EFFECTS OP MOISOTE STRESS AT DIFFERENT GROWIH STAGES ON THE PERFORMANCE AND YIELD OP WHEAT (Triticum aestivum L. em Thell.)

By

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CERTIFICATION

This Thesis entitled 'Effects of Moisture Stress at Different Growth Stages on the Performance and Yield of Wheat (Triticur aestivum L. em Thell.)' by Benjamin Chumang DATIRI, meets the regulations governing the Degree of Master of Science, Ahmadu Bello University, Zaria and is approved for its literary presentation and contribution to Scientific knowledge.

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ABSTRACT

In order to study the effects of moisture stress at different growth stages of wheat (Triticum aestivum L. em Thell), an experiment was conducted under field conditions during the 1980-81 dry, cool harmattan season at Irrigation Research Station, Kadawa, Nigeria. Two levels of moisture stress were imposed by omitting one and two irrigations at tillering, jointing, flowering and grain filling stages of wheat. These were then compared with a no-stress control treatment, which received a regular irrigation at 10-days interval.

Soil moisture profile studies revealed that the control treatment experienced no stress as its soil moisture tensions did not exceed 0.25 bars. The other treatments experienced different magnitudes of stress depending on how their soil moisture tensions exceeded 0.5 bars. From the soil suction and water content relationships (figure 2), it appeared that at about 0.5 bars most of the available water in the experimental plot had been lost. The ground water table during the growing season fluctuated between 80 and 100 cm from the soil surface.

Both levels of soil moisture stress slightly decreased the plant water potential. However, the water stress in plant was mild even in treatments with minus two irrigations at the various growth stages.

Plant growth, yield components and yield were generally decreased; whereas plant canopy temperatures, grain protein content and roots shoot ratio were increased by stress conditions. Thus the four selected growth, stages were sensitive to both levels of moisture stress. However, the most sensitive (critical) growth Stages under Kadawa conditions (with high water table) were jointing and flowering for treatments with minus two and one irrigations, respectively. These caused 36.2 and 18.6% reductions in grain yield. Generally, omitting two irrigations at all growth stages and one at flowering and grain filling were deleterious to wheat and should be avoided. In fact these caused significant reductions (between 16.3 and *36.2%)* in grain yield. However, omitting one irrigation during tillering and jointing could be tolerated since this reduced grain yield by only 12.9 and 10.7%, respectively.

Finally, it appeared that the 10-days irrigation interval (as in the control treatment) could be conveniently used at Kadawa and environs with similar conditions as the yield was good.

DEDICATION

This project Thesis is dedicated to my dear daughter, Sinidarwei Charity Datiri for the high level of understanding she demonstrated during the entire period of this work.

I am also dedicating this project Thesis to the Lord Jesus Christ for his great love and unfailing promises in the Holy Bible, which have kept me going in my academic pursuit.

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CHAPTER 1

INTRODUCTION

Plant growth, in general, is influenced by a wide range of physical factors including various climatic elements such as temperature, radiation, wind and humidity; but in many cases water availability is a major control. This is because a surplus supply of water as well as its deficit have deleterious effects on crop growth, development and production. Whilst excess moisture supply cause plant death due to development of unfavourable conditions such as waterlogging, high acidity, salinity, alkalinity and/or oxygen exclusion from the rootzone, a deficit causes plant death due to desiccation. In fact water availability affects almost every process occurring in plants; but it is pertinent to say that the links, however, are complex and that the relationship varies with plant characteristics, stage of development, as well as soil and climatic conditions (Chang, 1968).

The significance of water to plants cannot be overemphasized. However, the major ways in which water is important to plants can be listed as:

(a) It is a major constituent of plant protoplasm, sometimes making up as much as 95% of the total weight of plants.

Most organic substances in the protoplasm including carbohydrates, proteins and nucleic acids are hydrated in their natural state and removal of water affect their physical and chemical properties. Whenever the protoplasm is dehydrated, it becomes inactive and below a certain water content it is killed. One of the processes most affected by dehydration is photosynthesis (Jackson, 1977).

(b) Water takes part directly in quite a number of chemical reactions in the plant. Some of these reactions include water being a source of hydrogen atom for the reduction of CO_2 in photosynthesis and is a product of respiration. It is also important in hydrolytic processes such as in digestion.

(c) Water acts as a solvent in which many other substances (including mineral nutrients) dissolve and undergo chemical reactions.

(d) A considerable part of water in plants is found in vacuoles within the protoplasts and this is responsible for maintaining turgidity of cells and plants as a whole. If leaves lose their turgidity, the stomata guard cells close, thus preventing further uptake of carbon dioxide for photosynthesis.

(e) Water is a medium whereby dissolved substances move between cells and into the xylem and phloems through which they get transported from one part of the plant to another.

After highlighting the importance of water to plants, it becomes very evident that the most common probable cause of poor plant performance and sometimes death is the inadequate supply of water sufficiently enough to replace that loss by evapotranspiration and deep percolation. It is also evident that even the slightest water deficit can sometimes be fatal. However, plants have a number of ways of avoiding the build-up of water deficits (Levitts, 1972). Despite this, some growth stages have been found to be more sensitive to moisture stress than others (Aspinall et al., 1964; Campbell, 1968; Lehane and Staple, 1962). Usually, the most sensitive growth stage is referred to as the critical stage (Krishnan, 1972).

Wheat cultivation is not new in Nigeria. Evidence shows that the crop was grown in some parts of Northern Nigeria as early as 2,000 B.C. The present level of wheat production in Nigeria is estimated to be about 15,000 metric tons (Olugbemi, 1980). The area under cultivation at present is also estimated to be 200,000 hectares when the irrigation schemes around Lake Chad, Kano, Kaduna and Sokoto states are fully developed

in the next few years (CIMMYT Report, 1978; Olugbemi, 1980). Furthermore, at the farmers' present average production of 2 tons/ha, wheat production in Nigeria could reach an estimated value of about 414,000 metric tons in the near future (Olugbemi, 1980).

Meanwhile, it is pertinent to state that being a temperate crop, wheat thrives well only under low temperatures. Thus its distribution in Nigeria is presently restricted to latitudes 10° and 14°N, mainly in the Sudan and Sahel Savanna zones, where it is grown during the cool harmattan season. It is usually sown in Mid-November to early December and harvested in March/April. Minimum temperatures for the greater part of the growing period in Nigeria are between 12° to 20°C (Olugbemi, 1980).

Wheat production has been growing in Nigeria due to the onset of big irrigation schemes under the River Basin Development Projects. As such, wheat varieties are being screened and recommended for the various growing areas. Thus the cultivar Siete cerros was recommended for Kano State in 1975 (Olugbemi et al., 1979). Research on various aspects of wheat production in Nigeria has also been going on since 1959. Most of the work carried out so far has been by the Institute for Agricultural Research, Ahmadu Bello University, Zaria. The Institute has

identified some promising high yielding varieties under Nigerian conditions. These include Tousson; Sonora 63; (Lee x N10 - B) GB55) GB56 and Siete Cerros which under good management will produce at least 4,000Kg/ha of grain under Nigerian conditions. However poor management or failure to adhere to the recommended practices will adversely affect their performance. This explains why Nigerian farmers' average yield is only about 1,500 to 2,000 Kg/ha.

Even though research on wheat has been going on in Nigeria, it is unfortunate to say that its water management has been lagging behind. It is in this line that Redden (1979) reported that 'work on irrigation, drainage and farming systems has been lagging behind'. Moreover, little work has been done and reported on moisture stress effect on yield of wheat in Nigeria. However, the soil-plant-water relation studies under moisture stress conditions have never been carried out for various growth stages of wheat under the agroclimatic conditions of Nigeria.

The consistent rise of water table at Kadawa and its surroundings during the wheat growing season (Nwa, 1978) poses a threat of water logging conditions in the very near future if irrigation water is not judiciously applied. Population growth

which is increasing rapidly, as well as growth and development of industries would also necessitate a great need for judicious use of water to meet both industrial, domestic and crop production requirements. Consequently, water economy for crop production will, therefore, be inevitable in the very near future. Thus the present study was aimed at achieving the following objectives:

(1) To identify the most sensitive (critical) growth stage(s) of wheat to moisture stress.

(2) To examine the effects of two different levels of moisture status on internal plant water status, plant growth and yield of wheat.

(3) To assess the performance of wheat under 10-days irrigation interval and monitor fluctuations in water table during the growing season of the wheat crop.

(4) The results obtained will then form a basis on which farmers in the wheat growing areas (especially Kadawa and its environs) could be reliably advised as to what growth stage(s) and what level(s) of moisture stress should be avoided if losses in wheat yield have to be combated.

CHAPTER 2

LITERATURE REVIEW

Virtually no work on moisture stress effects on wheat has been published in Nigeria except those of Chari (1980) and Surma et al (1980). However, much work has been published on this subject in other parts of the world. Therefore it will be proper to review the literature of published work done on moisture stress effect on wheat in other parts of the world in order to fully understand the state of knowledge on the subject.

2 2.1 Moisture Stress

Moisture supply is one of the factors, if not the major factor, that affects plant growth and development. Moisture stress is the state of moisture when the supply is inadequate (Crafts, 1968). Crafts (1939) also stated that the term stress is somewhat ambiguous, but it might be defined as the state a plant enters when the water potential is sufficienctly low to inhibit normal plant processes. Ghosh et al (1975) found that wheat growth, especially the leaf area index (LAI) was greatly reduced when soil moisture tension was above 0.25 bars. Therefore it

could be deduced that for wheat, moisture stress conditions ensue when the soil moisture tension exceeds 0.25 bars. However, moisture stress of a plant is usually influenced indirectly by soil moisture status and directly by the plant water status. Thus moisture stress is a result of the development of plant water deficit and not necessarily soil water deficit. In fact, with adequate soil moisture supply, plant water deficit can still occur as a result of increased evaporative demand of the atmosphere.

Further, the plant water deficit that develop at any point in time is the result of a complex combination of soil, plant, and atmospheric factors, all of which interact to control the rates of water absorption and water loss (Kramer, 1959; 1963; Vaadia, et al., 1961). It has also been emphasized that the degree to which internal water deficits develop in the leaves of a plant depends on the evaporative demand, on the soil water potential at the root surface, ψ_{root} and on the gradients of water potential within the plant. In turn, these gradients depend on the degree of stomatal closure; and ψ_{root} depend on the volume of soil per unit length of root, the bulk value of soil water potential, ψ_{soil} and the hydraulic conductivity of the soil (Slatyer, 1967).

2.2 Development of Moisture Stress

As evapotranspiration from an initially wet soil (where soil water potential, Ψ soil is approximately zero) proceed from day to day, it progressively reduces soil water content and soil water potential. Since there must be a gradient of decreasing potential through the water pathway from soil to atmosphere to provide the driving force for water flow, there is usually a concomitant decline in plant water potential and plant water content. The consequence is that an internal water deficit develops and increases in magnitute. Thus Begg and Turner (1976) stated that plant water deficit develops as a consequence of water movement through the plant along a series of frictional resistances that result in gradients of water potential, with the largest drops in potential where the flow rates and resistances are largest. Therefore water deficit occurs as an inevitable consequence of the flow of water along a pathway in which frictional resistance and gravitational potential have to be overcome (Jarvis, 1975) and do not only occur when the loss of water from the leaves in transpiration exceeds the supply from the roots (Begg and Turner, 1976).

Since the plant can only extract water from the soil when the water potential in the plant is lower than that

in the soil, the water in the plant is seldom in equilibrium with the water in the soil. The differences in water potential between the plant and the soil depend on the rate of uptake of water from the soil and water conducting properties of the soil and the plant (Gardner and Nieman, 1964). Further, Slatyer (1967) asserted that the plant water potential, Ψ plant (especially the leaf potential) shows marked diurnal fluctuations and very little dependence on soil potential. In fact, Ψ soil merely sets the limit of recovery possible by the plant during the dark period, so that the maximum Ψ plant follows the decline in Ψ soil down to and beyond the wilting point.

Even with adequate soil water, moisture stress can still occur due to other stresses that influence and enhance its development. Such stresses include: Waterlogging stress; Wind stress; Salt stress; Heat stress; Population stress; Humidity stress and stress due to pests and disease attacks.

Waterlogging stress results in oxygen exclusion from the soil (Ganyushina and Lazarchik, 1971). This stress, when severe, results in killing of plant roots; increase fungal disease attacks and reduction in yield (Giha, 1976). If evaporative demand of the

environment remains the same while water absorption is much reduced or nil due to death of roots, moisture stress conditions ensue.

Wind stress increases the evaporative demand of the atmosphere and whenever absorption cannot cope up with this demand, moisture stress results. Hot dry winds (like the Sirocco winds), in particular, enhance stress development and senescence of plants. For example, hot dry winds may severely damage ears at and shortly after emergence, causing the death of the exposed floral parts of the ear. If these conditions occur between heading and ripening, they interfere with the maturation of the grains and result in shrunken grains and low yields.

Salt stress causes a physiological reduction in availability of water, which is further aggravated at low moisture potential. Here both moisture tension and osmotic potential work additively to create internal plant water deficit and so enhance moisture stress development.

Evaporation is an energy requiring process. The source of this energy is the sun and the form used is heat energy. However, excessive heat increases the rate of evaporation to a fatal level. Excessive heat

and/or cold both cause injury to plant roots. The increase in the rate of evaporation and/or injury to plant roots which reduces absorption, both enhance moisture stress development.

Population stress enhances moisture stress because plants usually compete for mineral nutrients, oxygen and moisture in the soil. The higher the population density, the more keen the competition. The consequence of this keen competition for moisture is moisture stress ensuing.

Relative humidity plays a great role in determining the evaporative demand of the atmosphere. Secondly, it could create conducive conditions for pests and diseases to thrive in. All these enhance moisture stress development.

Pest and disease attacks can damage roots and plant tissues; block or destroy conductive tissues and so accentuate moisture stress development.

2.3 Indicators of Moisture Stress

Moisture stress condition in plants is indicated by two basic parameters: the water content, θ or the energy status of the contained water usually expressed as the total water potential, Ψ (Slatyer and Taylor, 1961). These represent direct indicators of moisture stress in plants.

However, there are several indicators of moisture stress which can be grouped under indirect indicators of stress in plants. These indirect indicators were extensively reviewed by Hsiao (1973) and Begg and Turner (1976).

2.3.1 Measurement of Moisture Stress

The subject of measurement of crop water status has received considerable attention recently. Barrs (1968) provides a most comprehensive review of the methods for measuring the relative water content (R.W.C.); water potential, Ψ; Osmotic potential, π; pressure potential P; and Stomatal aperture. Reviews by Boyer (1969), Wiebe et al (1971), Sullivan (1971), Turner (1972), Slavik (1974), Ritchie & Hinckley (1975) and Begg and Turner (1976) all provide further details on measurement of crop water status. However, water potential, relative water content and tissue water content will be considered here.

2.3.1.1 Water Potential

Water potential is the total water potential when the gravitational potential is neglected. And, the total water potential is that amount of work that must be done per unit quantity of pure water to transport

reversibly and isothermally an infinitesimal quantity of water from a pool of pure water at a specific elevation and at atmospheric pressure to the soil or plant water at the point under consideration. There are several ways of measuring water potential. One of the accurate methods is that by thermocouple psychrometry (Yang and Jong, 1968) except in cases where large concentrations of solutes occur on the leaf surface or are released in the psychrometer chamber (Klepper and Barrs, 1968). However, strict temperature control and long equilibrium times restrict its use. To overcome these problems, certain equipments have been developed such as the temperature compensated thermocouple psychrometer (Hsieh and Lungate, 1970; Meeuwig, 1972; Hsieh et al., 1972; Calissendorff and Gardner, 1972) and dew point hygrometers (Neumann and Thurtell, 1972; Campbell et al., 1973; Campbell and Campbell, 1974; Neumann et al., 1974) to compensate the strict temperature control requirement. However, strict temperature control is still desirable in these devices. These consequently led to the development of insitu psychrometer or hygrometer for the measurement of water potential. But for field conditions, the most common equipment used is the pressure chamber (Begg and Turner, 1976; Ritchie and Hinckley, 1975) because it is

to a great extent insensitive to temperature (Tyree et al., 1974).

The technique is quite simple and the measurement of water potential can be made very rapidly (Ritchie and Hinckley, 1975; Fischer et al., 1977). However, there could be errors arising from rapid water loss, especially from excised leaves of actively transpiring plants (Turner and Long, 1980) or errors due to exclusion of plant parts from the pressure chamber during the determinations (Millar and Hansen, 1975). But with care and precautions, the values of water potential determined using the pressure chamber closely agree with those determined using the thermocouple psychrometer.

The units of water potential could be bars, joules/Kg or Pascals (1 bar = 100 J/Kg = 10^5 pa). Generally, the stressed plants have comparatively lower water potentials than non-stressed plants at any time of the day. This is why water potential has been used to indicate when stress ensues and affect various processes in the plant. For example, Crafts (1968) stated field and forage crops thrive well until - 16 bars potential is approached. However, Frank et al. (1973) reported that under controlled environment values of leaf water potential

of wheat required to halt stomatal conductance were - 13 bars at tillering; - 17 bars at heading; - 24 bars at flowering and - 31 bars at grain filling stages. Again, Johnson et al. (1974) reported that the water potential for initial (5%) inhibition of photosynthesis was - 10 bars; for 50% inhibition was - 15 bars and for 100% inhibition was - 30 bars. Meiri et al. (1975) reported that in field grown wheat, the water potential measured in a whole flag leaf was about 6 bars higher than that measured in the apical one third of the leaf. They further stated that water potential values in the transpiring shoots were 3 to 5 bars higher than in the leaves and that detopping the flower bud did not alter this pattern; indicating that the highest water potential in the shoot was in the stem. This invariably implies that plant water potential will always be higher than leaf water potential. Further, Millar and Denmead (1976) reported that the critical water potential for stomatal closure in wheat leaves varied from - 7 bars for leaves at the bottom of the stem, to - 14 bars for the next highest leaves, and ultimately to - 19 bars for the top leaves. It has also been found that plants that have undergone several cycles of stress or in which water deficit have developed slowly,

the leaf water potential for stomatal closure is lower than in plants quickly dehydrated or with no stress history (Brown, 1974; McCree, 1974). Also, Hsiao (1973) and Hsiao and Acevedo (1974), stated that various plant processes are affected at different levels of moisture stress. They showed that while processes like cell growth, wall synthesis and protein synthesis are affected at fairly higher water potential, other processes are affected as the water potential becomes more negative.

2.3.1.2 Relative Water Content:

Relative water content (RWC) is the water content (on a percentage basis) relative to the water content of the same tissue at full turgor (after floating on water to a 'constant' weight). At one time, RWC was less accurately termed, relative turgidity (Begg and Turner, 1976). RWC is also closely related to water potential of the same tissue, though the relationship is dependent on species and stages of growth (Connor and Tunstall, 1968; Gardner and Ehlig, 1965; Millar et al, 1968; and Sanchez Diaz and Kramer, 1971), on long-term alterations induced by environmental factors, and possibly even on the short-term water history of the plant (Jordan and Ritchie, 1971).

A major short coming is that RWC is a rather insensitive indicator of water status when moisture stress is not severe. In nearly saturated tissues, where a small change in water content could markedly affect pressure potential, a change of a few bars in water potential may correspond to only several percentage points in RWC. This is about the size of the random error in RWC measurement in many studies (Barrs, 1968). Perhaps for this reason, in some studies, RWC showed no significant change, although physiological processes were affected by the mild stress employed (Hsiao, 1970).

Other ways of expressing RWC are:

(a) Water Saturation Deficit (WSD) = $\frac{\text{(Fully Turgid wt. - Fresh wt.}}{\text{(Fully Turgid wt. - Dry wt.}}$

(b) Relative Saturation Deficit (RSD) = $\frac{\text{(Fully Turgid wt. - Fresh wt.}}{\text{(Fully Turgid wt.}}$

(c) Relative Turgidity (RT) = $\left(\frac{\text{Fresh wt. - Dry wt.}}{\text{Fully Turgid wt. - Dry wt.}}\right)$

RT and WSD are simply related as:

$$100 - RT = WSD.$$

2.3.1.3. Tissue Water Content

Tissue water content (percentage fresh weight) and fresh weight have also been used as indicators of water status. The unfortunate thing about this method is that water content

or fresh weight of tissue at full turgor is normally not given as a reference. Water content could, therefore, be very misleading because of its superficial resemblance to RWC.

However, small changes in the water content of vegetative tissue usually correspond to much larger changes in RWC (Barrs, 1968). For example, for a decrease in water content from 85% at full turgor to 80% under stress, the corresponding values of RWC are 100% and 71% respectively (Hsiao, 1973). Water content is usually most frequently used in studies of seeds and lower plants. And, except for one notable example by Wilson (1971), there is virtually nothing known about the relationship between water content and water potential. For this reason, it is not possible to have quantitative comparison of stress severity among different materials.

2.3.2 Indirect Methods of Characterizing Moisture Stress

Barrs (1968) refered to a number of indirect methods of characterizing stress in plants. Some of these are measurement of leaf temperature by infra - red thermometry; leaf thickness by β-gauging; or changes in stem diameter and fruit diameter; and stomatal aperture which could be used to estimate moisture stress conditions.

To elaborate on stomatal aperture, it is measured in the field as relative stomatal aperture, leaf permeability or diffusive conductance by employing infiltration techniques, portable mass flow or diffusion porometers respectively (Begg and Turner, 1976). These indirect methods could be calibrated against water potential or RWC and so provide a continuous and non-destructive estimation of stress conditions at the same time allowing other physiological measurements, like CO_2 assimilation to be carried out on the same leaf.

Visual symptoms such as wilting (leaf curling or folding) and colour changes of foliage can be used sufficiently accurate as measures of moisture stress in some instances, for example, in irrigation scheduling. But wilting is an unfortunate method of indicating stress because apart from depending on turgor pressure, it is a function of mechanical properties of cell wall and tissue. Thus it is well known that different species wilt at different water potentials or RWC. An extreme example is an oil palm which does not wilt visibly even when fatally desiccated (Hsiao, 1973). Moreover, as moisture stress develops, physiological processes are often affected long before wilting becomes apparent

(Redshaw and Meidner, 1972). Thus visual symptoms, especially wilting, should not be relied on as a sole indicator of moisture stress.

2.4 Effects of Moisture Stress

2.4.1 Morphological Effects

2.4.1.1 Cell division and elongation:- The growth and development of a plant depends on continuing cell division, on the progressive initiation of primordia and on the differentiation and enlargement of cells (Slatyer, 1973). Cell division is generally regarded as less sensitive to water deficits than cell enlargement (Vaadia et al, 1961; Clements, 1964; Gates, 1964; Salter and Goode, 1967; Slatyer, 1967; Hsiao, 1973). Evidence of this view is provided by the observation that plants exposed to water stress frequently have cell numbers of the same general order as the controls but cells of smaller sizes (Brouwer, 1963; Petinov, 1965), and by the phenomena of more rapid growth on recovery from stress compared to controls (Gates, 1955a, b). The effects of stress on cell division may be indirect because the cambial initials have to extend to a certain point before cell division occurs (Doley and Leyton, 1968). More recently, McCree

and Davis (1974) have suggested that cell division and cell enlargement are equally sensitive to water deficit in grain sorghum.

2.4.1.2 Leaf area, growth rate and number of tillers:- Leaf enlargement generally shows a marked decrease at values of leaf water potential below - 4 bars (Turner and Begg, 1978). One of the most important consequences of the sensitivity of cell enlargement to small water deficits is the marked reduction in leaf area, and the resulting reduction in crop growth rate, particularly when there is incomplete light interception. Water stress can also affect leaf area by reducing tillering and by hastening the death of leaves and tillers (Turner and Begg, 1978). Reduced tillering has also been observed in wheat (Turner, 1966). He also showed that water stress applied after maximum tiller development in wheat increased the death rate of tillers from 3 $day^{-1}m^{-2}$ in non-stressed to 11 $day^{-1}m^{-2}$ in stressed plants.

2.4.1.3 Root growth:- Although total plant growth is reduced during water stress, root growth is generally, but not always (Gerakis et al., 1975), favoured relative to shoot

growth as indicated by the frequently reported increase in the root: shoot ratio (Troughton, 1957; Pearson, 1966; Christie, 1975, Ng et al; 1975).

2.4.2 Physiological Effects

Since a number of reviews on physiological responses of plants to water deficits have been published recently (e.g. Crafts, 1968; Gates 1968; Hsiao, 1973 Slatyer, 1973; Boyer and McPherson, 1975; Begg and Turner, 1976; Turner and Begg, 1978), a general summary survey will be given here with special attention to wheat.

2.4.2.1. Stomatal behaviour:- The stomata occupy a key position in the pathway for gaseous exchange between plants and the atmosphere, and thereby regulate both photosynthesis and water loss. It is now generally recognized that the stomata do not respond to changes in leaf water potential or RWC until a critical threshold level of these parameters is reached, and then stomatal closure occurs over a narrow range of leaf water potential or RWC (e.g. Turner 1974a; Begg and Turner, 1976). Recently, the stomata of field grown wheat have been shown to close between - 7 to - 19 bars (Connor, 1975; Millar and Denmead, 1976). Turner (1974a), however, pointed out

that there is not unique value of leaf water potential for stomatal closure in any species or cultivar, but that the leaf water potential for stomatal closure varies with position of leaf in canopy (Turner, 1974b; Millar and Denmead, 1976), plant age (Frank et al, 1973) and growth conditions such as the number of cycles of stress (Brown, 1974; McCree, 1974) or whether the plants are grown in a controlled environment or field (Begg and Turner, 1976). However, Turner (1974a) also suggested that stomatal conductance may be better related to leaf pressure potential than leaf water potential since changes in stomatal aperture involve changes in the turgor relations of guard cells and or subsidiary cells (Meidner and Edwards, 1975). And so leaf pressure potential is considered a more reasonable stress indicator than leaf water potential for stomatal relations although the latter could be used in the absence of the former.

2.4.2.2 Photosynthesis:- Since stomatal regulate CO_2 exchange, water deficits that close stomata must also depress photosynthesis. In addition, water deficits may affect

the transfer and fixation of CO_2 internal to the stomata (Turner and Begg, 1978). Thus the initial reduction in photosynthesis due to increase plant moisture stress is generally considered to arise from changes in conductance of CO_2 through the stomata (Slatyer, 1973). Consequently, the change in net photosynthesis with leaf water potential follows that of stomatal conductance. In most species that have been studied, non stomatal effects on photosynthesis occur at stresses considerably below those that induce stomatal closure (Slatyer, 1973), but in some species non-stomatal effects on photosynthesis have been reported at similar levels of stress to those that induced stomatal closure (Boyer, 1971; Doley and Trivatt, 1974).

2.4.2.3 Respiration:- Dark respiration appears to be depressed whenever the water deficit is sufficient to close stomata and decrease photosynthesis, but the relative decrease in dark respiration is less than that of net photosynthesis (Turner and Begg, 1978). However, water deficits have also been reported to increase, decrease or have no effect on photorespiration (Begg and Turner, 1976).

2.4.2.4 Translocation and distribution of assimilates:- The translocation and distribution of assimilates can be influenced by water stress as it affects the rate of assimilation, the rate of utilization, the loading and unloading of sieve elements and/or the movement of assimilates in the phloem (Turner and Begg, 1978). However, the velocity of assimilate movement in wheat is unaffected by water potentials as low as - 30 bars (Wardlaw, 1967; 1969; 1971), but this water deficit did decrease the overall translocation of assimilates. Further, Wardlaw (1967) and Passioura (1976) both reported that in wheat under water stress, there is a greater movement of assimilates from the stems to the grains than when there was no stress. Again, in wheat where the sink for assimilates was less affected by water stress than the photosynthesis of the source leaf, the main factors limiting translocation were considered to be a reduced production of assimilates and reduction of loading into the vascular systems (Wardlaw, 1967; 1971).

2.4.3 Effects on hormonal balance and nitrogen metabolism

Changes in hormonal balance and nitrogen metabolism are quite important during moisture stress. Recent discoveries show that endogenous levels of abscisic acid

and proline increase several folds when plants are subjected to stress (e.g. Wright and Hiron, 1969; Barnnett and Naylor, 1966); and that abscisic acid closes stomata and reduces transpiration (e.g. Little and Eidt, 1968; Jones and Mansfield, 1970) while proline accumulation may be linked to drought resistance (Singh et al, 1972, 1973). More recent reviews on these topics include those by Naylor (1972) Livne and Vaadia (1972), Hsiao (1973), Milborrow, (1974) and Raschke (1975).

2.4.4 Effects of Moisture stress at different growth stages on yield of wheat.

Moisture stress, in general, reduces yields. The degree of yield reduction, however, depends on environmental conditions, soils, crop variety, and the growth stage at which the stress occurred. Thus Lehane and Staple (1962) found that the relationship between moisture and crop production varied with plant characteristics; stage of development; soil and climatic conditions.

Moisture supply is an essential factor controlling germination. There has to be a suitable supply of moisture for good germination to occur. Dasberg and Mendel (1971) observed a decrease in the rate of germination of wheat due to excessive moisture supply. On the other hand,

Milthorpe (1950) has defined and described the stage after which the germinating 'seeds' of wheat cannot tolerate moisture deficits. Before the first leaf emerges, the wheat seedlings are capable of passing through one or more cycles of dehydration, upto 98% loss in their moisture content, without any ill-effects.

Moisture stress at tillering has been found to cause losses in yield by several investigators (Aspinall et al., 1964; Day and Intalap, 1970; Bhardwaj et al., 1971; Vijar Kumar, 1979; Musick and Dusek, 1980) due to reduction in the number of spikes per plants as a result of increased tiller and stem senescence.

During jointing, moisture stress reduces crop yield due to reduction in plant size, photosynthetic area and seeds per spike (Day and Intalap, 1970; Falaki et al., 1979). However, certain authors (e.g. Nuthonson, 1955; Arnon, 1972; Chari, 1980) have reported that the flowering stage is the most critical to moisture utilization as this is the stage in wheat when the plant consumes alot of moisture. As such moisture stress at this stage, reduces grain yield greatly. Moreover, Falaki et al; (1979) stated that moisture stress at flowering stage influences number of tillers, sizes of ears on tillers and number of

effective ears. Wilson (1969) found that moisture stress before ear emergence has no effect on yield, number of ears per plant and number of grains per ear, and that the 1000 - grain weight was increased instead. Bunting and Drennan (1966) reported that moisture stress at the grain filling stage, including both the milk and hard dough stages, reduces yield due to reduction in size, duration and photosynthetic activity of the plant part that still remained green after ear emergence.

Concerning what growth stage was critical to moisture stress, Salter and Goode (1967) concluded from examination of large number of studies of cereal crops that the plant seems especially sensitive to moisture conditions during the shooting and earing stages when the development of the reproductive organs is taking place. They further stated that a shortage of moisture then, has the greatest effect upon yield and in many experiments this seemed irreversible; and that optimun moisture conditions later do not overcome the loss already incurred. Thus, sufficiently enough irrigation and/or rainfall at these stages have maximum beneficial effects.

Other workers, however, have arrived at slightly different conclusions. Day and Intalap (1970) examined three growth stages of wheat in Arizona and found that the jointing stage was critical. Water stress at that time resulted in fewer days from planting to flowering and reduced yield. They concluded, however, that moisture at any growth stage decreased grain yield, but that the jointing stage was critical. On the other hand, Hearn and Wood (1964), in Malawi, found a consistent, significant negative response to high irrigation rates and that the plants appeared to remain healthier when considerable moisture stress was allowed to develop. For wheat in the Sudan, ElNadi (1969) found that the flowering phase and stage of grain filling and maturation were more sensitive to drought than the vegetative period. ElNadi also found that yields were not reduced when the wheat crop suffered from cycles of water stress induced during the vegetative period if the crop received favourable water regimes afterwards. Lehance and Staple (1962) found that the critical moisture - sensitive stage were heading (earing) and grain filling.

The considerable importance of water influencing yields has been demonstrated in India by Gangopadhyaya and Sarker (1965). They analysed the impact of rainfall

occurring at different stages of growth of wheat and found that 75% of total variation in yield could be accounted for. In Nigeria, Chari (1980) found that the flowering period is more critical; whereas Surma et al (1980) reported that the jointing stage of wheat is more critical to moisture stress.

The different conclusions reached indicate something of the complexity of the subject. Responses of different varieties of wheat would seem to differ considerably. Thus Derera et al. (1969) examined the drought tolerance of fifteen varieties and found that the main factor seemed to be differences in the earliness of plant maturity. However, other factors such as root development and water use efficiency also appeared to be significant (Jackson, (1977)).

2.4.5 Recovery from Moisture Stress and consequent compensatory growth.

Alleviation of water stress results in rapid rise in leaf water potential and recovery of turgor, but there is frequently a delay in the opening of stomata and the recovery of photosynthesis (Schneider and Childers, 1941; Stalfelt, 1955; Iljin, 1957; Glover, 1959; Sanchez-Diaz

and Kramer, 1971; Kriedemann and Loveys, 1974; Loveys and Kriedemann, 1973). Although a small number of guard cells remained permanently closed (Iljin, 1957; Allaway and Mansfield, 1970) and the intercellular CO_2 concentration had a small carry-over effect (Fishcher, 1970; Allaway and Mansfiled, 1970), the major after effect of stress clearly resided in the guard cells and was subsequently shown to be due to the persistence of abscisic acid which has a direct effect on guard cells (Allaway and Mansfield, 1970; Jones and Mansfield, 1970; Kriedemann and Loveys, 1974; 1975). Other inhibitors may also have a role in after affects of stress. However, Nulsen and Thurtell (1978) showed that the main resistance to recovery of water potential after stress resided in the roots. Photosynthesis does not recover from stress as quickly as stomatal conductance and abscisic acid levels in the leaf (Begg and Turner, 1976). Kriedemann and Loveys (1975) and Kriedemann et al. (1975) provided evidence that phaesic acid, a derivative of abscisic acid, may inhibit photosynthesis at least under some conditions.

A more rapid rate of growth and development than in unstressed controls is frequently observed in plants recovering from stress (Gates, 1955a, 1968). Leaf enlargement has also been found to be higher for the stressed than for control plants on recovery (Boyer, 1970a, Hsiao et al., 1970; Acevedo et al., 1971). Full recovery

is possible if the stress is brief (Acevedo et al., 1971), but with long or severe stress full recovery did not occur (Boyer, 1970; Acevdo et al., 1971). Also, photosynthetic rate of leaves subjected to stress has been found to be greater on recovery than for leaves of similar chronological age that had not undergone stress (Ludlow and Ng, 1974).

The changes in growth and development induced by stress have been described as 'a senescent decline in growth during wilting and the development of a physiologically younger condition upon rewatering' (Gates, 1964). Recently, Ludlow (1975) has suggested that water stress merely suspends the aging of physiologically young leaves and Ng et al (1975) concluded that earlier studies showed the same results. However, it is difficult to visualize that all the processes contributing to aging cease and recommence at a single critical leaf water potential, since physiological and biochemical processes are affected at different degrees of stress (Hsiao, 1973).

In the light of yield compensation, Nicholls and May (1963) showed that in barley, the rate of primordia production of the apex was reduced by a soil water deficit, but alleviation of stress caused an accelerated rate of

primordium formation so that the final number of primordia and the apex length were the same as the controls. However, in determinate annuals, if ear has not emerged, florets have aborted, or fertilization has been incomplete, compensation by producing ears, florets or fertilized flower is out of the question. But, depending on the stage and degree of loss, compensation can occur such that yield need not be reduced either by increasing weight of grain panicle through increase in number of grains per panicle (Blum, 1973) or larger grains (Bagga et al., 1973); or by having larger and heavier grains (Turner, 1966). However, it is evident that a genotype has a maximum grain size (Fischer, 1973; Gallagher et al., 1975), so that the potential for compensation by increasing grain size or weight is limited. Further, until recent, the contribution of assimilates other than current photosynthates was considered to be a small component of yield (Thorne, 1966). However, Yoshida (1972) cited several studies with limited nitrogen fertilization of rice in which upto 40% of final grain yield was translocated from the stem, and Gallagher et al., (1975) showed that upto 70% of the final yield in barley was translocated from the stem under extreme conditions. Wardlaw (1967) also showed that under

water stress, wheat translocated assimilates from the stem and lower leaves to the grain to compensate for loss of flag leaf photosynthesis. The importance of this was highlighted by Passioura (1976). He showed that about two-thirds of the final grain weight came from redistribution of assimilates after anthesis and only one-third from current assimilation in the period after anthesis in severely stressed wheat plants grown on a limited amount of stored water.

2.4.6 Moisture-Nutrient interaction

A reduction in the uptake of nitrogen and phosphorus induced by a water deficit has been well documented (Gates, 1957; Storrier, 1965; Turner, 1966; Greenway et al., 1969; Greenway and Klepper, 1969). The uptake of several other elements has also been shown to be reduced by water stress (Greenway and Klepper, 1969; Gates, 1974). Greenway et al. (1969) showed that the uptake of phosphorus was reduced to - 2 bars and decreased linearly as the potential of the root medium was reduced further, until - 10 bars when phosphorus uptake was negligible. Sprent (1976) has also reviewed fully the effects of water stress on nitrogen fixation.

These results clearly suggest that the reduced growth observed as a result of moderate water deficit may, in part, arise from a disturbance in mineral nutrition as well as any direct effect of water deficits (Turner and Begg, 1978). The implications of this for the field are obvious. Nutrient levels are usually highest in the surface soil, which is the first to dry out. Although the plants may have roots penetrating the deeper and wetter part of the soil profile, the relative lack of nutrients in the sub-soil and the availability of nutrients in the dry surface soil may limit growth and yield more than the soil water deficit perse. This is supported by work done by Garwood and Williams (1967) and Simpson and Lipsett (1973).

Soil nutrient status can also markedly influence water use efficiency of crops, and hence the time of onset of stress or the strategy for irrigation where water supply is not limited. Further, under limited supply of water, heavy nitrogen fertilization or growth of wheat after a legume have been shown to produce vigorous vegetative growth that depletes soil water, and can lead to a lower yield than with low fertilizer application (Barley and Naidu, 1964; Fischer and Kohn, 1966 a,b,c; Bond et al (1971). Fischer (1970) also showed that

application of phosphorus to Stylosanthes humilis swards increased growth and water use in the vegetative phase and reduced the ability of the sward to withstand extended periods of drought due to earlier soil water depletion.

2.4.7 Water Use Efficiency

Water use efficiency (WUE) in terms of the dry matter per unit of water used in evapotranspiration is very important when the supply of water is limited. WUE and drought resistance are often taken loosely as synonymous, although they are frequently unrelated (Hsiao and Acevedo, 1974; Reitz, 1974). WUE refers to a parameter of yield, and a major objective of research in this area is to attain high WUE while maintaining high productivity (Turner and Begg, 1978). However, in drought resistance the emphasis is frequently on survival during a period of low water supply. In many cases, the ability to survive water stress is negatively correlated with productivity (Jarvis and Jarvis, 1963; Begg and Jarvis, 1968; Reitz, 1974).

There is no unique value for WUE of a species as it is also a function of the environment in which the species is grown. One of the main ways that environment influences

WUE is by influencing the boundary layer and stomatal resistance to gas exchange, and the internal resistances of CO_2 assimilation (Turner and Begg, 1978). Thus water stress increases WUE, but only at the expense of a reduction in the rate of photosynthesis.

WUE can be improved by either increasing dry matter production or decreasing water loss or both (Turner and Begg, 1978). Other methods of improving WUE include: the use of antitranspirants, which either close stomata, form a film over the leaf or increase plant reflectivity; the use of windbreaks; and CO_2 fertilization (Begg and Turner, 1976). These have little practical significance in crop production on a large scale. However, cultural practices such as the control of weeds, disease and insects, which have been reviewed recently by Begg and Turner (1976) also increase yield and WUE.

2.5 Adaptation to Moisture Stress

The ability of a crop variety or species to grow satisfactorily in areas subjected to periodic water deficits has been termed its drought resistance (May and Milthorpe, 1962; Levitt, 1972).

In order to withstand and adapt to water deficits, plants have developed both morphological and physiological

mechanisms to enable them to do so. Since the rate of evapotranspiration is determined by leaf area up to at least a leaf area index of three (Ritchie, 1974), the sensitivity of leaf expansion to water deficit is a mechanism of limiting the evaporative surface and delaying the development of further stress. Similarly, leaf shedding or accelerated leaf death is also an adaptive mechanism for reducing water use; and Turner (1966) provided indirect evidence that this alleviated severe deficits at a later stage of development. Whilst these mechanisms are important for survival of annual grasses, mechanisms of greater importance to crops and other plants are the positive movement of leaves resulting in their orientation parallel to the incident radiation (Parahelionasty) and the passive flagging or rolling of leaves when wilted, which reduces the effective leaf area and hence the energy load upon the plant (Begg and Tursell, 1974; Begg and Tursell, 1974; Begg and Turner, 1976). Other mechanisms that reduce the radiation load are the increased leaf hairiness and wax blooms that develop under stress (Chatterton, et al, 1975; Johnson, 1975). Further, the development of the root over the shoot under water stress is another adaptive mechanism

that enables the crop to explore a greater soil volume for water and it is clearly a useful morphological adaptation provided water is available at depths.

An important physiological mechanism of plants adapting to stress is the lowering of osmotic potential (Turner and Begg, 1978). Any loss of water from the cell must concentrate the solution within the cell and this leads to a decrease in osmotic potential. Apart from the decrease in osmotic potential due to solute concentration as water potential decrease, stress may also induce a net solute increase i.e. osmotic adjustment or osmoregulation (Hsiao, 1973; Ike and Thurtell, 1981). Thus, Turner and Begg (1978) made an inference that if the resulting decrease in leaf osmotic potential matches the decrease in leaf water potential, then turgor pressure will be maintained so that physiological processes that are turgor-dependent, such as leaf elongation, stomatal closure (Turner, 1974a; Meidner and Edwards, 1975; Begg and Turner, 1976) and hence photosynthesis, will be maintained as leaf water potential decreases. In practice, the decrease in osmotic potential is unlikely to occur as rapidly as the decrease in water potential so that ultimately the turgor potential

decreases to zero. This is because $\psi = \pi + P + \tau$, where

ψ = total water potential; π = osmotic potential;

P = pressure potential and τ = matric potential.

Consequently, Begg and Turner (1976) have made available some evidence of osmotic adaptation for a number of field crops.

Osmotic adjustment provides some explanation for the decrease in the threshold water potential for stomatal closure after a series of cycles of stress (Brown 1974; McCree, 1974) and could also contribute to the differences between field and controlled environment studies. Osmotic adaptation of roots (Greacen and Oh, 1972) may also be important in allowing preferential growth of roots under stress (Hsiao and Acevedo, 1974). The solutes accumulating during osmotic adjustment are largely unknown; but Turner and Begg (1974) reported that osmoregulators proposed include sugar alcohols (Lewis and Smith, 1967), organic acids (Osmond, 1963; Dhindsa et al., 1975) and soluble carbohydrates. Proline is responsible for osmotic adjustment in some microorganisms (Tempest et al., 1970) and halophytes, but may be insufficient to account for significant change in osmotic potential in grasses (Chu et al., 1976). Thus Turner and Begg (1978) have suggested that it appears that the rise in soluble carbohydrates (Iljin, 1957; Wilson and Ng, 1975) may be the primary source of net solute increase in pasture species.

CHAPTER 3

MATERIALS AND METHODS

The study was carried out under irrigation during the cool dry harmattan season of 1980-81, at the irrigation Research Station of the Institute for Agricultural Research, Ahmadu Bello University at Kadawa. The station (11°39'N, 08°02'E, 500 m above sea level) is located in the Sudan ecological zone. The meteorological data for the 1980-81 dry cropping season as well as the previous cropping history of the experimental plot are given in table 1.

3.1 SOILS

Soils of Kadawa have been classified as Eutric Cambisol (FAO/UNESCO) and Typic Ustropept (Soil Taxonomy) by Ojanuga et al. (1979). The soil parent materials are said to be aeolian sandy drift over ironpan. The soils of the area have been reported to be moderately deep, sandy clays with loamy sand tops. They are also moderately to imperfectly drained to a depth of about 89 cm because of the perched water table resting on the underlain ironpan at depths varying between 91 and 152 cm.

Table 1: Meteorological data for 1980-81 dry cropping season and previous cropping history of Kadawa.

(a) Meteorological data for Kadawa, 1980-81 dry season

MONTH	TEMPERATURE °C				Windrun	Rainfall
	Dry bulb		Wet bulb			
	AM(9)	PM(4)	AM(9)	PM(4)	(Km)	(Cm)
NOVEMBER	27.7	33.0	17.9	20.0	105.3	0.00
DECEMBER	22.2	28.2	14.5	20.2	110.9	0.00
JANUARY	20.5	27.0	11.6	17.2	412.0	0.00
FEBRUARY	21.8	30.6	13.6	18.6	538.6	0.00
MARCH	27.3	34.7	16.9	20.5	975.2	0.00

Source: Progress Report on Irrigation Research Programme 1980-81, P.5. IAR., A.B.U., Zaria.

(b) Previous Cropping History of Kadawa Field Plot, F3.3.

SEASON	CROPS GROWN		
	1978-79	1979-80	1980-81
WET	Maize	Maize	Fallow
DRY	Wheat	Wheat	Wheat

The ground water table in the experimental field plot fluctuated between 80 to 100 cm during the 1980-81 dry cropping season (figure 1).

3.1.1 Soil Physical Properties:

The data on soil physical properties are presented in table 2 and the moisture characteristic (desorption) curves for the different soil layers up to 60 cm are presented in figure 2.

According to the U.S.D.A. classification, the textural class was loamy sand and sandy loam at 0 to 20 cm and 20 to 60 cm depths respectively. The particle size distribution varied with depth. The clay content increased with depth from the surface, whereas the silt, fine and coarse sand contents decreased. This was probably due to the influence of parent materials and the various processes of soil formation involved.

Soil moisture retention capacity was found to increase from the surface to greater depths as a consequence of textural influence. Thus, for instance, the water saturation percentage (i.e. the moisture content at zero suction) values were 24.7, 26.5 and 30.1 for 0 to 20 cm, 20 to 40 cm and 40 to 60 cm depths, respectively.

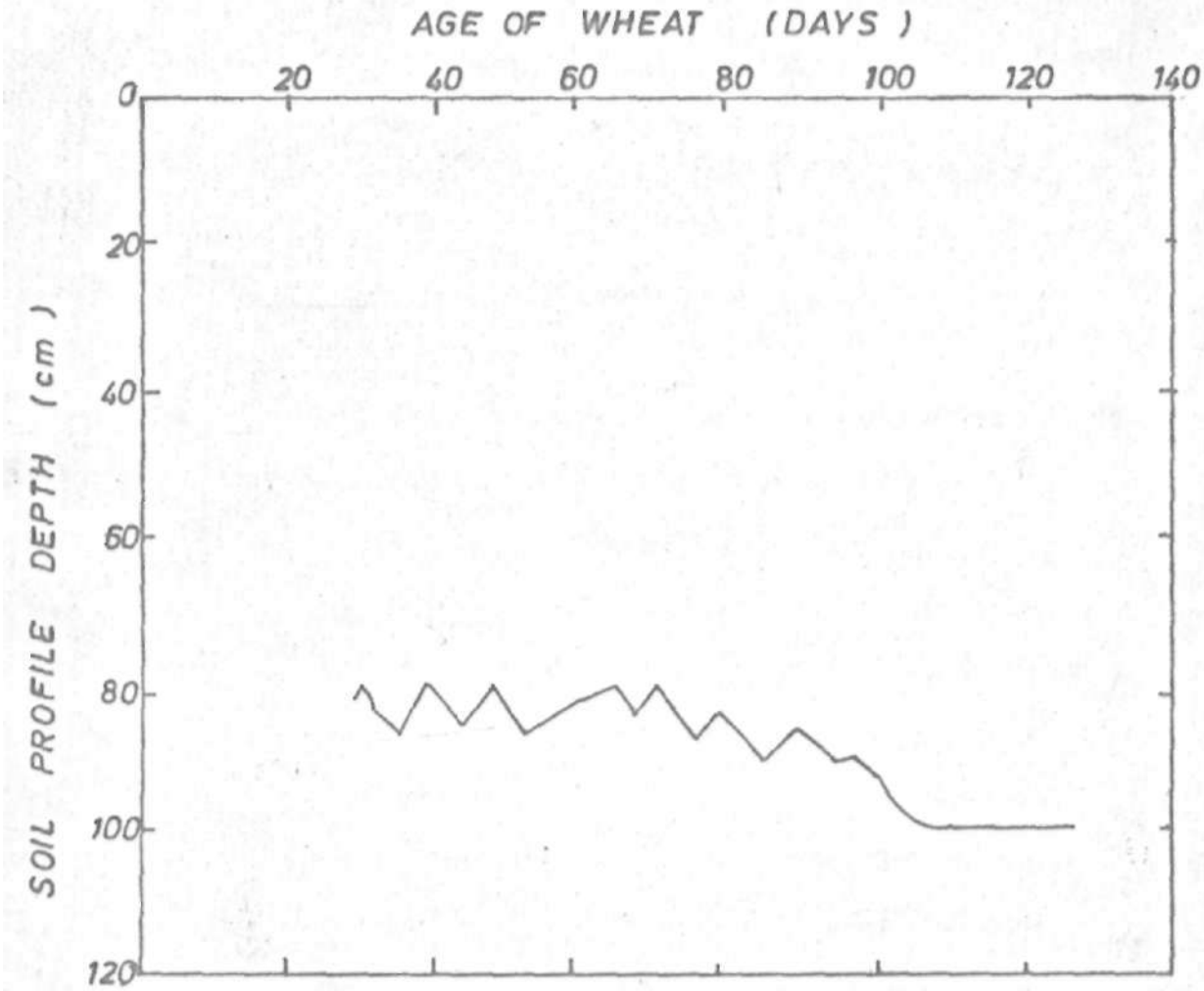


FIG. 1 : Water table variation during the growing season of wheat, 1980-81

Table: 2 Some Selected Soil Physical Properties of the Experimental Site

Soil Depth (Cm)	Soil Separates (%)				Soil Moisture Content (% by weight) at different Suctions (Bars).						Bulk Density ($g\ cm^{-3}$)
	Clay	Silt	Fine Sand	Coarse Sand	0.00	0.10	0.33	1.00	5.00	15.00	
0-20	5.00	15.00	75.60	4.40	24.68	21.52	13.30	12.49	11.76	11.16	1.52
20-40	9.00	14.00	73.20	3.80	26.45	23.97	17.57	15.77	14.66	13.79	1.45
40-60	14.00	12.00	72.21	1.79	30.06	25.59	18.72	17.07	15.46	14.60	1.43

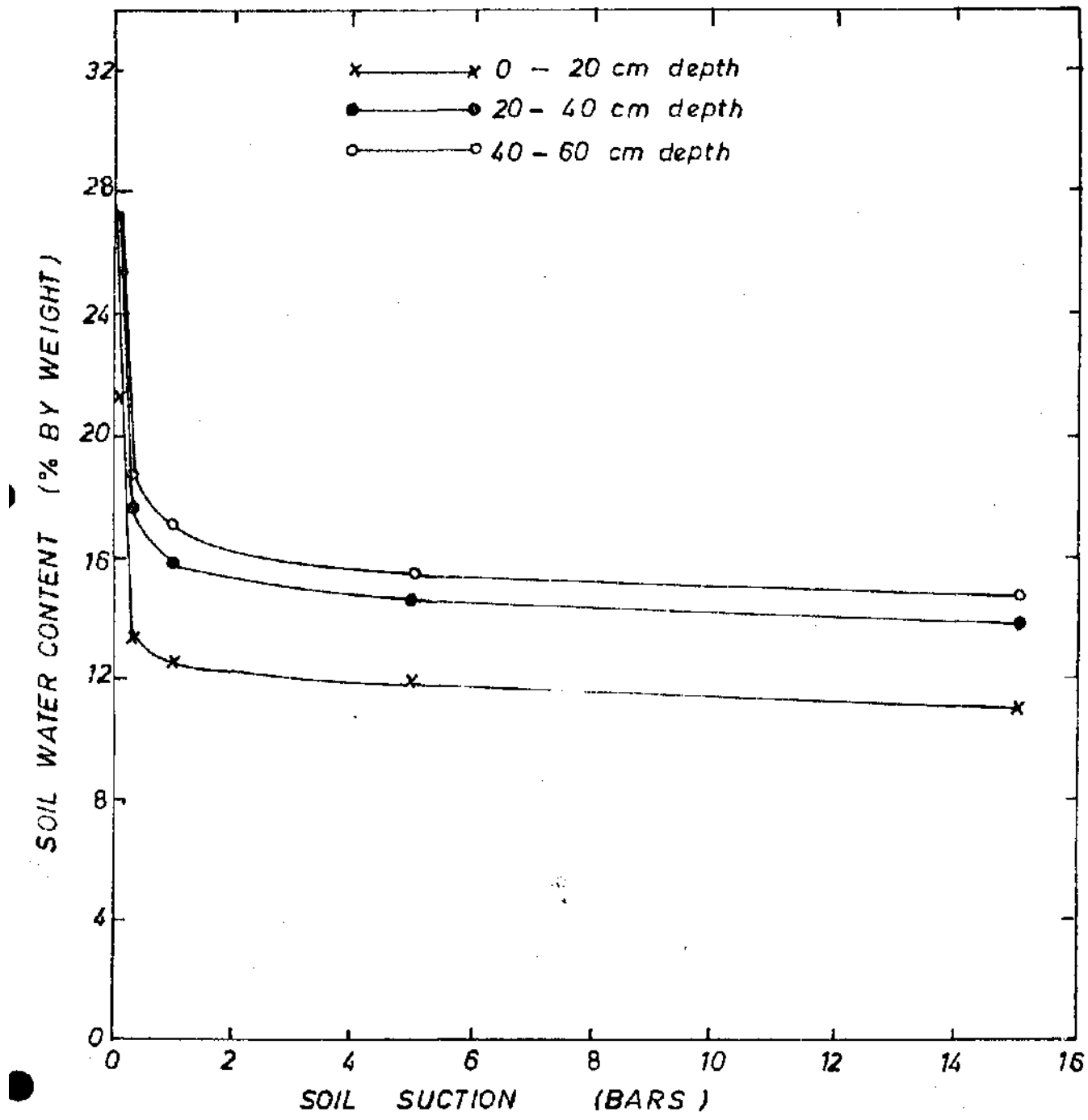


FIG. 2 ; Soil moisture characteristic curves for three different depth ranges

Further, the moisture characteristic curves for these three depths showed that at about 0.5 bars suction, most of the availa'le moisture had been removed while the remaining one had become difficultly available.

Bulk density was found to decrease with soil depth. The surface 0 to 20 cm soil layer had the highest bulk density (1.52 gcm^{-3}). However, the difference between the 20 to 40 cm and 40 to 60 cm depth ranges was not much, with bulk density values of 1.45 gcm^{-3} and 1.43 gcm^{-3}, respectively. While the higher bulk density at the surface layer could be due to mechanical soil compaction caused by tractors and other implements used during land preparation, the lack of difference in the deeper layers is due to the textural difference mentioned earlier.

3.1.2 Soil Chemical Properties

Data on pH, exchangeable cations, effective cation exchange capacity, organic carbon, total nitrogen (N), available phosphorus (P) and available Potassium (K) for the different soil layers upto 60 cm are presented in table 3.

able: 3 Some Selected Soil Chemical Properties of the Experimental Site.

Soil Depth (cm)	pH ($0.01MCaCl_2$)	Exchangeable Cations (meq/100g)					Effective Cation Exchange Capacity (meq/100g)	Organic Carbon (%)	Total N (%)	Available P (Bray - 1) (ppm)	Available K (ppm)
		Ca^{2+}	Mg^{2+}	K^{+}	Na^{+}	$(H^{+} + Al^{3+})$ Exchangeable acidity					
0–20	5.55	4.12	0.99	0.44	0.02	0.02	5.59	0.38	0.038	12.00	174.00
20–40	6.02	4.45	1.23	0.49	0.02	0.00	6.19	0.29	0.021	7.00	194.00
40–60	5.80	4.97	1.26	0.39	0.03	0.02	6.67	0.20	0.013	2.22	155.00

The pH of the soil was highest in the 20 to 40 cm depth (pH = 6.02) due to lack of hydrogen (H^+) and aluminium (Al^{3+}) ions in that layer. But pH generally decreased with soil depth.

The amounts and distribution of the following cations: Ca^{2+}, Mg^{2+}, K^+ and Na^+ were generally found to be maximum in the subsoils, a pattern which seemed to be related to clay content of the soil. However, exchangeable acidity ($H^+ + Al^{3+}$) was the same (0.02 meq/100g) at 0 to 20 cm and 40 to 60 cm depths but lacking (zero) at 20 to 40 cm depth layer. But, the effective cation exchange capacity, the total sum of all exchangeable cations including exchangeable acidity, was found to increase with depth due to the influence of clay content.

The organic carbon was highest in the surface soil and decreased with soil depth. This is because of the crop residues that increased surface organic matter. The total nitrogen was also found to have a similar pattern with organic carbon, because most of the nitrogen in the soil is usually associated with organic matter. Moreover, fertilizers are usually applied onto the soil surface. Thus available P also decreased with soil depth as P is not very mobile. However, available K increased from

174 at 0 to 20 cm depth to 194 ppm at 20 to 40 cm depth and decreased quite much to 155 ppm at 40 to 60 cm depth. This could be due to the leaching of added K as fertilizer from the surface layer. The leached K then got trapped in the 20 to 40 cm depth layer which had a relatively high clay content.

3.2 Treatments:- Two levels of moisture stress were imposed by omission of one or two irrigations at four selected physiological growth stages of wheat viz: Tillering, Jointing, Flowering and grain filling. Basically, there were three irrigation treatments.

(i) Irrigating at all growth stages (control treatment) at 10-days interval.

(ii) Irrigating at all growth stages minus one irrigation at each of the selected growth stages.

(iii) Irrigating at all growth stages minus two irrigations at each of the selected growth stages.

Details of the treatments used in the study are given in table 4.

3.3 Experimental Design:- In the study, the 9 treatments were replicated four times in a randomized block design. The layout of the experimental plots is given in figure 3. Check basin irrigation system was used.

Table 4: Treatments used in the study

TREATMENT DESIGNATION	NATURE OF STRESS	IRRIGATION SCHEDULING (DAYS AFTER SOWING)											DESCRIPTION OF TREATMENT
		1	6	16	25	36	46	56	66	76	86	96	
T_1	No stress	x	x	x	x	x	x	x	x	x	x	x	Control, no irrigation missed until irriga- was cut off after the 96th day.
T_2	minus one irrigation	x	x	-	x	x	x	x	x	x	x	x	One irrigation missed during Tillering (16 - 35 days*)
T_3	minus one irrigation	x	x	x	x	-	x	x	x	x	x	x	One irrigation missed during Jointing (36 - 58 days*)
T_4	minus one irrigation	x	x	x	x	x	x	-	x	x	x	x	One irrigation missed during flowering (59 - 74 days*)
T_5	minus one irrigation	x	x	x	x	x	x	x	x	-	x	x	One irrigation missed during grain filling (75 - 105 days*)
T_6	minus two irrigations	x	x	-	-	x	x	x	x	x	x	x	Two irrigations missed during Tillering
T_7	minus two irrigations	x	x	x	x	-	-	x	x	x	x	x	Two irrigations missed during Jointing
T_8	minus two irrigations	x	x	x	x	x	x	-	-	x	x	x	Two irrigations missed during flowering
T_9	minus two irrigations	x	x	x	x	x	x	x	x	-	-	x	Two irrigations missed during grain filling

N.B. x is irrigate; - is miss irrigation; * is days after sowing, Source:- Kumar and Yayock, 1980.

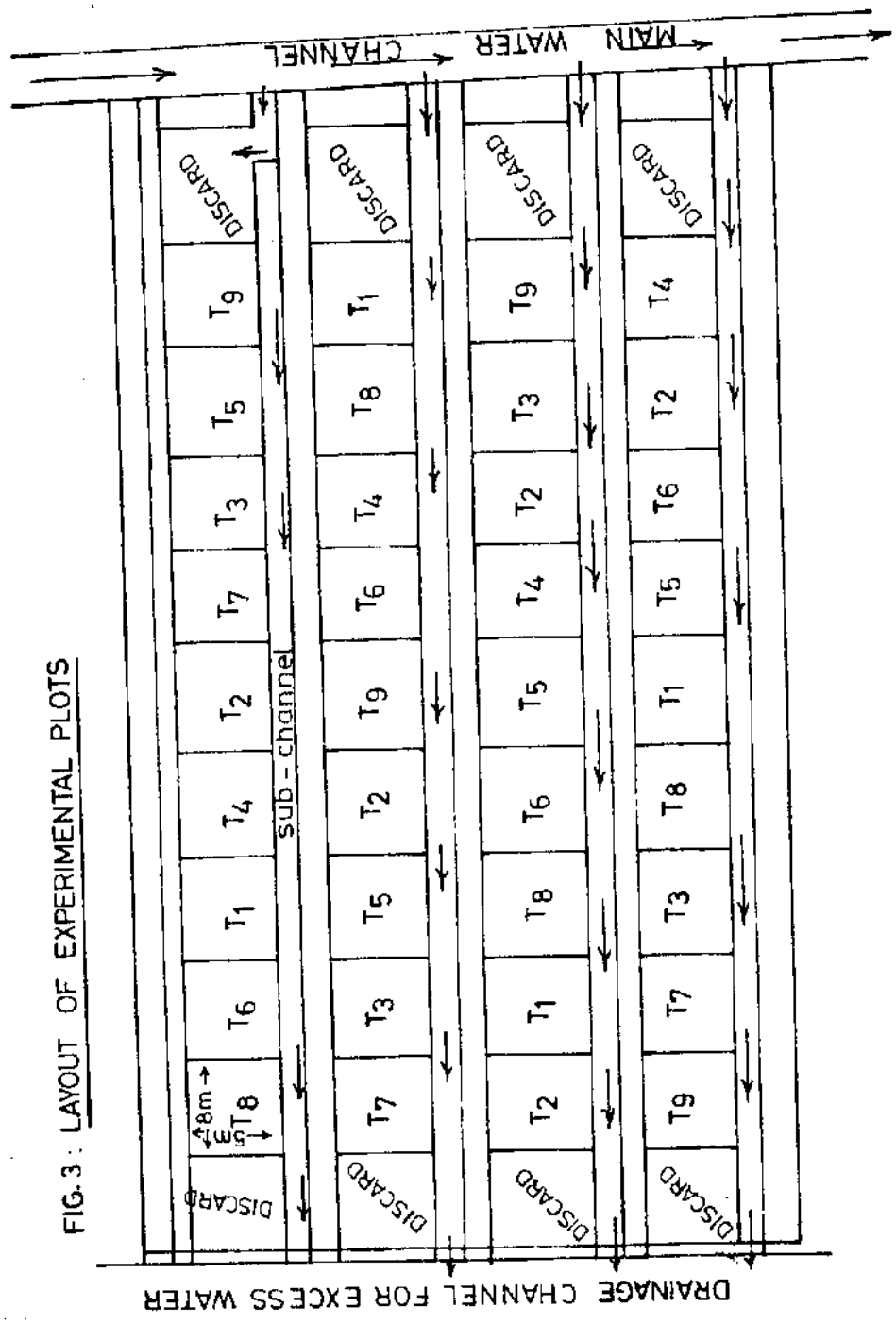


FIG. 3 : LAYOUT OF EXPERIMENTAL PLOTS

3.4 Cultural Operations:-

3.4.1 Land preparation and plot size:- The experimental area was disc harrowed once, followed by manual hand levelling. Thirty-six plots, each 8 m x 5m were then marked out. These rectangular plots were then prepared for planting after a basal application of compound fertilizer.

3.4.2 Fertilizer application:- Compound fertilizer (15:15:15) was broadcasted onto the plots at the rate of 60Kg each of N; P_2O_5 and K_2O per hectare. This was worked into the seedbeds before sowing was done. A second dose of nitrogen at the rate of 60 Kg N/ha as urea was topdressed after 6 weeks of planting .

3.4.3 Planting:- Wheat, Cultivar Siete cerros was sown on 18th November, 1980 by drilling 100 Kg seeds/ha in rows 25 cm apart. The plots were immediately irrigated on that same day.

3.4.4 Weeding:- The crop was weeded three times before harvest. The first weeding was about three weeks after sowing. The second (just before the second dose of nitrogen was applied) and the third weedings were carried out about six and eleven weeks after sowing, respectively. All weeding operations were done manually and completed within two days.

3.4.5 Irrigation:- Irrigation was by gravitational method. Water was conveyed from the main channel into sub-channels that led into plots using plastic pipe siphons. Water was let in to a plot by blocking the sub-channel and opening a gate into the check basin plot (figure 3). Five centimeters of water was applied during each irrigation. Two general irrigations were given on the first and sixth days after sowing to ensure good germination. Differential treatment started on the sixteenth day after sowing. Thereafter, a regular 10 days irrigation interval was followed as in the control treatment, missing irrigation(s) only at the appropriate time(s) to impose the desired moisture stress in the treatments as indicated in table 4. The last irrigation was on the 96th day after sowing.

3.4.6 Harvesting:- The wheat crop was harvested at deadripe stage, on 19th March, 1981 about 126 days after sowing. Harvest for yield assessment was done taking samples from net plots measuring 3.0 m x 1.0 m; while the rest of the crop was harvested in bulk. Harvesting, threshing, winnowing and cleaning of seeds were all done manually.

3.5. Soil and Plant Studies

3.5.1 Soil Studies

3.5.1.1 Soil Moisture Profile:- Soil moisture retentions were recorded at 10-days interval by reading the tensiometers installed at 15, 30, 45, 60 and 75 cm soil depths. Five plots, one each for treatments T_1, T_6, T_7, T_8, and T_9 were selected randonly within the experimental plots. Tensiometers were then instz led in these selected plots about two weeks after sowing. The tensiometers' readings were recorded until the 96th day.

Bulk density and soil moisture retention at various suctions were determined after the crop had been harvested. The ground water table was monitored continuously during the crop growth period. Four holes were dug up to 100cm deep within the experimental plot. Ground water table measurements were then taken using a bell indicator. This was done at weekly interval.

3.5.2 Plant Studies

3.5.2.1 Plant water potential:- Diurnal fluctuation in plant water potential for stressed and non-stressed treatments were determined at two-hours interval from 6.00 a.m. to 6.00 p.m. during jointing and flowering growth stages, using the pressure bomb (chamber) apparatus. During each determination, four plants were used for every treatment considered. Details of the pressure chamber method used in this study is described in Scholander et al. (1965) and Fischer et al (1977).

The plant water potential determinations were usually done a day before the next irrigation, when the stress was probably at its maximum.

3.5.2.2 Plant canopy temperature:- Diurnal fluctuation in plant canopy temperature was determined concurrently with plant water potential for stressed and non-stressed treatments using thermometers. The thermometers were hung just below the canopy of the crop with the aid of wooden planks.

3.5.2.3 Plant height:- This was measured at weekly interval till full or final height was attained at about the grain filling stage. Plant height was measured from the soil surface to shoot apex or tip of ear after heading. A meter rule was used in the measurements.

3.5.2.4 Dry Matter Harvested:- This was determined at weekly interval during the growth period of the crop. During each determination, 25cm row of crop was sampled from about mid-way in each plot. The samples were dried in the oven at 85°C for 24 hours and later at 105°C for 2 hours and weighed. The dry matter harvested per hectare was then calculated for each treatment from the dry matter harvested per 25cm row of crop.

3.5.2.5 Leaf area retention (LAR):- This was estimated by sampling 25cm row of wheat crop and measuring length and breadth (mid-point) of each leaf. Leaf area (LA) was calculated by multiplying the length and breadth of each leaf and then summing the leaf areas of all the leaves from the 25 cm row of wheat crop. The leaf area per hectare was calculated from leaf area per 25 cm row; and then LAR estimated as:

$$LAR = \frac{LA\ (Cm^2)}{\text{Land area } (Cm^2)}$$

Only leaves or leaf portions still green were considered. The LAR was estimated at weekly interval during the crop growth period.

3.5.2.6 Leaf area duration (LAD):- This is a measure of leaf area per plant. It gives an estimate of the area of photosynthetic green leaf portion still remaining per plant. In the present study, it was estimated as leaf area per unit area divided by the number of tillers in that unit area.

$$LAD = \frac{LA}{\text{Number of tillers (Plants).}} \ (Cm^2)$$

This was also estimated at weekly interval during the crop growth period.

3.5.2.7 Number of tillers:- This was estimated by counting the number of tillers per 25 cm row of wheat crop, from which the number of tillers per hectare was calculated. The number of tillers were estimated at weekly interval throughout the crop growth period. The number of effective tillers (the tillers that produced ears) was also noted for each treatment.

3.5.2.8 Root: Shoot ratio:- At maturity, samples for roots were taken using an 8 cm diameter bucket-type soil auger, after the shoots had been cut. Root sampling was to a depth of 30 cm on crop rows and 15 cm in the furrows after which there were no roots observed.

The cut shoots from each treatment were oven-dried at 85°C for 24 hours and then at 105°C for 2 hours and weighed. The root samples from the crop rows as well as the furrows for each treatment were washed thoroughly, oven-dried at 85°C for 24 hours and then at 105°C for 2 hours, bulked and also weighed. The root: shoot ratio was obtained by dividing weight of the roots by the weight of shoots. Because of the tideous job involved,

especially in washing the root samples, only nine samples, one each from the nine treatments in the study were taken.

3.5.2.9 Shoot nitrogen content:- Shoots were cut from 25 cm row of wheat crop at the heading stage, air-dried ground and then the nitrogen content determined using the colometrical method described by Jennings (1961).

3.5.2.10 Grain protein content:- The grains were analysed for nitrogen using the colometrical method described by Jannings (1961). The nitrogen content values of the grains were then multiplied by 6.25 to get the protein content (Jackson, 1962).

3.5.2.11 Time to heading:- It was recorded when plants in each treatment started and completed heading.

3.5.2.12 Time to maturity:- It was recorded when plants in each treatment started and completed maturing i.e. when the flag leaves started and completed becoming halve green - halve yellow in each treatment.

3.5.2.13 Length of ear:- This was measured using a meter rule for five ears randomly sampled from each plot. The mean length of ear for each treatment was then calculated.

3.5.2.14 Number of spikelets:- Five ears were sampled randomly per plot and the spikelets per ear counted. The mean number of spikelets per ear for each treatment was then calculated.

3.5.2.15 Number of grains:- Five ears were sampled randomly per plot and then the number of grains per ear counted. The mean number of grains per ear for each treatment was then calculated

3.5.2.16 Unit grain weight:- One thousand grains were counted from the product of each plot and weighed. Then the mean 1000 - grain weight for each treatment was calculated.

3.5.2.17 Grain (Economic) Yield:- This was obtained after threshing, winnowing, cleaning and weighing grains from net plots (3.0m x 1.0m) sampled during harvest. The grain yield per hectare was then calculated from those of the net harvested plots for each treatment.

3.5.2.18 Biological yield:- It is the total dry matter of all plant parts (excluding roots) produced at harvest. It was obtained by weighing all the crop's produce above ground level(straw and grains). Roots were excluded because of the difficulty in getting roots from the soil. The same net plots as in grain yield

assessment were used and the biological yield per hectare calculated for each treatment.

3.5.2.19 Straw yield:- This was obtained as the difference between biological yield and economic (grain) yield for each treatment.

3.5.20 Estimated loss in yield:- The control treatment was used as the standard and losses in yield of the other (stressed) treatments were calculated as yield differences from the control. The losses in yield were calculated for the biological yield, economic yield and straw yield of the stressed treatments and then each was expressed as a percentage loss in yield.

3.5.2.21 Cummulative depth of water used:- This was estimated by multiplying the water applied (in depth units) during each irrigation (5 cm) by the total number of irrigations applied during the crops growth period.

3.5.2.22 Harvest Index (HI):- Obtained as a percentage of economic yield to biological yield (Donald and Hamblin, 1976). It was estimated as:

$$HI = \frac{\text{Economic yield}}{\text{Biological yield}} \times 100$$

3.5.2.23 Water Use Efficiency (WUE):- This was estimated as:

$$WUE = \frac{\text{Economic (grain) yield (Kg/ha)}}{\text{Cummulative depth of water used (Cm)}}$$

3.6 Statistical Treatment of Data

The various data collected during the study were statistically analysed, wherever applicable, for variance as described by Snedercor and Cochran (1967). Duncan's multiple range test was then used to compare the means for significant differences as described by Duncan (1955).

CHAPTER 4

RESULTS AND DISCUSSIONS

4.1 SOIL STUDIES:

4.1.1 Soil Moisture Profile

The soil moisture profile reading in bars, using tensiometers, are giving in table 5 for treatments T_1, T_6, T_7, T_8, and T_9. The results revealed that the control treatment, T_1 had soil moisture tensions below 0.2 bars in the rootzone except on the 95th day after planting. This would suggest that there was no soil moisture stress experienced in this treatment before the 95th day. In general wheat growth was greatly reduced only after soil moisture tension was greater than 0.25 bars. This was in agreement with the findings of Ghosh et al (1975) with wheat grown on sandy loam soils. The soil moisture stress observed on the 95th day at the surface 15cm soil depth of the control treatment, T_1 was due to the high rate of water consumption at the later growth stage of wheat and was necessary and good for crop ripening.

Table 5: Soil Moisture tension readings (bars) using tensiometers.

TREATMENT	DEPTH (cm)	DAYS AFTER SOWING							
		25	35	45	55	65	75	85	95
T_1	15	0.08	0.08	0.05	0.02	0.07	0.06	0.18	0.72
	30	0.06	0.06	0.08	0.05	0.07	0.09	0.14	0.40
	60	0.02	0.01	0.02	0.02	0.01	0.02	0.04	0.29
T_6	15	0.36	0.71	0.10	0.18	0.62	0.76	F	F
	30	0.08	0.65	0.70	0.62	0.60	F	F	F
	45	0.08	0.22	0.44	0.32	0.56	0.63	F	F
	60	0.03	0.02	0.03	0.03	0.06	0.04	0.09	0.24
	75	0.03	0.02	0.01	0.00	0.02	0.00	0.07	0.22
T_7	15	0.08	0.12	0.62	*	0.29	0.20	0.22	0.15
	30	0.09	0.18	0.76	*	0.47	0.66	*	*
	60	0.04	0.06	0.42	*	0.45	0.60	*	*
T_8	15	0.09	0.23	0.43	0.56	0.70	*	*	*
	30	0.07	0.15	0.28	0.36	0.65	*	*	*
	60	0.04	0.10	0.18	0.26	0.36	*	*	*
T_9	15	0.14	0.30	0.20	0.56	0.64	0.78	*	*
	30	0.06	0.28	0.60	0.40	0.58	0.72	*	*
	60	0.07	0.04	0.06	0.03	0.49	0.45	*	*

* Soil too dry for tensiometers.
F Failure due to tensiometer breakdown.

Unlike in the control treatment, soil moisture data (moisture tension greater than 0.25 bars) of the other treatments indicated that there was stress whenever irrigation was missed. Also, stress conditions were alleviated whenever irrigation was restored. However, the degree of stress development and recovery from stress depended on the level of the moisture stress as well as the growth stage at which it was imposed. For instance results of treatment T_6, where two irrigations were missed during tillering, indicated that soil moisture tension started increasing when irrigation was missed on the 16th day after planting. This continued until a peak value of 0.71 bars was recorded on the 35th day at 15cm soil depth. When irrigation was restored on the 36th day, soil moisture tension started falling. The soil moisture tension then remained relatively low until about the 65th day when it was noticed to have increased considerably. And by the 75th day, tensiometers started failing to give any readings. This was most probably due to the breakdown of the instruments or the drying up of the soil. But it is worthwhile to note that up till the 95th day when observation was stopped, the soil at 60cm depth

and below had soil moisture tensions below 0.25 bars. This could be due to the influence of capillary rise from the perched ground water table.

Treatment T_7 (where two irrigations were missed during jointing) indicated that by the 55th day when there was high moisture stress, the tensiometers had failed to give any readings. When re-watered on the 56th day, the tensiometers started functioning (after they had been serviced). However, failure was again observed as from the 85th day as soils were drying up. In the treatments (T_8 and T_9) where two irrigations were missed during flowering and grain filling, soil moisture tension rose above 0.25 bars and stress symptoms (leaf curling and wilting) were observed even before irrigation was missed. And when stress was imposed in these treatments, tensiometers failed since the soil was too dry by then. Infact, after 85 days of planting, all the tensiometers in treatments T_7, T_8 and T_9 stopped functioning due to high soil moisture tension. This was a consequence of the high rate of water consumption by wheat during the second half of its life cycle than during the first.

In general, soil moisture tension was much lower at greater soil depths than at the surface layers. This was mainly due to the presence of the perched water table. However, during the later growth stage of wheat the soil moisture tension also became high at greater soil depths. This was due to the high rate of water consumption by wheat at that stage which subsequently lowered the water table depth. Infact the ground water table observation (fig.1) revealed that as from the 29th day after planting until the 85th day, the water table fluctuated between 80 and 90cm below the soil surface. But as from the 89th day, the water table started falling gradually until it got to 100cm depth by the 108th day.

4.2 PLANT STUDIES

4.2.1 Plant Water Potential

The diurnal fluctuations in plant water potential at jointing and flowering stages of wheat under various moisture stress conditions are given in figure 4. Plant water potential was observed during jointing and flowering because these stages of wheat have been reported more

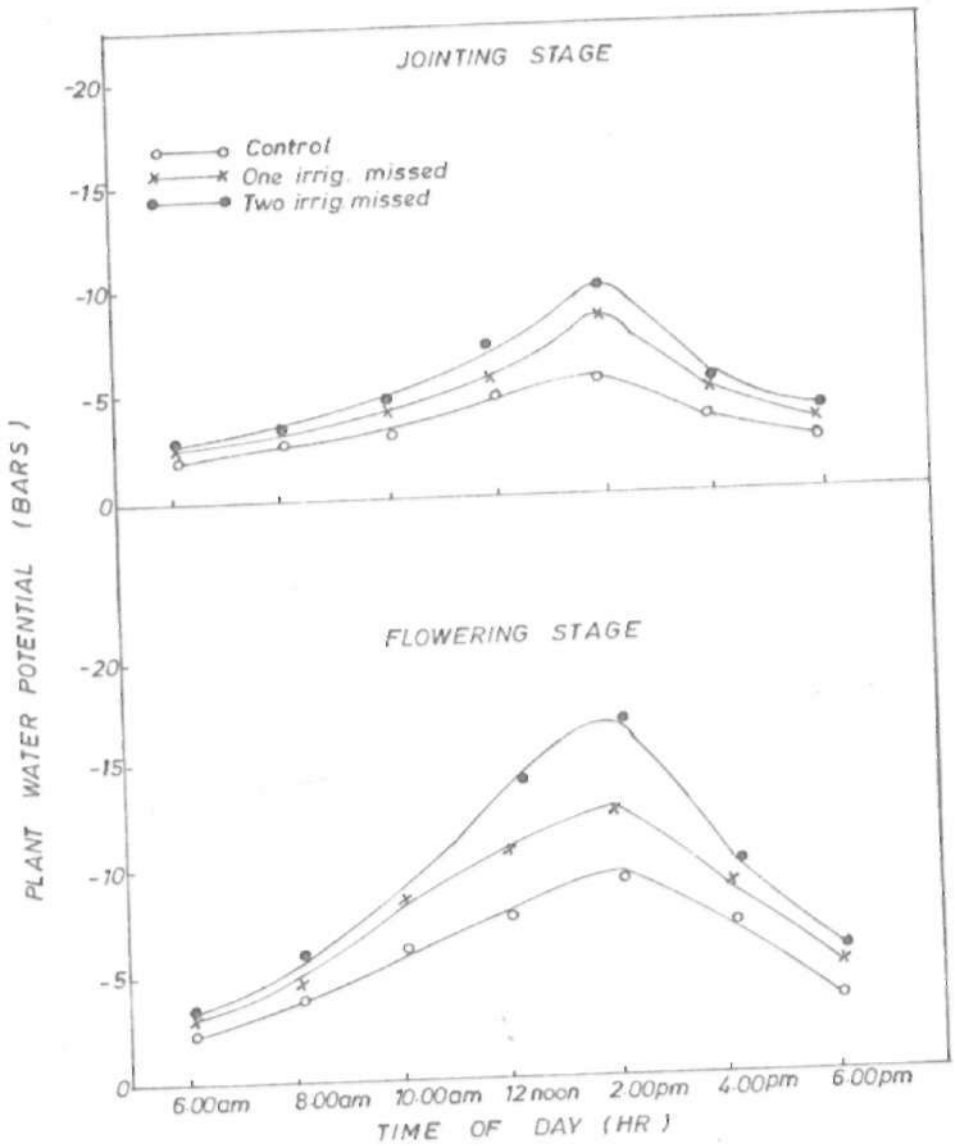


FIG. 4 : Diurnal fluctuation in plant water potential at jointing and flowering growth stages of wheat under various moisture stress conditions

sensitive to moisture stress in Nigeria (Chari, 1980; Surma et al; 1980). The result indicated that at both growth stages considered, the diurnal fluctuations of the plant water potential were consistently lowest in the control treatment. The greatest fluctuations were in treatments where two irrigations were missed (henceforth referred to as minus two irrigation treatments), and then those where minus one irrigation was missed (henceforth referred to as minus one irrigation treatments). However, the plants generally had higher plant water potential values during jointing than flowering. Furthermore, the plant water potential at 6.00 p.m. (1800hrs.) generally returned more closely to the predawn measurement during jointing than flowering. But at both growth stages, the plant water potential at 1800hrs returned closer to the predawn measurement in the control treatment, followed by treatments with minus one irrigation and then those with minus two irrigations, respectively. Thus, the result revealed that the greater the moisture stress imposed, the lower the plant water potential at any growth stage at anytime of the day; and also the slower the recovery from stress (fig. 4).

Plant water potential was lowest at about 2.00 pm in all the treatments at both growth stages. The 2.00 pm plant water potential values at the jointing and flowering stages were -5 and -9 bars for the control treatment; -8 and -13 bars for the minus one irrigation treatments and then -10 and -16 bars for the minus two irrigations treatments, respectively. And since the control treatment experienced no stress as indicated by results of soil moisture tension, the plant water potential threshold values for stress to ensue would therefore be -5 and -9 bars for the jointing and flowering stages, respectively.

Environmental temperature, soil moisture status and wind have all been reported to have great influences on evapotranspiration and consequently on plant water potential (Frank et al., 1973; Tanner, 1963). Thus visible wilting and/or leaf curling were observed in the stress treatments especially between the hours of about 11.00am and 4.00pm whenever plant water potential was determined. The differences between the plant water potential values of the control treatment and those of the stress treatments occurred between the hours of about

11.00am and 4.00pm due to the effect of higher temperatures during this period. Infact, the differences between the plant water potential values of the control treatment and those of the stress treatments (treatments with minus one and two irrigations) would represent the various degrees of stress experienced by the stress treatments. However, the magnitudes of the stress experienced were rather mild and/or moderate than severe since the lowest water potential values attained by the different treatments were about -15 bars or greater. Thus severe stress did not develop even when two irrigations were missed during jointing and flowering, most probably due to the effect of the perched water table at Kadawa. Maurya (1981) also found that plant water potential values for wheat grown at Kadawa do not get as low as those obtained at Samaru. He attributed this observation to the effect of the high water table at Kadawa (fluctuating between 70 and 120cm from the soil surface) and the higher air temperature at Samaru during the wheat growing season.

Further, the plant water potential values in bars/day was calculated for the various treatments during

jointing and flowering. The result is presented in the table below.

GROWTH STAGE	TREATMENTS	PLANT WATER POTENTIAL (BARS/DAY).
JOINTING	Control	- 71.5
	One irrigation missed	- 85.0
	Two irrigations missed	- 106.0
FLOWERING	Control	- 105.0
	One irrigation missed	- 147.0
	Two irrigation missed	- 168.0

It is, therefore, very apparent that treatments with irrigation missed during flowering suffered higher degrees of stress than those during jointing.

4.2.2 Plant Canopy Temperature

The diurnal fluctuations in plant canopy temperature at jointing and flowering growth stages of wheat under various moisture stress conditions are presented in figure 5. During both growth stages, plant canopy temperature reached their highest values at about 2.00pm. Also, the plant canopy temperatures for all treatments at both growth stages did not return to predawn measurements by 6.00pm. Further, the control treatment had lower canopy

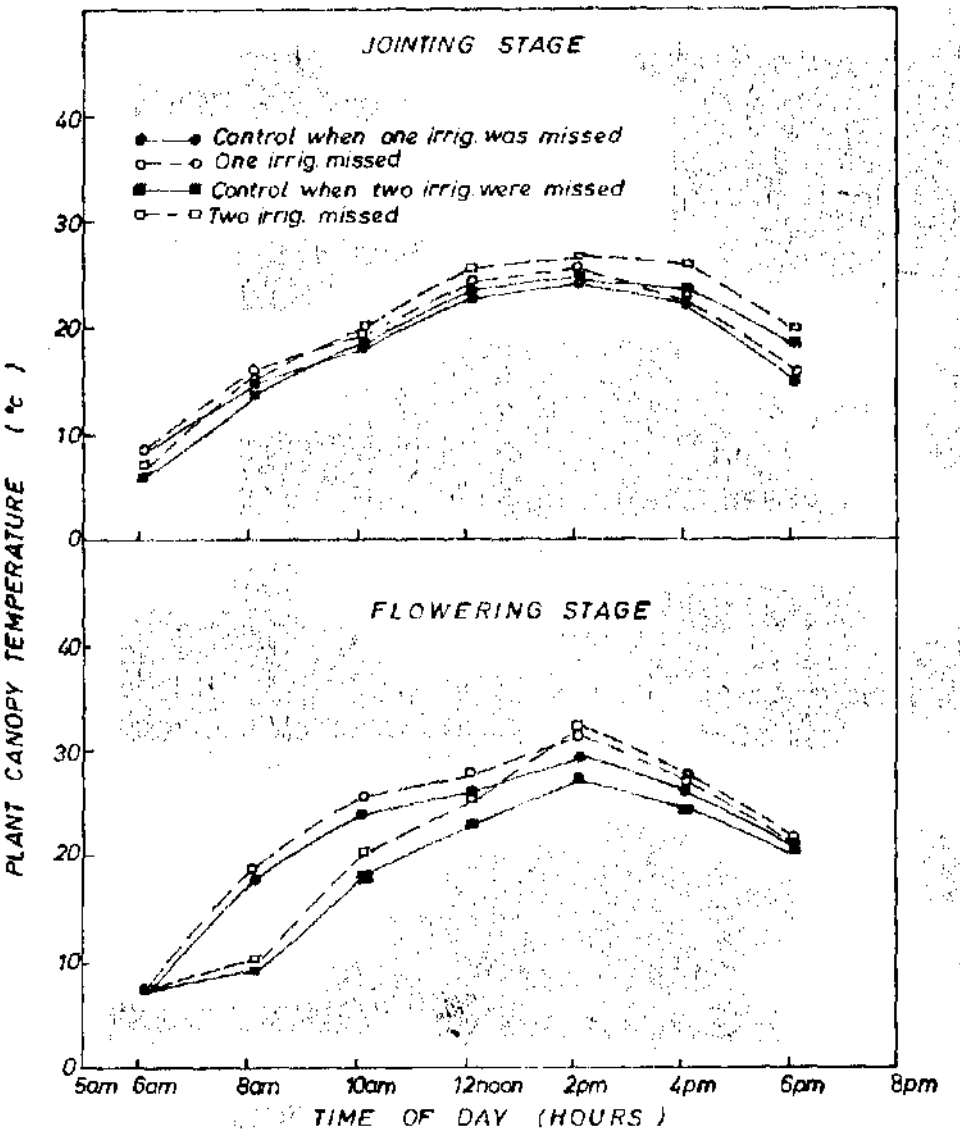


FIG. 5 : Diurnal fluctuation in canopy temperature at jointing and flowering growth stages of wheat under various moisture stress conditions

temperatures than minus one or minus two irrigations treatments at any growth stage. These results could be attributed to the fact that both environmental temperature as well as the soil moisture status influence evapotranspiration rate and subsequently the plant canopy temperature (Tanner, 1963). Frank et al. (1977) also reported that the canopy temperature of wheat crop was strongly influenced by shelter as well as soil-water content. They also observed that shelter plus good soil moisture status treatments produced higher leaf water potential and lower canopy temperature. And Ehrler et al. (1978) found that high relative humidity plus good soil water supply reduced plant canopy temperature.

4.2.3 Plant Height.

The variation in plant height as affected by different levels of moisture stress conditions at different growth stages is presented in figure 6. The control treatment had higher plant height at all growth stages than all other treatments except treatment, T_8 in which two irrigations were missed during flowering. Generally, moisture stress at any

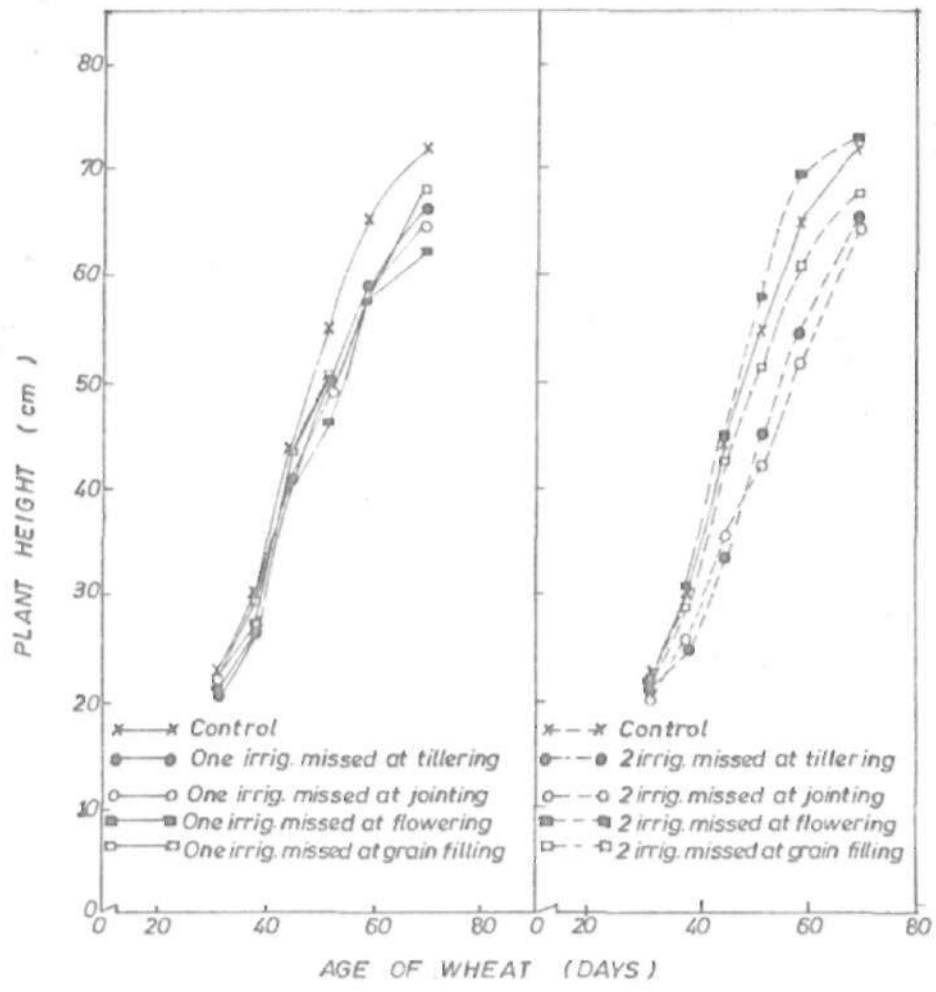


FIG. 6 :Plant height as affected by different levels of moisture stress conditions at different wheat growth stages

growth stage, especially before heading reduced plant height considerably. However the reduction in plant height was more in treatments with minus two irrigations before heading. This is because it is the period of active and maximum growth in wheat, usually referred to as the vegetative stage. In fact, Florell and Faulkner (1934) reported that no growth occurred after blossoming had been completed in wheat, but before then growth was continuous. The reduction in plant height was due to lack of cell elongation as evidenced by the rate of plant elongation presented in table 6. Whenever stress was imposed the rate of plant elongation reduced; but as soon as stress was alleviated, a more rapid rate of plant elongation was observed in the stressed plant than in the control. This was quite pronounced when plants were stressed by missing one or two irrigations during tillering and jointing. The rapid growth rate observed after stress alleviation, could be attributed to the rapid elongation of cells already formed during stressed conditions; since moisture stress has been reported to affect cell enlargement more than cell division (Gates, 1965a; 1968; Boyer, 1970; Hsiao et al., 1970 and Acevedo et al., 1971).

Table 6: Rate of plant elongation (mm/day)

Treatment	AGE OF WHEAT (Days)					
	0-30	31-37	38-44	45-51	52-58	59-69
T_1	7.50	10.71	20.00	15.43	14.57	6.80
T_2	6.83	9.00	23.86	9.29	12.86	10.00
T_3	7.33	10.71	15.71	12.14	13.29	8.57
T_4	7.10	12.14	15.00	8.14	15.71	7.14
T_5	7.27	7.43	19.71	13.86	9.71	15.29
T_6	7.10	5.29	14.00	14.57	15.00	13.57
T_7	6.67	77.57	14.29	9.57	14.00	17.43
T_8	7.17	12.86	29.07	18.29	16.43	5.00
T_9	7.43	9.57	19.71	12.43	13.29	9.29

The final plant height (height at maturity) is given in table 8. Treatment, T_8 had a slightly higher final plant height (72.75cm) than other treatments but it was statistically the same with treatments T_1, T_2, T_3, T_5, T_6 and T_9. On the other hand, treatment T_4 had a slightly lower final plant height (62.00cm) but this was statistically the same with treatments T_2, T_3, T_5, T_6, T_7 and T_9.

4.s 4 Dry Matter Harvested

The dry matter harvested showing the effects of various levels of moisture stress at different growth stages is presented in figure 7. The dry matter harvested was consistently higher in the control treatment than in all the other treatments throughout the life cycle of the wheat crop. Whenever moisture stress was imposed at the various growth stages, dry matter harvested was suppressed. The suppression was more in treatments where two irrigations were missed. This was because all activities responsible for dry matter production (e.g. water and nutrient uptake and consequently growth) were considerably affected by the moisture stress. For instance there was a considerable reduction in nutrient uptake (especially nitrogen) when two irrigations were

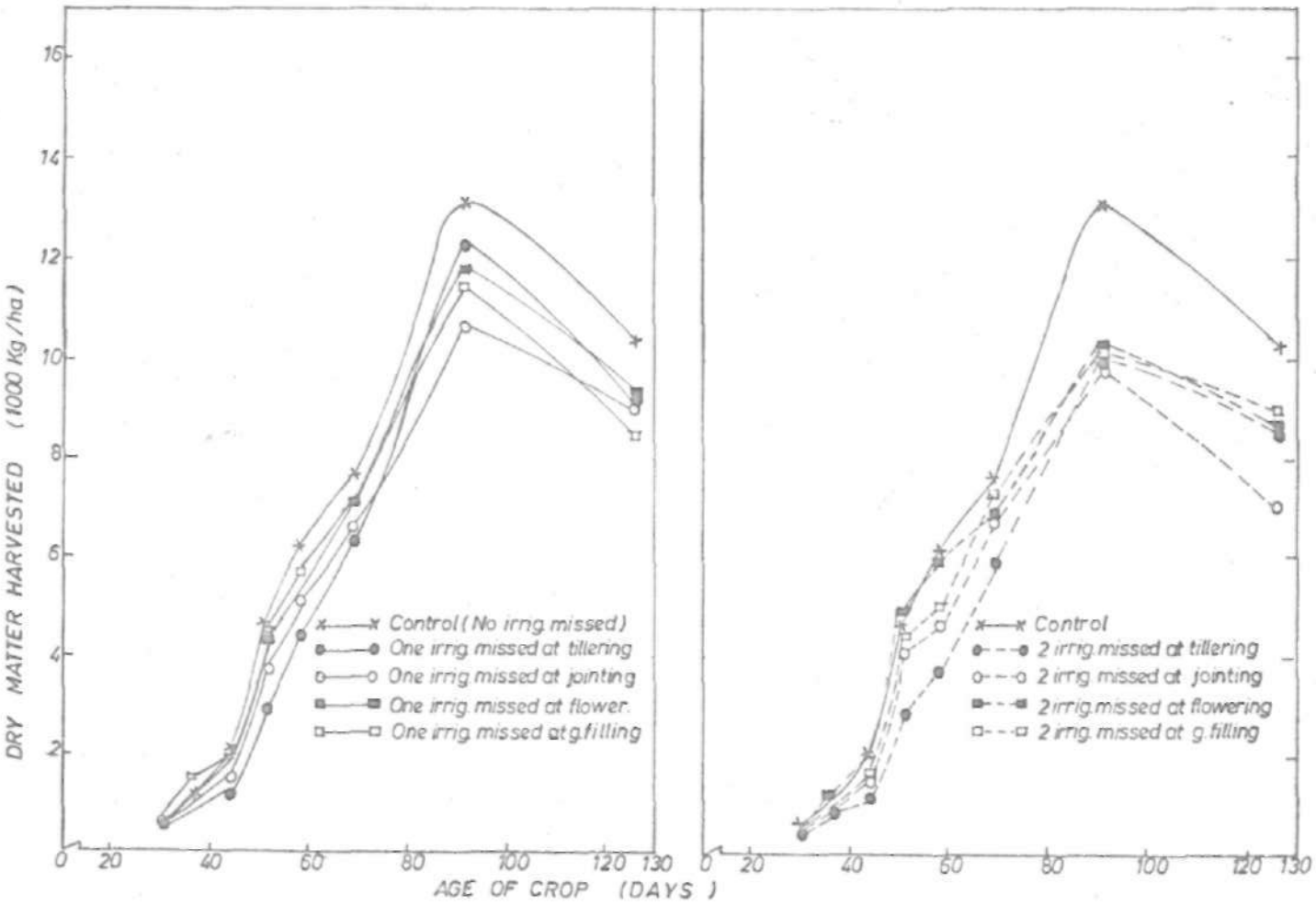


FIG. 7 : Dry matter harvested as affected by different levels of moiture stress conditions at different wheat growth stages

missed during jointing, as evidenced by the shoot nitrogen content at flowering (see table 7). Thus growth was consequently reduced too; more so because the second dose of nitrogen applied during this jointing stage was not fully utilized. However, there was recovery in dry matter accumulation harvested as soon stress was alleviated by restoring good moisture supply. But the recovery was less in treatments where two irrigations were missed than in treatments with one irrigation missed. It is also pertinent to state that recovery was least in treatments that suffered moisture stress, especially minus two irrigations treatments during jointing and grain filling. This is because both stages experienced much senescence and shedding of leaves. Infact during grain filling stage the moisture stress also hastened maturity and so there was no time lapse allowed for recovery. Finally, the result also indicated that the dry matter harvested generally increased reaching a peak about the 90th day after planting in all the treatments and then falling to values at harvest. This could be attributed to the senescence and shedding of leaves which were not picked from the ground. The fall in dry matter harvested from

the peak to values at harvest was generally more in the control treatment, all minus one irrigation treatments and treatments with minus two irrigations during grain filling (fig. 7). This is because these treatments didnot experience much senescence and shedding of leaves until after the 96th day when irrigation was cut-off.

4.2.5 Leaf Area Retention (LAR)

The estimated variations in leaf area retention as affected by different levels of moisture stress at different wheat growth stages are presented in figure 8. LAR is a measure of green leaf area per unit area of land. It could be used to estimate plant growth. Thus the greater the LAR, the more the ground is covered and the greater the light interception. And since photosynthesis takes place in the presence of light, the greater would be the photosynthates produced. The consequence will be better plant growth. The results obtained in this study indicated that moisture stress reduced LAR. This is as a result of marked decrease in leaf enlargement which occurs whenever plant water potential values fell below - 4 bars (Turner and Begg, 1978). Moreover, it has been found (Ghosh et al, 1975)

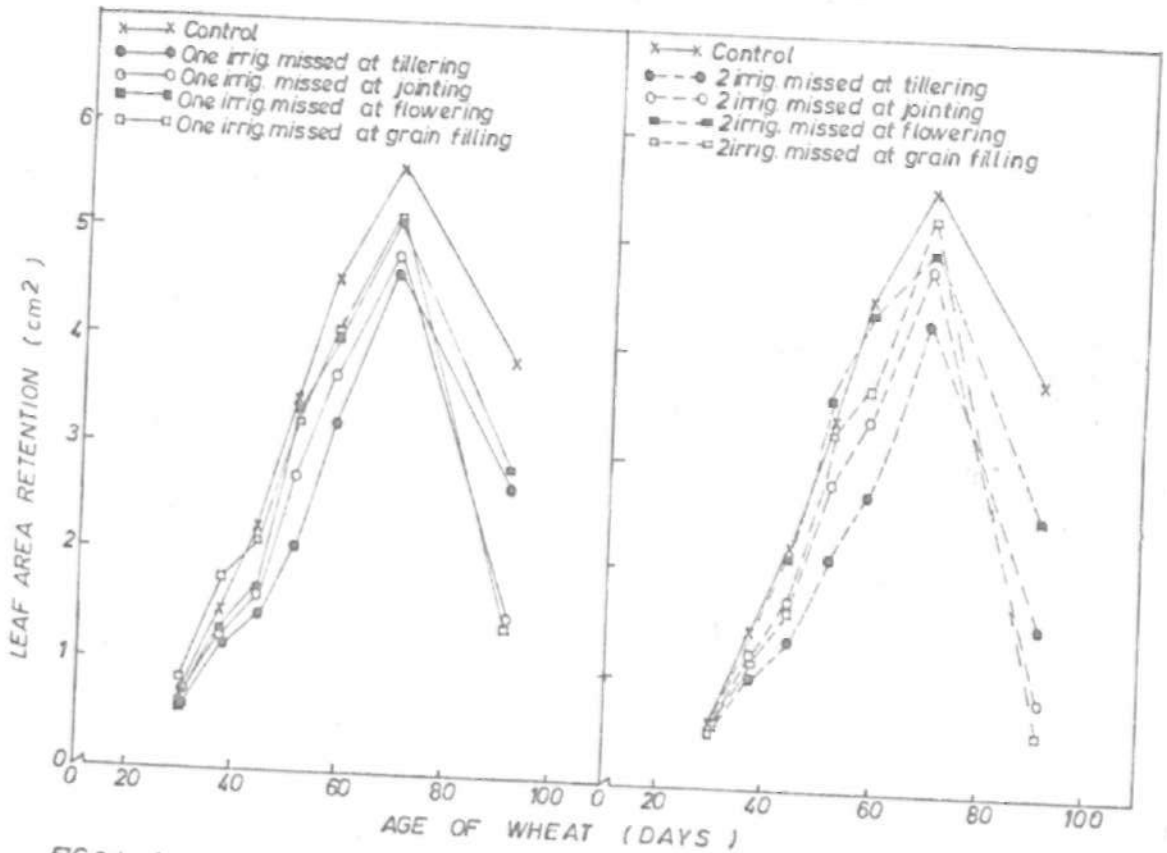


FIG. 8: Leaf area retention as affected by different levels of moisture stress at different wheat growth stages

that soil moisture tension greater than 0.25 bars would reduce leaf area index as well as LAR. And as discussed earlier, moisture stress in this study produced soil moisture tension greater than 0.25 bars and plant water potential lower than - 4 bars. Generally, LAR was highest in the control treatment followed by treatments with one irrigation and then those with two irrigations missed at any growth stage. Thus reduction in LAR was highest in treatments that had two irrigations missed, especially during jointing and grain filling. This is because moisture stress hastened senescence and shedding of leaves which were not included in LAR measurements. This effect was more pronounced in the minus two irrigations treatments. Infact, the minus two irrigations treatment during jointing had the greatest reduction in LAR because moisture stress had an indirect effect on nutrient (especially nitrogen) availability which aggravated plant senescence. At the later wheat growth stage, moisture stress during grain filling also hastened maturity and plant senescence. Thus LAR was

much more reduced than in any of the other treatments except the minus two irrigation treatment during jointing. Finally it is worthwhile noting that LAR reached it maximum values in all the treatments during the flowering stage. This is most probably, because growth had been completed in wheat during this stage as reported by Florell and Faulkner (1934).

4.2.6 Leaf Area Duration (LAD)

The estimated variations in leaf area duration as affected by different levels of moisture stress at different wheat growth stages are presented in figure 9. LAD is an estimated measure of the photosynthetic plant portions (leaves) that are still green. It is sometimes simply defined as the leaf area per plant. And since tillers were considered in this study as individual plants for LAD estimations, LAD variations in the different treatments depended on tiller production and/or mortality; as well as on the degree of plant (especially leaves) senescence. Thus the LAD of the control treatment was higher than those of most of the other treatments. The results in figure 9 also indicated that LAD for all the

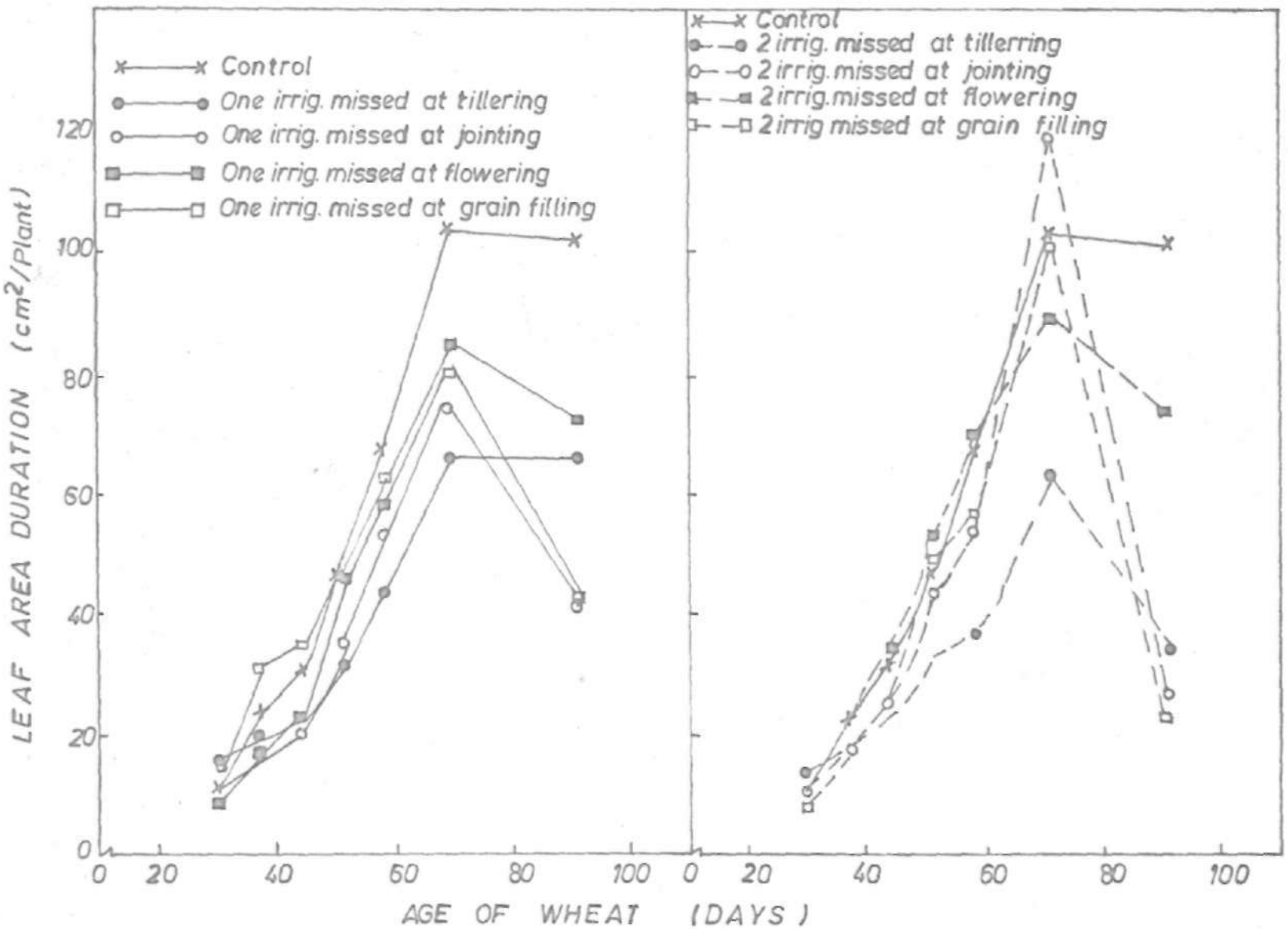


FIG. 9 : Leaf area duration as affected by different levels of moisture stress at different wheat growth stages

treatments attained their maximum values by the 70th day after sowing. The highest LAD (about 118cm^2 plant) was, however, attained by the treatment with minus two irrigations during jointing. This is because this same treatment had the greatest tiller mortality, which invariably resulted in the highest LAD attained at about the 70th day. However when senescence ensued in the remaining 'older' tillers, the LAD of this same treatment fell sharply. On the other hand, treatments which had moisture stress (especially the minus two irrigation treatment) during tillering suffered most in term of LAD. This was due to the initial plant stunting and senescence when the stress was imposed. Secondly there was a regeneration of tiller production in great numbers when the stress was alleviated. This invariably kept LAD of stressed treatments during tillering relatively low.

The LAD of the control treatment from the 70th day to about the 90th day after sowing remained fairly constant and slightly above 100cm^2/plant. However, the LAD of the other treatments fell to values below those attained at about the 70th day. By the 90th day, LAD had fallen to about 40cm^2/plant or below in treatments that suffered from moisture stress during jointing and grain filling.

However, it never fell below 20cm^2/plant. In fact, apart from the control treatment, LAD was least affected in treatments which had irrigation missed during flowering. This is because LAI in those treatments did not fall below 70cm^2/plant by the 90th day after sowing when the observations were stopped.

4.2.7 Number of Tillers

The variations in number of tillers as affected by different levels of moisture stress are presented in figure 10. The control treatment had a continuous increase in number of tillers until a peak value of about 7.6 million tillers/ha was attained at the jointing stage. The number of tillers then started decreasing until a value of about 3.75 million tillers/ha was attained at the grain filling stage, This was because not all tillers produced, reached the flowering stage. A similar observation was reported by Friend (1965). He further explained that some of the tillers died before heading, while others (especially those borne on the upper nodes of the stems) formed rudimentary ears that never emerged. This was also observed in the present study.

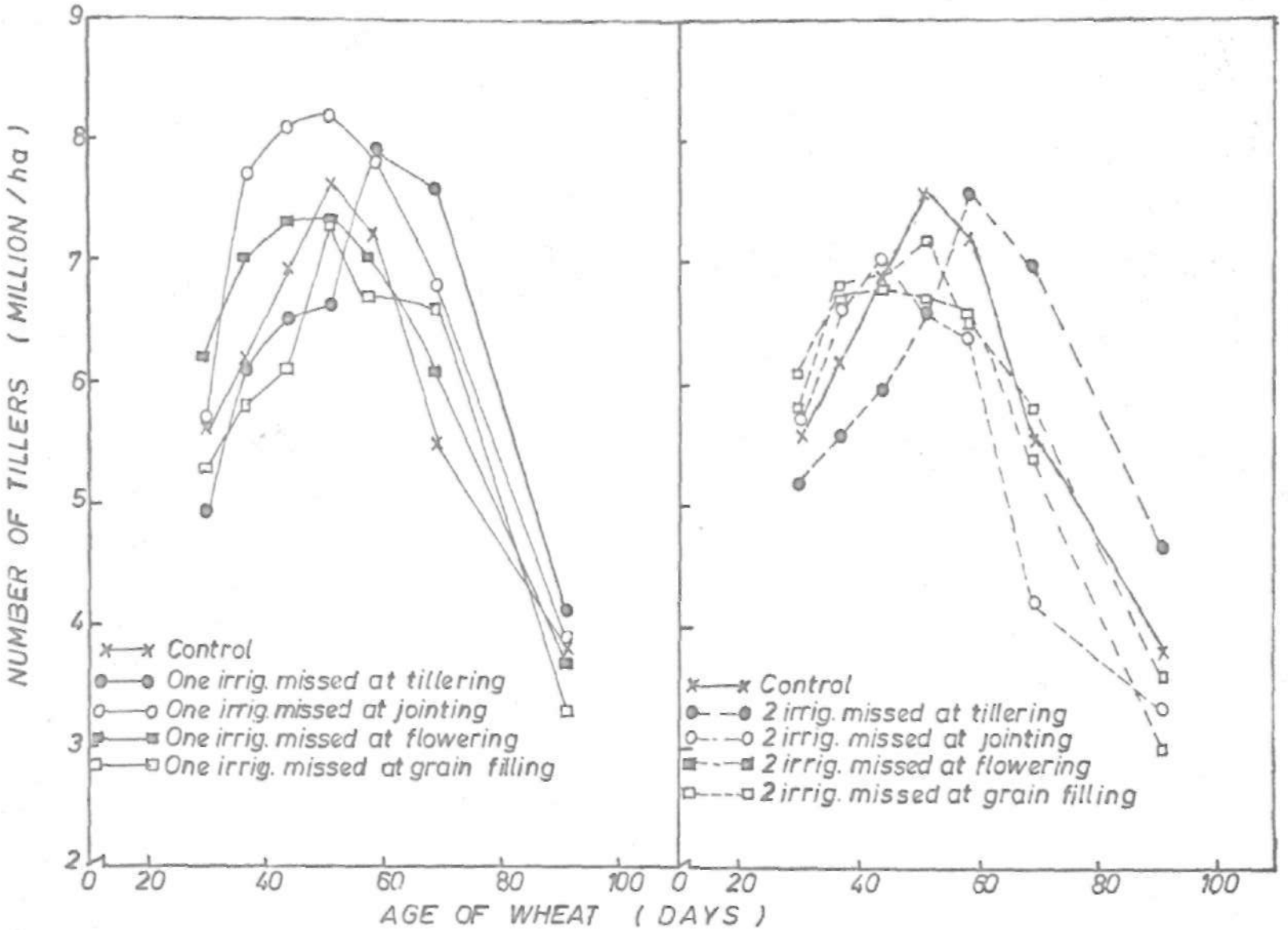


FIG.10 : Number of tillers as affected by different levels of moisture stress conditions at different wheat growth stages

Generally, moisture stress suppressed tillering and increased the death of tillers, especially the late ones that emerged just before the stress. However, tillering although being suppressed during moisture stress was actually stimulated upon alleviation of the stress. The effect of moisture stress on tillering was greater at early growth stages of the wheat crop. A similar observation was reported by Aspinall et al. (1964) and they attributed these findings to nutrient uptake and distribution within the plant. This could explain why the number of tillers decreased sharply in the treatments where irrigations were missed during jointing. The effect of tillering stimulation after rewatering was clearly observed in treatments that suffered moisture stress during the tillering stage. As such peak values of about 7.9 and 7.6 million tillers/ha were attained during the jointing-heading period by treatments with minus one and two irrigations during tillering, respectively. Infact these same treatments had the highest number of effective tillers at about the 90th day after sowing (grain filling) with about 4.1 and 4.7 million tiller/ha for treatments with minus one and two irrigations during tillering, respectively. The treatment with more stress during tillering had grater number of tillers

than the one with less stress, most probably due to nutrient uptake and distribution in the plants. It was also observed that all the treatments in this study had their highest number of tillers at about jointing – heading period. This is due to the fact that some of the tillers died before heading. Moisture stress increased the death of tillers. However, apart from death of tillers, moisture stress after heading increased the number of rudimentary ears. The consequence of all these is the reduction in effective tillers. The number of effective tillers was analysed statistically and the result is given in table 8. It revealed that treatment T_6 with minus two irrigations during tillering, had a significantly higher number of effective tillers (4.68 million/ha) than the other treatments. But this was statistically the same with treatments T_1, T_2, and T_3. On the other hand, treatment T_9, which had two irrigations missed during grain filling, had a significantly lower number of effective tillers (3.04 million/ha); but it was at par with treatments T_8, T_7, T_5, T_4, T_3 and T_1.

4.2.8 Root: Shoot Ratio

The root: shoot ratio for the various treatments is presented in table 7. Under well-defined environmental conditions the root: shoot ratio has a practically constant value for each growth stage in any given species. However, many factors of agronomic significance such as nitrogen supply, moisture supply, high light intensity, shade and temperature all affect this ratio differently (Brouwer, 1966). The result of root: shoot ratio obtained in this study revealed that treatment T_6, where two irrigations were missed during tillering had the highest value (0.052). This was closely followed by treatment T_7 (0.050), where two irrigations were missed during jointing and then treatment T_2, where one irrigation was missed during tillering with 0.046 root: shoot ratio. All other treatments had root: shoot ratios below 0.040, with the lowest value of 0.030 in treatment T_4, where one irrigation was missed during flowering. Thus moisture stress generally increased root: shoot ratio except in treatments which suffered moisture stress during flowering, where the ratios were lower than that of the control treatment (0.035). The root: shoot

Table 7: Root: shoot ratio; shoot nitrogen content at flowering; grain protein content; time to heading and time to maturity as affected by different levels of moisture stress during different wheat growth stages.

TREATMENTS	Root: shoot ratio	Shoot nitrogen content at flowering (%)	Grain protein content (%	Time to heading (Days)	Time to maturity (Days)
T_1	0.035	3.5	8.13	53-65	112-118
T_2	0.046	3.3	9.38	46-56	105-109
T_3	0.039	3.8	11.88	49-58	102-106
T_4	0.030	3.7	8.13	53-65	104-109
T_5	0.035	3.5	9.38	53-65	100-104
T_6	0.052	3.1	9.38	46-56	105-109
T_7	0.050	2.3	10.63	49-58	102-106
T_8	0.034	3.3	14.38	53-65	104-109
T_9	0.040	3.0	15.63	53-65	100-104
Mean	0.0401	3.28	10.77		
Standard Deviation (S.D.)	0.0076	0.45	2.68		
Coefficient of Variation (%)	19.05	13.71	24.93		

ratio was increased by moisture stress before flowering because root growth was still very active and favoured by stress during this period. Moreover, Strebeyko et al. (1963) have reported that root growth was negligible at flowering as it slows down or ceases entirely about the time of ear formation.

During root sampling, it was also found that most roots concentrated in the ploughed surface 0-15cm of the soil. But few easily traceable roots extended to about 45cm deep. A similar observation was also reported by Dunham (1979). Thus this could serve as an explanation for the responses to more frequent irrigation reported by some researchers working under the high water table conditions of Kadawa experimental site.

4.2.9 Nitrogen Content of Plant

Data of shoot nitrogen content is presented in table 7. The shoot nitrogen content was determined during flowering, because nitrogen accumulation by the plants is mostly completed by the time of anthesis, although it could still continue until the plants mature (Boatwright and Haas 1961). The result indicated that the highest shoot nitrogen content (3.8%) was obtained in treatment T_3, where one

irrigation was missed during jointing. This was followed by treatment T_4 (3.7%N). All other treatments had shoot nitrogen content values between 3.0 and 3.5% except treatment T_7, (2.3%N). The considerable lower shoot nitrogen content in treatment T_7 is an evidence that minus two irrigations during jointing, reduced nitrogen uptake. Inspite of the second dose of nitrogen applied during this same growth stage, plants could not make use of the applied nitrogen due to soil moisture stress. Since nitrogen is an essential plant nutrient for healthy growth and development, this treatment had the greatest reduction in growth and yield due to this indirect effect of soil moisture stress.

4.2.10 Grain Protein Content

The grain protein content determined for the various treatments in this study is presented in table 7. The highest grain protein content (15.63%) was obtained in treatment T_9 which had minus two irrigations during grain filling. This was followed by treatment T_8 with 14.38% grain protein content. All the other treatments had grain protein content values between 8.13 and 11.88%. The result also revealed that moisture stress

generally increased the grain protein content. But to be more specific moisture stress at the later growth stage of wheat (flowering and grain filling), especially the treatments with longer periods of stress, gave higher grain protein contents. This is because moisture stress at the later growth stage hastened maturity and formation of shrivelled kernels due to shortened period of photosynthates transfer from the plant organs to the kernels. Consequently, the kernels had higher nitrogen and lower starch contents. This was also reported by Shutt and Hamilton (1964) and Shollenberger et al. (1949). And since grain protein content was calculated from grain nitrogen content, it followed that higher nitrogen content implied higher protein content. Finally, the grain protein content (8.13%) of the control treatment was only 0.17% lower than that reported for Siete cerros wheat cultivar by Olugbemi et al (1979).

4.2.11 Time to Heading and Maturity

The average periods taken to heading and maturity are presented in table 7. The result revealed that the periods to heading were between

53 to 65 days; 46 to 56 days and 49 to 58 days for the control treatment, treatments stressed during tillering and treatments stressed during jointing, respectively. Also, the control treatment matured between 112 to 118 days whereas treatments stressed during tillering; jointing; flowering; and grain filling stages matured between 105 to 109 days; 102 to 106 days; 104 to 109 days; and 100 to 104 days, respectively. Thus moisture stress generally reduced the ultimate period from sowing to maturity. However, whilst moisture stress before heading reduced the period to heading; that after heading shortened the period to maturity. Similar results have been reported by Aspinall et al. (1964) and Day and Intalap (1970). It is also pertinent to state that moisture stress at the later growth stage, especially that due to minus two irrigations, reduced the period to maturity considerably.

4.2.12 Length of Ear

Data for length of ear is presented in table 8. The result indicated that the control treatment, T_1 had a longer length of ear (9.08cm) than the other treatments. But this was statistically the same

Table 8: Effective tillers; final plant height; length of ear; number of spikelets per ear; number of grains per ear and 1000-grain weight as affected by different levels of moisture stress during various wheat growth stages.

TREATMENTS	Effective tillers (million/ ha)	Final Plant height (cm)	Length of ear (cm)	Number of spikelets per ear	Number of grains per ear	100-grain weight (g)
T_1	3.84 abc	71.75 ab	9.08 a	16.50 a	68.92 a	37.35 abc
T_2	4.12 ab	66.00 abc	8.68 abc	15.00 ab	54.25 a	38.25 ab
T_3	3.88 abc	64.25 abc	8.93 ab	15.75 ab	62.54 a	37.08 bc
T_4	3.68 bc	62.00 c	8.78 abc	16.25 ab	60.88 a	38.75 ab
T_5	3.28 bc	68.00 abc	8.93 ab	15.00 ab	64.29 a	35.90 bc
T_6	4.68 a	65.00 abc	8.33 c	14.50 b	58.96 a	36.80 bc
T_7	3.32 bc	64.00 bc	8.53 bc	14.50 b	54.58 a	40.50 a
T8	3.60 bc	72.75 a	8.98 ab	16.00 ab	51.48 a	38.38 ab
T_9	3.04 c	67.25 abc	9.00 ab	15.25 ab	59.38 a	34.35 c
Mean	3.72	66.78	8.80	15.42	59.47	37.48
Standard of Deviation (S.D)	0.49	3.58	0.25	0.74	5.47	1.77
Coefficient of Variation (%)	13.30	5.	2.82	4.80	9.20	4.72

Values followed by different letter(s) in the column are significantly different at 5% level.

with the length of ear in treatments T_2, T_3, T_4, T_5, T_8 and T_9. On the other hand, treatment T_6 had a significantly shorter length of ear (8.33cm) than the other treatments. However this was also statistically the same with the length of ear in treatments T_7, T_2 and T_4. In general, the reduction in length of ear was more prominent in treatments which were stressed for 20-days before heading occurred. This was probably due to the resultant stunted growth caused by the stress in those treatments.

4.2.13 Number of Spikelets

The number of spikelets per ear for the various treatments is given in table 8. The result showed that the control treatment, T_1 had a significantly higher number of spikelets per ear (16.50 spikelets/ear) than the other treatments. However this was statistically the same with the number of spikelets per ear in treatments T_2, T_3, T_4, T_5, T_8 and T_9. Contrarily, treatments T_6 and T_7 (minus two irrigations treatments during tillering and jointing) had significantly lower numbers of spikelets per ear (14.50 spikelets/ear). But this was statistically

the same with number of spikelets per ear in treatments T_2, T_3, T_4, T_5, T_8 and T_9. Thus the number of spikelets per ear was only prominently reduced in longer stressed treatments during tillering and jointing. Similar results have been reported by Aspinall et al. (1964); Day and Intalap (1970) and Musick and Dusek (1980). This significant reduction in the number of spikelets per ear due to moisture stress could be attributed to the the resultant stunted growth in those treatments as a result of the stress. Aspinall et al (1964) also reported that it could be attributed to the process of spikelet initiation which occurs prior to anthesis.

4.2.14 Number of Grains

The number of grains per ear for the various treatments is presented in table 8. The result indicated that there was no significant difference statistically in all the treatments. However, the control treatment had the highest number of grains per ear (68.92), whereas the lowest number of grains per ear (51.46) was in treatment T_8, which had minus two irrigations during flowering. All the other treatments had numbers of grains per ear between 54.25 and 64.29. The reduction caused by moisture stress during tillering was mainly due to the reduction in ear size. The



reduction caused by moisture stress during jointing and flowering could be a consequence of an effect associated with the process of spikelet initiation and later with the formation of gametes (Aspinall et al, 1964). Furthermore, Arnon (1972) stated that nitrogen deficiency caused complete cessation of ear development and/or degeneration of florets in the remaining ears. This could be the reason for the lower number of grains per ear in the minus two irrigations treatment during jointing. Finally, the reduction in number of grains per ear due to moisture stress during grain filling could be attributed to hastened senescence and maturity; which consequently terminated the development or caused poor development and/or abortion of the already formed gametes.

4.2.15 Unit Grain Weight

Data for 1000-grain weight is presented in table 8. Treatment T_7, which had minus two irrigations during jointing, had a significantly higher 1000-grain in weight (40.50g) than the other treatments. However, this was statistically the same with the 1000-grain weights in treatments T_1, T_2, T_4, and T_8. On the other hand, treatment T_9, which

had minus two irrigations during grain filling, had a significantly lower 1000-grain weight (34.35g). But this was statistically the same with 1000-grain weights in treatment T_1, T_3, T_5 and T_6. Thus moisture stress before flowering generally increased the 1000-grain weight. Wilson (1969) also reported that 1000-grain increased due to moisture stress prior to ear emergence. This is an adaptation of yield compensation as described by Turner (1966). Contrarily, moisture stress after heading, especially during grain filling, caused a significantly lower unit-grain weight. This was due to hastened senescence and maturity that produced shrunken grains which weighed less.

4.2.16 Biological Yield

The biological yield of the various treatments is presented in table 9. The control treatment T_1, had a significantly higher biological yield (10395.83Kg/ha) than all the other treatments. However, this was statistically the same with the biological yields in treatments T_2, T_3, T_4, T_5, T_8 and T_9. On the other hand, treatment T_7 with minus two irrigations at jointing had a significantly lower biological yield

Table 9: Yield and losses in yield due to different levels of moisture stress during different wheat growth stages.

TREATMENT	BIOLOGICAL YIELD (Kg/Ha	ECONOMIC (GRAIN) YIELD YIELD (Kg/Ha)	STRAW YIELD (Kg/Ha)	ESTIMATED LOSSES (%)		
				Biological Yield	Economic Yield	Straw Yield
T_1	10395.83 a	4611.67 a	5784.16 a	0.00	0.00	0.00
T_2	9169.17 ab	4016.67 ab	5152.50 abc	11.80	12.90	10.92
T_3	9007.50 abc	4118.34 ab	4889.16 bc	13.36	10.70	15.74
T_4	9295.00 ab	3754.17 abc	5540.83 ab	10.59	18.59	4.21
T_5	8862.49 abc	3858.33 abc	5004.16 abc	14.75	16.34	13.49
T_6	8604.16 bc	3554.17 bc	5049.99 abc	17.23	22.93	12.69
T_7	7060.00 c	2941.67 c	4118.33 c	32.09	36.21	28.80
T_8	9047.50 ab	3650.00 bc	5397.50 ab	12.97	20.85	6.69
T_9	8742.50 abc	3479.17 bc	5263.33 ab	15.90	24.56	9.00
Mean (X)	8909.35	3776.02	5133.33	16.09	20.39	12.69
Standard Deviation (S.D)	865.87	465.03	473.04	6.81	7.96	7.50
Coefficient of Variation (%) (C.V)	9.72	12.32	9.22	42.36	39.06	59.12

Values followed by different letter (s) in the column are significantly different a 5% level

(7060.00Kg/ha) than the other treatments. But this was statistically the same as the biological yields in treatments T_3, T_5, T_6 and T_9. Thus moisture stress at any growth stage, generally reduced the biological yield. The highest loss in biological yield (32.09%) was incurred in treatment T_7. Other treatments had losses in biological yield between 10.59 and 17.23%. The loss was considerably higher in treatment T_7 than in all the other treatments because of the effect of the moisture stress perse as well as the indirect effect of reduced nitrogen availability to and uptake by the plants in this treatment (as evidenced by the shoot nitrogen content in table 7). These consequently depressed growth and yield considerably.

4.2.17 Economic (grain) Yield

The economic yield of the various treatments is presented in table 9. The control treatment, T_1 had a significantly higher economic yield (4611.67Kg/ha) than all the other treatments. But this was statistically the same with the economic yields of treatments T_2, T_3, T_4 and T_5. Contrarily, treatment T_7 had a significantly lower economic yield (2941.67Kg/ha). This was statistically the same as the economic yields of treatments

T_4, T_5, T_6, T_8 and T_9. Thus moisture stress generally reduced economic yield. Whether the reduction was significant or not depended on the level of stress and when it was imposed. The highest loss in economic yield (36.21%) occurred when two irrigations were missed during jointing. The other treatments, which had minus two irrigations at various growth stages, had losses in economic yield between 20.85 and 24.56%. For treatments which had minus one irigation during tillering, jointing, flowering and grain filling stages, the losses in economic yield were 12.90, 10.70, 18.59 and 16.34%, respectively. Losses in economic yield due to moisture stress before anthesis were mainly as a result of reduction in length of ear, number of spikelets/ear and number of grains/ear. However 1000-grain weight and effective tillers also contributed in the minus two irrigations treatments during tillering and jointing. On the other hand, losses in economic yield due to moisture stress after anthesis were mainly as a consequence of reduction in effective tillers and number of grains per ear; plus 1000-grain weight at the grain filling stage only.

4.2.18 Straw Yield

The straw yield for the various treatments is also presented in table 9. The result revealed that the control treatment, T_1 had a significantly higher straw yield (5784.16Kg/ha) than all the other treatments. But this was statistically the same as straw yield of treatments T_2, T_4, T_5, T_6, T_8 and T_9. On the other hand, treatment T_7 where two irrigations were missed during jointing had a significantly lower straw yield (4889.16 Kg/ha). However, this was statistically the same as straw yields of treatments T_2, T_3, T_5 and T_6. Moisture stress, therefore, generally caused losses in straw yield. The highest loss (28.80%) occurred in treatment T_7. This was due to the effect of moisture stress perse as well as the indirect effect of reduced nitrogen availability and uptake which occurred in this treatment. The losses in straw yield of the other treatments were not much and were between 4.21 and 15.74%.

4.2.19 Harvest Index (HI)

The harvest index (HI), expressed as a percentage, for the various treatments is presented in table 10. The result revealed that treatment T_3, where one irrigation was missed during jointing, had a significantly higher HI (45.8%) than the other treatments.

Table 10: Cummulative depth of water applied; harvest index and water use efficiency as affected by different levels of moisture stress at different wheat growth stages.

TREATMENT	No. of irrigations	Cummulative depth of water applied (cm)	Harvest Index (%)	Water use efficiency (Kg/Ha/cm water).
T_1	11	55	44.5 ab	83.85 a
T_2	10	50	43.8 ab	80.33 a
T_3	10	50	45.8 a	82.37 a
T_4	10	50	40.9 ab	75.59 a
T_5	10	50	43.5 ab	77.17 a
T_6	9	45	42.8 ab	78.98 a
T_7	9	45	42.5 ab	65.37 a
T_8	9	45	41.3 ab	81.11 a
T_9	9	45	40.5 b	77.32 a
Mean	9.67	48.33	42.83	78.01
Standard of Deviation (S.D)	0.71	3.54	1.77	5.43
Coefficient of Variation (%)	7.31	7.31	4.13	6.96

Values followed by different letter(s) in the column are significantly different at 5% level.

But this was statistically the same as the HI of all the other treatments except treatment T_9. On the contrary, treatment T_9, which had two irrigations missed during grain filling, had a significantly lower HI (40.5%). This was, however, statistically the same as the HI of all the other treatments except treatment T_3. Thus the result also indicated that Siete cerros wheat cultivar had a fairly constant HI despite periodic moisture stress of different levels at the different growth stages. The same result about constant HI values in Siete cerros wheat cultivar has also been reported by Surma et al. (1980).

4.2.20 Water Use Efficiency (WUE)

Data for total water applied and water use efficiency (WUE) are presented in table 10. The control treatment received 55cm total irrigation water, whereas minus one and two irrigations treatments received 50 and 45cm, respectively. The result indicated that there was no significant difference between WUE of the various irrigation treatments. This could be due to contributing effects of the perched water table. However, the result also indicated that the control

treatment, T_1 had the highest WUE (83.85Kg/ha/cm water). This was followed by treatment T_3 with WUE value of 82.37Kg/ha/cm water. The lowest WUE value (65.37Kg/ha/cm water) was obtained in treatment T_7 due to the reduced nitrogen availability and uptake that consequently reduced growth and yield in this treatment. All the other treatments had WUE values between 75.59 and 81.1'K;/ha/cm water.

The WUE values obtained in this study are similar to those reported by Chari (1979) for moisture stress experiment conducted at Kadawa. Also, the WUE values of all the treatments in the present study except that of treatment T_7 were higher than the highest value (66.00Kg/ha/cm water) reported by Chaudhury and Kumar (1980) for moisture stress experiment on dwarf wheat.

Olugbemi et al. (1979) reported that if planting is at recommended time (usually mid-November to early December) and the recommended cultural practices are observed, Siete cerros wheat cultivar along with other promising varieties in Nigeria could produce at least 4000Kg/ha of grain yield. Again, Olugbemi et al. (1981) reporting on wheat breeding under irrigation at Kadawa, stated that yields were generally low (for reasons not well understood) with a mean value of 3957 Kg/ha.

They also reported that Siete cerros cultivar during the same period yielded a mean of 3500Kg grains/ha. All these results were obtained for the traditional 7-days irrigation interval, with about 5cm depth of water applied during each irrigation. In the present study, where 10-days irrigation interval was used with about 5cm depth of water applied during each irrigation and moisture stress imposed at different growth stages, Siete cerros generally yielded higher than the 3500Kg/ha obtained under the wheat breeding programme. The only exceptions were treatments T_7 and T_9 which suffered stress of minus two irrigations each during jointing and grain filling and whose grain yields were 2941Kg/ha and 3479Kg/ha, respectively. Infact the control treatment of the present study, which had a regular 10-days irrigation interval, yielded 4611.67Kg grain/ha. This excelled the minimum expected 4000Kg grain/ha under good management conditions in Nigeria. Moreover, Siewierski (1980) reported that giving irrigation at 10-days regular interval to early boot and then weekly later until maturity of Siete cerros wheat cultivar under Kadawa conditions, gave the highest yield (4860Kg/ha). This he reported, was significantly higher than the yields

of other treatments considered. This yield (4860Kg/ha) is also only about 250Kg higher than that obtained in the control treatment of the present study. Thus from the foregoing discussion and the observation on soil moisture profile and water table, it becomes very evident that a 10-days irrigation interval could be conveniently used at Kadawa and its environs. Maurya (1981) also reported that 10 to 11 days irrigation interval is quite economical under the high water table conditions of Kadawa provided appropriate drainage is done. It could also be inferred, from the results of yield in the present study, that omitting one irrigation in a regular 10-days irrigation interval schedule could be tolerated during tillering and jointing. However, omitting two irrigations during all growth stages and one during flowering and jointing should be avoided as these would reduced yields considerably.

CHAPTER 5

SUMMARY AND CONCLUSIONS

The effects of moisture stress at tillering, jointing, flowering and grain filling growth stages of semi-dwarf wheat (Triticum aestivum L. em Thell.) were studied under field conditions during the 1980-81 cool dry harmattan season at Irrigation Research Station Kadawa, Nigeria. Wheat plants were subjected to two levels of moisture stress by missing one and two irrigations at each of these four growth stages. These were then compared with a no-stress control treatment which received a regular irrigation at 10-days interval.

The following is the summary of the results and conclusions derived from the study.

1. Soil moisture profile studies revealed that the control treatment experienced no stress as soil moisture tensions were below 0.25 bars at 45cm soil depth. Other treatments experienced slight stress whenever irrigations were missed. Generally, the stress was experienced more in the surface 0-10cm layer than deeper layers of the soil profile. The ground water table fluctuated between 80 and 100cm from the soil surface during the crop growth period. The capillary rise from the perched water table maintained low soil moisture tension at the lower layers of the soil profile.

2. Plant water potential was slightly lowered due to soil moisture stress. The treatments with minus two irrigations were more effective in decreasing the plant water potential. The plants generally gave lower plant water potential values at flowering than jointing. The lowest plant water potential values were observed at about 2.00 p.m. Plant water potential measurements clearly indicated that the water stress in plants appeared to be mild even in treatments of minus two irrigations.

3. Soil moisture stress resulted in higher plant canopy temperatures. However canopy temperatures were generally higher at flowering than jointing.

4. At all growth stages, both levels of moisture stress decreased plant height, dry matter accumulation harvested, leaf area retention, leaf area duration, time to heading and maturity, length of ear, number of spikelets and grains per ear, yield and water use efficiency. However, grain protein content and root: shoot ratio (except for stress treatments during flowering) were generally increased. Effective tillers increased when stress was imposed before, and decreased when stress was imposed after, flowering. Unit grain weight decreased due to stress at only grain filling stage. Ultimately, the

treatments with minus two irrigations caused poorer development of wheat plants and subsequently lower yields than the control and minus one irrigation treatments.

5. The most sensitive (critical) growth stages were jointing and flowering, for treatments of minus two and one irrigations, respectively. The losses in economic yields were 36.2% in the minus two irrigation treatment at jointing and 18.6% in the minus one irrigation treatment at flowering.

6. An omission of two irrigations at all growth stages and one irrigation at flowering and grain filling were deleterious and should be avoided as these caused considerable reduction in yield. Infact, the reductions in grain yields were be between 16.3 and 36.2%. However, omitting one irrigation at tillering and jointing could be tolerated since this reduced grain yield by only 12.9 and 10.7%, respectively.

7. A 10-days irrigation interval could be conveniently used for wheat production at Kadawa and its environs, which experience high water table during the growing season. Provision of appropriate drainage systems to avoid increase in ground table and salinity development will further enhance the suitability of this 10-days irrigation interval.

8. The reduction in yield was not only due to the direct effect of soil moisture stress. In fact, it was also due to the unavailability of the top-dressed fertilizer applied after about one month. Thus, a soil moisture stress due to the omission of two irrigations at any growth stage could be as productive as the control treatment, under a high water table (80-100cm) condition, provided fertilizer is placed in the moist layer to make it available to the plants.

BIBLIOGRAPHY

Acevedo, E., Hsiao, T.C. and Henderson, D.W. (1971). Immediate and Subsequent Growth Responses of Maize Leaves to changes in Water Status. Plant Physiol. 48 : 631-636.

Allaway, W.G., and Mansfield, T.A. (1970). Experiments and observations on the after effect of wilting on stomata of Rumex Sanguineus. Can. J. Bot. 48 : 513-521.

Arnon, I. (1972). Crop Production in Dry Regions. Vol. II: Systematic Treatment of the Principal Crops. A Plant Science Monograph. Pp. 1-72. Leonard Hill, London.

Aspinall, D., Nicholls, P.B. and May, L.H. (1964). The effects of soil moisture stress on the growth of Barley. 1: Vegetative development and grain yield. Aust. J. Agric. Res. 15 : 729-746.

Bagga, A.K., Ghare, M.M., and Asana, R.D. (1973). Physiological analysis of the responses of sorghum hybrids 'CSH1' and CSH2" to rain-fed cultivation. Indian J. Agric. Sci. 43 : 225-229.

Barley, K.P., and Naidu, N.A. (1964). The performance of three Australian Wheat varieties at high levels of nitrogen supply. Aust. J. Exp. Agric. Anim. Husb. 4 : 39-48.

Barnett, N.M. and Naylor, A.W. (1966). Amino Acid and Protein Metabolism in Bermude Grass During Water Stress. Plant Physiol. 41 : 1222-1230.

Barra, H.D. (1968). Determination of Water Deficit in Plant Tissues. In "Water Deficits and Plant Growth" (T.T Kozlowski, ed.), Vol. 2, Pp. 235-368. Academic Press, New York.

Begg, J.E., and Jarvis, P.G. (1968). Photosynthesis in Townsville (Stylosanthis humilis H.B.K.). Agric. Meteorol. 5 : 91-109.

Begg, J.E. and N.C. Turner (1976). Crop Water Deficits. Adv. Agron. 28 : 161-217.

Bhardwaj, R.B.L; Gantam, R.C. and Singh, A. (1971). Irrigate your wheat crop at critical stages of growth. Indian farming 20 (10) : 11-13.

Blum, A. (1973). Components analysis of yield responses to drought of Sorghum hybrids. Exp. Agric. 9 : 159-167.

Boatwright, G.O. and Haas, H.J. (1961). Development and composition of spring wheat as influenced by nitrogen and phosphorus fertilization. Agron. J. 53 : 33-36.

Bond, J.J., Power, J.F., and Willis, W.O. (1971). Soil Water Extraction by N-fertilized Spring Wheat. Agron J. 63 : 280-283.

Boyer, J.S. (1969). Measurement of the Water Status of Plants. Annu. Rev. Plant Physiol. 20 : 351-364.

Boyer, J.S. (1970). Leaf Enlargement and Metabolic Rates in Corn, Soyabean, and Sunflower at various leaf water potential. Plant Physiol. 46 : 233-235.

Boyer, J.S. (1971). Nonstomatal Inhibition of Photosynthesis in Sunflower at Low Leaf Water Potentials and High Light Intensities. Plant Physiol. 48 : 532-536.

Boyer, J.S., and McPherson, H.G. (1975). Physiology of Water Deficits in Cereal Crops. Adv. Agron. 27 : 1 -23.

Brouwer, R. (1963). The Influence of the suction tension of the nutrient solutions on growth transpiration and diffusion pressure deficits of bean leaves. Acta Bot. Nearl. 12 : 248-260.

Brouwer, R. (1966). Root growth of grasses and cereals. Pp. 153-166 in The growth of Cereals and Grasses (Ed. F.L. Milthorpe and J.D. Ivins.) Butterworth, London, xii + 359 pp., illustr.

Brown, K.W. (1974). Calculations of Evapotranspiration from Crop Surface Temperature. Agric. Meteorol. 14 : 199-209.

Bunting, A.H., and Drennan, D.S.H. (1966). Some aspect of the morphology and physiology of cereals in the vegetative phase. Pp. 20-30 in "The Growth of Cereals and Grasses" (Ed. F.L. Milthorpe and I.D. Evins). Butterworth, London, xii + 359 pp., illustor.

Calissendorf, C., and Gardner, W.H. (1972). A temperature - compensated leaf psychrometer for insitu measurements of water potential. In "Psychrometry in Water Relation Research" (R.W. Brown and B.P. Van Haveren, eds), Pp. 224-228. Utah Agric. Exp. Stn., Logan.

Campbell, C.A. (1968). Influence of soil moisture stress applied at various stages of Growth on the yield components of chinook wheat. Can. J. Plant Sci. 48 : 313-320.

Campbell, E.C., Campbell, G.S., and Barlow, W.K. (1973). A Dewpoint Hygrometer for Water Potential Measurement. Agric. Meteorol. 12 : 113-121.

Campbell, G.S. and Campbell, M.D., 1974. Evaluation of a Thermocouple Hygrometer for Measuring Leaf Water Potential insitu. Agron. J. 66 : 24-27.

Chang, J.H. (1968). Climate and Agriculture, Aldine, Chicago.

Chari, A.V. (1980). "Moisture Stress", in Institute for Agricultural Research Progress Report on Irrigation Crop Research Programme, 1979-80; Pp. 48-50.

Chatterton, N.J., Hanna, W.W., Powell, J.B., and Lee, D.R. (1975). Photosynthesis and transpiration of bloom and bloomless sorghum. Can J. Plant Sci. 55 : 641-643.

Choudhury, P.N. and Kumar, V. (1980). The Sensitivity of Growth and Yield of Dwarf Wheat to Water Stress at Three Growth Stages. Irrigation Science 1 : 223-231.

Christian, J.H.B. and Waltho, J.A. (1964). The Composition of Staphylococcus aureus in Relation to the Water Activity of the Growth Medium. J. Gen. Microbiol. 35 : 205-213.

Christie, E.K. (1975). Physiological Responses of Semi-arid Grasses. III. Growth in Relation to Temperature and Soil Water Deficit. Aust. J. Agric. Res. 26 : 447.

Chu, T.M., Aspinall, D. and Paleg, L.G. (1976). Stress Metabolism. VII. Salinity and Proline Accumulation in Barley Aust. J. Plant Physiol. 3 : 219-228.

CIMMYT Report on Wheat Improvement. 1978.

Clement, H.F. (1964). Interaction of Factors affecting Yield. Annu. Rev. Plant Physiol. 15 : 409-442.

Connor, D.J. 1975. Growth, Water Relations and Yields of Wheat Aust. J. Plant Physiol. 2 : 353-366.

Connor, D.J. and Tunstall, B.R. (1968). Tissue Water Relations for Brigalow and Mulga. Aust. J. Bot. 16 : 487-490.

Crafts, A.S. (1939). Solute transport in plants. Science 90 : 337.

Crafts, A.S. (1968). Water Deficit and physiological Processes. In "Water Deficit and Plant Growth (Ed. T.T. Kozlowski) Vol. 2. pp. 85-133 (Academic Press: New York).

Curtis, D.L. and Andrews, D.J. (1966). Annual Report I.A.R. for 1964-65.

Dasberg, S., and Mendel K. (1971). The effect of Soil Water and aeration on seed germination. Journal of Exp. Bot. 22 : 992-998.

Day, A.D. and Intalap, S. (1970). Some effects of moisture stress on the growth of wheat. Agron. J. 62 : 27-29.

Derera, N.F., Marshall, D.R. and Balaam, L.N. (1969). 'Genetic variability in root development in relation to drought tolerance in spring wheats'. Experimental Agriculture, 5 : 327-337.

Dhindsa, R.S., Beasley, C.A., and Ting, I.W. (1975). Osmoregulation in Cotton Fiber. Accumulation of Potassium and Malate during Growth. Plant Physiol. 56 : 394.

Doley, D. and Leyton, L. (1968). Effects of Growth Regulating Substances and Water Potential on the Development of Secondary Xylem in Fraxinus. New Phytol. 67 : 579-594.

Doley, D. and Trivett, N.B.A. (1974). Effects of Low Water Potential on Transpiration and Photosynthesis in Mitchell Grass (Astrebla lappacea). Aust. J. Plant Physiol. 1 : 539-550.

Donald, R.C.M. and Hamblin, J. (1976). Biological yield and harvest index. Adv, Agron. 28 : 361-405.

Duncan, D.B. (1955). Multiple range and Multiple F. test. Biometrics, II : 1-42.

Dunham, R. (1979). Rooting Pattern of Irrigated Wheat in 'History status of Wheat Research in Nigeria'. Samaru Miscellaneous Paper 85 : 49-50.

Ehrler, W.L., Idso, S.B., Jackson, R.D. and Reginato, R.J. (1978). Diurnal Changes in Plant Water Potential and Canopy Temperature of Wheat as Affected by drought. Agron. J. 70 : 999-1004.

El Nadi, A.H. (1969). 'Efficiency of Water use by irrigated wheat in Sudan'. Journal of Agricultual Science, 73 (2) : 261-266.

Falaki, A.M., Ibrahim, A.A. and Asenime, I.O.E. (1979). Water Management of Barley and wheat in northern Nigeria. Paper presented at 6th Nigerian Irrigation Seminar, 26th - 28th September, 1979.

Fischer, R.A. (1970). After-effect of Water Stress on Stomatal Opening Potential. J. Exp. Bot. 21 : 386-404.

Fischer, R.A. (1973). The effect of water stress at various stages of development yield processes in wheat. In "Plant Response to Climatic Factors" (R.O. Slatyer, ed.), Pp. 233-241. UNESCO, Paris,

Fischer, R.A. and Kohn, G.D. (1966a). The Relationship between Evapotranspiration and Growth in the Wheat Crop. Aust. J. Agric. Res. 17 : 255-267.

Fischer, R.A. and Kohn G.D. (1966b). Soil Water Relative Turgidity of Leaves in the Wheat Crop. Aust. J. Agric. Res. 17 : 269-280.

Fischer, R.A., and Kohn, G.D. (1966c). The Relationship of Grain Yield to Vegetative Growth and Post-flowering Leaf Area in the Wheat Crop under conditions of Limited Soil Moisture. Aust. J. Agric. Res. 17 : 281-295.

Fischer, R.A. Sanchez, M. and Syme, J.R. (1977). Pressure chamber and air flow proporometer for rapid field indication of water status and stomatal condition in wheat. Expl. Agric. 13(4) : 241-251.

Florell, V.H., and Faulkner, B. (1934). Growth of Wheat during the heading period. J. Amer. Soc. Agron. 26 : 954-964.

Frank, A.B., Harris, D.G. and Willis, W.O. (1977). Plant water relationships of spring wheat as influenced by shelter and soil water. Agron. J. 69 : 906-910.

Frank, A.B., Power, J.F. and Willis, W.O. (1973). Effect of Temperature and Plant Water Stress on Photosynthesis, Diffusion Resistance, and Leaf Water Potential in Spring Wheat. Agron. J. 65 : 777-780.

Friend, D.J.C. (1965). Tillering and leaf production in wheat as affected by temperature and light intensity. Can. J. Bot. 43 : 1063-1076.

Gallagher, J.N., Biscoe, P.V. and Scott, R.K. (1975). Barley and its environment. V. Stability of grain weight. J. Appl. Ecol. 12 : 319-336.

Ganyushina, E.V. and Lazarchik V.M. (1971). Effect of excessive soil moisture at different stages of spring wheat growth on its biochemistry and yields. Vestnik Moskovskogo Universiteta, 6 Biologiya, Pochvove denie (1971) No. 5, 1188-120 (cited in Field Crop Abstracts, 1973).

Gangopadhyaya, M. and Sarker, R.P. (1965). Influence of rainfall distribution on the yield of wheat crop! Agric. Meteorol. 2 : 331.

Garner, W.R. and Ehlig, C.F. (1965). Physical aspects of the internal water falations of plant lwaves. Plant Physiol. 40 : 705-710.

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

Garwood, E.A. and Williams, T. E. (1967). Growth, Water use and nutient uptake from the subsoil by grass swards. J. Agric. Sci. 69 : 125-130.

Gates, C.T. (1955a). The response of the young tomato plant to a brief period of water shortage. I : The whole plant and its principal parts. Aust. J. Biol. Sci. 8 : 196-214.

Gates, C.T. (1955b). The response of the young tomato plant to a brief period of water shortage. II : The individual leaves. Aust. J. Biol. Sci. 8 : 215-230.

Gates, C.T. (1957). The responses of the young tomato plant to a brief period of water shortage. III : Drifts in nitrogen and Phosphorus. Aust. J. Biol. Sci. 10 : 125-146.

Gates, C.T. (1964). The effect of water stress on plant growth. J. Aust. Inst. Agric. Sci. 30 : 3-22.

Gates, C.T. (1968). Water deficits and growth of herbaceous plants. In "Water Deficits and Plant Growth" (T.T. Kozlowski, ed.) Vol. 2, pp. 135-190. Academic Press, New York.

Gates, C.T. (1974). Water Shortage and Agriculture: Some Responses. J. Aust. Inst. Agric. Sci. 40 : 121-142.

Gerakis, P.A., Guerrero, F.P. and Williams, W.A. (1975). Growth, Water relations and nutrition of three annuals as affected by drought. J. Appl. Ecol. 12 : 125.

Ghosh, K.K., Jana, P.K. and Maity, S.P., (1975). Ingluence of Soil Moisture Tension and Nitrogen on growth dynamics in wheat. Indian Agriculturalist 19 (1) : 51-57.

Giha, O.H. (1977). Fungi associated with foot and root-rot disease of irrigated wheat in the northern states of Nigeria. (P ANS 22 (4) : 1976, pp. 479-487).

Glover, J. (1959). The apparent behaviour of Maize and Sorghum Stomata during and after drought. J. Agric. Sci. 53 : 412-416.

Greacen, E. L. and Oh, J.S. (1972). Physics of root growth. Nature (London), New Biol. 235 : 24-25.

Greenway, H., Hughes, P.G. and Klepper, B. (1969). Effects of Water Deficits on Phosphorus nutrition of Tomato Plants. Physiol. Plant 22 : 199-207.

Greenway, H. and Klepper, B. (1969). Relation between Anion Transport and Water Flow in Tomato Plants. Physiol. Plant. 22 : 208-219.

Hearn, A.B. and Wood, R.A. (1964). "Irrigation control ecperiments on dry season crops in Nyasaland; Empire Journal of Experimental Agriculture. 32 : 1-17.

Hsiao, T.C. (1970). Rapid Changes in Levels of Polyribosomes in Zea mays in Response to Water Stress. Plant Physiol. 46 : 281-285.

Hsiao, T.C. (1973). Plant responses to water stress. Annu. Rev. Plant Physiol. 24 : 519-570.

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

Hsiao, T.C., Acevedo, E. and Handerson, D.W. (1970). Maize Leaf Elongation: Continuous Measurements and Close Dependence on Plant Water Stress. Science 168 : 590-591.

Hsieh, J.J.C., Enfield, C.G. and Hungate, F.P. (1972). In "Psychrometry in Water Relations Research" (R.W. Brown and B.P. Van Haveren, eds.), pp. 154-158. Utah Agric. Exp. Stn., Longan.

Hsieh, J.J.C. and Hungate, F.P. (1970). Temperature Compensated Peltier Psychrometer for measuring Plant and soil Water Potentials. Soil Sci. 110 : 253-257.

Ike, I.F. and Thurtell, G.W. (1981). Osmotic adjustments in indoor grown cassava in response to water stress. Physiol. Plant. 52 : 257-262.

Iljin, W.S. (1957). Drought resistance in Plant Physiological processes. Annu. Rev. Plant Physiol. 8 : 257-274.

Jackson, I.J. (1977). Climate, Water and agriculture in the tropics. Longman, London and New York.

Jackson, M.L. (1962). Nitrogen determinations for Soils and plant tissues. Soil Chem. Anal. pp. 190. Constable and Co. Ltd. 10 Orange St., London W.C.2.

Jarvis, P.G. (1975). In "Heat and Mass Transfer in the Biosphere". I. Transfer Processes in Plant Environment (D.A. de Uries and N.H. Afgan, eds) pp. 369-394. Halsted Press, Wash., D.C.

Jarvis, P.G., and Jarvis, M.S. (1963). The Water relations of tree seed seedings. IV. Some aspects of the tissue water relation and drought resistance. Physiol. Plant 16 : 501-516.

Jennings, A.C. (1961). Determination of the nitrogen content of cereal grain by colometric methods. Cereal Chem. 38 (6) : 467-469.

Johnson, H.B. (1975). Plant pubsscence : An ecological perspective Bot. Rev. 41 : 233-258.

Johnson, R.R., Frey, N.M. and Moss, D.N. (1974). Effect of water stress on photosynthesis and transpiration of flag leaves and spikes of barley and wheat. Crop Science 14 : 728-731.

Jones, R.J., and Mansfield, T.A. (1970). Supression of stomatal opening in leaves treated with abscisic acid. J. Exp. Bot. 21 : 714-719.

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.

Karchi, Z. (1963). (Economize seeds in Winter Cereals - in Hebrew) Hassadeh 43 : 397-399, 557-560.

Klepper, B. and Barrs, H.D. (1968). Effects of Salt Secretion on Psychrometric Determinations of Water Potential of Cotton Leaves. Plant Physiol. 43 : 1138-1140.

Kramer, P.J. (1959). The role of Water in the Physiology of Plants. Adv. Agron. 11 : 51-70.

Kramer, P.J. (1963). Water Stress and Plant Growth. Agron. J. 55 : 31-15.

Kriedemann P.E., and Loveys, B.R. (1975). Hormonal influences on Stomatal Physiology and photosynthesis. In "Environmental and Biological Control of Photosynthesis" (R. Marcelie, ed.), pp. 227-236. Junk, The Hague.

Kriedemann, P.E. and Loveys, B.R. (1974). Hormonal mediation of plant responses to environmental stress. R. Soc. N.Z., Bull. 12 : 461-465.

Kriedemann, P.E. and Loveys, B.R. and Downton, W.J.S. (1975). Internal Control of Stomatal Physiology and Photosynthesis. II. Photosynthetic Responses of Phaseic Acid. Aust. J. Plant Physiol. 2 : 553-567.

Krishnan, A. (1972). Agroclimatological research problems related to dry land agriculture. Indian Farming 21 (11) : 22-24.

Kumar, V. (1979). Water Stress and Crop Growth. Agronomy Departmental Seminar given on 27th July, 1979.

Kumar, V. and J.Y. Yayock (1980). Growth stages and Productivity of wheat at two dates of planting at Samaru. Paper presented at 7th National Irrigation Seminar at Bagauda Lake Hotel, Kano, September, 8-12.

Lehane, J.J. and Staple, W.J. (1962). Effects of soil moisture tension on growth of wheat. Can J. Soil Sci. 42 : 180-188.

Lehane, J.J. and Staple, W.J. (1965). Influence of Soil texture, depth of soil moisture storage, and rainfall distribution on wheat yields in south-western saskatchewan. Can J. Soil Sci. 45 : 207-219.

Levit, J. (1973). "Response of Plants to Environmental Stresses", Academic Press, New York.

Lewis, D. H. and Smith, D.C. (1967). Sugar alcohols (Polyols) in fungi and green plants. I Distribution, Physiology and metabolism. New Phytol. 66 : 143-184.

Little, C.H.A. and Eidt, D.C. (1968). Effects of abscisic acid on bud break and transpiration in woody species. Nature (London) 220: 498-499.

Livne, A. and Vaadia, Y. (1972). Water Deficits and Hormone Relations. In "Water Deficits and Plant Growth" (T.T. Kozlowski, ed), Vol. 3, pp 255-275. Academic Press, New York.

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. L

Ludlow,.M.M. (1975). In "Environmental and Biological control of Photosynthesis" (R. Marcelle, ed.), pp 123-134. Junk, The Hague.

Ludlow, M.M. and Ng, T.T. (1974). Water Stress suspends leaf ageing. Plant Sci. Lett. 3 : 235-240.

Maurya, P. R. (1981). Water balance studies along with vertical salt movement at varying amount of irrigation water. I.A.R. Progress Report on Irrigation Research Programme, 1980-81, p. 53-57.

May, L.H., Milthorpe, E.J. and Milthorpe F.L. (1962). Pre-sowing Hardening of Plants to drought. An appraisal of the contribution by P.A. Genkel. Field Crop Abs. 15 : 93-98.

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

McCree, K.J. and Davus, S.D. (1974). Effects of water stress and temperature on leaf size and on size and number of epidermal cells in grain sorghum. Crop Sci. 14 : 751-755.

McFadden, E.S. and Sears, E.R. (1946). "The origin of Triticum Spelta and its free-threshing hexaploid relatives. J. Hered. 37 (3) : 81-89.

Meeuwig, R.O. (1972). A low-cost thermocouple Psychrometer recording system. In "Psychrometry in Water Relation Research" (R.W. Brown and B.P. Van Haveren eds.), pp. 131-135. Utah Agric. Exp. Stn., Logan.

Meidner, H., and Edwards, M. (1975). Direct Measurements of turgor pressure potentials of guard cells. J. Exp. Bot. 26 : 319-330.

Meiri, A., Plant, Z. and Shimshi, D. (1975). The use of the pressure chamber Technique for Measurement of the water potential of Transpiring plant organs. Physiol. Plant. 35 : 72-76.

Milborrow, B.V. (1974). The chemistry and physiology of abscisic acid. Ann. Rev. Plant Physiol. 25 : 259-307.

Millar, B.D. and Denmead, O.T. (1976). Water relations of wheat leaves in the field. Agron. J. 68 : 303-307.

Millar, A.A., Duysen, M.E. and Wilkinson, G.E. (1968). Internal Water Balance of Barley Under Soil Moisture Stress. Plant Physiol. 43 : 8968-972.

Millar, B.D. and Hansen, G.K. (1975). Exclusion Errors in Pressure chamber Estimates of leaf water potential. Ann. Bot., 39:915-20

Milthorpe, F.L. (1950). Changes in the drought resistance of wheat seedling during germination. Ann. Bot., 14 : 79-89.

Musick, J.T. and Dusek, D.A. (1980). Planting Dates and Water Deficit Effects on Development and Yield of Irrigated Winter Wheat. Agron. J. 72 (1) : 45-52.

Naylor, A.W. (1972). Water Deficit and Nitrogen Metabolism. In "Water Deficits and Plant Growth" (T.T. Kozlowski, ed.) Vol. 3 pp. 241-254. Academic Press, New York.

Neumann, H.K., and Thurtell, G.W. (1972). A peltier cooled thermocouple dew-point hygrometer for in situ measurement of water potentials. In "Psychrometry in Water Relations Research" (R.W. Brown and B.P. Van Haverm, eds.), pp. 103-112. Utah Agric. Exp. Stn., Logan.

Neumann, H.H. Thurtell, G.W. Stevenson, K.R. and Beadle, C.L. (1974). Leaf Water content and potential in corn sorghum, soybean and sunflower. Can J. Plant Sci. 54:185-195.

Ng, T.T. Wilson, J.R. and Ludlow, M.M. (1975). Influence of Water Stress on Water Relations and Growth of a Tropical (C_4) Grass, Panicum maximum var, trichoglume Aust. J. Plant Physiol. 2 : 581-595

Nicholls, P.B. and May, L.H. (1963). Studies on the growth of the barley apex. I. Interrelationships between primordium formation, apex length and spikelet development. Aust. J. Biol. Sci. 16 : 561-571.

Nulsen, R.A. and Thurtell, G.W. (1978). Recovery of Conrn Leaf Water Potential After Severe Water Stress. Agron J. 70 (6) : 903-906.

Nuttonson, M.Y. (1955). Wheat climate relations and the use of phenology in ascertaining the thermal and photothermal requirements of wheat. Amer. Inst. Crop Ecology. Washington.

Nwa, E.U. (1978). Groundwater Table in Irrigated Areas. IAR, Progress Report on Irrigated Crop Research Programme, 1977-78; pp. 78 - 81.

Ojanuga, A.G., Valette, J. and Khawaja, I.A. (1979). Seventh Annual Joint Meeting of the National Soil Correlation Committee and Soil Science Society of Nigeria, Kano, 21st - 27th October, 1979.

Olugbemi, L.B. (1973). Wheat Research in Nigeria. Proceedings of the Fourth F.A.O./Rockefeller Foundation, Wheat Seminar, Tehran 21st May -5th June, 1973 : 92-96.

Olugbemi, L.B. (1980) Bread: The road to Self-sufficiency in Nigeria. Ahmadu Bello University public lecture, 12th March, 1980.

Olugbemi, L.B., Orakwue, F.C. and Aguda, E.V. (1981). Wheat Breeding under Irrigation: 1980/81 Season. I.A.R. Progress Report on Irrigation Research Programme, 1980-81, Pp. 6-11.

Olugbemi, L.B. Redden, R. and Aguda, E.V. (1979). "Variety Screening" in History and Status of Wheat Research in Nigeria. Samaru Miscellaneous paper 85 : 3-16.

Osmond, C.B. (1963). Oxalates and Ionic Equilibria in Australian Salt bushes (Atriplex). Nature (London) 198 : 503-504.

Passioura, J.B. (1976). Physiology of Grain Yield in Wheat Growing on Stored Water. Aust. J. Plant Phyiol 3 : 559-565.

Pearson, R.W. (1966). Soil Environment and Root Development. In "Plant Environment and Efficient Water Use". (eds. W.H. Pierre, D. Kirkham, J. Pesek and R. Shaw.) p. 95 (Am. Soc. Agron. and Soil Sci. Soc. Am. : Madison, Wisconsin.

Peterson, R.F. (1965). Wheat : Botany, cultivation, and utilization. World Crops Books (Ed. N. Polunin). Leonard Hill, London, & Interscience, New York, xxiv + 422 pp. illustr.

Petinov, N. S. (1965). The Physiology of irrigated agricultural plants: an abstract with commentary. Field Crop Abstr. 18 : 1-8.

Raschke, K. (1975). Stomatal action. Annu. Rev. Plant Physiol. 26 : 209-340.

Redden R. (1979). In 'History and Status of Wheat Research in Nigeria'. Samaru Miscellanous Paper 85 : 1-2.

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.

Reitz, L.P. (1974). Breeding for more effective Water Use. Is it real or a mirage? Agric. Meteorol. 14 : 3-11.

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

Ritchie, G.A. and Hinchley, T.M. (1975). The Pressure Chamber as and Instrument for Ecological Research Adv. Ecol. Res. 9 : 165-254.

Salter, P.J. and Goode, J.E. (1967). "Crop Responses to Water at Different Stages of Growth". Common W. Agric. Bur., Farnham Royal, Bucks, England.

Sanchez-Diaz, M.F. and Kramer, P.J. (1971). Behaviour of Corn and Sorghum under Water Stress and during Recovery. Plant Physiol. 48 : 613-616.

Schneider, G.W. and Childers, N.F. (1941). Influence of Soil moisture on photosynthesis, respiration and transpiration of apple leaves. Plant Physiol. 16 : 565-583.

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

Shollenberger, J.H., Curtis, J.J. Jaeger, C.M., Earle, F.R. and Bayles, B.B. (1949). Effect of environment on the nitrogen content of wheat kernels. Tech. Bull. U.S. Dept. Agric., 1995, 33 pp., Illustr.

Shutt, F.T. and Hamilton, S.S. (1934). The quality of wheat as influenced by environment. Emp. J. Exp. Agric., 2 : 119-138.

Siewierski, E. (1980). Irrigation Frequency and Amount of Water Use Verses Ground Water Table. I.A.R, Progress Report on Irrigated Crop Research Programme, 1979-80; P. 54-60.

Simpson, J.R., and Lipsett, J. (1973). Effects of Surface moisture supply on the subsoil nutritional requirement of lucerne (Medicago sativa L.). Aust. J. Agric. Res. 24 : 199-209.

Singh, T.N., Aspinall, D. and Paleg, L.G. (1972). Proline accumulation and varietal adaptibility to drought in barley: A potential metabolic measure of drought resistance. Nature (London), New Biol. 236, 188-190.

Singh, T.N. Paleg, L.G. and Aspinall, D. (1973). Stress Metabolism. III. Variation in response to water deficit in the barley plant. Aust. J. Biol. Sci. 26 : 65-76.

Single, W.V. (1964). The influence of nitrogen supply on the fertility of the wheat ear. Aust. J. Exp. Agric. Annim. Husb., 4 : 165-160.

Slatyer, R.O. (1967). "Plant-Water Relationships". London and New York, Academic Press 366 pp.

Slatyer, R.O. (1973). The effect of internal Water status on plant growth, development and yield. In "Plant Response to climatic Factors" (R.O. Slatyer, ed,) pp. 177-191. UNESCO, Paris.

Slatyer, R.O. and Taylor, S.A. (1961). Terminolgy in Plant-and-Soil-water relations. Nature 187 : 922.

Slavik, B. (1974). "Methods of Studying Plant Water Relations". Springer-Verlag, Berlin and New York.

Snedecor, G.W. and Cochran, W.G. (1967). Statistical Methods, 6th ed. Lowa State Univ. Press. AMOS, Iowa, U.S.A.

Sprent, J.I. (1976). Water Deficits and Nitrogen-fixing Root Nodules. In "Water Deficits and Plant Growth" (T.T. Kozlowski, ed.) Vol. 4, pp Academic Press, New York.

Stalfelt, M.G. (1955). The stomata as a hydrophotic regulator of the water deficit of the plant. Physiol. Plant. 8 : 572-593.

Stowrier, R.R. (1965). The influence of water on wheat yield, plant nitrogen uptake, and Soil mineral nitrogen conentration. Aust. J. Exp. Agric. Anim. Husb. 5 : 310-316.

Strebeyko, P. Wislocka, M. and Kzywack, T. (1963). Dynamics of Growth and development in spring wheat. Physiologia Pl., 16 : 359-367.

Sullivan, C.Y. (1971). Techniques for measuring plant drought stress. In "Drought Injury and Resistance in Crops" (K.L. Larson and J.D. Eastin, eds.), Publ. No. 2, pp. 1-18. Crop Sci. Soc. Amer. Madison, Wisconsin.

Surma, D.A. Gupta, U.S. and Olugbemi, L.B. (1980). The possibility of Economizing Irrigation Water in two distinct Varieties of wheat. Paper present at the 7th National Irrigation Seminar at Bagauda Lake Hotel Kano. September, 8-12, 1980.

Tanner, C.B., 1963. Plant Temperature. Agron, J. 55 : 210-211.

Tempest, D.W., Meers, J.L. and Brown, C.M. (1970). Influence of Environment on the Content and Composition of Microbial Free Amino Acid Pools. J. Gen. Microbiol. 64 : 171-185.

Thorne, G.N. (1965). Photosynthesis of ears and flag leaves of wheat and barley. Ann. Bot. 29 : 317-329.

Thorne, G.N. (1966). Physiological aspects in grain yield of cereals. In "The Growth of Cereals Grasses" (F.L. Milthorpe and J.D. Ivins, eds.), pp. 88-105. Butterworth, London

Troughton A. (1957). The underground organs of herbage grasses. Distribution of roots in the soil. Bull. Common W. Bur. Pasture Field Crops. Hurley Berks 44 : 41-46.

Turner, N.C. (1966). Grain production and water use of wheat as affected by plant density, defoliation and Water Status. Ph.D. Thesis, University of Adelaide, Australia.

Turner, N.C. (1974a). Stomatal responses to light and water under field conditions. R. Soc. N.Z., Bull. 12 : 423-432.

Turner, N.C. (1974b). Stomatal Behaviour and Water Status of Maize, Sorghum and Tobacco under Field Conditions. Plant Physiol. 53 : 360-365.

Turner, N.C. and Begg, J.E. (1978). Responses of Pasture plants to Water Deficits. Plant Relations in Pastures (ed. J.R. Wilson) Pp. 50-66. CSIRO, Melbourne.

Turner N.C. and Long, M.J. (1980). Errors arising from Rapid Water Loss in the Measurement of Leaf Water Potential by the Pressure Chamber Technique. Aust. J. Plant Physiol., 7 : 527-537.

Tyree, M.T., Dainty, J. and Hunter, D.M. (1974). The water relations of hemlock (Tsuga canadensis). IV. The dependence of the balance pressure on temperature as measured by pressure - bomb technique. Can. J. Bot. 52 : 973-978.

Vaadia, Y. Raney, F.C. and Hagan, R.M. (1961). Plant Water Deficits and physiological processes. Annu. Rev. Plant Physiol. 12 : 265-292.

Wardlaw, I.F. (1967). The effect of water stress on translocation in relation to photosynthesis and growth. I. Effect during grain development in wheat. Aust. J. Biol. Sci. 20 : 25-39.

Wardlaw, I.F. (1969). The effects of waters stress on translocation in relation to photosynthesis and growth. II. Effects during leaf development in Lolium temuletum. Aust. J. Biol. Sci. 22 : 1-16.

Wardlaw, I.F. (1971). The early stages of grain development in wheat: Response to water stress in a single variety. Aust. J. Biol. Sci. 24 : 1047-1055.

Wiebe, H.H. Campbell, G.S., Gardner, W.H. Rawlins, S.L., Cary, J.W. and Brown, R.W. (1971). Measurement of Plant and Soil Water Status. Utah, Agric. Exp. Stn., Bull. 484 : 1-71.

Wilson, A.M. (1971). Amylase Synthesis and Stability in Crested Wheat grass seeds at Low Water Potentials. Plant Physiol. 48 : 541-546.

Wilson, J.H. (1966). The influence of water on yield components of wheat. Rhod. J. Agric. Res. 7 (2) : 129-133.

Wilson, J.R. and Ng, T.T. (1975). Influence of Water Stress on Parameters Associated with Herbage Quality of Panicum maximum var. trichoglume. Aust. J. Agric. Res. 26 : 127-136.

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 (London) 224 : 719-720.

Yang, S.J. and deJong E. (1968). Measurement of internal water stress in wheat plants. Can. J. Plant Sci. 48 : 89-95.

Yoshida, S. (1972). Physiological aspects of grain yield. Annu. Rev. Plant Physiol. 23 : 437-464.