}$	1.03 $_{a}$	0.70 $_{b}$	1.05 $_{c}$	0.92 $_{b}$	0.97 $_{b}$
-15	1.00 $_{a}$	0.60 $_{b}$	0.99 $_{c}$	0.52 $_{b}$	0.83 $_{b}$

* Means within the same column followed by the same letter are not significantly different at the 5% level of probability as determined by Duncan's Multiple Range Test.

Table 4 Relative growth rates net assimilation rates (NAR). Root/Shoot ratio and specific leaf weight in cowpea as influenced by leaf water potential.

Leaf Water Potential (Bars)	RGR (mg/day)	NAR_2 (mg/cm^2 Leaf area/ day)	Root/Shoot Ratio.	SLW_2 (mg/cm^2 Leaf Area)
-5	0.04_a	0.36_a	0.10_a	6.25_a
-10	0.02_a	0.233_b	0.24_b	4.58_a
$-12._c$	0.02_a	0.14_c	0.31_b	4.73_a
-15	-0.004_b	-0.19_c	0.24_b	7.74_a

* Means within the same column followed by the same latter are not significantly different at the 5% level of probability.

Table 5A Stomatal vresistance, nitrate reductase activity and nodulation as influenced by leaf water potential

Leaf Water Potential (Bars)	Stomatal resistance (sec/cm)	(NRA MNO_3^-/g fresh tissue / hr)	Number of effective nodules
-5	2.56_a	0.42_a	26.83_a
-10	3.84_a	0.201_a	17.33_a
-12.5	4.03_a	0.13_b	5.50_b
-15	140.25_b	0.08_b	1.67_b

* Means within the same column followed by the same letter are not significantly different at the 5% level of probability.

Table 6A Total chlorophyll, chlorophyll a and chlorphyll b in relation to leaf water potential.

Leaf Water Potential (Bars)	Chlorophyll (mg/plant)			Chlorophyll (mg/g fresh tissue)		
	Total Chl	Chl.a	Chl.b	Total Chl.	Chl.a	Chl.b
-5 a	3.45_{a}	2.12_{a}	1.33_{ab}	79.17_{a}	33.24_{a}	31.27_{a}
-10 b	5.22_{a}	3.15_{a}	2.07_{a}	53.42_{a}	33.57_{a}	19.86_{a}
-12.5 c	2.81_{ab}	1.79_{ab}	1.02_{b}	55.20_{a}	30.55_{a}	24.66_{a}
-15 d	0.62_{b}	0.41_{b}	0.21_{c}	28.79_{a}	18.80_{a}	11.21_{a}

* Means within the same column followed by the same letter are not significantly different at the 5% level of probability

Table 8A Starch, total soluble carbohydrates, reducing sugars and amino acids in relation to leaf water potential*

Leaf Water Potential (Bars)	Starth		Total soluble Carbohydrates		Reducing Sugars (ng.)		Total Amino Aci (mg.)	
	(mg/plant)	(mg/g fresh tissue)	mg/plant)	(mg/g fresh tissue)	(mg/plant)	(mg/g fresh tissue)	(mg/plant.	(mg/ fresh
-5	235.52_a	34.76_a	125.54_a	5.27_a	60.28_a	6.84_a	5.69_a	0.28_a
-10	61.31_b	14.55_b	87.26_{ab}	17.90_a	54.37_a	7.93_a	2.66_a	0.66_b
-12.5	10.60_b	3.82_b	64.54_b	35.67_b	26.37_b	8.38_a	2.28_a	1.75_c
-15	5.09_b	2.95_b	50.39_b	33.44_b	20.42_b	10.37_a	2.74_a	2.50_a

* Means within the same column followed by the same letters are not significantly different at the 5% level of probability.

Table 7A. Total, soluble and insoluble proteins in relation to leaf water potential

Leaf Water Potential (Bars)	Total Protein (mg/plant)	Soluble Protein (mg/plant)	Insoluble Protein (mg/Plant)
-5	790.40_{a}	330.00	460.40_{ab}
-10	849.33_{a}	220	629.33_{a}
-12.5	436.40_{b}	190.60	209.06_{b}
-15	373.00_{b}	176.00	197.06_{b}

* Means within the same column followed by the same letter are not significantly different at the 5% level of probability.

Table 9A Seed yield and some of its components as influenced by leaf water potential.

Leaf Water Potential (Bars)	Seed Yield (g/plant)	Seed Weight (g/pod)	Seed size (g/seed)	pod/seed ratio
-5	10.89_a	2.75_a	0.19_a	0.67_a
-10	3.44_b	1.47_b	0.18_a	0.81_a
-12.5	1.29_b	0.56_c	0.23_b	1.47_a
-15	0.37_b	0.37_c	0.28_c	1.43_a

* Means within the same column followed by the same letter are not significantly different at the 5% level of probability.

Table 10A Pod density, length, and yield an seed number/pod in relation to leaf water potential*

Leaf Water Potential (Bars)	Pod density (pods/plant)	pod length (cm/pod)	pod dry weight (g/pod)	number of seeds/pod
-5	4.23_a	19.63_a	0.29_a	12.30_a
-10	2.17_b	13.00_b	0.22_a	7.23_b
-12.5	1.67_{bc}	10.67_b	0.16_a	3.77_a
-15	1.00_c	5.17_c	0.196_a	1.67_d

* Means within the same column followed by the same letter are not significantly different at the 5% level of probability.

REFERENCES

1. Acevedo, E., Hsiao, T.C., and Anderson, D.W. 1971. Immediate and subsequent growth responses of maize leaves to changes in water stress. Plant Physiol. 48: 631-636

2. Ackerson, R.C. 1980. Stomatal response of cotton to water stress and abscisic acid as affected by water stress history. Plant Physiol. 65: 455-459.

3. Adjei-Twum, D.C. 1975. Studies on the germination, growth, and development of soybean (Glycine max Merr. L.) used as a vegetable. PH.D Thesis University of Illionois.

4. Adjei-Twum, D.C., and Splittstoesser, W.E. 1976. The effect of soil water regimes on leaf water potential, growth, and development of soybeans. Physiol. Plant 38: 131-137.

5. Adjei-Twum, D.C., 1982. Some research methods in agronomy and crop physiology. IAR/Ethiopia, Agronomy and Crop Physiology Bulletin. No. 1.

6. Afridi, M.M.K., and Hewitt, E.J. 1964. The inducible formation and stability of nitrate reductase in higher plants. I. Effects of nitrate and molybdenum on enzyme activity in cauliflower (Brassica oleraceae var. botrytis). J. Exp. Bot. 15: 251-271.

7. Aggarwal, P.K., and Sinha, S.K. 1984. Effect of water stress on grain growth and assimilate partitioning in two cultivars of wheat contrasting in their yield stability in a drought environment. Ann. Bot. 53: 329-340.

8. Alberte, R.S., Thronber, J.P., and Ficus, E.L. 1977. Water stress effects on the content and organization of chlorophyll in mesophyll and bundle sheath chloroplasts of maize. Plant Physiol. 59: 351-353.

9. Allen, J.R. and Obura, R.K. 1983. Yield of corn, cowpea and soybeans under different intercropping systems. Agron. J. 75: 1005-1009.

10. Arnon, D.I. 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in Beta vulgaris. Plant Physiol. 24: 1-15.

11. Arnon, I. 1972. Crop Production in Dry Regions Vol. II. Systematic Treatment of the Principal crops. Leonard Hill Book. London, pp. 250-254.

12. Arnon, I. 1975. Physiological principles of crop production. In U.S.Gupta (ed.). Physiological aspects of dryland farming. Oxford and IBM publishing Co. New Delhi. pp 3-146.

13. Asana, R.D. 1965. Measurement of drought resistance in crop plants. In F.E. Eckardt (ed.). Methodology of Plant Eco-Physiology UNESCO. pp 413-430.

14. Ashenden, T.W., Stewart, W.S., and Williams, E. 1975. Growth responses of sand dune populations of Dactylis glomerata L. to different levels of water stress. J. Ecol. 63: 97-108.

15. Bardzik, J.M., March, H.V., and Havis, J.R. 1971. Effect of water-stress on the activities of three enzymes in maize seedlings. Plant Physiol. 47: 828-831.

16. Barlow, E.W.R., Boersma, L., and Young, J.L. 1976. Root temperature and soil water potential effects on growth and soluble carbohydrate concentration of corn seedlings. Crop Sci. 16: 59-62.

17. Barlow, E.W.R., Munns, R., Scott, N.S., and Reisner, A.H. 1977. Water potential, growth and polyribosome content of the stressed wheat apex. J. Exp. Bot. 28: 909-916.

18. Barnett, N.M., and Naylor, A.W. 1966. Amino acid and protein metabolism in Bermudagrass during water stress. Plant Physiol. 41: 1222-1230.

19. Begg, J.E., and Turner, N.C. 1970. Water potential gradients in field tobacco. Plant Physiol. 46: 343-346.

20. Begg, J.E., and Turner, N.C. 1976. Crop water deficits. Adv. Agron. 28: 161-217.

21. Bentson, C., Klockare, B., Klockare, R., Larsson, S., and Sundgvist, C. 1978. The after-effect of water stress on transpiration rate and changes in abscisic acid content of young wheat plants. Physiol. Plant. 41: 149-154.

47. Denmead, O.T., and Shaw, R.H. 1960. The effect of soil moisture at different stages of growth on the development and yield of corn. Agron. J. 52: 272-274.

48. Devlin, R.M., and Witham, F.H. 1983. Plant Physiology 4th ed. Willard Grant Press. Boston.

49. Dhindsa, R.S., and Cleland, R.E. 1975. Water stress and protein synthesis. Differential inhibition of protein synthesis. Plant Physiol. 55: 778-781.

50. Dittrich, P., and Raschke, K. 1977. Malate metabolism in isolated epidermis of Commelina communis L. in relation to stomatal functioning. Planta 134. 77-81.

51. Douglas, T.J. and Paleg, L.G. 1981. Lipid composition of Zea mays seedlings and water stress induced changes. J. Exp. Bot. 32: 499-508.

52. Duncan, W.G. 1975. Maize. In L.T. Evans (ed.). Crop physiology some case histories. Cambridge University Press. London.

53. Dunham, R.J., and Nye, P.H. 1976. The influence of soil water content on the uptake of ions by roots: III. Phosphate, potassium, calcium and magnesium uptake and concentration gradients in soil. J. Appl. Ecol. 13: 967-984.

54. Duyson, M.E., and Freeman, T.P. 1974. Effect of moderate water deficit (stress) on wheat seedlings growth and plastid pigment development. Physiol. Plant. 31: 262-266.

55. Erlandson, G., Pettersson, S., and Suensson, B.B. 1978. Rapid effect on ion uptake in sunflower roots. Physiol. Plant. 43: 380-384.

56. Fanjul, L., and Rosher, P. 1984. Effects of water stress on internal water relations of apple leaves. Physiol. Plant. 62: 321-328.

57. Feller, U.K., Soong, T.J., and Hageman, R.H. 1977. Leaf proteolytic activities and sen escence during grain development of field grown corn (Zea mays L.) Plant Physiol. 59: 290-294.

58. Fereres, E., Acevedo, E., Henderson, D.W., and Hsiao, T.C. 1978. Seasonal changes in water potential and turgor maintenance in sorghum and maize under water stress. Physiol. Plant. 44: 261-267.

59. Fischer, R.A., and Hsiao, T.C. 1968. Stomatal opening in isolated epidermal strips of Vicia faba II. Responses to KCl concentration and the role of potassium absorption. Plant Physiol. 43: 1953-1958.

60. Fukutoku, H., and Yamada, J. 1982. Accumulation of carbohydrates and proline in water stressed soybean (Glycine max). Soil Science and Plant Nutrition. 28: 147-151.

61. Gale, J., and Hagan, R.M. 1966. Plant antitranspirants. Ann. Rev. Plant Physiol. 17: 269-282.

62. Gallacher, A.E., and Sprent, J.T. 1978. The effects of different water regimes on growth and nodule development of green-house-grown Vicia faba. J. Exp. Bot. 29: 413-423.

63. Gallagher, J.N., Biscoe, P.V., and Hunter, B. 1976. Effects of drought on grain growth. Nature 264: 541-542.

64. Gates, C.T. 1968. Water deficits and growth of herbaceous plants. In T.T. Kozlowski (ed.), Water Deficits and Plant Growth. Vol. II. Academic Press, New York. pp. 135-190.

65. Girma, F.S., and Krieg, D.R. 1984. Comparisions of water relations components in cotton and cowpea. Plant Physiol. (supplement) 75: 174.

66. Gornall, A.C., Bardwill, C.J., and David, M.M. 1949. Determination of serum proteins by means of the buiret reaction. J. Biol. Chem. 117: 751-766.

67. Greenway, H., Hughes, P.G., Klepper, B. 1969. Effects of water deficit on phosphorus nutrition of tomato plants. Physiol. Plant. 22: 199-207.

68. Gupta, U.S. (ed.) 1975. Physiological Principles of Dry land Farming. Oxford and IBM Publishing Co. New Delhi.

69. Hall, A.E., and Dancette, C. 1978. Analysis of fallow farming systems in semi-arid Africa using a model to stimulate the hydrologic budget. Agron. J. 70: 816-823.

70. Hall, A.E., Shulze, E.D. 1980. Drought effects on transpiration and leaf water status of cowpea in controlled environments. Aust. J. Plant Physiol. 7: 141-147.

71. Hall, H.K., McWha, J.A. 1981. Effects of abscisic acid on growth of wheat. Ann. Bot. 47: 427-433.

72. Harper, J.E., and R.H. Hageman, 1972. Seasonal profiles of nitrate reductase in soybeans. (Glycine max L. Merr.). Plant Physiol. 49: 146-154.

73. Harrison, M.A., and Walton, D.C. 1975. Abscisic acid metabolism in water stressed bean leaves. Plant Physiol. 56: 250-254.

74. Hartung, W., and Funfer, C. 1981. Abscisic acid and apical dominance in Phaseolus coccineus L. the role of tissue age. Ann. Bot. 47: 371-375.

75. Hassid, W.Z., and Neufeld, E.F. 1964. Quantitative determination of starch in plant tissue. In Whistler, R.L., Smith, R.J., BeMiller, J.N. and Walfrom, M.L. (eds.). Methods in Carbohydrates. Chemistry IV: 33-36.

76. Hatch, M.D., and Slack, C.R. 1970. Photosynthetic CO_2 fixation pathways. Ann. Rev. Plant Physiol. 21: 141-162.

77. Henckel, P.A. 1964. Physiology of plants under drought Ann. Rev. Plant Physiol. 15: 363-386.

78. Herbert, S.J., Baggerman, F.D. 1983. Cowpea response to row width, density, and irrigation. Agron.J. 75: 982-986.

79. Hiler, E.A., van Bavel, C.H.M., Hossam, M.M., and Jordan, W.R. 1972. Sensitivity of southern peas to plant water deficit at three growth stages. Agron. J. 64: 60-63.

80. Hodgson, J.M. 1973. Lipid deposition on leaves of Canada thistle ecotypes. Weed Sci. 21: 169-172.

81. Hodgson, J.D., and Lorio, P.L., 1969. Carbohydrates and nitrogen fractions of the inner bark of loblolly pines under moisture stress. Can.J.Bot. 47: 1651-1657.

82. Hsiao, T.C. 1970. Rapid change in levels of polyribosomes in Zea mays in response to water stress. Plant Physiol. 46: 281-285.

83. Hsiao, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24: 519-570.

84. Hsiao, T.C., Acevedo, E. and Henderson, D.W. 1970. Maize leaf elongation: continuous measurments and close dependence on plant water status. Science 168: 590-591.

85. Hsiao, T.C., Acevedo, E., Fereres, E., and Henderson, D.W. 1976. Water stress, growth, and osmotic adjustment. Phil. Trans. R. Soc. Lond. B. 273: 479-500.

86. Humble, G.D., and Raschke, K. 1971. Stomatal opening quantitatively related to potassium transport. Plant Physiol. 48: 447-453.

87. Ilahi, I., and Dorffling, K. 1982. Changes in abscisic acid and proline levels in maize varieties of different drought resistance. Physiol. Plant. 55: 129-135.

88. Institute of Agricultural Research (IAR) Melka Werer Research Station. 1970. Progress Report for the Period March 1968 to March 1969. pp. 59.

89. Irvine, F.R. 1974. West African Crops. Oxford University Press, Oxford.

90. Itai,C., and Vaadia, Y. 1965. Kinetin-like activity in root exudate of water stressed sunflower. Physiol. Plant. 18: 941-944.

91. Janes, B.E. 1970. Effect of carbondioxide, osmotic potential of nutrient solution, and light intensity of transpiration and resistance to flow of water in peeper plants. Plant Physiol. 45: 95-103.

92. Jordan, W.R. and Ritchie, J.T. 1971. Influence of soil water stress on evaporation, root absorption and internal water status of cotton. Plant Physiol. 48: 783-788.

93. Kanemasu, E.T., and Tanner, C.B. 1969. Stomatal diffusion resistance of snap beans. I. Effect of leaf water potential. Plant Physiol. 44: 1547-1552.

94. Kanemasu, E.T., Thurtell, G.W., and Tanner, C.B. 1969. Design, calibration and field use of a stomatal diffusion porometer. Plant Physiol 44: 881-885.

95. Karani, E., Drieg, D.R., and Quisenberry, J.E. 1980. Water stress effects on CO_2 assimilation, photosynthetic partioning, stomatal resistance and nodule activity in soybean. Crop Sci. 20: 431-345.

96. Kay, D.E. 1979. Food Legumes. Tropical Products Institute London.

97. Keck, R.W., and Boyer, J.S. 1974. Chloroplast response to low leaf water potentials: III. Differing inhibition of electron transport and photophorylatio Plant Physiol. 53: 474-479.

98. Keim, D.L., and Kronstad, W.E. 1981. Drought response of winter wheat cultivars grown under field stress conditions. Crop Sci. 21: 11-15.

99. Klepper, L.A., Flesher, D. and Hageman, R.H. 1971. Generation of reduced nicotimide adenine dinucleotid for nitrate reduction in green leaves. Plant Physiol. 48: 580-590.

100. Koeppe, D.E., Miller, R.J., and Bell, D.T. 1973. Drought-affected mitochondrial processes as related to tissue and whole plant responses. Agron J. 65: 307-310.

101. Kramer, P.J. 1969. Plant Soil Water Relationships: Modern synthesis. McGraw-Hill Book Co. New York.

102. Kramer, P.J. 1974. Fifty years of progress in water relations research. Plant Physiol. 54: 463-471.

103. Laetsch, W.M. 1968. Chloroplast specialization in dicotyledons possessing the C_4- dicarboxylic acid pathway of photosynthetic CO_2 fixation. Amer. J. Bot. 55: 875-883.

104. Lambers, H. 1976. Respiration and NADH - oxidation of the roots of flood-tolerant and flood-intolerant Senecio species as affected by anaerobiosis. Physiol. Plant. 37: 117-122.

105. Lambers, H., Steingrover, E., and Smakma, G. 1978. The significance of oxygen transport and of metabolic adaptation in flood tolerance of Senecio species. Physiol Plant. 43: 277-281.

106. Larson, K.L. 1975. Drought injury and resistance of crop plants. In U.S. Gupta (ed.). Physiological aspects of dryland farming. Oxford and IBM Publishing Co. New Delhi. pp. 147-166.

107. Lawlor, D.W. 1970. Absorption of polyethlene glycols by plants and their effects on plant growth. New Phytol. 69: 501-513.

108. Lee, J.A. and Stewart, G.R. 1971. Desiccation injury in mosses. I. Intraspecific difference in the effect of moisture stress. New Phytol. 70: 1061

109. Leek, G.L., Weete, T.D., and Peterson, C.M. 1977. Effects of water stress on epicuticular wax and lipid formation in cotton leaves. Plant Physiol. (Supp.) 59: 53.

110. Leopold, A.C. 1970. Plant Growth and Development McGraw-Hill Book Company. New York.

111. Levitt, J. 1965. The measurement of drought resistance In. F.E. Eckardt (ed.). Methodology of Plant Eco-Physiology. UNESCO. pp. 407-412.

112. Levitt, J. 1980. Responses of plants to environmental stresses. vol. II. Water, radiation, salt, and other stresses. Academic Press. New York. pp 25-280.

113. Lockhart, J.A. 1965. Cell extension. In. J. Bonner and J.E. Varner (eds). Plant Biochemistry. Academic Press, New York. pp. 826-849.

114. Loveys, B.R., and Kriedemann, P.E. 1973. Rapid changes in abscisic acid like inhibitors following alterations in vine leaf water potential Physiol. Plant. 28: 476-479.

115. Loveys, B.R., and Kriedemann, P.E. 1974. Internal control of stomatal physiology and photosynthesis: I. Stomatal regulation and associated changes in endogeneous levels of abscisic and phaseic acids. Aust. J. Plant. Physiol. 1: 407-415.

116. Ludlow, M. 1982. Leaf turgor maintenance during water stress. Plant Physiol. (suppl.). 69(4): 14

117. Maranville, J.W., and Paulsen, G.M. 1970. Alteration of carbohydrate composition of corn (Zea mays L.) seedlings during moisture stress. Agron.J. 62: 605-608.

118. May, L.H., and Milthorpe, F.L. 1962. Drought resistance of crop plants. Field Crop Abstr. 15: 171-179.

119. McPherson, H.G., and Boyer, J.S. 1977. Regulation of grain production by photosynthesis in maize subjected to a water deficiency. Plant Physiol. (supp.) 59: 53.

120. MacRobbie, E.C. 1981. Effects of abscisic acid on "isolated" guard cells of Commeline communis L. J. Exp. Bot. 32: 563-572.

121. Mengel, K., and Von Braunschweig, L.C. 1972. The effect of soil moisture upon the availability of potassium and its influence on the growth of young maize plants (Zea mays L.). Soil Sci. 114: 142-148.

122. Milborrow, B.V., and Noddle, R.C. 1970. Conversion of 5-(1,2- Ephoxy-2, 6, 6-trimethylcyclohexyl)-3-methylpenta-cis-2-trans-4- dienoic acid into abscisic acid in plants. Biochem. J. 119: 727-734.

123. Mohanty, P., and Boyer, J.S. 1976. Chloroplast response to low leaf water potentials: IV. Quantum yield reduced. Plant Physiol. 57: 704-609.

124. Morilla, C.A., Boyer, J.S., and Hageman, R.J. 1973. Nitrate reductase activity and polyribosomal content of corn (Zea mays) having low water potential. Plant Physiol. 51: 817-824.

125. Naidu, K.M., Appala, B., and Venkateswarlu, B. 1967. Influence of soil moisture on sugar and nitrogen contents of Pennisetum typhoides. Agr. J. 14: 143-148.

126. Nelson, N. 1964. A photometric adaptation of the somogyi method for the determination of glucose. J. Biol. Chem. 153: 347-378.

127. Nobel, P.S. 1970. Plant Cell Phsyiology a Physiochemical Approach. W.H. Freeman and Company. San Franscisco.

128. Certil, J.J. 1971. A whole system approach to water physiology in plants. In L. Chandra (ed.). Advanced Frontiers of Plant Sciences vol. 27. pp. 1-200.

129. Osmond, C.B. 1978. Crassulacean acid metabolism, a curiosity in context. Ann. Rev. Plant Physiol. 29: 379-414.

130. O'Toole, J.C., Crookston, R., Treharne, K.J., and Ozbun, J.L. 1976. Mesophyll resistance and carboxylase activity: A comparision under water stress conditions. Plant Physiol. 57: 465-468.

131. O'Toole, J.C., Ozbun, J.L., and Wallace, D.H. 1977. Photosynthetic response to water stress in Phaseolus vulgaris. Physiol. Plant. 40: 111-114.

132. Outlaw, W.H. 1983. Current concepts on the role of potassium in stomatal movements. Physiol. Plant. 59: 302-311.

133. Parsons, L.R., and Howe, T.K. 1984. Effect of water stress on the water relations of Phaseolus vulgaris and drought resistance of P. acutifolius Physiol. Plant. 60: 197-202.

134. Penadasa, M.A. 1979. Movements of abaxial and adaxial stomata. New Phytol 82: 69-80.

135. Penadasa, M.A. 1983. Effects of KCl concentration on changes and malate levels in abaxial and adaxial epidermis in relation to stomatal opening. J. Exp. Bot. 34: 514-522.

136. Pereira, J.S., and Kozlowski, T.T. 1976. Leaf anatomy and water relations of Eucalyptus camaldulenis and E. globulus seedlings. Can.J.Bot. 54: 2868-2880.

137. Peterson, D.M., Housley, T.L., and Schrader, L.E. 1977. Long distance translocation of sucrose, serine, leucine, lysine and CO_2 assinilates. II Oats. Plant Physiol. 59: 221-224.

139. Plaut, Z. 1974. Nitrate reductase activity of wheat seedlings during exposure to and recovery from water stress and salinity. Physio Plant. 30: 212-217.

140. Pratt, H. , and Geoschl, J.D. 1969. Physiological roles of ethylene in plants. Ann. Rev. Plant Physiol. 20: 541-548.

141. Price, C.A. 1974. Molecular Approaches to Plant Physiology. Tata McGraw-Hill Publishing Company Ltd. New Delhi.

142. Purseglove, J.W. 1968. Tropical Crops: Dicotyledons I. Longmans, Green and Co. Ltd. London.

143. Purseglove, J.W. 1976. The orgins and migrations of crops in tropical Africa. In J.R. Harlan, J.M.G. DeWet, and A.B.L. Stemler (eds.). Origins of African Plant Domestication. Nouton Publishers. The Hague pp. 211-221.

144. Quarrie, S.A., and Jones, A.G. 1979. Genotypic variation in leaf water potential, stomatal conductance and abscisic acid concentration in spring wheat subjected to artificial drought stress. Ann. Bot. 44: 323-332.

145. Radford, P.J. 1967. Growth analysis formulae. Their use and abuse. Crop Sci. 7: 171-176.

146. Raschke, K. 1970. Leaf hydraulic system: rapid epidermal and stomatal responses to changes in water supply. Science 167: 189-191

147. Raschke, K. 1975. Stomatal action. Ann. Rev. Plant Physiol. 26: 309-340.

148. Redshaw, A.J., and Meidner, H. 1972. Effects of water stress on the resistance to uptake of carbon dioxide in tobacco. J. Exp. Bot. 23: 229-240.

149. Reid, C.P.P. 1974. Assimilation, distribution and root exudation of ^{14}C by ponderosa pine seedlings under induced water stress. Plant Physiol. 54: 44-49.

151. Rodriguez, J.L., and Davies, W.J., 1982. The effects of temperature and abscisic acid on stomata of Zea mays L. J. Exp. Bot. 33: 977-987.

152. Saunier, R.E., Hull, H.M., and Ehrenreich, J.H. 1968. Aspects of drought tolerance in creosotebush (Larrea divaricata). Plant Physiol. 43: 401-404.

153. Scholander, P.F., Hammel, H.T., Bradstreet, E.D., and Hemmingsen, E.A. 1965. Sap pressure in vascular plants. Science 148: 339-346.

154. Schnable, H., and Raschke, K. 1980. Potassium chloride as stomatal osmoticum in Allium cepa L. a species devoid of starch in guard cells. Plant Physiol. 65: 88-95.

155. Seidlova, F., Kohli, R.K., and Pavlova, L. 1981. Effects of abscisic acid on the growth pattern of the shoot apical meristem and on flowering in Chenopodium rubrum L. Ann. Bot. 48: 777-785.

156. Shah, C.B., and Loomis, R.S. 1965. Ribonucleic acid and protein metabolism in sugar beet during drought. Physiol. Plant. 18: 240-254.

157. Sheikholeslam, S.N., and Currier, H.B. 1977. Effect of water stress on turgor differences and ^{14}C-assimilate movement in phloem of Ecballium elaterium. Plant Physiol. 59: 381-383.

158. Shouse, P., Dasberg, S., Jury, W.A., and Stolzy, L.H. 1981. Water deficit effects on water potential, yield and water use of cowpeas. Agron. J. 73: 333-336.

159. Silvius, J.E., Johnson, R.R., and Peters, D.B. 1977 Effect of water stress on carbon assimilation and distribution in soybean plants at different stages of development. Crop Sci. 17: 713-716.

160. Sionit, N., and Kramer, P.J. 1976. Water potential and stomatal resistance of sunflower and soybean subjected to water stress during various growth stages. Plant Physiol. 58: 537-540.

161. Slatyer, R.O. 1967. Plant Water Relationships Academic Press. London.

162. Slavik, B. 1975. Water stress, photosynthesis and the use of photosynthates. In J.P. Cooper (ed.). Photosynthesis and Productivity in Different Environments. Cambridge University Press, Cambridge. pp. 511-556.

163. Smith, R.C., St.John, B.H., and Parrondo, R. 1973. Influence of mannitol on absorption and retention of rubidium by excised corn roots. Amer.J.Bot. 60: 839-845.

164. Sojka, R.E., Stolzy, L.H., and Kaufmann, M.R. 1975. Wheat growth related to rhizosphere temperature and oxygen levels. Agron. J. 67: 591-596.

165. Soong, T.T., and Hageman, R.H. 1977. Changes in leaf proteolytic enzymes as function of water deficit in corn (Zea mays L.). Plant Physiol. (suppl.) 59: 53.

166. Sprent, J.I. 1971a. The effects of water stress on nitrogen fixing root nodules. I. Effects on the physiology of detached soybean nodules. New Phytol. 70: 1-17.

167. Sprent.J.I. 1971b. Effect of water stress on nitrogen fixation in root nodules. Plant and Soil, special volume: 225-228.

168. Steele, W.N. 1979. Cowpeas. In N.W. Simmonds (ed.) Evolution of crop plants. Longman Group Ltd. London. pp. 200-205.

169. Stewart, C.R. 1973. The effect of wilting on proline metabolism in excised bean leaves in the dark. Plant Physiol. 51: 508-511.

170. Stewart, C.R., Boggess, S.F., Aspinall, D., and Paleg, L.G. 1977. Inhibition of proline oxidation by water stress. Plant Physiol. 59: 930-932.

171. Stickler, F.C. 1964. Row width and plant population studies with corn. Agron. J. 56: 438-441.

172. Stillwell, W., and Tien, H.T. 1977. Protection of chlorophyll by phospholipids from photoxidation. Biochem. Biophys. Res. Commun. 76: 232-238.

173. Stocker, R., and Weatherley, P.E. 1971. The influence of the root system on the relationship between the rate of transpiration and depression of leaf water potential. New Phytol. 70: 547-554.

174. Summerfield, R.J., Huxley, P.A., Dart, P.J., and Huges, A.P. 1976. Some effects of environmental stress on seed yield of cowpea (Vigna unguiculata (L Walp.) cv. "Prima". Plant Soil 44: 527-546.

Talha, M., and Osman, F. 1975. Effect of soil water stress on water economy and oil composition in sunflower (Helianthus annuus L.). J. Agric. Sci. 84: 49-56.

176. Taylor, H.M., and Klepper, B. 1974. Water relations of cotton: I. Root growth and water use as related to top growth and soil water content. Agron.J. 66: 584-588.

177. Taylor, H.M., and Klepper, B. 1978. The role of rooting characteristics in the supply of water to plants. Adv. Agron. 30: 99-128.

178. Terry, N., Waldron, L.J., and Ulrich, A. 1971. Effects of moisture stress on the multiplication and expansion of cells in leaves of sugar beet. Planta, 97: 281-289.

179. Turk, K.J., and Hall, A.E. 1980a. Drought adaptation of cowpea II. Influence of drought on plant water status and relations with seed yield. Agron. J. 72: 421-427.

180. Turk, K.J., and Hall, A.E. 1980b. Drought adaptation of cowpea. III. Influence of drought on plant growth and relations with seed yield. Agron. J. 72: 428-433.

181. Turk, K.J., and Hall, A.E. 1980c. Drought adaptation of cowpea. IV. Influence of drought on water use, and relations with growth and seed yield. Agron. J. 72: 434-439.

182. Turk, K.J., Hall, A.E., and Asbell, C.W. 1980. Drought adaptations of cowpea. I. Influence of drought on seed yield. Agron. J. 72: 414-420.

183. Wardlow, I.F. 1969. The effect of water stress on translocation in relation to photosynthesis and growth II. Effect during leaf development in Lolium tenulentum L. Aust. J. Biol. Sci. 22: 1-16.

184. Wample, R.L., and Reid, D.M. 1975. Effect of aeration on the flood-induced formation of adventitious roots and other changes in sunflower (Heliantus annus L.) Planta 127: 263-270.

185. Wardle, K., and Short, K.C. 1983. Stomatal responses and the senescence of leaves. Ann. Bot. 52: 411-412.

186. Wardle, K., and Short, K.C. 1981. Responses of stomata in epidermal strips of Vicia faba to carbon dioxide and growth hormones when incubated with potassium chloride and potassium iminodiacetate. J. Exp. Bot. 32: 303-309.

187. Watts, S., Rodriguez, J.L., Evans, S.E., and Davies W.J. 1981. Root and shoot growth of plants treated with abscisic acid. Ann. Bot. 47: 595-602.

188. Westphal, E. 1974. Pulses in Ethiopia. Their taxonomy and agricultural significance. Center for Agricultural Publishing and Documentation. Wageningen

189. Weyers, J.D.B., Patterson, N.W., Fitzsimons, P.J., and Duddley, J.M. 1982. Metabolic inhibitors block ABA induced stomatal closure. J. Exp. Bot. 33: 1270-1278.

190. Wignarajah, K., Greenway, H., and John, C.D. 1976. Effect of water-logging on growth and activity of alcohol-dehydrogenase in barley and rice. New Phytol. 77: 585-592.

191. Willmer, C.M., Rutter, J.C., and Meidner, H. 1983. potassium involvement in stomatal movements of paphiopedilum. J. Exp. Bot. 34: 507-513.

192. Wright, S.T.C., and Hiron, R.W.P. 1969. (+) - Abscisic acid, the growth inhibitor induced in detached wheat leaves by a period of wilting. Nature 224: 719-720.

193. Yemm, E.W., and Cocking, E.C. 1955. The determination of amino acids with ninhydrin. Analysist 80: 209-213.

194. Zabadal, T.J. 1974. A water potential threshold for the increase of abscisic acid in leaves. Plant Physiol. 53: 125-127.

195. Zeevaart, J.A.D. 1980. Changes in the levels of abscisic acid and its metabolites in excised leaf blades of Xanthium strumarium during and after water stress. Plant Physiol. 66: 672-678.

196. Zeiger, E., and Field, C. 1982. Photocontrol of the functional coupling between photosynthesis and stomatal conductances in the intact leaf. Plant Physiol. 70: 370-375.

197. Ziska, L.H., Hall, A.E. 1983. Soil and plant measurements for determining when to irrigate cowpeas (Vigna unguiculata (L.) Walp) grown under planned water deficitys. Irri. Sci. 3: 247-257.

D E C l A R A T I O N

I, the undersigned, declare that this thesis is my work and that all sources of materials used for the thesis have been dully acknowledged.

Masresha Fetene

Addis Ababa University,
Faculty of Science
June, 1985