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Responses of Grain Sorghum to Variable Water Supply under High and Normal Irrigation Frequencies

By

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TABLE OF CONTENTS

Page

I. INTRODUCTION 1

II. LITERATURE REVIEW 4

A. Soil Water Extraction by Sorghum 4

B. Measurements of Plant Water Status 7

C. Plant Responses to Water Stress 10

D. Sorghum Yield as Affected by Water Supply. 13

E. Effects of Irrigation Frequency on Crop Yields 15

III. MATERIALS AND METHODS 18

A. Crop Culture, Irrigation and Plot Layout 18

A.1 Experiment I 19

A.2 Experiment II 21

B. Measurements 22

B.1 Measurement of Water Applied in the Line Source Sprinklers 22

B.2 Soil Water Content 22

B.3 Leaf Area 23

B.4 Ground Cover 23

B.5 Leaf Water Potential 24

B.6 Leaf Diffusive Resistance 25

B.7 Relationship Between Relative Water Content (RWC) and Leaf Ψ 25

B.8 Panicle Size 27

B.9 Dry Matter Accumulation 27

Page

B.10 Yields and Yield Components 27

IV. RESULTS AND DISCUSSION 29

A. Water Applied in Experiment I 29

B. Soil Water Depletion 29

B.1 Soil Water Extraction Patterns in Experiment I 29

B.2 Soil Water Extraction Patterns in Experiment II 35

B.3 Evapotranspiration (ET) in the Different Treatments 37

C. Plant Responses 39

C.1 Vegetative Growth 39

C.1.1 Leaf Area Development. 39

C.1.2 Radiation Interception by the Crop canopy 43

C.1.3 Main Stem Leaf Area Index and Ground Cover Relationships. 43

C.2 Plant Water Status 49

C.2.1 Diurnal Evolution of Leaf Water Potential (Ψ) in Early Stages of Growth 49

C.2.2 Treatment Effects on Leaf Ψ. . 52

C.2.3 Seasonal Evolution of Leaf Water Potential (Ψ) 54

C.2.4 Relation Between Relative Water Content (RWC) and Leaf Water Potential (Ψ). 57

C.2.5 Diurnal Changes in Leaf Diffusive Resistance (r_ℓ) and the Relation Between r_ℓ and Leaf Ψ 60

Page

C.3 Panicle Development 63

C.3.1 Panicle Development Affected by Water Stress 63

D. Dry Matter Accumulation 67

D.1 Dry Matter Accumulation in Experiment I 67

D.2 Dry Matter Accumulation in Experiment II 72

E. Yield Response Functions as Affected by the Irrigation Regime and Yield Components 72

E.1 Relationship Between Yield and Total Seasonal ET 74

E.2 Yields and Yield Components in Experiment I 79

E.3 Yields and Yield Components in Experiment II 80

E.4 Tiller Contribution to Grain Yields . 80

V. SUMMARY AND CONCLUSIONS 85

VI. LITERATURE CITED 90

INIA
BIBLIOTECA

I. INTRODUCTION

There is ample evidence in the literature to demonstrate that total dry matter and harvestable crop yields decrease as the evapotranspiration decreases below its potential rate. In semi-arid regions where rainfall is insufficient to meet the evapotranspirative demand, irrigation is needed to maintain ET at the potential rate, thus maximizing crop productivity.

At present, the normal irrigation practices are oriented towards irrigating as infrequently as possible while attempting to maximize economic yields. An increase in irrigation frequency above that needed to satisfy the allowable water depletion of a given soil seems unjustified because of increased irrigation costs. However, this is not a factor in the modern, permanent, fully automated irrigation systems. Rawlins and Raats (1975) have recently advocated the use of high frequency irrigation as a means of minimizing crop water stress and percolation losses. In this technique, water is applied at very frequent intervals with amounts equivalent to the current evapotranspirative demand.

An additional development along the same line is the use of deficit high-frequency irrigation (Miller and Aarstad, 1976). Here, the amounts of water applied at frequent intervals are less than the ET, presumably resulting in crop water deficits. Surprisingly, Miller (1977) has shown that harvestable yields of bean, wheat and sugarbeets were maintained under deficit-high-frequency irrigation even though ET was reduced below that of treatments where the ET demand was fully met. Some of these results are open to question since Miller (1977) did not make any comparisons between high and normal irrigation frequencies, and, furthermore, the total dry matter yields of his experiment were not reported. Also, there are some uncertainties in the contribution of the stored soil water at planting time to seasonal ET in some of the treatments.

Sorghum has long been considered a drought resistant crop. It is said to have a more efficient root system than other cereals and more effective control of stomata behaviour (Slatyer, 1955). The topic of grain sorghum responses under variable water supply has been the subject of many studies (Blum, 1973; Lewis _et_ _al_. 1974; Fereres, 1976; Fisher _et_ _al_. 1976; Stanhill _et_ _al_. 1976). Several studies conducted at Davis, California (Vega, 1972; Fereres, 1976) have shown that there was no significant difference in the grain yield of irrigated and unirrigated sorghum, provided that the deep loam soil profile was fully charged at planting time.

In view of these results, and the apparent advantages of deficit, high-frequency irrigation in decreasing ET while still maintaining yields, it is interesting to study whether this is the case in grain sorghum under a situation where the contribution of stored soil water to ET is kept at a minimum.

Therefore, the objectives of this research were to study the effects of the irrigation regime on the yield response function of grain sorghum to variable water supply. To obtain a better understanding of the mechanisms responsible for the yield responses, parameters such as main stem leaf area index, ground cover, leaf water potentials, stomatal opening, dry matter accumulation, yields and yield components were monitored throughout the growing season. Irrigation treatments include high frequency (irrigations each other day) and normal frequency irrigations each 10 to 14 days), flood and sprinkler irrigations and a full range of water applied, varying from extremely deficient to slightly excessive.

II. LITERATURE REVIEW

A. Soil Water Extraction by Sorghum

A primary function of a root system is the supply of water and nutrients to the plant shoot (Brouwer, 1965). The shoot, in turn, supplies assimilates to roots which are required for growth and maintenance. Root growth is also dependent on environmental factors such as temperature, aeration, water content, and mechanical impedence of the soil (Peters and Runkles, 1974).

Sorghum plants have a vigorous and deep root system (Miller, 1916; Vega, 1972); this has been often invoked as one reason for the ability of this crop to withstand drought. For instance, Miller (1916) and Martin (1930), indicated that sorghum was more drought-resistant than corn because sorghum had twice as many secondary roots per unit of primary root as did corn. However, Vega (1972), in a study comparing root growth of unirrigated corn and sorghum, found few differences in root development between the two species. In that study, sorghum developed roots to a depth of 2.4 m, in an open Yolo loam soil at Davis when the profile was wetted throughout at the beginning of the growing season. Ajmad (1975) confirmed Vega's results for unirrigated sorghum, finding that sorghum roots extracted water to a depth of 2.7 m. Fereres (1976) observed similar patterns of water extraction in unirrigated sorghum also at the University of California at Davis.

In the absence of rain or irrigation, plant growth is dependent on the water stored in the soil. The utilization of water by the plant is determined by the rate of water movement to the root surface and the rate at which roots are growing into the moist soil. Therefore, the water supply to a crop will be determined by the interaction of root growth, hydraulic conductivities of the soil and water potential gradients (Hsiao et al., 1976a). It has been shown by Vega (1972), Ajmad (1975), and Fereres (1976), working in Yolo loam soil that the water stored in a fully charged profile at planting time (around 35 to 40 cm of water depth; Ajmad, 1975) was sufficient to grow a sorghum crop to maturity without reducing grain yields significantly below those of a well-irrigated treatment. This was due in part by the continuous exploration of moist subsoil layers by sorghum roots. Unfortunately, the above mentioned authors did not study root growth under conditions of partially dry subsoil.

It is generally established that root growth decreases as soil water potential decreases (Peters, 1957 and Kmoch et al., 1957). For instance, Gingrich and Russell (1957), studying corn root growth as affected by water stress, found that root elongation rate was very sensitive to the soil water potential in the range -1/2 to -3 bars, and decreased linearly in the -3 to -12 bars range. However, a reduction in root growth produced by moderate water stress will not inhibit the essential functions of a root system such as water and nutrient absorption (Peters and Runkles, 1974). When soils are partially wetted, the hydraulic conductivity of the soil is usually too small to support significant water movement to the root over great distances, so extension of roots into moist regions of the soil profile is necessary for absorption of water (Cadwell, 1976). In recent work, Taylor and Klepper (1975), conducting an experiment with cotton at the Auburn rhizotron, also found that rooting density and water uptake rate per unit root length decreased as the soil water content decreased. Portas and Taylor (1976) found that some root growth occurred in corn and tomato at soil water potentials more negative than -40 bars. Hunter and Kelley (1946), growing corn in tar paraffin pots filled with moist soil and surrounded by air-dry soil, surprisingly found that corn roots penetrated the wall of the pot and extended in the dry soil which presumably was at 1000 bars tension. However, Hendrickson and Veihmeyer (1931) found that bean and sunflower roots grew only a few millimeters in a soil at or below the permanent wilting point. Roots were found to adjust osmotically between soil water potentials of -2.8 and -8.3 bars, thus maintaining a nearly constant turgor in root cells through buildups of solutes regardless of the variation in soil water potential (Greacen and Oh, 1972). From the above, it can be tentatively concluded that some root growth may occur at very low soil water content, although its significance in terms of coping with drought stress has not been clearly established.

B. Measurement of Plant Water Status

Hsiao (1973) has pointed out some parameters which can be used as indicators of the plant water status. Among them, leaf water potential (Ψ), which is the chemical potential of water on a volume basis relative to a standard reference state, is the most commonly used to indicate plant water status.

The total Ψ is the sum of the following components: Solute potential (Ψ_s), pressure potential (Ψ_p) and matrix potential (Ψ_m) (Kramer, 1969). Plant Ψ_s, due to the high solute concentration in the plant cell is considered a major component of total Ψ. Plant Ψ_p, which includes the hydrostatic pressure responsible for turgor is also a significant component of total Ψ. Plant Ψ_p is positive when the plant is under high water status and decreases to a negligible value as plant tissues dehydrate (Hsiao, 1973). Plant Ψ_m may be neglected for mesophytic plants (Boyer, 1967).

Leaf Ψ can be measured by several methods as reviewed by Barrs (1968). Among them, thermocouple psychrometry is widely used. This technique uses a thermocouple psychrometer of the Peltier type (Spanner, 1951) or the wet-loop type

(Richard and Ogata, 1958). However, the pressure chamber technique (Scholander et al., 1965) has been used recently by many workers to measure leaf Ψ, assuming that xylem Ψ_s is negligible (Boyer, 1967; De Roo, 1969; Barrs et al., 1970; Blum, Sullivan and Eastin, 1973). The pressure chamber method is based on sealing a leaf inside a chamber where pressure is increased until the sap menisci appear at the surface of the severed xylem vessels (Blum, Sullivan, and Eastin, 1973). This technique, in contrast with the thermocouple psychrometry, is simple and can be easily used under field conditions (De Roo, 1969).

De Roo (1969) and Blum, Sullivan and Eastin (1973), estimated leaf Ψ of sorghum with the pressure chamber and compared this technique to thermocouple psychrometry. De Roo (1969) found very good agreement between both methods. In contrast, the results obtained by Blum et al. (1973) showed that pressure chamber readings in sorghum could not be directly used as an accurate estimate of leaf Ψ, but should be corrected according to a calibration against thermocouple psychrometer. Sample preparation, rate of pressure increase and high values of xylem Ψ_s may be reasons for the discrepancy between the two techniques (Waring and Cleary, 1967). Blum et al. (1973) found that xylem Ψ_p was a better estimate of leaf Ψ in sorghum when the rate of pressure increase was changed from .33 to .38 bars sec^{-1}. Therefore, the pressure chamber can be a very useful field technique, but a calibration against thermocouple psychrometry measurements of Ψ may be needed if accurate estimates of leaf Ψ are required.

Another useful indicator of plant water status is relative water content (RWC), which is defined as the percentage of water content of the tissue at sampling relative to the water content in the tissue when fully turgid. There is a direct relationship between RWC and Ψ, although this relationship is dependent on plant species (Sanchez, Diaz, and Kramer, 1971), age of the plant (Gardner and Ehlig, 1965), time of day (Acevedo, 1975; Fereres, 1976), and other environmental factors (Knipling, 1967).

The osmotic and pressure components of the potential are not independent. Because of the elastic nature of the cell wall, changes in turgor pressure causes changes in cell volume due to changes in cell water content. This in turn will change the cell concentration and thus the Ψ_s. The tissue Ψ_s has been found to be inversely proportional to the RWC of the leaf (Gardner and Ehlig, 1965). In general, when a plant tissue is fully turgid, a small reduction in tissue RWC causes a large drop in Ψ, and a decrease in turgor pressure (Ψ_p). At the same time, there will be a slight decrease in tissue Ψ_s. As the tissue loses water and Ψ_p approaches zero, most of the decrease in Ψ can be accounted by decreases in Ψ_s (Gardner and Ehlig, 1965; Hsiao and Acevedo, 1975).

C. Plant Responses to Water Stress

Important advances in the field of plant-water relations have occurred in the last decade. Kramer (1974) has attributed them to: 1) The universal acceptance of the term water potential as an indicator of plant and soil water status; 2) the improvement of methodology for measuring water potential and stomatal resistance, and 3) the acceptance of the soil-plant-atmosphere continuum concept. In the last few years, several reviews have been published on effects of water stress in plant growth and development (Slatyer, 1969; Hsiao, 1973; Boyer and McPherson, 1975; Begg and Turner, 1976). All reviewers agreed that water stress may affect almost all biophysical and biochemical processes in the plant. Hsiao (1973) pointed out that cell growth is one of the most sensitive processes affected by water stress. Plant growth ultimately results from the processes of cell division and cell expansion, both being very sensitive to water stress (Hsiao, 1973), although cell division is less sensitive than cell expansion (Slatyer, 1969; Hsiao, 1973; Clough and Milthorpe, 1975).

Maintenance of turgor pressure seems to be crucial for cell expansion to occur (Hsiao, 1973). Consequently, Boyer (1968) hypothesized that expansive growth must occur during the night when plant water status is most favorable and turgor pressure is maximum. However, recent field data (Hsiao _et_ _al_., 1976a) indicate that corn growth rate was high at midday presumably because turgor pressure was maintained at a high level via osmotic adjustment.

An important effect of water stress on plants is induction of stomatal closure. Processes of transpiration and CO_2 assimilation use the same pathway (stomata) between the air and cell surfaces within the leaf. Stomatal closure, due to water stress, reduces plant transpiration and also causes a reduction in CO_2 assimilation by reducing the inward movement of CO_2 into the leaf. CO_2 assimilation for many species has been shown to be sensitive to moderate but not to mild water stress (Hsiao, 1973).

The relationship between leaf Ψ and stomatal diffusive resistance has been studied in many species, and it has been shown that there is a threshold value of leaf Ψ below which the leaf diffusive resistance increases sharply. The threshold Ψ for stomatal closure is very variable among species (Hsiao, 1973); for instance Duniway (1971) found a threshold value of -7 to -9 for tomato in greenhouse, and Jordan and Ritchie (1971) reported that stomata of cotton in the field did not close at a leaf Ψ of -27 bars. Even for the same species, the threshold Ψ may be different depending on growing conditions (Cutler and Rains, 1977), stress history (McCree, 1974), and plant age (Fereres, 1976). Other environmental factors such as light, temperature, CO_2 concentration and air humidity, affect stomatal behaviour (Hall, Shulze and Lange, 1976). In general, it appears that stomatal opening is not very sensitive to water stress (Hsiao, 1973).

Sorghum growth and development is influenced by microclimate factors such as temperature, water vapor, wind speed, radiation and CO_2 concentration (Owonubi, Kanemasu and Powers, 1975). Recent studies in micrometereology of sorghum canopies suggest that the microclimate can be used to change photosynthesis and evapotranspiration through cultural practices (Chin Choy and Kanemasu 1976). Stickler (1964) and Blum (1970) found that when soil moisture is not limiting, closer row spacing of sorghum crops use water more efficiently and increases production. Kanemasu and Arkin (1976) also found that the sorghum narrow rows intercepted more light and that there was an 11.6% increase in net photosynthesis over the wide-row sorghum. Owonubi et al. (1975) found that the seasonal evapotranspiration for sorghum planted in narrow and wide rows (both having similar plant population) were very similar.

An important consequence of the sensitivity of cell growth to water stress is a marked reduction in leaf area that will reduce the rate of crop growth (Hsiao and Acevedo, 1974; Begg and Turner, 1976). As leaf area is more sensitive to water stress than CO_2 assimilation, crops harvested for total dry matter as economical yield are often more sensitive to water stress than those where only a part of the crop is harvested such as cereals. The stage of growth at which water stress occurs also influences markedly plant responses such as photosynthesis and stomatal behaviour (Sullivan and Eastin, 1974). Sullivan (1972) found that leaf tissue of several sorghum varieties was less susceptible to desiccation injury at severe water stress levels (about -33 bars) prior to anthesis than at the post anthesis stage.

D. Sorghum Yield as Affected by Water Supply

The marketable yield in sorghum is ultimately determined by the number of panicles, number of grains per panicle and weight of individual grains. Numerous reports in the literature show that the degree duration and timing of water stress are critical factors in determining growth and yield responses in many graminae (Begg and Turner, 1976). Salter and Goode (1967) have shown abundant evidence that in cereals, the most sensitive developmental stages to water stress were floral development and flowering, and that the grain filling period was less sensitive. Slatyer (1969, 1973) and Begg and Turner (1976) reported that water stress during inflorescence development reduced the number of primordia and the development of those into florets.

Photosynthesis of ears, stems and leaves during the grain filling period is the major contributor to grain yields in cereals (Thorne, 1966; Evans _et al_., 1975). Therefore, a reduction of the photosynthetic area of cereals during that period has a major impact on grain yields.

Sorghum, like most graminae, has the ability to produce tillers. Tiller can be an important contribution to grain yield. For instance, Stickler and Pauli (1961) found that tiller contributed from 3 to 67% of the total yield depending on genotypic and environmental factors. Ajmad (1975) reported that low water supply reduces the tiller yield contribution. Fereres (1976) confirmed Ajmad's hypothesis finding that the percent yield contributed by tillers was 39.7% in the irrigated treatment and only 28.2% in the non-irrigated treatment. Henderson as cited by Hsiao et al. (1976b) found that severe stress at panicle emergence may result in complete death of panicle, and new branch heads may form if the stress is released, increasing the yield contributed by these branch panicles. He also reported that severe stress around heading time may reduce yields substantially. However, the reduction was slight or nil when stress was either much earlier or later. Lewis et al. (1974) reported that sorghum is sensitive to water stress around the time of flowering. He found that the major effect was a reduction in the number of grains per panicle. Stickler (1964) reported that there is a compensation process among the different yield components of sorghum; for that reason, he found constant yields from different plant populations. Also, compensation among the yield components is considered an important factor in maintaining sorghum yields under water stress (Blum, 1973).

E. Effects of Irrigation Frequency on Crop Yields

One important way of increasing agricultural productivity in semi-arid zones is by developing land for irrigation. In most parts of the world, the best quality land is already under irrigation, and it appears that intensifying and developing the present irrigation systems should be easier and more feasible than developing new land (Rawlins and Raats, 1975). Presently, the normal irrigation practice is to irrigate as infrequently as possible in order to minimize irrigation costs (Rawlins, 1973). Recently, several studies in which irrigations were given at very frequent intervals (daily or even more frequent) have appeared in the literature, (Phene and Beale, 1976; Phene and Sanders, 1976; Miller and Aarstad, 1976; Miller, 1977). The above authors referred to this technique as high-frequency irrigation. Under this regime, soil water content can be kept continually high if enough water is applied to meet the evaporative demand. Also, the plant Ψ presumably is kept high except for periods of high transpiration demand if the absorption of water by roots is temporarily insufficient to meet the evaporative demand. Hsiao (1973) suggested that even though some water stress may occur at midday in plants growing under high soil water status, it is not likely to significantly affect the total dry matter production. Other advantages are advocated for the use of high-frequency irrigation; Rawlins and Raats (1975) concluded that deep percolation can be avoided and better salinity control may be achieved using this technique. Also, under high irrigation frequency, the use of the soil as a storage reservoir of water and nutrients is minimized (Phene and Beale, 1976). This characteristic can be an important advantage in sandy soils that have a low water-holding capacity. Also, nitrogen losses by leaching can be minimized (Rawlins, 1973). Productivity studies using high-frequency irrigation have shown high yield with the high-frequency treatments, although comparisons between high and normal irrigation frequencies using the same irrigation method are lacking. Phene (1974) found that grain yield produced per unit of water used of trickle-irrigated sweet corn was higher than that of sprinkler or furrow irrigated plants. Later, Phene and Beale (1976) confirmed Phene's results, showing a 12% to 14% increase in sweet corn grain yield in high-frequency trickle irrigated plots as compared to furrow and sprinkler irrigated plots. Jensen and co-workers (1965, 1971) found that sugarbeets and potatoes can be grown satisfactorily with frequent and light irrigations. Recently, Miller (1977), growing sugarbeets, wheat, and beans in a soil with moderately high water-holding characteristics, concluded that the irrigation requirements through daily sprinkler applications can be decreased without affecting yields. Also, the total water used by the crop was reduced under this regime, although this was not clearly demonstrated. Thus, high frequency irrigation appears promising as a technique to decrease peak irrigation requirements and possibly to obtain high yields without fully meeting the seasonal evapotranspiration demand. However, definitive data are lacking to substantiate this point.

III. MATERIALS AND METHODS

A. Crop Culture, Irrigation and Plot Layout

Two experiments were conducted in 1977 at the Experimental Farm of the University of California at Davis in a deep Yolo loam soil which is easily penetrable by roots.

The summer in Davis is extremely dry and the evaporative demand is high. Pruitt, Lourence, and Oettingen (1972) indicated that the mean monthly grass evapotranspiration for July was 208.3 mm. Precipitation during the 1977 growing season occurred on May 19 and 26, September 17, 19, and 20, amounting to 2.6, 5.3, 2.3, 15.0 and 1.5 mm, respectively.

Sorghum bicolor, (L.) Moench, cultivar "Pioneer 846" was planted on May 18, on east-west rows 76 cm apart. The soil was fertilized prior to planting and on day 15 after planting respectively with 72 and 93.5 Kg of N per hectare in the form of ammonium nitrate (33.5% of N). The whole area was pre-irrigated on May 12 with 3.8 cm of water. Emergence started 7 days after planting but was not complete. Therefore two light irrigations of 3.8 and 1.2 cm were given on days 12 and 21 after planting, respectively, to improve stand establishment. Three weeks after planting, the plots were thinned to approximately 11 plants per meter, equivalent to a population of 145,000 plants per hectare.

All the plots were sprayed with Malathion and Kelthane at 58, 66 and 99 days after planting to control aphids and mites. Nevertheless some insect damage was noticeable in two plots of Experiment II. After heading, nets were extended above the plant canopy to protect the grain against bird damage. The nets caused essentially no shading.

Figure 1 presents the experimental layout of both experiments showing the plot locations, neutron access tube and catching can locations.

A.1 Experiment I

Experiment I was performed in the western part of the experimental layout where the subsoil was dry; the volumetric soil water content was less than 18% from 60 to 210 cm deep.

Two similar line source sprinkler plots (27.4 m x 36.6 m, each) were used: one for normal irrigation frequency (NF) and the other for high irrigation frequency (HF). The line source sprinkler produces a uniform water application pattern down the length of the plot which decreases linearly from the source (Hanks et al., 1976). A line source, 36 m long with 6 sprinklers 6 m apart, was placed parallel to the row direction in the middle of both plots on June 27.

A two-nozzle sprinkler head (Model 30, Rainbird Sprinkler Manufacturing Company, Glendora, California) with nozzle sizes of 3.6 and 2.4 mm, was used. The sprinklers were placed on risers 60 cm long at the beginning of the growing season, and later were raised to a height of 180 cm.

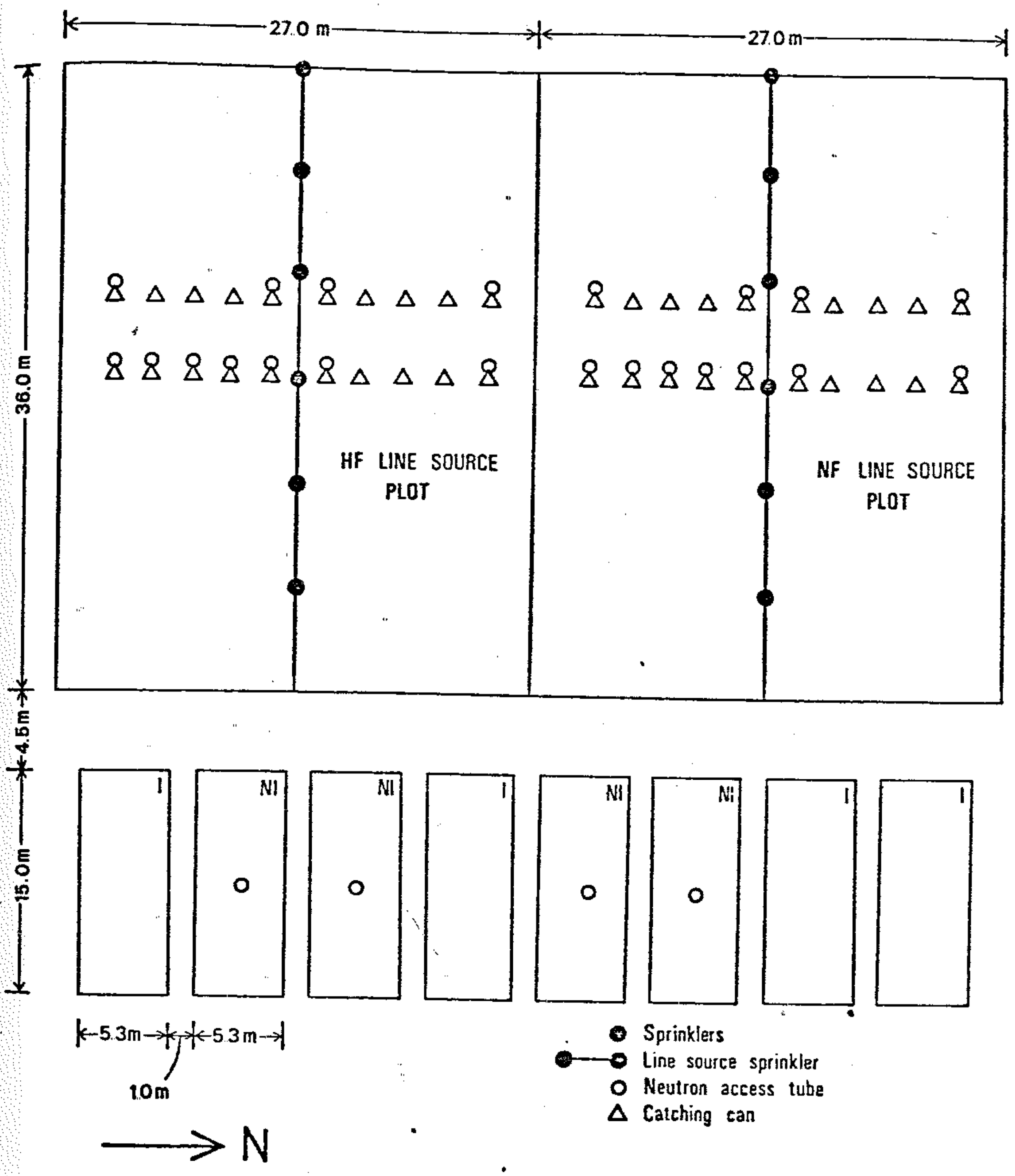

Figure 1. Experimental layout of Experiment I (HF and NF line source plots) and Experiment II (I and NI plots).

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The sprinklers were operated at 3.0-3.4 atmospheres and produced a wetted radius of approximately 12.8 m. As any wind drastically altered the sprinkler pattern, most irrigations were applied under calm conditions.

Five locations at right angle to the line source were chosen as sites for the different treatments in both irrigation regimes. There was substantial variability in soil water content within each sprinkler plot. However, the locations selected for experimental purposes had fairly uniform soil water content throughout the profile. Treatment differential was based on irrigation regime and amount of applied water (Table 1).

Table 1. Irrigation Treatments in Experiment I

Applied Water % ET	Irrigation Regime	
	High Frequency	Normal Frequency
100	HF-5	NF-5
76	HF-4	NF-4
52	HF-3	NF-3
35	HF-2	NF-2
23	HF-1	NF-1

A.2 Experiment II

A completely randomized design experiment was conducted in an area with a fully charged profile adjacent to experiment

I. Two irrigation treatments were used on 4 replicate plots (5.3 m x 150 m):

1) No irrigation after germination (NI), and 2) weekly basin irrigations of 6 to 8 cm of water per irrigation (I).

B. Measurements

B.1 Measurement of Water Applied on the Line Source Sprinklers

At the beginning of the growing season, 20 catching cans were placed 40 cm above the soil surface in each line source plot (Fig. 1). Later in the season, the cans were raised to a height of 160 cm, to avoid water interception by the plant canopy. After each irrigation, the amount of water caught in each can was measured with a graduate cylinder.

B.2 Soil Water Content

The soil water content was measured with a neutron probe (Moisture gauge Model 140A and scaler Model 2601, Troxler Electric Lab., Inc.). Volumetric water content was calculated using the calibration curve obtained by Acevedo (1975) for a nearby area with the same neutron probe. Experiment I was provided with 22 aluminum access tubes and Experiment II, with 4 (Fig. 1). The tubes were placed between rows to a depth of 300 cm.

On days 36, 53, 71 and 92 after planting, and at harvest, readings were taken at 30 cm intervals starting from 15 cm below the soil surface to 285 cm.

B.3 Leaf Area

Leaf area was determined by multiplying leaf length by the maximum leaf width and a factor of 0.74 (Ajmad, 1975). From 35 to 92 days after planting, leaf area measurements were taken for two representative plants per replicate. Leaf area was measured in the north and south side of the line source in treatments HF-5, HF-3, HF-1, NF-5, NF-3 and NF-1. Main stem leaf area index (area of leaf blade in main stems per unit area of soil surface) was calculated taking into account the length of row that each main stem occupied in the sites where measurements were taken.

After heading, the panicle area (calculated as the external area of a cylinder) was included in the leaf area calculation.

B.4 Ground Cover

Soil shade measurements were taken each 7 to 11 days at solar noon (between 1200 and 1300) to minimize the effects of the angle of sun rays.

Shading of the soil surface was measured using the technique developed by Adams, Arkim and Ritchie (1976), which consists of placing a meter stick on the soil surface parallel to the plant rows and counting shaded distance in several positions between rows. In this experiment, the shaded distance on the meter stick was counted, then the meter stick was moved 5 cm from the first position and parallel to it, and the shaded distance was measured again. This procedure was repeated until the whole distance between two rows was measured by the stick.

Ground Cover (GC) was computed by the formula:

$$\text{GC (\%)} = \frac{\text{Total cm of shade x 100}}{\text{Length of stick in cm x number of traverses}}$$

B.5 Leaf Water Potential

Leaf water potential (leaf Ψ) was measured in the field with a pressure chamber (Model 3005, Soil Moisture Equipment Corporation).

The apex (20-30 cm) of an expanded leaf was rolled around the central leaf vein, and placed in the silicone rubber gasket of the pressure chamber. Pressure was applied from a small cylinder of compressed nitrogen and increased at a rate around .50 bars/sec. until the sap began to bubble from cut ends of the vein, at this time, the pressure was read from the pressure gauge. In young plants, the whole plant top was placed in the pressure chamber.

To check the pressure chamber technique, leaf Ψ was measured in 17 leaves under different water status with both the pressure chamber (Scholander _et al_. 1965) and isopiestically by thermocouple psychrometer (Boyer and Knipling, 1965). The regression line obtained (Ψ psy = 0.83 Ψchamber + 2.50; r^2 = 0.84) indicated that the pressure chamber measurements were reliable and are presented as leaf Ψ values in this study (Fig. 1A). The leaf Ψ in both pressure chamber and psychrometer is expressed in bars.

B.6 Leaf Diffusive Resistance

Leaf diffusive resistance was measured on days 41 and 66 in the exposed, upper leaves with a diffusion porometer (Kanemasu, Thurtell and Tanner, 1969). The porometer used was manufactured by Lambda Institute Corporation, Lincoln, Nebraska. The sensor was calibrated at the beginning of the growing season and this calibration was used for calculations.

B.7 Relationship Between Relative Water Content (RWC) and Leaf Ψ.

Ten leaves of the HF-5, HF-3, HF-1, NI and I treatments were saturated by partial immersion in deionized distilled water for at least three hours then leaves were removed from water and exposed to the atmosphere. Leaves were then allowed to dry and measurements of leaf Ψ and weight were taken at frequent intervals (from 5 to 20 minutes). Leaf Ψ was measured in the pressure chamber and leaves weighed on an analytical balance. When leaf Ψ reached values below -30 bars, the leaf was oven dried at 70°C for 24 hours to determine its dry weight.

RWC was calculated by the formula:

$$\text{RWC (\%)} = \frac{\text{Water content in tissue at sampling x 100}}{\text{Water content in tissue when fully turgid}}$$

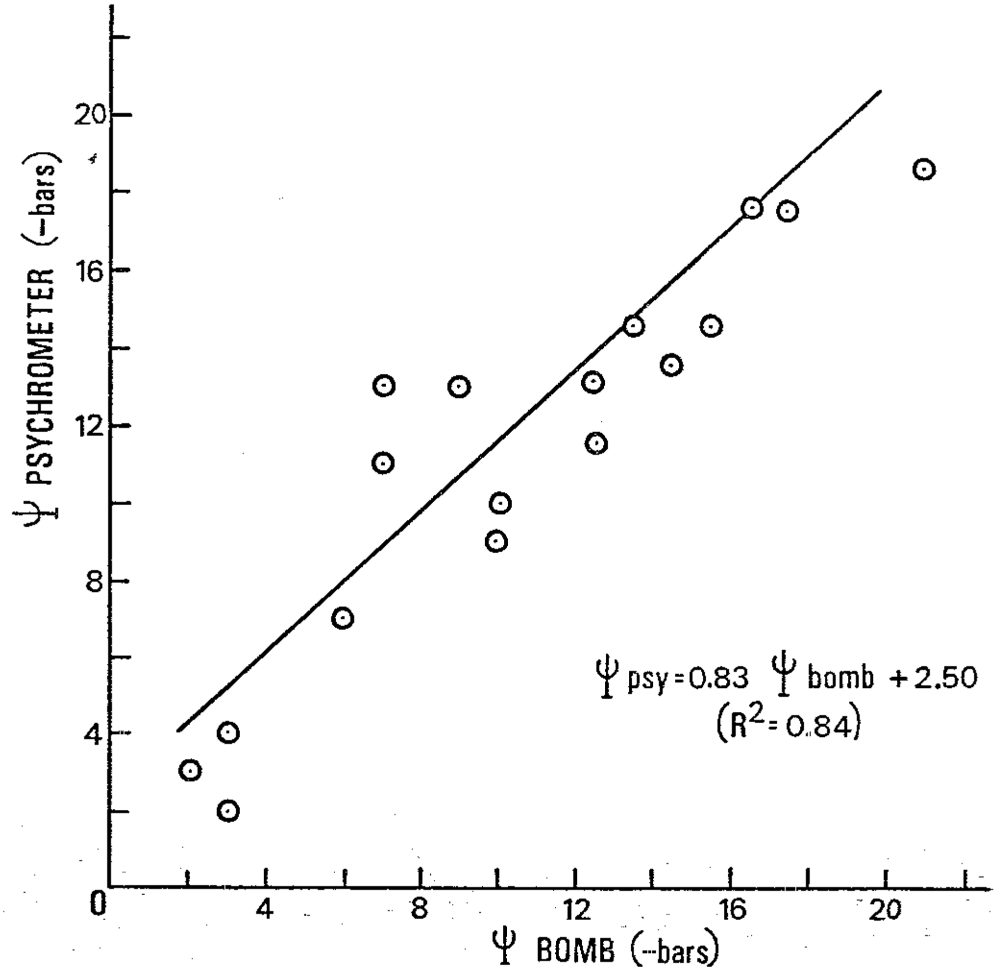

Figure 1A. Relation between the water potential measured with the pressure chamber and termocouple psychrometer. Points and individual observations.

B.8 Panicle Size

On day 60 after planting, leaf Ψ and panicle size were measured in plants under different water status to determine a possible relationship between these parameters. The panicle was assumed to be a cylinder, and its size was estimated as the external area of this cylinder.

B.9 Dry Matter Accumulation

The above-ground parts of the main stems of two plants were harvested from each replicate at 7 to 14 day intervals. Stems, leaves and panicle were separated and oven dried at 70 to 80°C for at least 50 hours and then weighed. Here again, because of variability in tiller development, tillers were ignored in these measurements.

B.10 Yields and Yield Components

Grains were considered mature and ready to harvest when the black layer at the base of the mature grain had formed (Martin _et_ _al_., 1976), since Eastin _et_ _al_. (1973) have shown that translocation to the grain is negligible after the black layer is formed. The earliest treatments (HF-5, HF-4, NF-5 and NF-4) reached physiological maturity as judged by the formation of the black layer 117 days after planting. The most stressed treatments (HF-3, HF-2, HF-1, NF-3, NF-2 and NF-1) reached maturity around 150 days after planting, since many new branch heads appeared which delayed the harvest.

Three meters from each of the two middle rows (4.56 m^2 of land area) in each plot were harvested to determine yield and yield components. The number of plants per m^2 and number of panicles from main-stem and panicles from tillers were counted. The tiller panicles and main-stem panicles were separated, oven dried at 70°C for 72 hours, weighed and then threshed to obtain the grain yield.

To determine percent dry matter in the vegetative parts (stems and leaves), a subsample was taken, weighed, oven dried, and weighed again.

A thousand grains were counted and weighed from each replicate (electronic counter, manufactured by Agricultural Specialty Company, Inc., Beltsville, Maryland).

IV. RESULTS AND DISCUSSION

A. Water Applied in Experiment I.

Differential treatments started in both plots 41 days after planting, one day after the line source sprinklers were installed. In the normal frequency irrigation regime (NF), irrigations were applied every 10 to 14 days with a total of 9 irrigations during the growing season. In the high frequency irrigation regime (HF), water was applied every other day for a total of 29 irrigations.

Cummulative applied water is plotted in Figure 2 for both irrigation regimes and for the five discrete locations across each line source that were chosen as treatments. A statistical analysis was performed using a factorial experimental design in which one of the factors was irrigation frequency and the other was the amount of applied water (Table 2). The analysis of variance showed that there were no significant differences between the water application patterns in the HF and NF irrigation regimes and that there were significant differences at the 1% level among the five locations across the line source in the amount of applied water. Therefore we can conclude that treatments in the HF regime received the same seasonal amount of water as analogous treatments in the NF regime.

B. Soil Water Depletion

B.1 Soil Water Extraction Patterns in Experiment I.

Crop water uptake was estimated assuming that deep

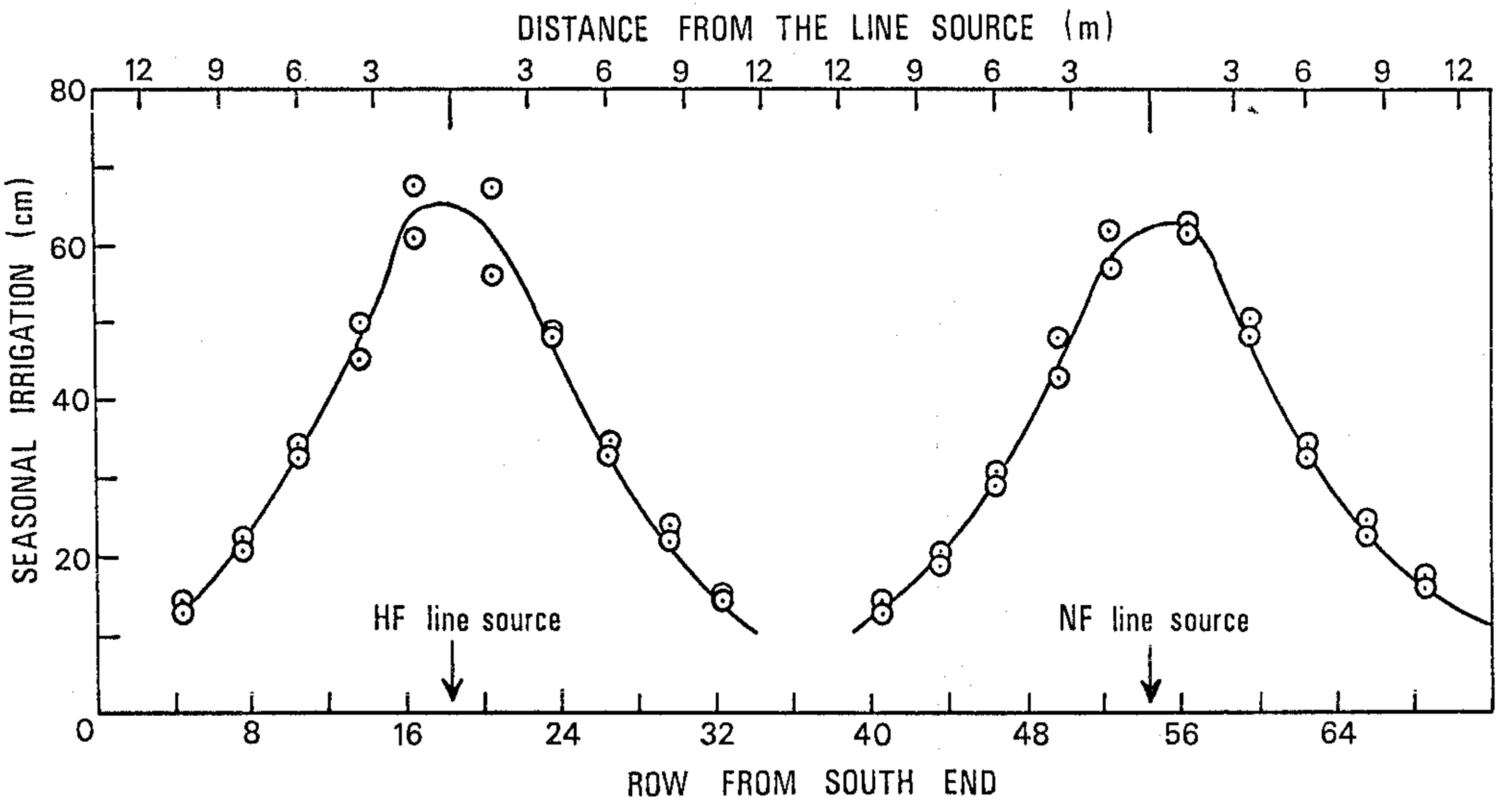

Figure 2. Cumulative water applied as a function of the distance from the sprinkler pipe line in the HF and NF regimes. Each point represents seasonal applied water at each catching can site.

Table 2. Analysis of variance of applied water in Experiment I.

Source	DF	SS	MS	F
Treatments	9	1836.04	204.00	188.89 **
Irrigation frequency	1	1.01	1.01	.93 NS
Amount of water applied	4	1832.66	458.17	424.23 **
Interaction	4	2.37	.59	.55 NS
Error	30	32.38	1.08	

*,** significant at 5% and 1% level of probability respectively.

NS Non significant at less than 10% level of probability.

percolation was negligible. This assumption is probably correct because the subsoil was very dry from 60 to 210 cm deep (less than 18% on a volume basis, equivalent to around -2 to -8 bars soil matric potential as measured by Acevedo (1975) in a nearby plot). Soil water depletion was calculated from differences in the volumetric water content of 30 cm layers at the beginning and at the end of the growing season. Figures 3 and 4 show soil water content as a function of depth at three times during the growing season in treatments HF-5, HF-1, NF-5 and NF-1. Soil water depletion increased with greater distance from the line source, and was therefore greater as the applied water decreased in both irrigation regimes. For example, depletion in HF-5 was very low (1.3 cm), while in HF-1 it was 13.7 cm of water (Table 3). Similarly, depletion in NF-5 and NF-1 was 1.8 and 15.7 cm of water, respectively.

In HF-5, most of the water uptake occured in the surface layers. There was no apparent water uptake below 1.3 meters in this treatment. However in NF-5 it appears that there was some extraction from deeper layers (water content at 255 cm had decreased from 32% on day 38 to 29% on day 120). In treatments 3, 2 and 1 of HF and NF regimes, significant soil water depletion in deeper layers had occured by the end of the growing season. For instance, soil water content at 255 cm in HF-1 and NF-1 had decreased from 26.0 and 27.0% on day 38 to 21.5 and 17.5%, respectively, at

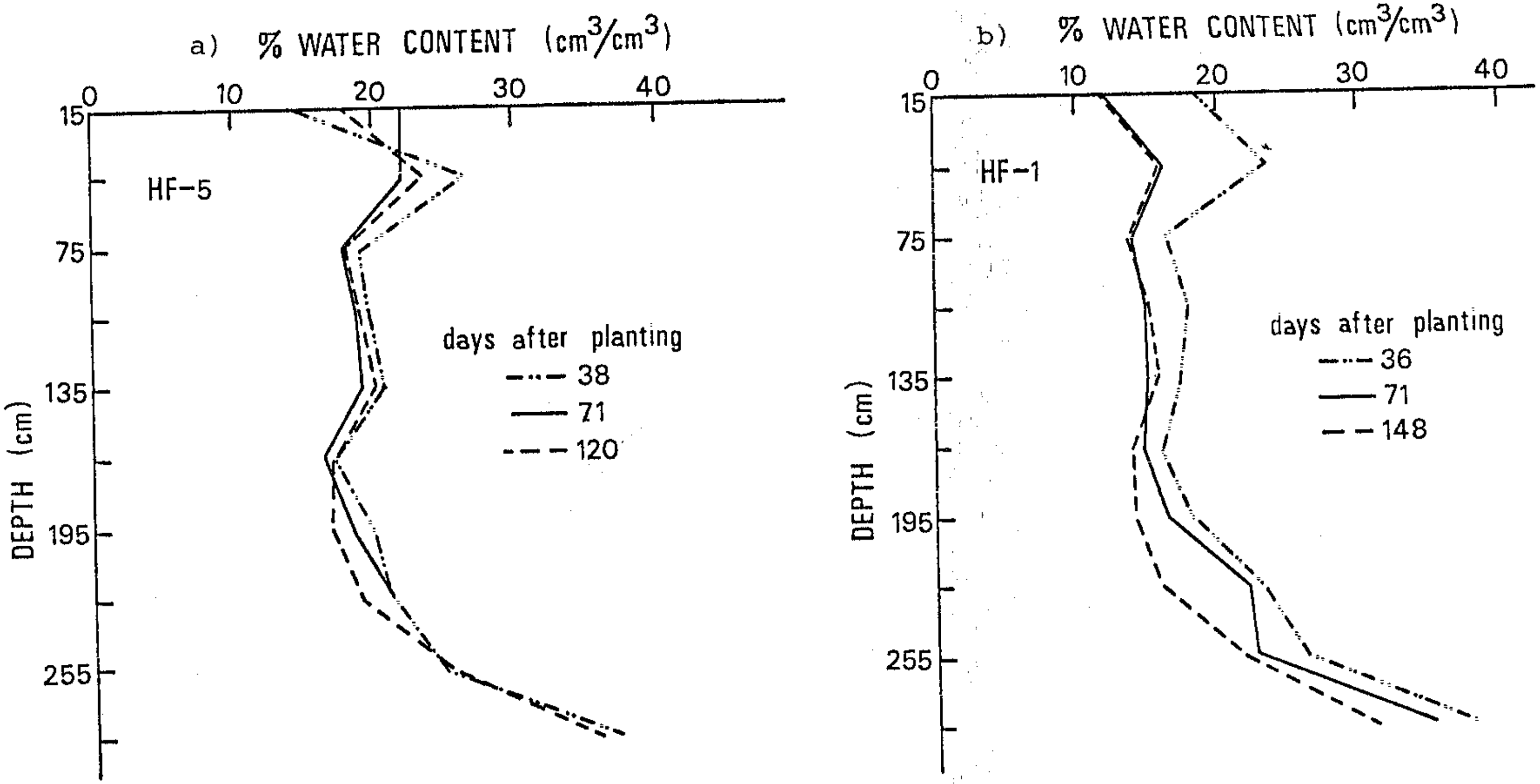

Figure 3. Volumetric water content profiles for a) HF-5 on days 38, 71 and 120, and b) HF-1 on days 26, 71 and 148. Each point is the average of four replicates.

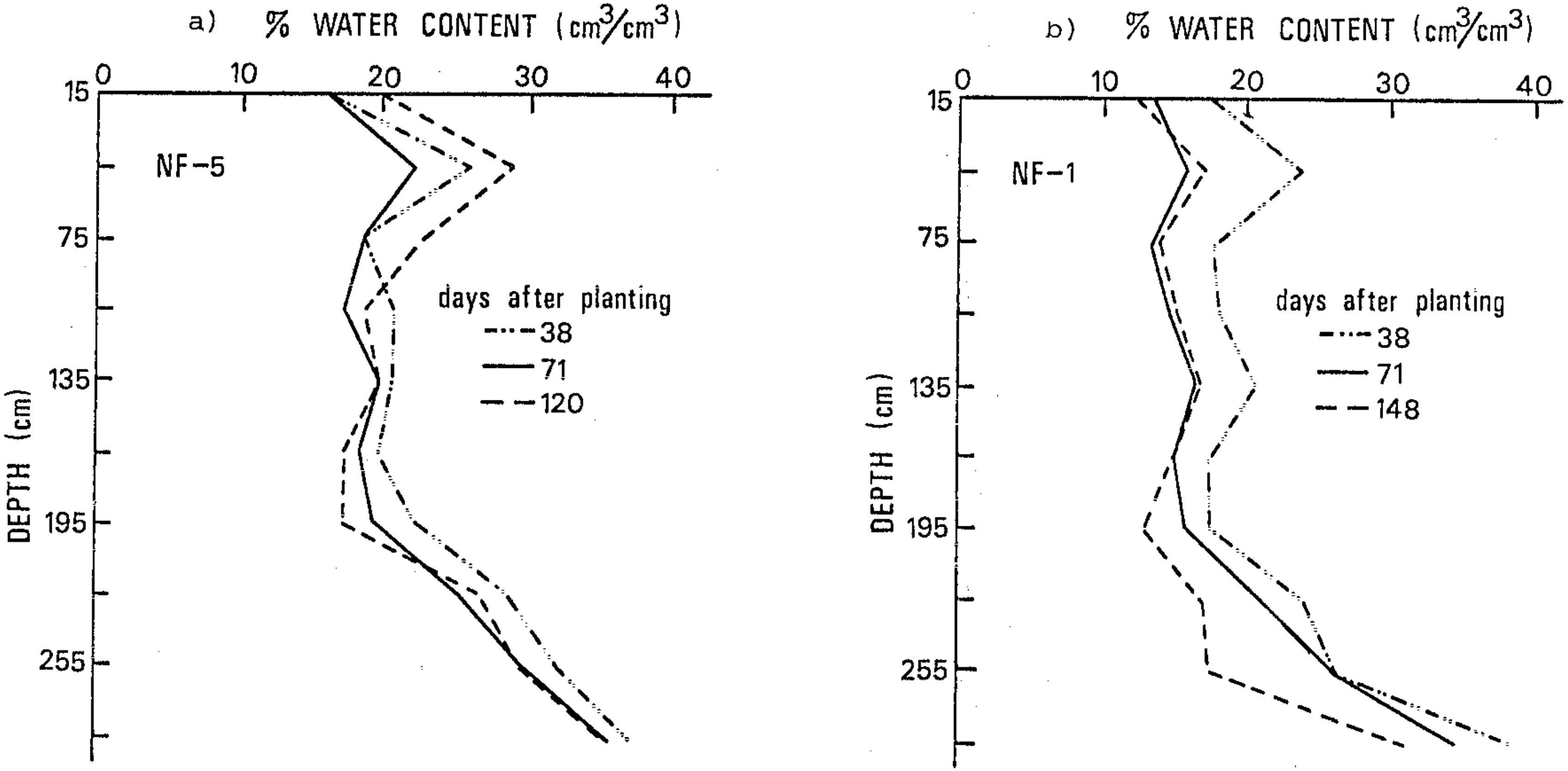

Figure 4. Volumetric water content profiles for a) NF-5 on days 38, 71 and 120, and b) NF-1 on days 38, 71 and 148. Each point is the average of four replicates.

harvest time. The only explanation for this observed depletion is that roots grew into the dry soil and penetrated the subsoil layers (below 2.1 meters) that had more available water.

In general, soil water depletion was less in any HF treatment than in the analogous treatment of the NF regime. The largest difference was observed in HF-2 and NF-2 that extracted 12.1 and 17.9 cm of water respectively.

B.2 Soil Water Extraction Patterns in Experiment II.

Here, in contrast with Experiment I, the soil profile was moist at planting time (soil water content was higher than 30% on a volume basis from 30 to 150 cm deep). Figure 5 presents data of soil water content as a function of soil depth in the non irrigated (NI) treatment. Water uptake occured in the upper layers of the soil at the beginning of the growing season, but as the season progressed, root absorption took place from lower layers in the profile. Vega (1972), Ajmad (1975) and Fereres (1976) in unirrigated sorghum and Vega (1972) and Acevedo (1975) in unirrigated maize, working under similar conditions at Davis, all found patterns of water absorption similar to those presented in Figure 5. These patterns of soil water content variation with soil depth give a good picture of the pattern of root growth. It appears that in the NI treatment there was very little root water absorption in the

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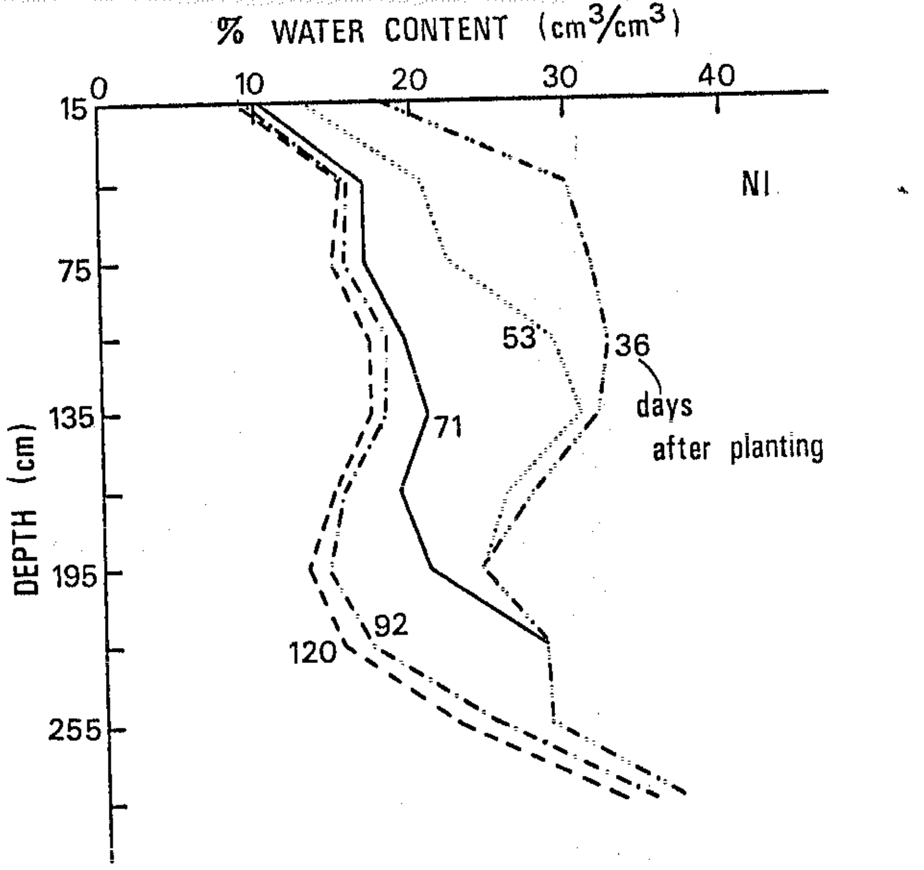

Figure 5. Volumetric water content profiles for the non-irrigated treatment of Experiment II on days 36, 53, 71, 92 and 120. Each point is the average of four replicates.

layer from 270 to 300 cm (the soil water content decreased from 37.0 on day 36 to 34.5% at harvest time). Therefore, the stored soil moisture down to 270 cm was probably enough to grow the crop to maturity.

B.3 Evapotranspiration (ET) in the Different Treatments.

Table 3 presents seasonal data of soil water depletion, applied water, rainfall and crop evapotranspiration (ET). ET was calculated by summing the soil water depletion, rain, and the applied water. In treatments HF-5 and NF-5, very little water was depleted from the soil, thus the actual ET was very similar to the applied water. Treatments HF-5 and NF-5 had a seasonal ET of 65.1 and 63.7 cm respectively. It was assumed that HF-5 and NF-5 had an actual ET equivalent to the potential ET based on the following: 1) Stewart _et al_. (1975) found at Davis that the maximum ET of grain sorghum was 58.7 cm, when the soil was at field capacity to below a depth of 3 meters at planting time and subsequently irrigated to keep ET at its potential rate. 2) The sorghum ET at Davis for the 1977 season as calculated by the data of evaporation pan and the crop coefficients developed by Fereres (unpublished data), amounted to 67.5 cm. This value was very close to the actual ET of HF-5 and NF-5). And 3) total above ground dry matter production of HF-5 and NF-5 did not differ signi-

Table 3. Soil water extraction, applied water as irrigation, rainfall and evapotranspiration (ET).

	Treatment	Water extracted from soil	Applied water as irrigation	Rainfall	ET
Expt. I	HF-5	1.3	63.0	.8	65.1
	HF-4	2.8	50.2	.8	53.8
	HF-3	11.9	33.0	2.7 *	47.6
	HF-2	12.1	21.8	2.7 *	36.6
	HF-1	13.7	14.0	2.7 *	30.4
	NF-5	1.8	61.1	.8	63.7
	NF-4	4.8	47.1	.8	52.7
	NF-3	12.0	29.8	2.7 *	44.5
	NF-2	17.9	20.4	2.7 *	41.0
	NF-1	15.7	15.2	2.7 *	33.6
Expt. II	NI	35.0	5.1	.8	40.9
	I	--	77.0	.8	--

*1.9 cm of rainfall fell on Sept. 17 and 19, when treatments 4 and 5 of Experiment I and both of Experiment II had already been harvested.

ficantly from that of the I treatment of Experiment II, which was never short of water.

C. Plant Responses

C.1 Vegetative Growth

C.1.1 Leaf Area Development

All plants of Experiment I suffered water deficit prior to starting of irrigation. Seasonal evolution of main stem leaf area index (main stem LAI) for treatments 1, 3 and 5 of both irrigation regimes is plotted in Figures 6 and 7. The LAI values presented here were calculated using the main stem leaf area of selected plants which were monitored throughout the growing season, and the initial plant population. The contribution of tillers to LAI which has been shown to be very significant in other studies (Ajmad, 1975; Fereres, 1976) was not considered here in the calculations of main stem LAI. Tillering was highly variable among treatments in time of appearance, final leaf area and death rate. Therefore a meaningful treatment comparison of leaf area development could only be performed if tiller contribution to LAI is ignored.

Treatment differences in main stem LAI were marked 9 days after the differential irrigation treatments were started. Maximum main stem LAI values for treatment 5 were 4.5 and 4.0 as compared to 1.6 and 1.9 for treatment 1 of the HF and NF regimes respectively. The low main stem

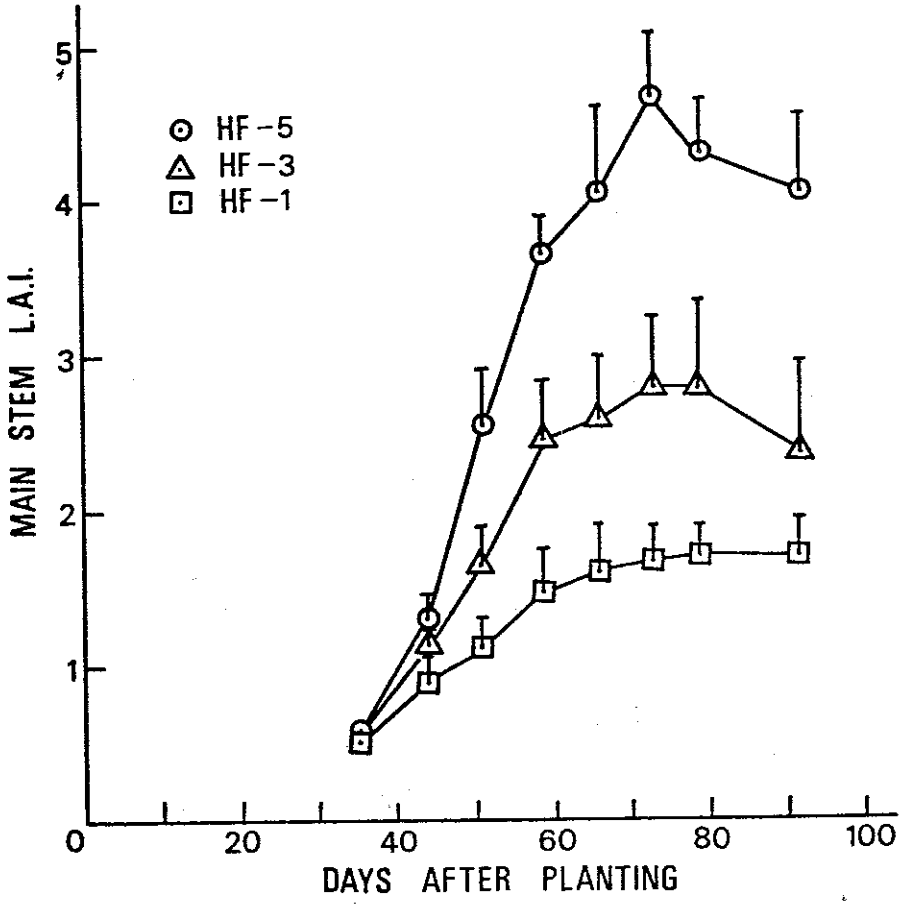

Figure 6. Main stem leaf area index evolution in treatments 5, 3 and 1 of the HF regime. Each point is the average of 4 measurements. Length of the bar indicates the standard error.

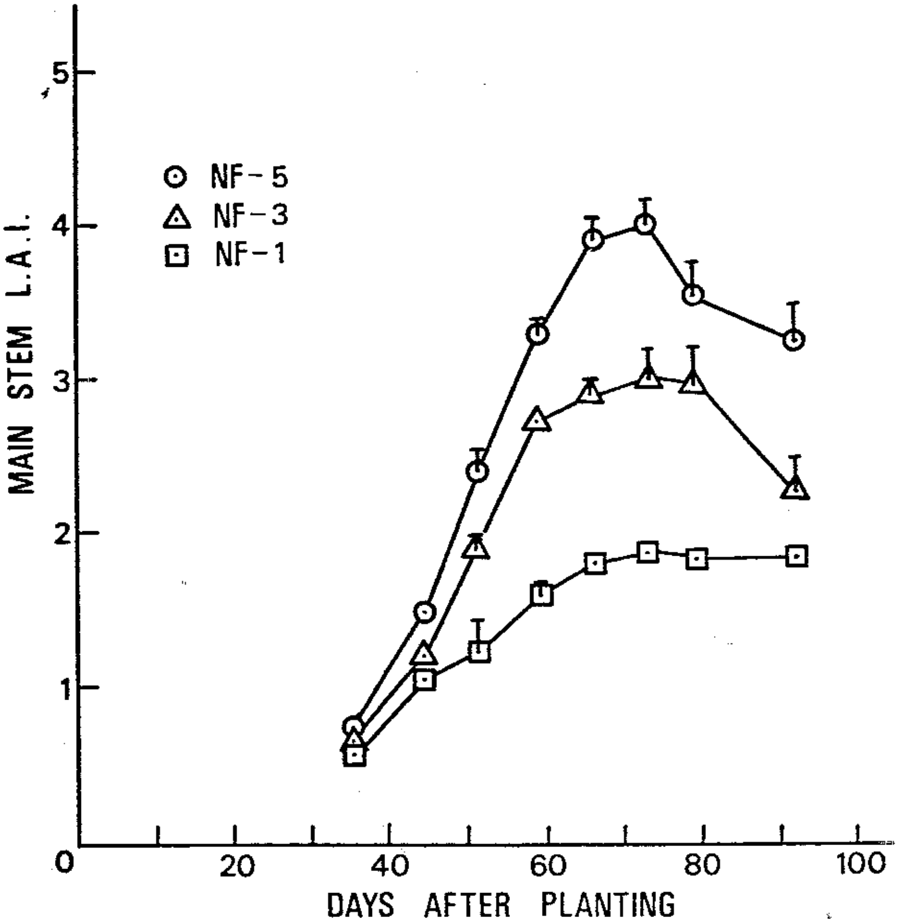

Figure 7. Main stem leaf area index evolution in treatments 5, 3 and 1 of the NF regime. Each point is the average of 4 measurements. Length of the bar indicates the standard error.

values of HF-1 and NF-1 indicate that vegetative growth was severely restricted in these two treatments. The maximum main stem LAI values for HF-3 and NF-3 were 2.9 and 3.0 respectively.

Main stem LAI increased with time in all treatments, reaching maximum values on day 72. After that time senescence of lower leaves started in all treatments, but the effect on main stem LAI was partially offset by the contribution of panicle area which was included. Particularly in treatments HF-1 and NF-1, main stem LAI was maintained or even increased after day 72 due to the contribution of new branch panicles to the main stem LAI. Panicle area contribution to main stem LAI on day 72 was about 40% for both HF-5 and NF-5 and 25 to 30% for HF-3 and NF-3. In treatments HF-1 and NF-1, the contribution was around 40% on day 91 and increased thereafter. Those high values may be due in part to the way panicle area was calculated as the area of a cylinder which may overestimate the actual area exposed. In other sorghum experiments at Davis, Fereres (1976) obtained a maximum value of LAI of 6.7 in the irrigated treatment. Ajmad (1975), using a plant population of 129,000 pl/ha, obtained a maximum LAI of 4.8, even though the panicle area was not included in his calculations. Maximum values of LAI of Fereres' and Ajmad's data were higher than the maximum main stem LAI calculated in this study, because the tiller contribution to LAI was included.

C.1.2 Radiation Interception by the Crop Canopy

Changes in the proportion of radiation intercepted by the canopy of the treatments 5, 3 and 1 of the HF and NF regimes are presented in Figures 8 and 9. Percent ground cover (GC) was measured at 7-14 day intervals starting on day 35 and ending on day 100. As can be clearly seen in Figures 8 and 9, this parameter was also very sensitive to the variation in applied water. Maximum GC value for HF and NF regimes were: 77 and 74 for treatment 5; 58 and 62 for treatment 3 and 39 and 44 for treatment 1. The rate of increase in GC was 12% per week in both HF-5 and NF-5 for the period between day 41 and day 64. In contrast, the average rate of increase in treatments 3 and 1 were 8 and 2% per week, respectively, for the same period. From day 64 to day 100, GC increased slightly in all treatments. This continued increase was mainly due to: 1) the higher inclination of the sun rays as the season progressed; 2) wider leaf insertion angle; and 3) shading produced by dry leaves which were not considered in the main stem LAI.

C.1.3 Main Stem Leaf Area Index and Ground Cover Relationships

LAI and GC are parameters very closely related. For instance, Stoner _et_ _al_. (1976) on plotting LAI versus GC of a corn canopy, found that the 98% of the variation in GC was explained by variations of LAI. This relationship

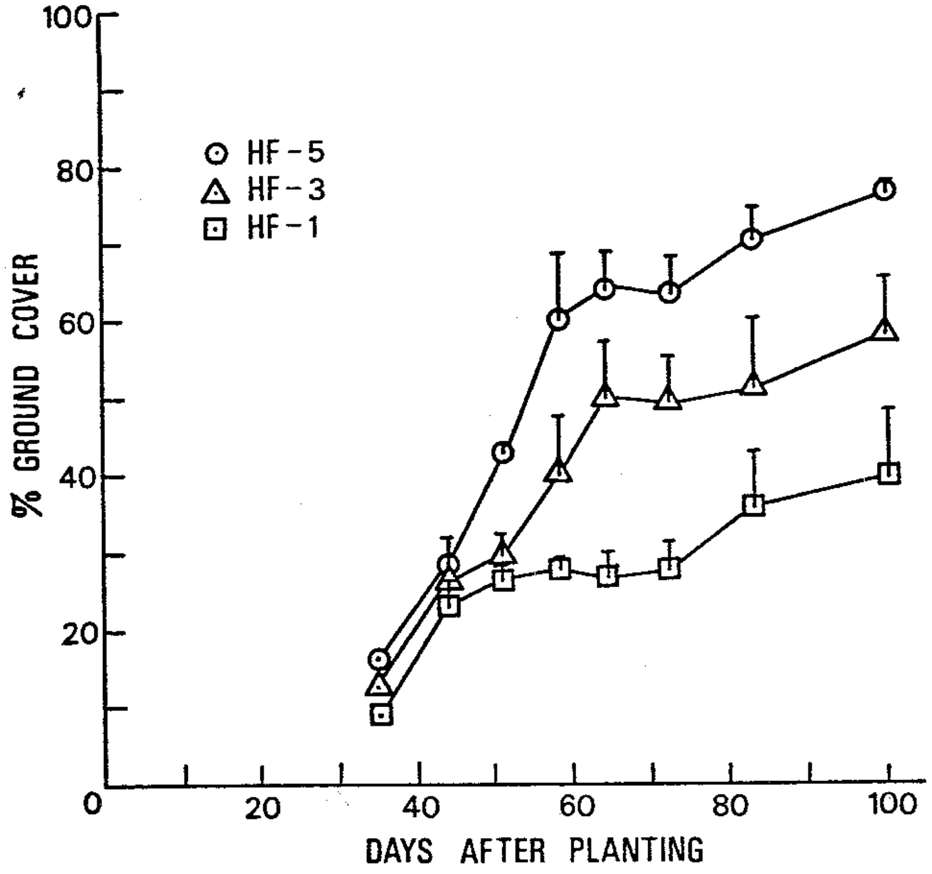

Figure 8. Evolution of ground cover in treatments 5, 3 and 1 of the HF regime. Each point is the average of two measurements. Length of the bar represents the standard error.

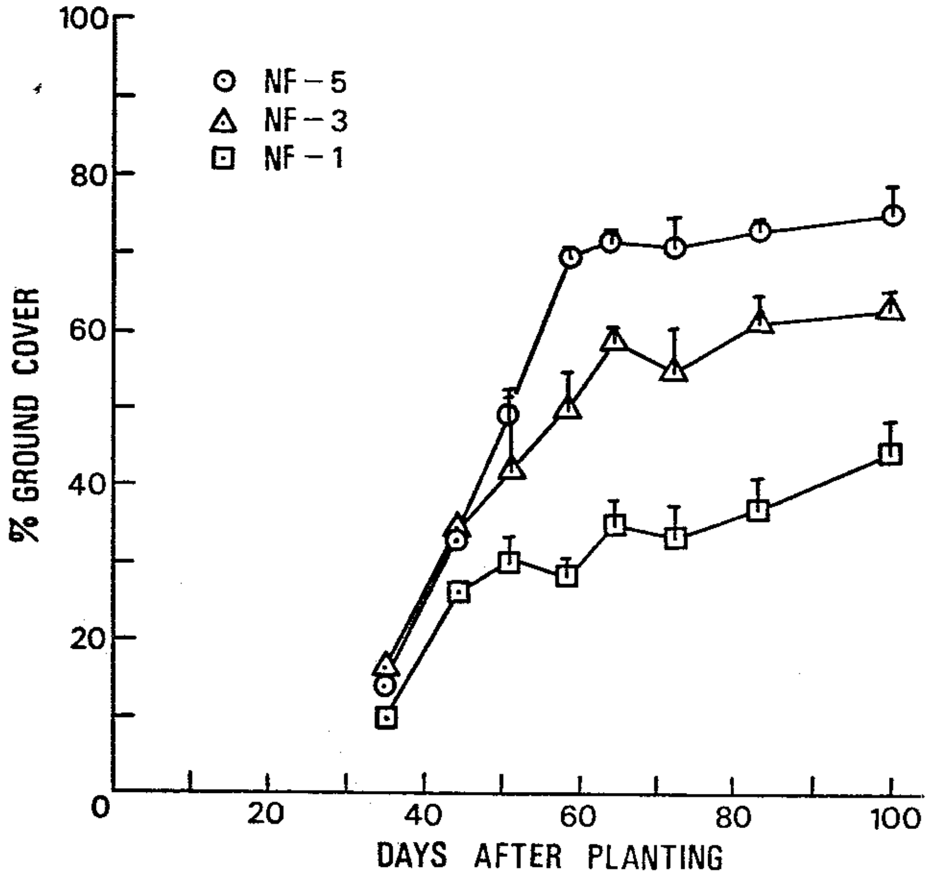

Figure 9. Evolution of ground cover in treatments 5, 3 and 1 of the NF regime. Each point is the average of two measurements. Length of the bar represents the standard error.

was best fitted by a second order equation. An attempt to quantify the relationship between these two parameters in this study is presented below. From day 28 until day 66, the relationship between main stem LAI and GC for both HF and NF regimes was studied (Figures 10 and 11). This period ending on day 66 was chosen to avoid the influence in GC of the late tillers which were very numerous in treatments 1, 2 and 3 of both regimes. Linear regressions were performed for both sets of data and the equations obtained were: main stem LAI = 6.7 GC - 0.44 (R^2 = .97) for the HF regime and main stem LAI = 5.3 GC - 0.16 (R^2 = .97) for the NF regime. The high correlation coefficient values indicate that linear regression is adequate to represent this relationship for the period studied. A comparison between the regression coefficients of the equations representing the HF and NF regimes, indicated that they were significantly different at the 1% level. For any given main stem LAI, GC was higher in the NF regime than in the HF regime. This would indicate that the canopy architecture was different between the two irrigation regimes from about midseason on. This may have been due to differences in leaf insertion angle and the degree of leaf rolling. It appeared that leaves of the HF regime remained more erect than those of the NF regime. Fereres (1976) reported that when plant water status is low, sorghum leaves remained erect and rolled, presenting less exposed surface to the sun rays.

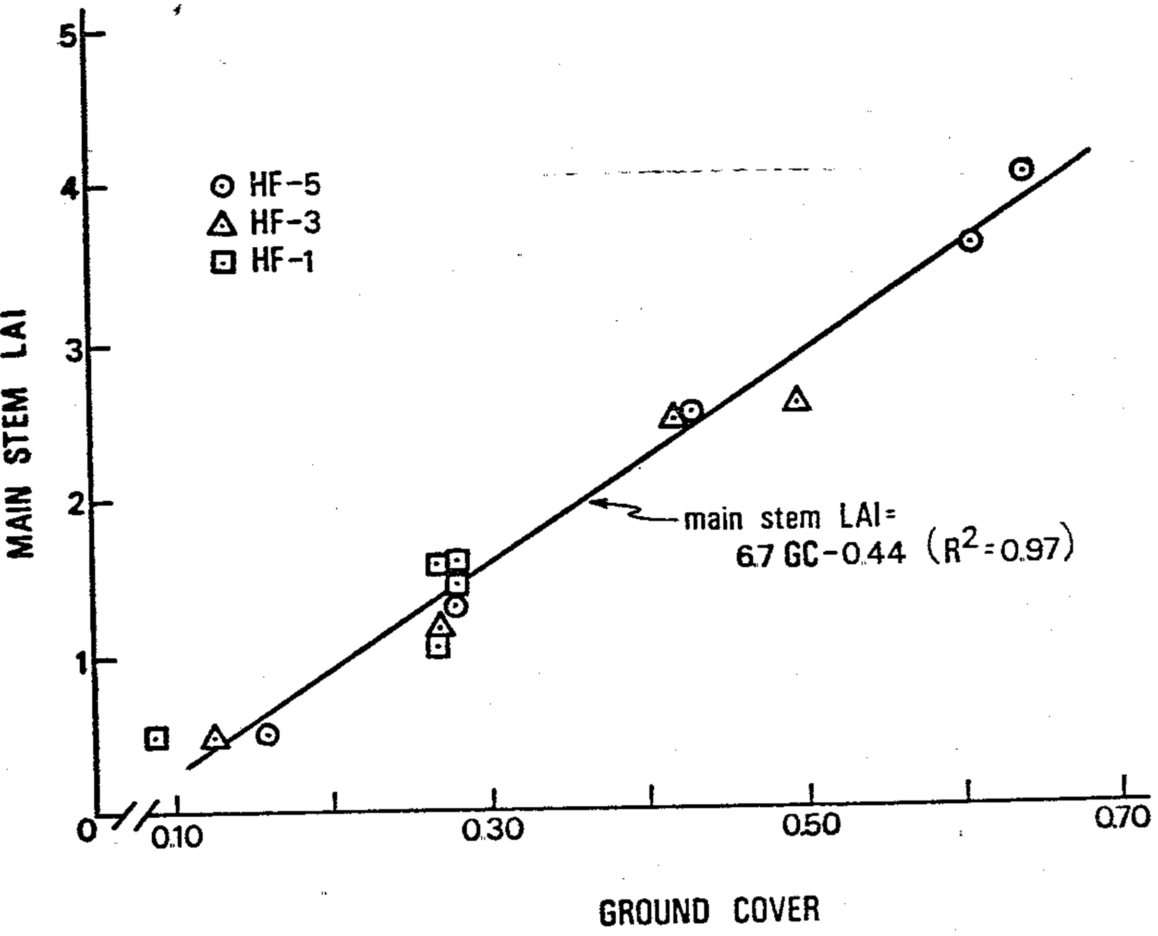

Figure 10. Relationship between main stem LAI and percent ground cover in the HF regime. Data were collected in the period of day 28 to day 66 after planting.

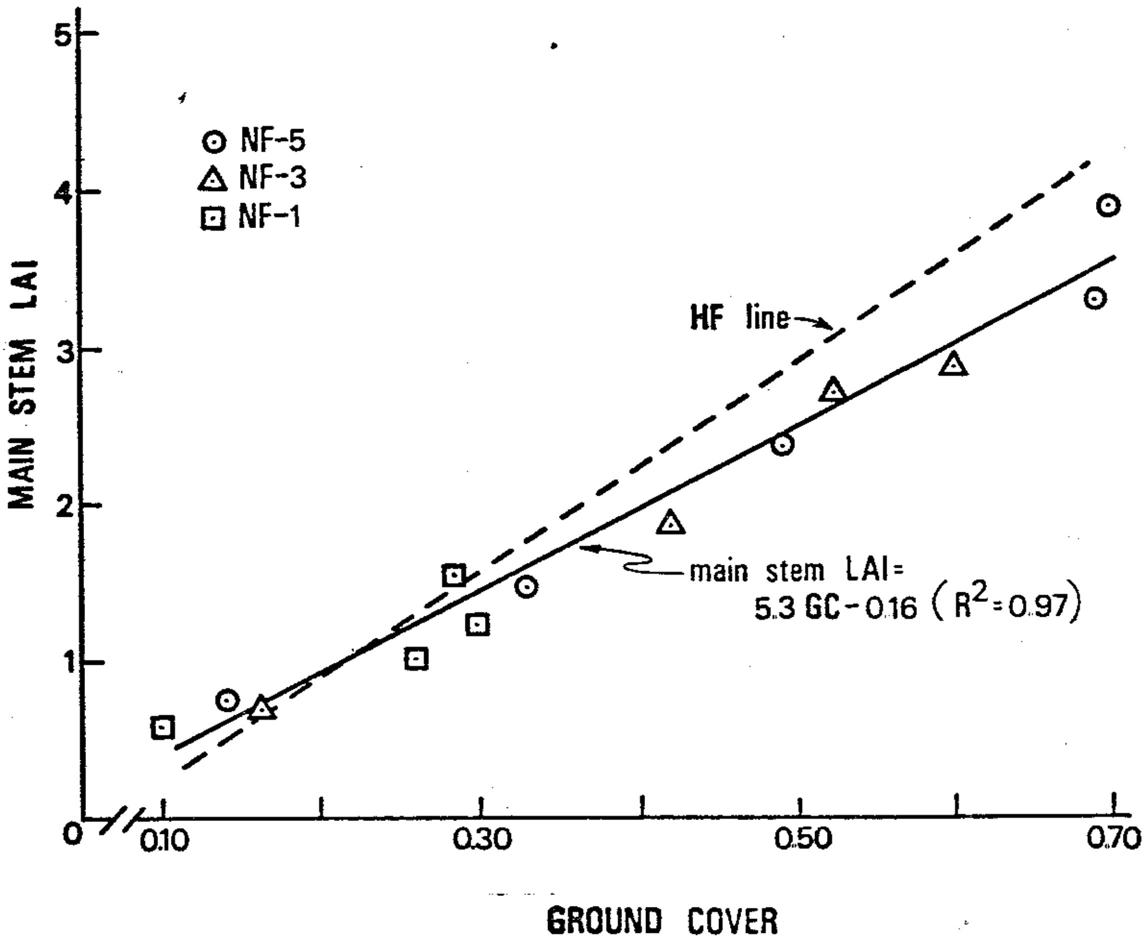

Figure 11. Relationship between main stem LAI and percent ground cover in the NF regime (solid line). The dotted line represents the HF regime of Fig. 10. Data were collected in the period of day 28 to day 66 after planting.

C.2 Plant Water Status

C.2.1 Diurnal Evolution of Leaf Water Potential (Ψ) In Early Stages of Growth

Diurnal oscillations of leaf Ψ are controlled both by transpiration and soil water status (Kramer, 1969). Diurnal oscillations of leaf Ψ on days 17, 27 and 39 are presented in Figure 12. All measurements were taken before the differential treatments were started. Early in the morning, the incoming energy from the sun increases and transpiration increases, therefore leaf Ψ decreases to maintain a Ψ gradient from the soil to the leaves (Slatyer, 1967). In this study, the minimum leaf Ψ values were reached between 1300 and 1400 hours when the incoming energy and transpiration were maximum. These minimum values were -10.0, -11.0 and -18.0 bars on days 17, 27 and 39 respectively. In the afternoon, leaf Ψ increased as the evaporative demand decreased (solar radiation decreased). The maximum leaf Ψ values, which were reached at night when the stomata were closed and plants had recovered, were -3.7, -1.9 and -5.5 bars on days 17, 27 and 39 respectively. The maximum leaf Ψ on day 39 was significantly lower than on the early dates. The differences between maximum and minimum leaf Ψ values may be used as an indicator of the degree of water stress. These differences were only 6 and 5 bars on days 17 and 27 and increased to 13 bars on day 39. It appears that by day 39, the soil had dried out (the

Figure 12. Daily leaf water potential patterns on days 17 (A), 27 (B) and 39 (C). In (A) and (B) the whole plant was placed in the pressure chamber. In (C) leaf Ψ was placed in the pressure chamber in the last expanded leaf (leaf #7). Each point is average of 6 to 9 measurements. The length of the bar indicate twice the standard error. All measurements were taken before the starting of irrigation treatments.

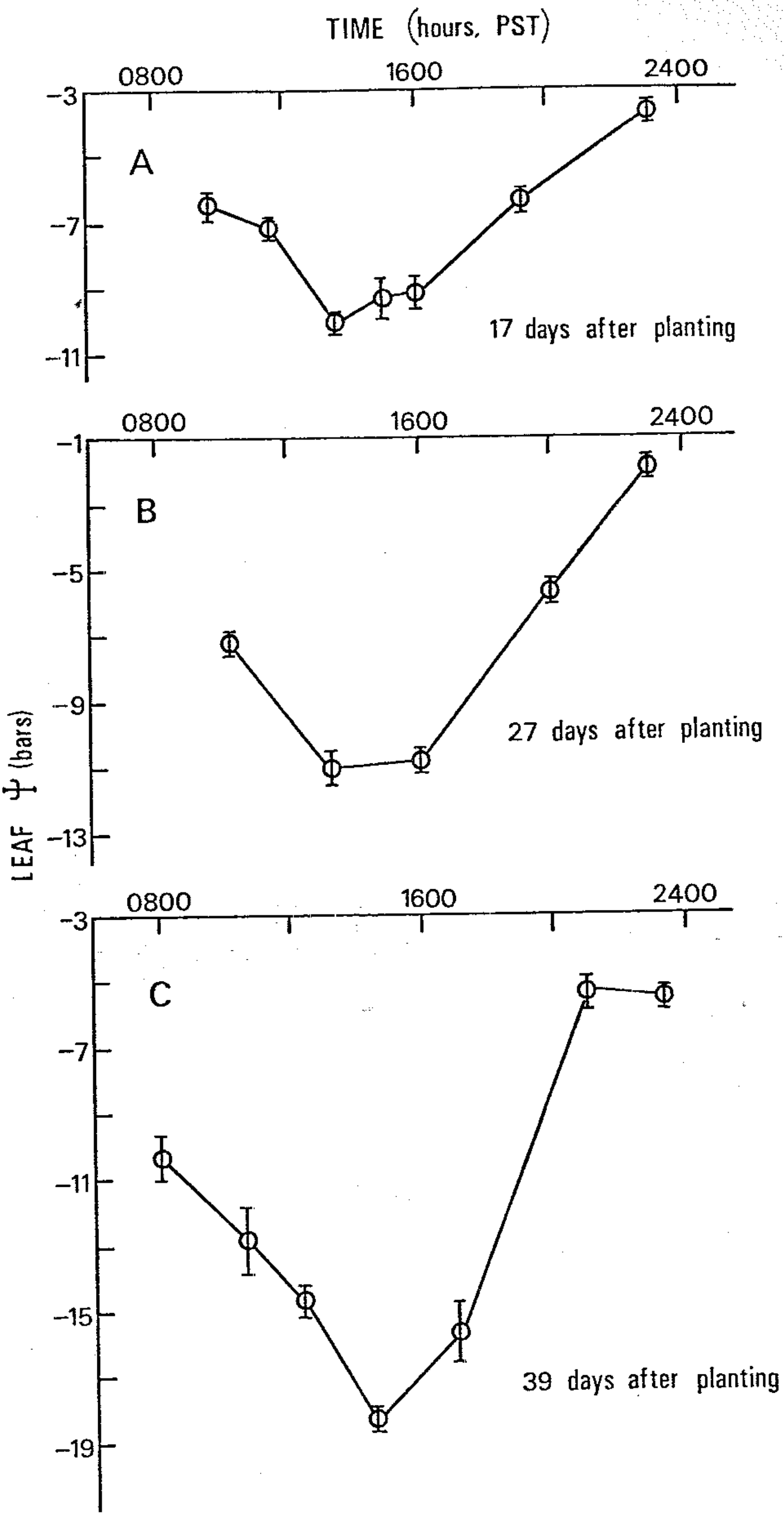
TIME (hours, PST)
0800
1600
2400
-3
-7
-11
A
17 days after planting
0800
1600
2400
-1
-5
-9
-13
B
27 days after planting
LEAF Ψ (bars)
0800
1600
2400
-3
-7
-11
-15
-19
C
39 days after planting

Figure 12

soil water content was below 17%), and as the evaporative demand was increasing due to longer days, greater water stress developed. Also, as the plants were getting older, the plant resistances possibly increased, and this also may have contributed to the higher water stress on day 39 (Reicosky et al. 1975). Kramer (1969) concluded that long term water stress was mostly produced by decreasing availability of soil water.

C.2.2 Treatment Effects on Leaf Ψ

Figure 13 shows the variation in leaf Ψ for both HF and NF regimes on day 58. Measurements of leaf Ψ were taken at midday just after an irrigation in the HF regime and 8 days after irrigation in the NF regime.

Midday leaf Ψ was around -14 bars in both HF-5 and NF-5. Midday leaf Ψ for HF-3, HF-1, NF-3 and NF-1 were -15.7, -18.2, -17.8 and -20.4 bars respectively. As can be seen from these results, there was a clear gradient in leaf Ψ across the line source in both HF and NF regimes as expected because of the different amount of water applied.

Another important result is that for this particular day, leaf Ψ was maintained higher in the HF than in the NF regime. This difference may be explained because 8 days had passed since the last irrigation in the NF regime, and the water which had been applied in treatments 3 and 1 was not enough to meet the evaporative demand. Therefore

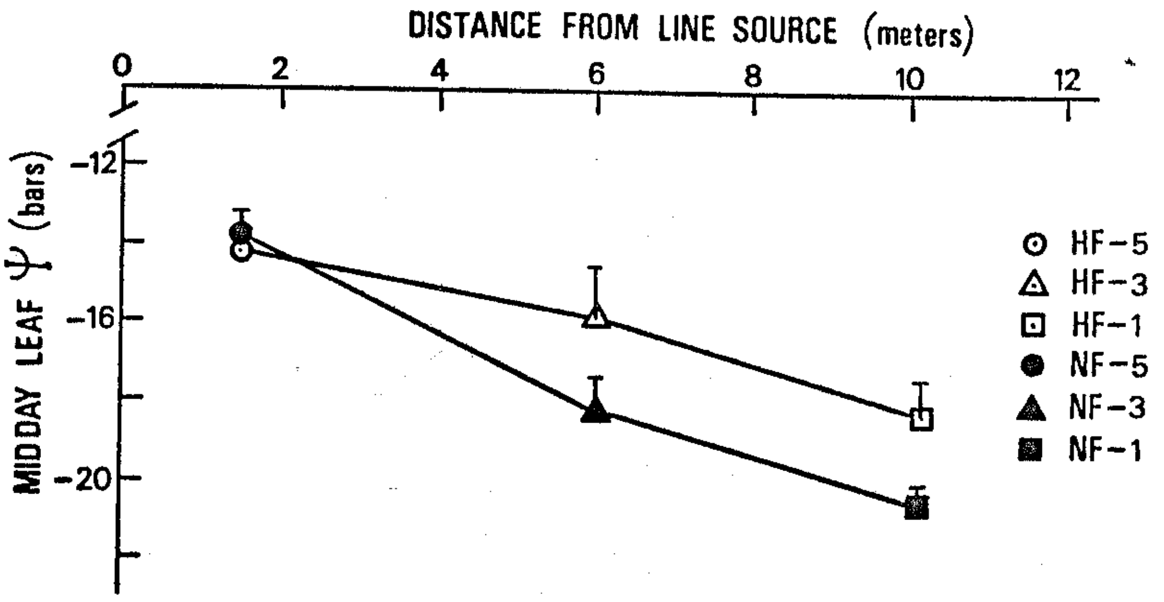

Figure 13. Midday leaf Ψ in the HF and NF regimes on day 58. Each point is average of 5 measurements. Length of the bar represents the standard error

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it appears that plant water balance fluctuated more in the NF regime, and that in the stressed treatments of the HF regime leaf Ψ did not decrease to as low values as in the NF regime.

Diurnal changes in leaf Ψ during an irrigation cycle were studied in the HF regime on days 77 and 78 (Figure 14). On day 77, the minimum leaf Ψ values were -11.8, -14.8 and -15.8 bars for HF-5, HF-3 and HF-1 respectively. At night, leaf Ψ increased in all the treatments to -3 to -5 bars. Unfortunately no measurements of leaf Ψ were taken after 1300 pm on day 78 but it appears that the diurnal pattern was similar to the day before. On day 58 the minimum leaf Ψ in HF-1 was -18.2 bars in contrast to -15.8 bars in the same treatment on day 77. This indicates that water stress was partially released at day 77, possibly because roots were reaching wet subsoil layers.

C.2.3 Seasonal Evolution of Leaf Water Potential

Midday leaf Ψ was plotted against time in the HF and NF regimes (Figure 15). As can be seen before the differential treatments had started (day 41), substantial water stress had developed. Midday leaf Ψ dropped to -18.2 bars on day 39. After this date, the leaf Ψ recovered in all treatments up to day 78. The only exception was in the NF-1 treatment, where leaf Ψ dropped to -21.8 bars on day 60. After day 78, there was a general decline in leaf Ψ.

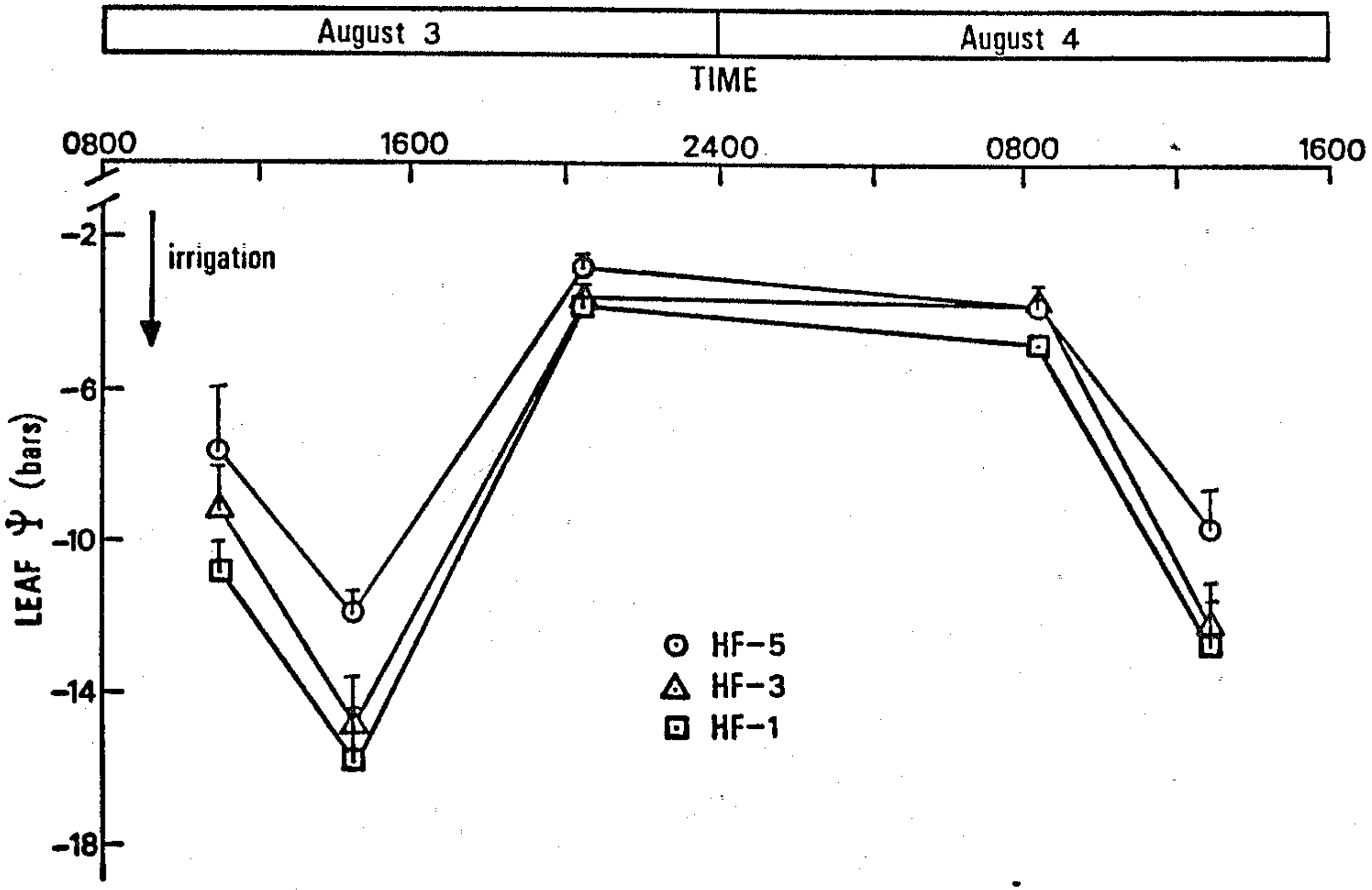

Figure 14. Daily leaf Ψ in the HF regime during an irrigation cycle. Each point is average of 6 measurements on leaf #2 or 3 (considering flag leaf as #1). Length of the bar represents the standard error.

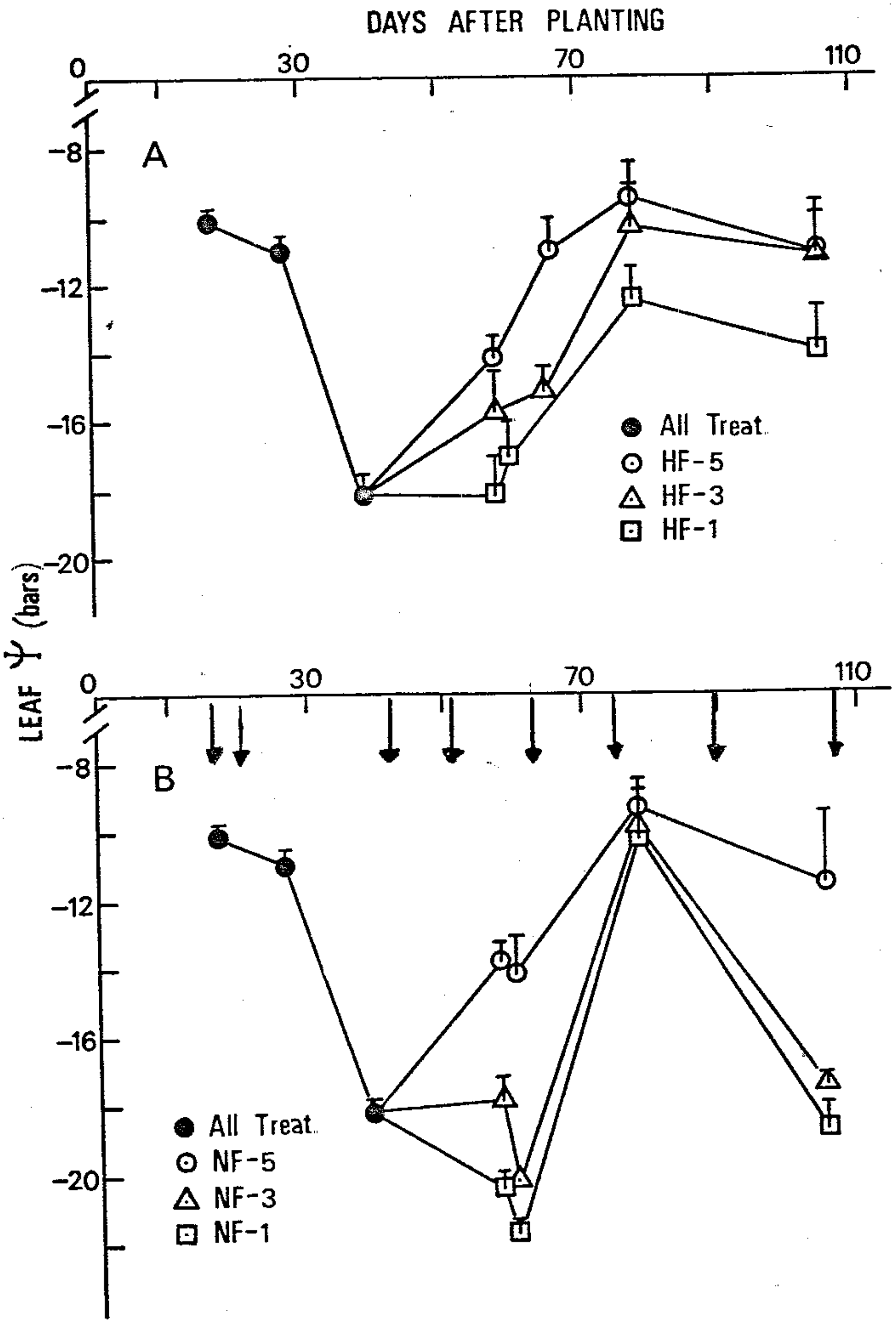

Figure 15. Leaf Ψ evolution in A) HF regime treatments and B) NF regime treatments. Each point is the average of 4 to 10 measurements. The arrows indicate the days of irrigation.

Fereres (1976) also observed a decline in midday leaf Ψ as the season progressed. However, leaf Ψ was maintained higher in the wetter treatments than in the drier treatments. The high leaf Ψ values on day 78 in the NF regime were possibly due to the fact that measurements were taken just after an irrigation. The general increase in midday leaf Ψ after day 39 was probably due to the combination of two factors; the release of the stress by irrigation and particularly in the stressed treatments (HF-1 and NF-1) and water absorption from deeper layers. Fluctuation in leaf Ψ was more drastic in the NF regime where lower Ψ values were observed (Figure 15). In view of the dependence of leaf expansion on leaf Ψ (e.g. Acevedo et al., 1971) one would expect treatments 1 and 3 in the HF regime to have a greater LAI than those in corresponding NF treatments, but this was not the case as LAI were similar for both regimes or even less in HF regime. Perhaps the infrequent irrigations allowed for more complete recovery of plant growth from water stress.

C.2.4 Relation Between Relative Water Content (RWC) and Leaf Water Potential (Ψ)

The relation between RWC and leaf Ψ (moisture release curve) was studied in three treatments of the HF regime and in the I and NI treatments of Experiment II on day 60 (Figure 16). The results indicated that the moisture release

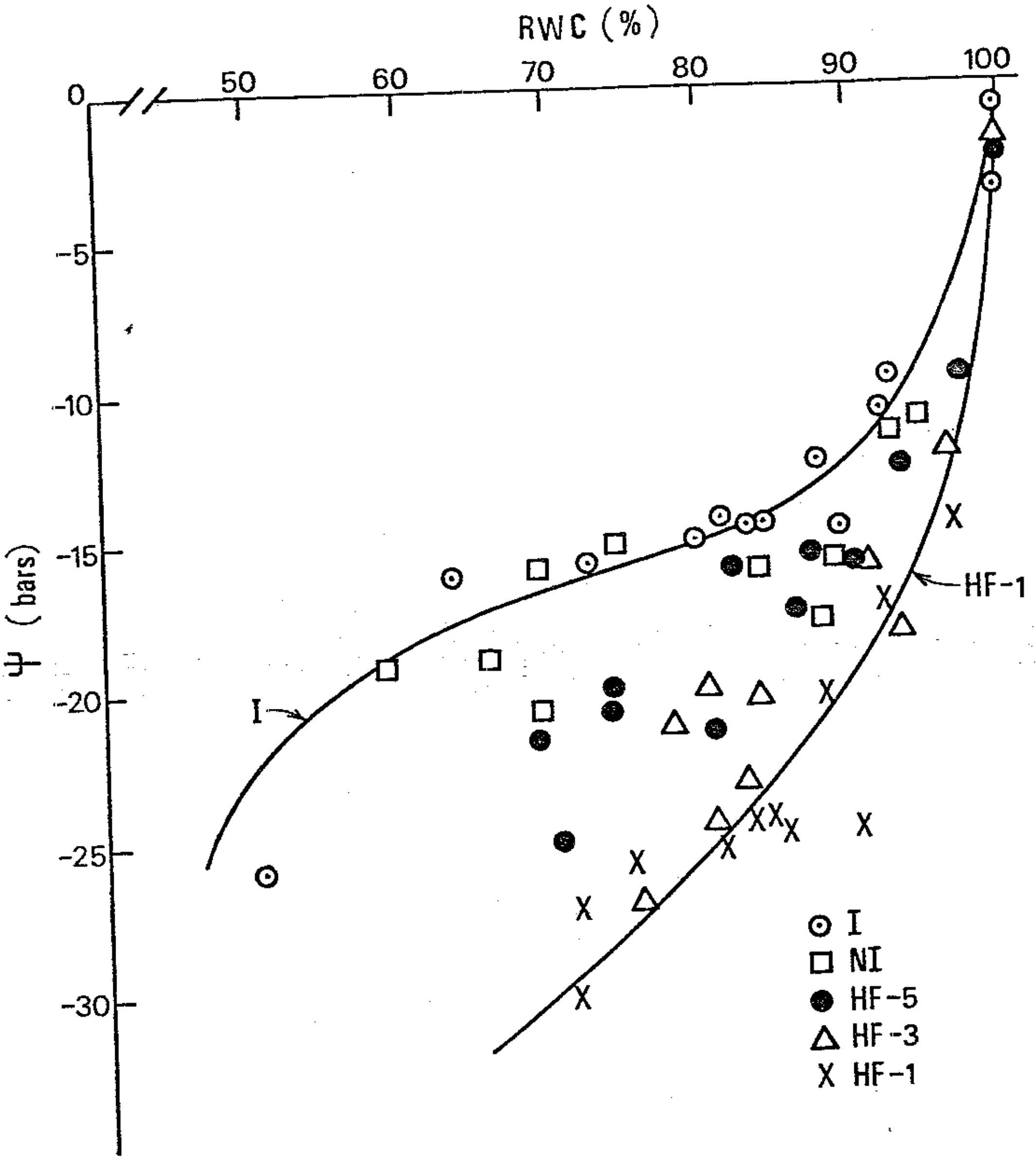

Figure 16. Relationship between RWC and Ψ for the same leaf in different treatments. Two leaves were used for each treatment. Data points are individual observations.

curves differ for the different treatments, however, due to the scatter of the data, only the two extreme curves (for I and HF-1 treatments) were drawn. As can be seen in Figure 16, all data from the other treatments fell between the two extreme curves. The water stressed plants (HF-1) maintained a higher RWC than the nonstressed plants (I) at the same leaf Ψ. Using the plot of 1/Ψ versus RWC (Scholander _et al_. 1964), it was found that at 100% RWC the solute potential in the I treatment was -11.1 bars in contrast to a value of -18.9 bars for the HF-1 treatment. Leaf Ψ at zero turgor was -12.8 bars in the I treatment and -23.8 in the HF-1 treatment. Recently, Hsiao _et al_. (1976a) and Begg and Turner (1976) have emphasized the significant role of osmotic adjustment in maintaining turgor in plants under water stress. However, Weatherley (1970) pointed out that an increase in elasticity could also maintain the turgor potential under water deficit. The lower Ψ at zero turgor in the stressed treatments could arise then from either osmotic adjustment (Hsiao _et al_., 1976a) or an increase in tissue elasticity (Weatherley, 1970). In a greenhouse study, Jones and Turner (1978), recently found complete evidence of osmotic adjustment in leaves of two sorghum varieties under water stress and no increase in cell wall elasticity. The data presented above confirm earlier evidence (Hsiao _et al_., 1976a; Fereres, 1976) that osmotic adjustment in sorghum as a response to water stress is common under field conditions. However it should be pointed out that the treatment that showed the maximum degree of osmotic adjustment (HF-1) was the most affected by water stress in terms of vegetative growth (maximum main stem LAI was only 1.6) indicating that adaptation had probably occured at the expense of reduced plant growth and development.

C.2.5 Diurnal Changes in Leaf Diffusive Resistance (r_ℓ) and the Relation Between r_ℓ and Leaf Ψ.

Leaf Ψ and r_ℓ were measured in the same leaf of plants that had different water status on days 39 and 66. On day 39 before the differential treatments were started, measurements were taken at frequent intervals in order to obtain the diurnal trend of r_ℓ (Figure 17). Leaf diffusive resistance was 5 sec/cm at 1215 indicating that the stomata were partially open. However, between 1400 and 1500 the r_ℓ increased to 12.4 sec/cm indicating a reduction in stomatal opening, presumably due to water stress. At 1700, r_ℓ had decreased again to a value of 6.4 sec/cm possibly as a response to lower radiation levels and partial tissue rehydration. After 1700 pm, r_ℓ increased sharply and at night (2300 pm) reached a value of 45 sec/cm. The next day, after sunrise stomata opened and r_ℓ decreased to small values (4 to 5 sec/cm).

Figure 18 shows the relation between r_ℓ and leaf Ψ for

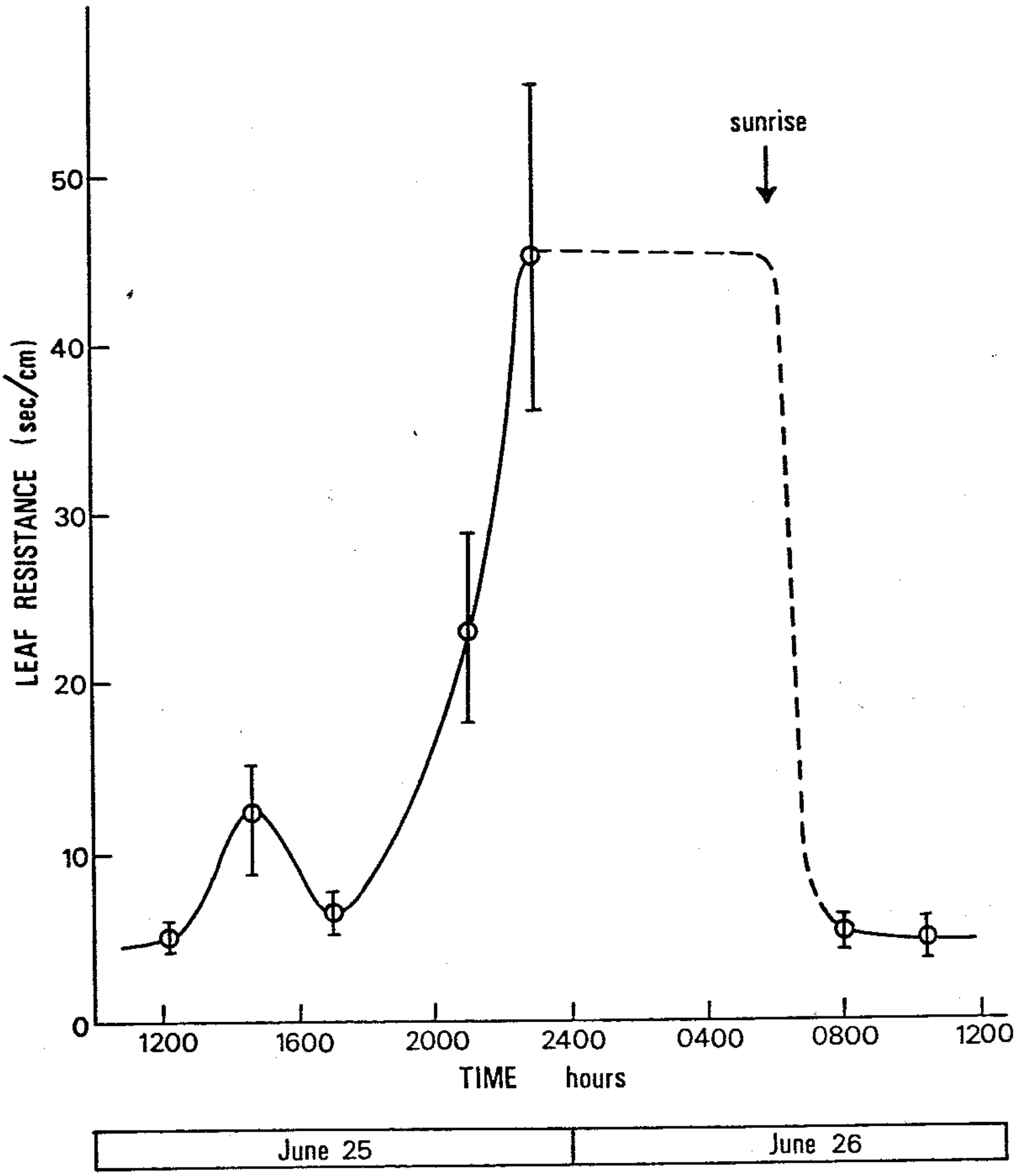

Figure 17. Diurnal variation of leaf diffusive resistance in a hot and sunny day (day 39). Each point is average of 6 measurements in different leaves. The length of the bar indicates twice the standard error.

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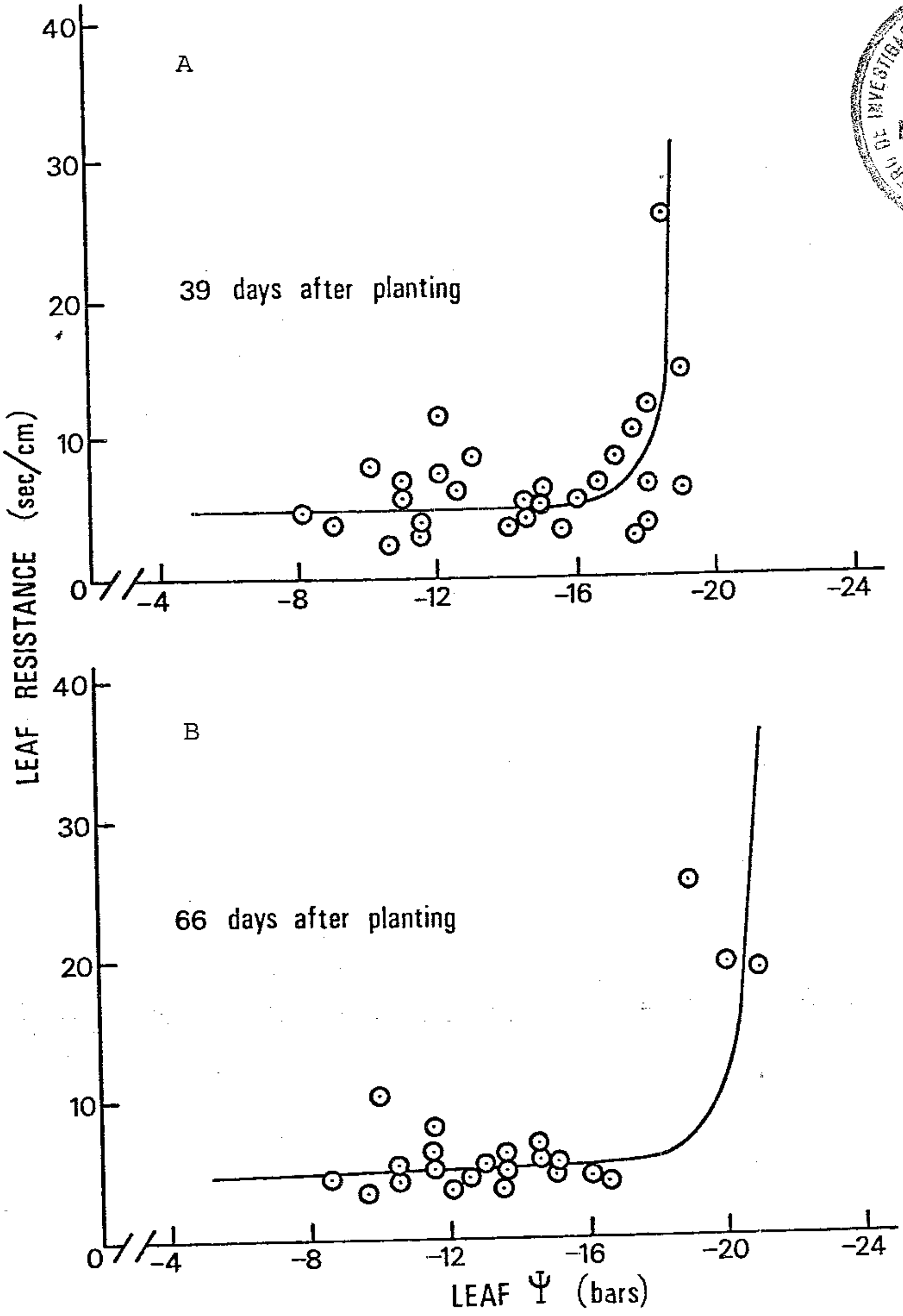

Figure 18. Relationship between diffusive resistance (r_ℓ) and leaf water potential (Ψ) in sorghum leaves on (A) day 39 and (B) day 66. On day 39 differential treatments were not started. On day 66 measurements were taken in all treatments in the HF and NF regimes. Points are individual data of r_ℓ measured between 1000 and 1700. All leaves were fully exposed.

part of the daylight period (from 1000 am to 1700 pm) on days 39 and 66. On day 39 stomata remained open at leaf Ψ values higher than -18 bars and closed at leaf Ψ values below -18 bars. A very similar curve was obtained on day 66, although no values were found in the transition to stomatal closure. On day 66, it appears that the threshold value for stomata closure was around -19 bars. Turner (1974) found for grain sorghum in the field that r_ℓ increased sharply when leaf Ψ dropped to -20 bars. A lower threshold value of stomatal closure is indicative of adaptation to drought (McCree, 1974). Fereres (1976) found that r_ℓ increased dramatically at values around -16 bars in sorghum plants where water stress developed very fast. However, he also found that adapted, older plants where water stress developed very slowly, stomata did not close, even though leaf Ψ was as low as -21 bars. Stress developed faster in this study than in the one conducted by Fereres (1976) because in this case, the subsoil was partially dry. No conclusion can be drawn from examination of Figure 18 in terms of stomatal adaptation to drought because data were too scattered and limited.

C.3 Panicle Development

C.3.1 Panicle Development Affected by Water Stress.

Panicle development is a key process in the determination of the final yield of many cereal crops (Begg and

Turner, 1976). Severe stress during inflorescence development can kill most of the florets, thus fewer grains per panicle are formed and the yield may be considerably reduced (Whiteman and Wilson, 1965). In treatments 1, 2 and 3 of both regimes, water stress severely affected the panicles of the main stem. In many of those panicles, the florets were killed and did not produce grain. In these treatments new branches developed from the uppermost four nodes and branch panicles were formed which attained physiological maturity later in the season. These branch panicles contributed markedly to the yield. Henderson's results as reported by Hsiao <u>et al</u>. (1976b) showed also that new branch panicles developed in sorghum plants when severe water stress occured during inflorescence development.

Great differences in panicle development were observed around flowering time (around 60 days after planting). On day 60, an experiment was conducted in order to determine the impact of the severity of water stress on panicle size. Plants from different treatments were sampled for midday leaf Ψ and the panicle area was measured (Figure 19). The data showed that plants under severe water stress (midday leaf Ψ below -19 bars), had very small panicles and so did plants with a high water status (midday leaf Ψ around -10 bars). Plants under moderate water stress (leaf Ψ between -12 and -15 bars) had the largest panicles. These results indicate that moderate water stress enhances panicle

Figure 19. Trend of panicle area versus leaf Ψ on day 60. Panicle area was estimated as the area of a cylinder. Points are individual observations.

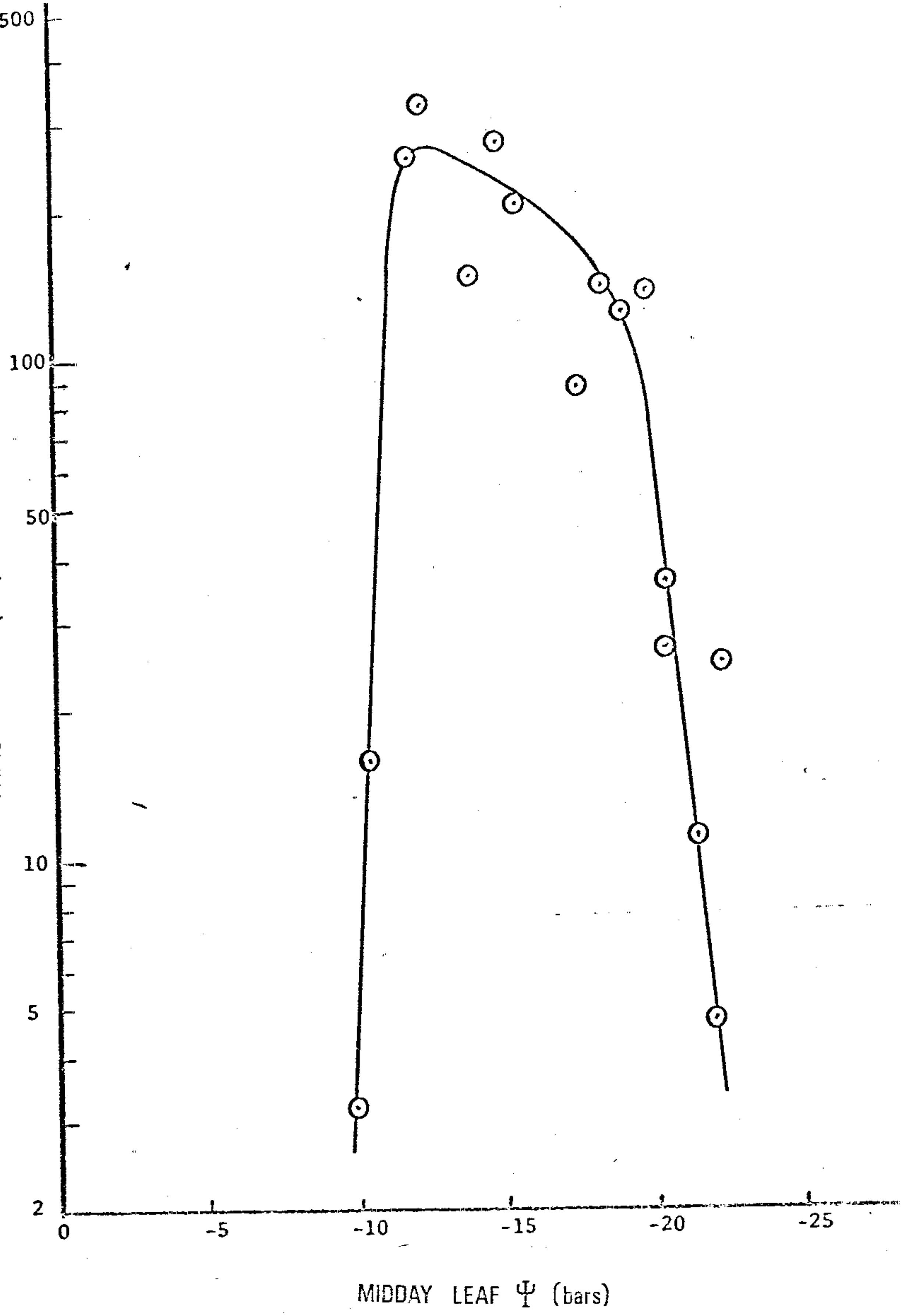

Figure 19

development as compared to plants with ample water supply (midday leaf Ψ of -10 bars or less) in sorghum. Panicles of plants under severe stress and without stress both showed retarded physiological maturity. However, the final panicle size reached at maturity was much larger in the control plants.

D. Dry Matter Accumulation

D.1 Dry Matter Accumulation in Experiment I.

Above-ground dry matter data during the growing season for all treatments of HF and NF regimes are plotted in Figure 20. In both HF and NF regimes, the amount of applied water greatly affected the dry matter accumulation patterns. Treatment 5 of both HF and NF regimes gave the highest values of dry matter accumulation throughout the growing season. For instance, on day 92 dry matter in HF-5 and NF-5 were 940 and 860 gm/m^2, respectively, while HF-1 and NF-1 yielded only 440 and 530 gm/m^2, respectively. Treatments 4, 3 and 2 of both HF and NF regimes had values between the extreme values of treatments 5 and 1.

The average rate of dry matter accumulation for HF-5, HF-3 and HF-1 was 113.6, 70.0 and 30.0 gm/m^2 per week, respectively, and for NF-5, NF-3 and NF-1, 126.2, 68.8 and 60.8 gm/m^2 per week respectively for the period between day 50 and day 111. For treatments 5 and 3, the dry matter accumulation rates were very similar in both regimes but

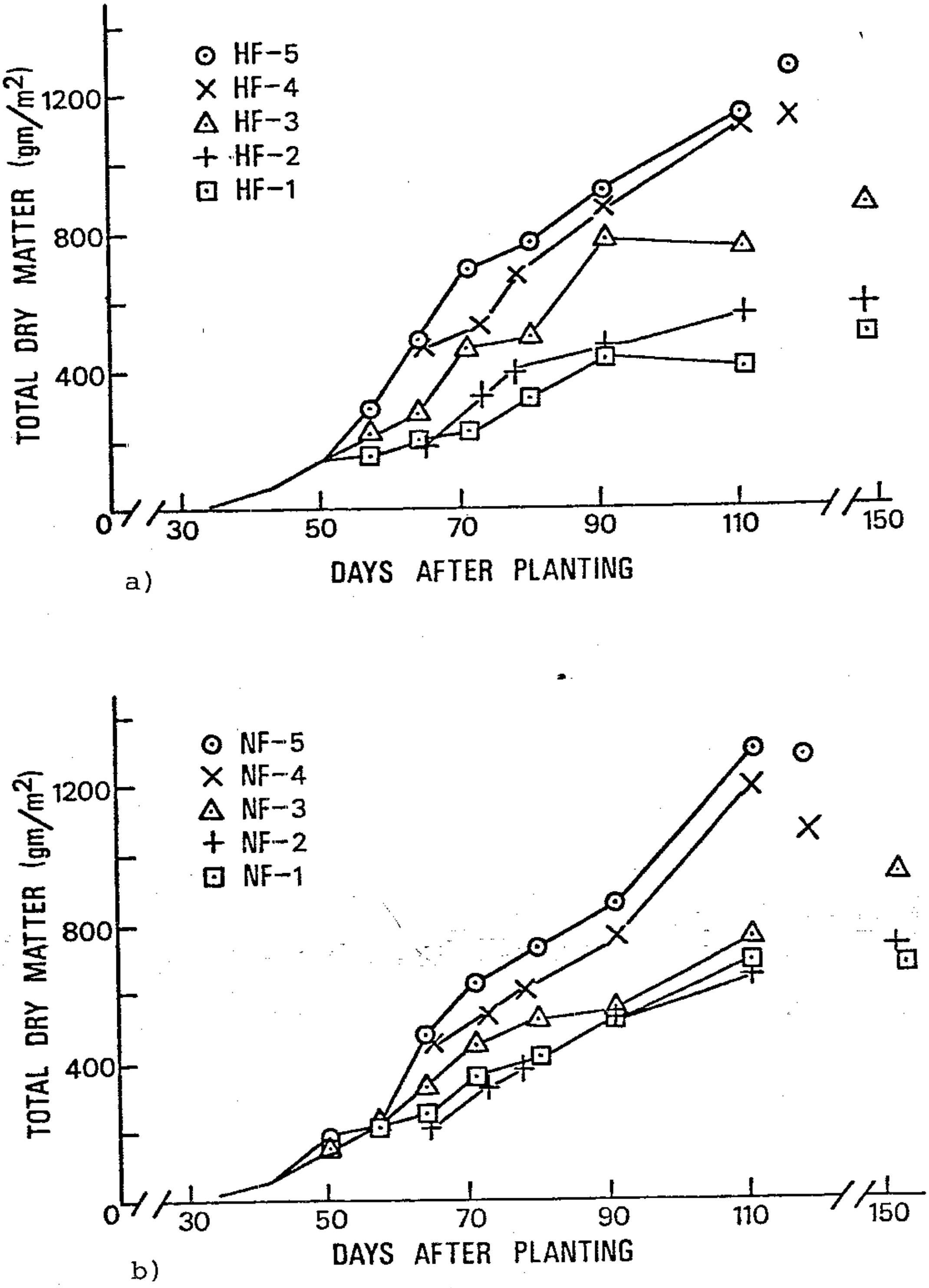

Figure 20. Above ground dry matter accumulation of main stems on a) HF regime, b) NF regime. Each point is average of two measurements of two plants each. Isolated points indicate the average total dry matter including tillers at harvest of four replicates.

in NF-1 the rate was twice as great as in HF-1. However main stem LAI and GC values did not show a corresponding difference between treatments NF-1 and HF-1. Dry matter accumulation in treatments HF-1 and NF-1 was very small due to the small photosynthetic area of the plants.

Final dry matter was also plotted in Figure 20 for all treatments. Dry matter accumulation was calculated using the main stem of two plants per replicate. Due to the variability in tillering, tillers were not considered in the evolution of dry matter. However, tillers were included in the total dry matter at harvest (isolated points of Figure 20).

The distribution of total dry matter in the different plant parts differed among treatments (Figures 21 and 22). For instance, on day 91, the contribution of leaves to total dry matter production was 26, 59, 31 and 61% in the HF-5, HF-1, NF-5 and NF-1 treatments, respectively, and that of stems was 15, 22, 14 and 25% for the same respective treatments. The corresponding contribution of the panicle was 59, 19, 55 and 14% respectively. Thus there was increasing panicle contribution to the total dry matter in wetter treatments. The small panicle contribution to total dry matter in treatments HF-1 and NF-1 can be explained by the relations between sink (panicle) and source (stem and leaves). In these treatments the sink was very small due to the very low number of grains per panicle so conceivably

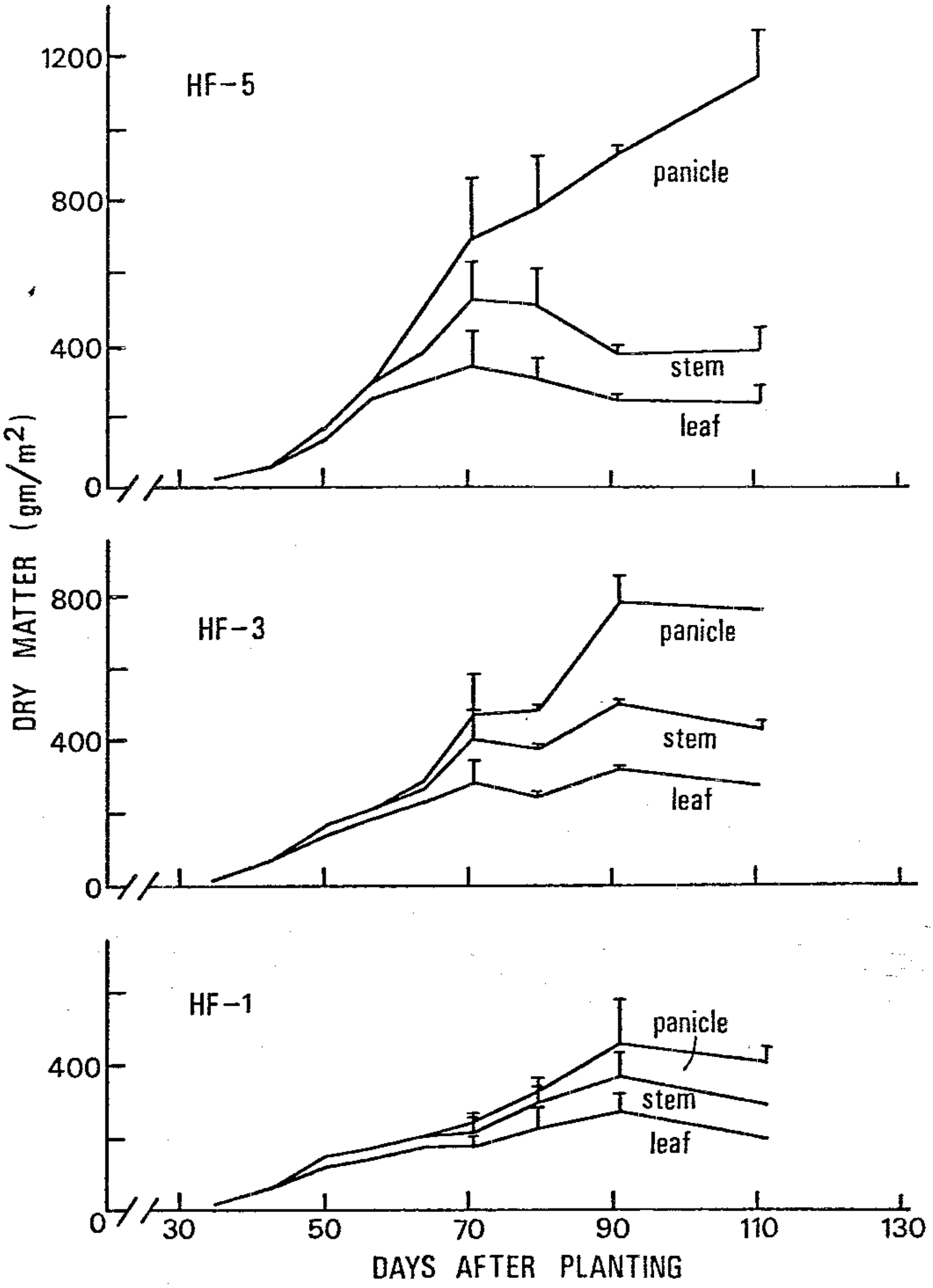

Figure 21. Dry matter yield of leaves, stems and panicle during the growing season in the HF regime. Each point is average of two measurements of two plants each. Length of the bar represents the standard error.

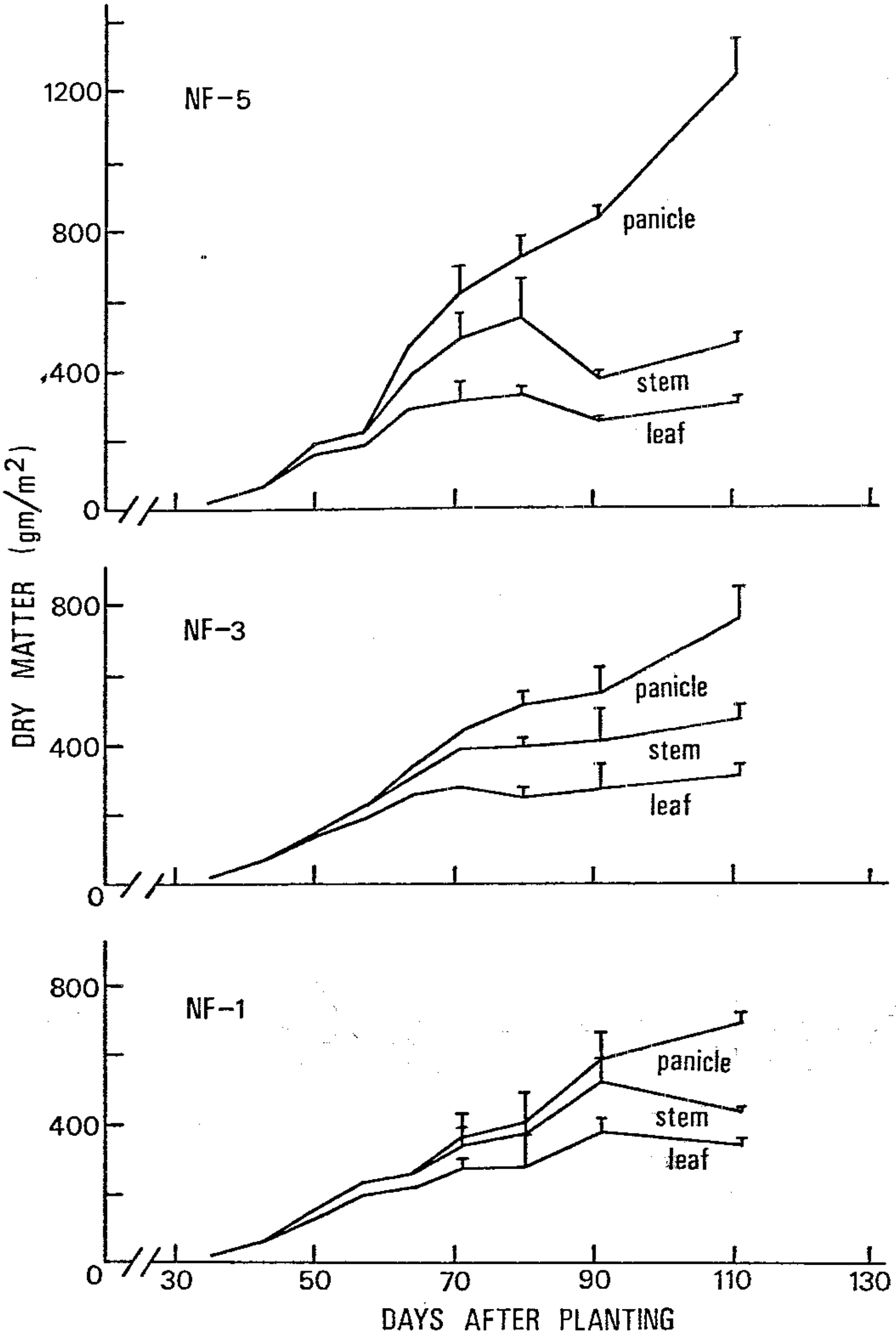

Figure 22. Dry matter yield of leaves, stems and panicle during the growing season in the NF regime. Each point is average of two measurements of two plants each. Length of the bar represents the standard error.

the transport of assimilates from the leaves to the panicle was restricted.

D.2 Dry Matter Accumulation in Experiment II

Dry matter accumulation in the NI treatment was substantially higher than in the treatments 1 and 3 of Experiment I because of the wet subsoil conditions of Experiment II.

Above-ground dry matter accumulation of the I treatment plants was higher than in the NI treatment although there were no significant differences between the two treatments on days 91 and 107 (Figure 23). The distribution of the different plant parts in total dry matter production was different in the two treatments (Figure 23). On day 91 the contribution of leaves, stems and panicle to total dry matter production for I treatment was 40, 21 and 39%, respectively. In contrast, for the NI treatment these contribution values were 29, 15 and 56%, respectively. The higher value of panicle contribution in the NI treatment probably was because of faster rate of panicle development in the NI treatment. The rate of dry matter accumulation in NI was very low after day 91, while this rate was much higher in the I treatment. This result indicated hastened maturity in the NI treatment.

E. Yield Response Functions as Affected by the Irrigation Regime and Yield Components.

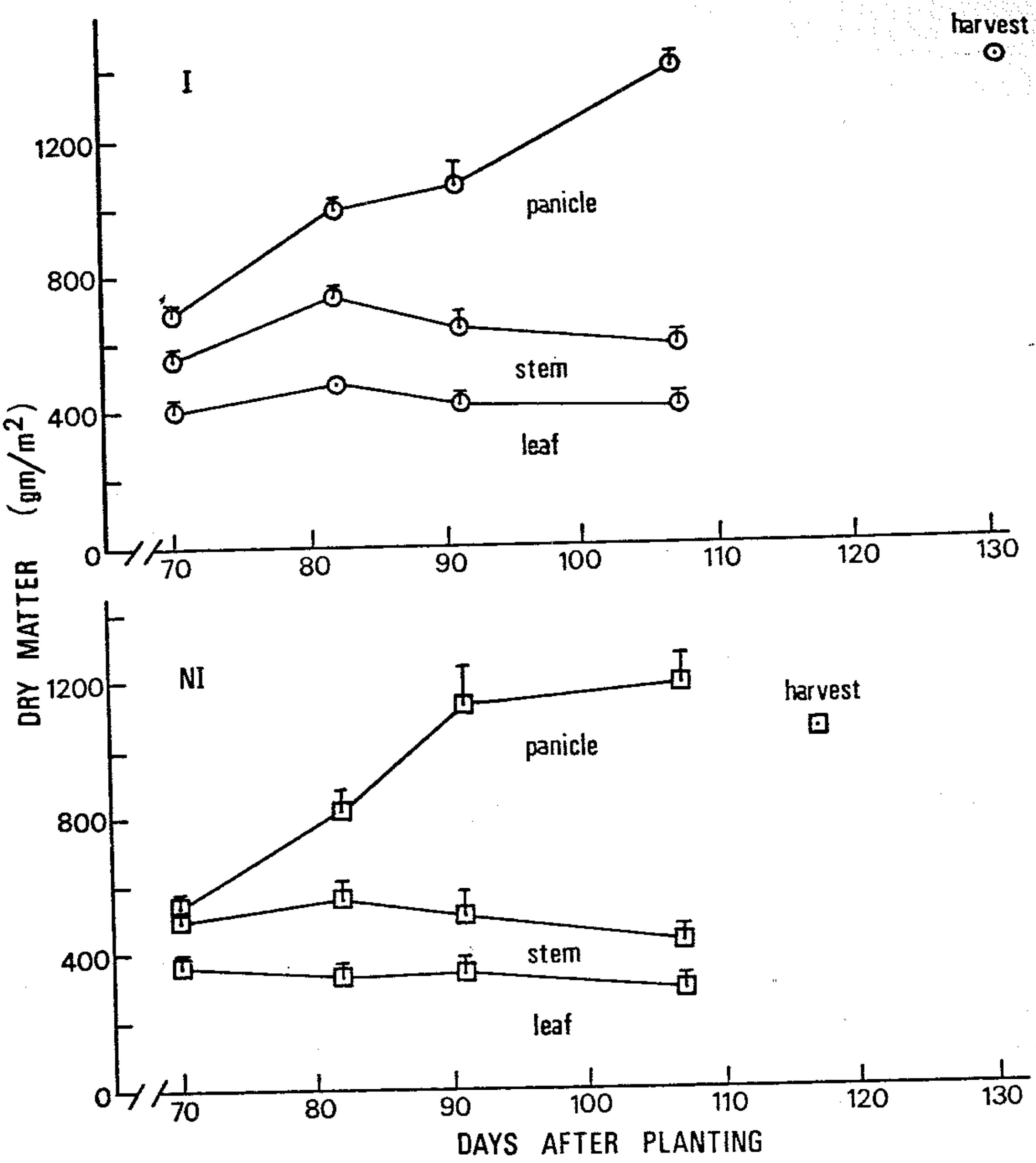

Figure 23. Dry matter yield of leaves, stems and panicle during the growing season in Experiment II. Each point is average of two plant per replicate plot. The isolated points are data at harvest. The length of the bar represents the standard error.

E.1 Relationship Between Yield and Total Seasonal ET

Yield response functions relating the total dry matter production and grain yield to seasonal evapotranspiration, were developed for both HF and NF (Figures 24 and 25). Linear regressions fitted very well the data for both total dry matter and grain yield in both HF and NF regimes. This was shown by the very high correlation coefficients, ranging from 0.936 to 0.975.

Statistical analysis showed that the slopes of the HF and NF lines were different at the 1% level in total dry matter production versus total seasonal ET. The slopes of the lines were also different at the 5% level in the plots of total grain yield versus total seasonal ET. When the actual ET was high (near potential ET), there were no differences in dry matter production or grain yield in the two irrigation regimes. However, as the actual ET decreased, total dry matter production and grain yield in the HF regime decreased more dramatically than in the NF regime. This difference is possibly because of the direct water evaporation from the soil in the HF regime when ground cover is not complete as in the stressed treatments of this work. As indicated previously, the maximum % GC for treatment 5 in HF and NF regime was 77 and 74% in contrast with 39 and 44% in treatments HF-1 and NF-1. Thus, it seems that when the % GC is high (more than 70%), the irrigation frequency did not affect the production level. However, when

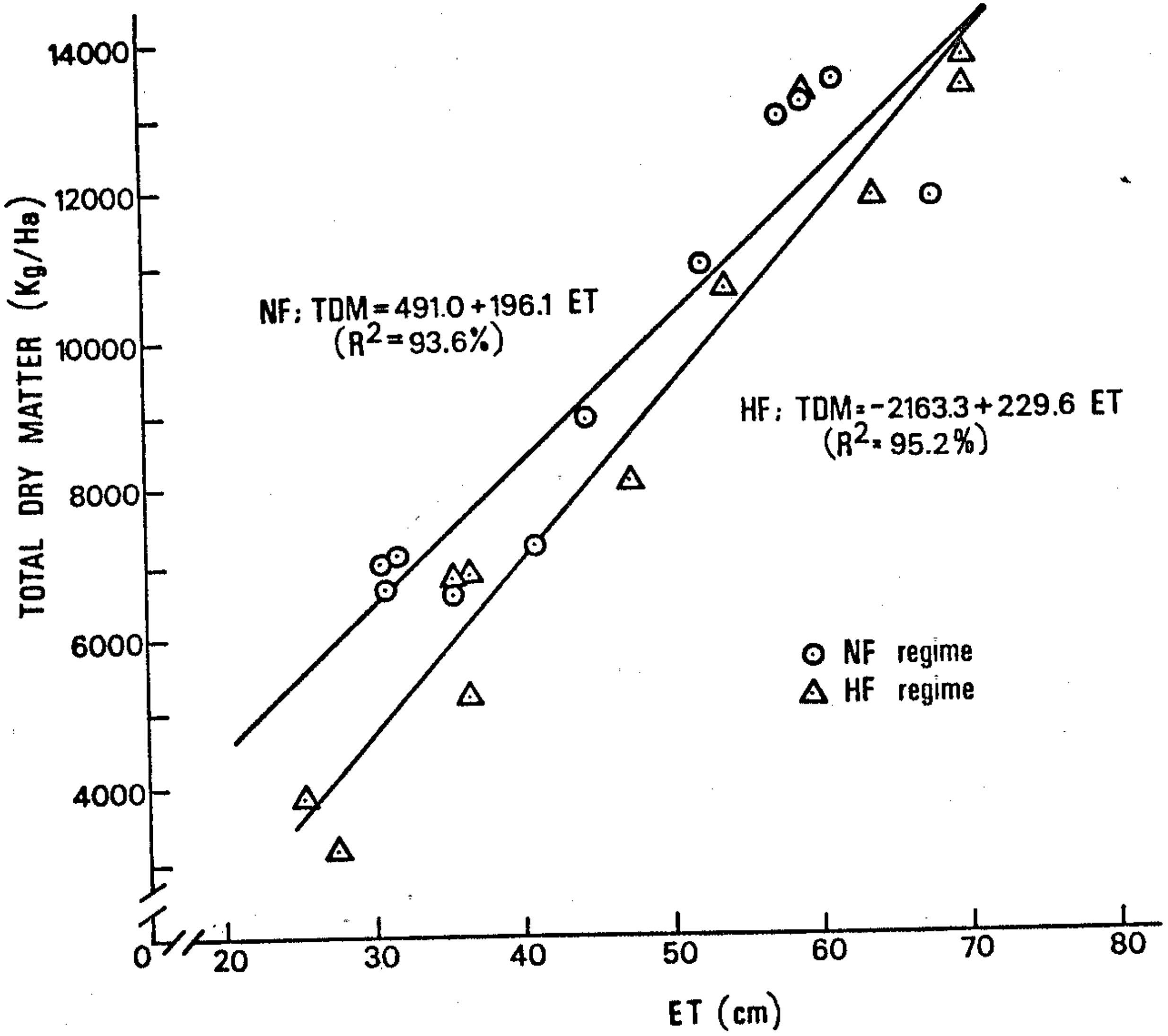

Figure 24. Linear regressions of sorghum total dry matter on seasonal ET for both HF and NF regimes.

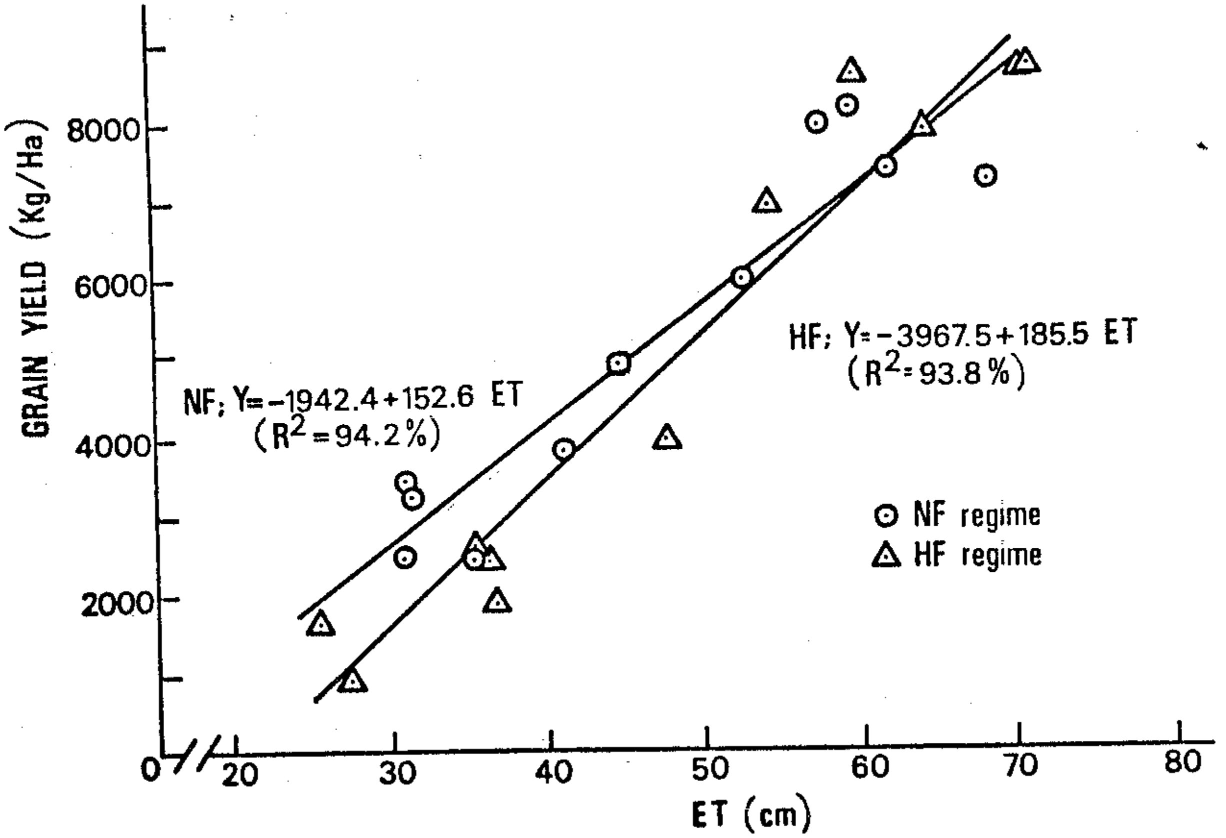

Figure 25. Linear regressions of sorghum total grain yield at 12% water content on seasonal ET for both HF and NF regimes.

the % GC is small, the high frequency regime produces less.

Water stress that occured early in the season in Experiment I (Figures 12 and 15) probably reduced the number of tillers in all treatments, therefore reducing the percentage of ground cover shaded by the crop later in the season. For instance, treatments HF-5 and NF-5 never reached full cover, while, in contrast the I treatment of Experiment II reached full cover around day 70 after planting. This reduction in ground cover may have resulted in a lower water use efficiency in treatments 1 through 4 of Experiment II.

Plotting the yield response functions in relative terms, that is as percent of maximum yield and maximum ET allows comparison with data of Stewart <u>et al</u>. (1975). They studied the water production function of sorghum in Davis and also found that a linear relation fitted their data. However, the equations obtained in this study differ noticeably from Stewart's equation, as can be seen in Figure 26. The line obtained by Stewart <u>et al</u>. was above both the HF and NF lines. Probably this disagreement was caused by the difference in soil water availability at planting time. In Stewart's experiment all the plots were pre-irrigated to assure field capacity to a depth beyond 3 m at planting time while in this work (Experiment I), the soil profile was very dry. This hypothesis was confirmed by plotting the data from 4 replicate plots of the NI

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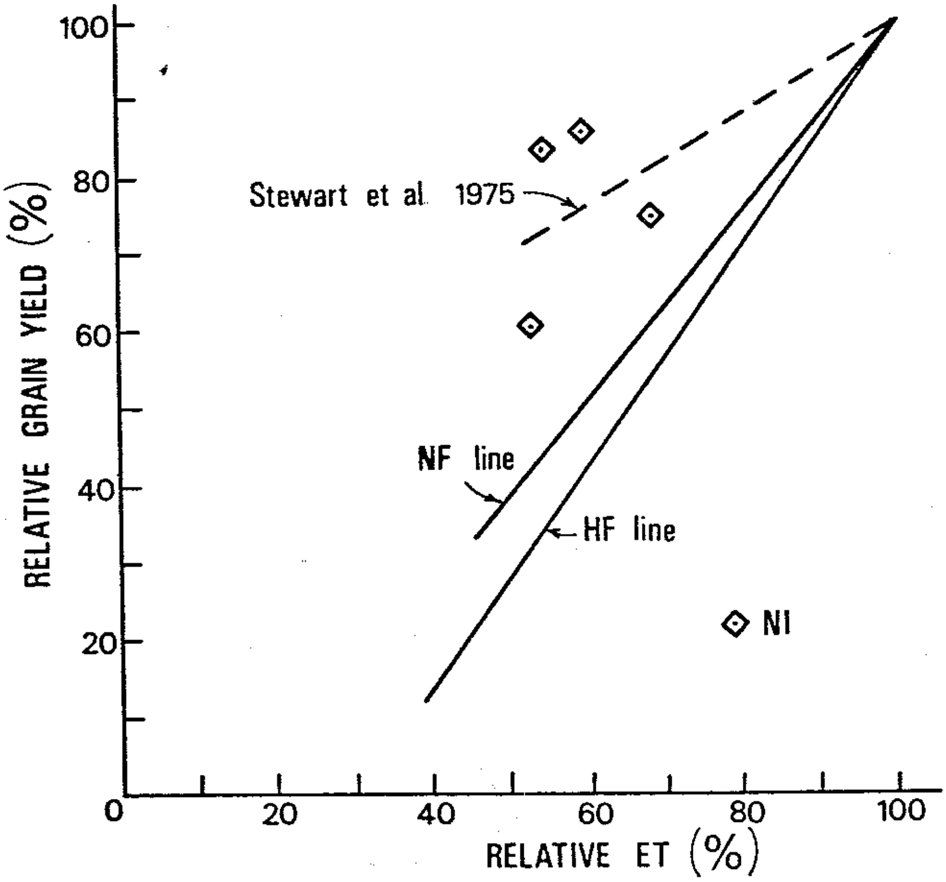

Figure 26. Lines of relative grain yield versus relative ET for both HF and NF regimes (solid lines). The dashed line corresponds to the equation obtained by Stewart *et al.* (1975) when put in relative terms. Symbols indicate points from NI plots relative to the NF-5 treatment.

treatment of Experiment II which had wet soil profile at planting. These data, as can be seen in Figure 26, fitted Stewart's equation better than the HF or NF lines.

B.2 Yields and Yield Components in Experiment I

In Experiment I, the replicates within each treatment can not be considered "true" replicates because the treatments could not be randomized due to the characteristics of the line source sprinkler plot. Therefore the treatment comparison must be discussed with caution. The maximum dry matter production and grain yield was obtained in treatments HF-5 and NF-5 (Table 4). Grain yields of treatments 5 and 4 of the HF regime appear higher than the ones in the analogous treatments of the NF regime. However, the opposite was true in treatment 1. Grain yield of HF-1 was 189.2 gm/m^2 in contrast to 289.2 gm/m^2 in NF-1. In both HF and NF regimes there was a gradient of decreasing total dry matter production, grain yield, weight of grain per panicle, number of grains per panicle and harvest index, with the maxima in treatment 5 and the minima in treatment 1. However, the number of heads per m^2 increased in the opposite direction. The head of the main stem was very damaged by water stress in treatments 1, 2 and 3 of HF and NF regimes. However heads from new branches appeared in these treatments.

E.3 Yields and Yield Components in Experiment II

Yields and yield components of the treatments of Experiment II also are presented in Table 4. The grain yield of the I treatment was 797 gm/cm^2 compared to 663 gm/m^2 in the NI treatment. However, these differences were not statistically significant because of the unusual plot to plot variability (Table 5). In earlier work in Davis, Fereres (1976) also found no differences in grain yield of I and NI sorghum when the soil profile was wet at planting time. No significant differences were found in the other yield components in the two treatments of Experiment II. The harvest index of the I and NI was 45.9 and 51.2% respectively but they were not significantly different (Table 6). However, Fereres (1976) found values of 0.42 and 0.48 for I and NI respectively and they were statistically different.

E.4 Tiller Contribution to Grain Yields

Table 7 shows the tiller contribution and yield components in both Experiment I and II. In Experiment I, the yield contributed by tillers in HF-5 and NF-5 was 18.0 and 15.4% respectively. In both HF and NF regimes, as water stress increased in severity, the tiller contribution to the final yield increased in importance. However, the % yield contributed by tillers was slightly greater in NF regime than in HF regime. The maximum value of yield contributed by tillers was 68.4% in NF-1, followed by 61.2%

in NF-2 and 48.2% in HF-1. The yield tiller contribution in treatments 1, 2 and 3 of both irrigation regimes was from the new branch heads.

In Experiment II, the yield contributed by tillers was 17.5 and 6.3% for I and NI respectively. Very few tillers developed in the NI treatment because early plant development was affected by stress and insufficient irrigation. Fereres (1976) reported values of 39.7 and 28.2% for I and NI respectively.

Table 4

Yields

	Treatment	Total Dry Weight gm/m^2	Grain Yield (12%) gm/m^2	# heads/ m^2	Weight of grain (12%) panicle gm/ panicle	# grains/ panicle	Weight of 1000 grains gm/1000 grains	Harvest Index %	# of plants/m^2
Exp. I	NF-5	1289	767	18.5	41.6	1257	33.1	50	13.4
	NF-4	1071	580	17.3	33.6	975	34.4	45	12.9
	NF-3	966	454	27.3	18.6	543	34.3	39	13.4
	NF-2	747	337	28.9	12.8	395	32.1	38	12.5
	NF-1	686	289	33.0	9.1	299	30.3	35	14.6
	NF-5	1302	844	17.3	49.1	1557	31.6	52	12.7
	NF-4	1163	763	17.2	44.4	1371	32.4	54	12.8
	NF-3	911	418	19.2	22.5	647	35.1	40	13.6
	NF-2	607	303	25.1	12.1	371	32.4	33	12.7
	NF-1	517	189	24.5	7.8	257	30.1	31	12.0
Exp. II	F-NI	1058	663	14.0	47.4	1789	26.6	51	12.5
	F-1	1440	797	16.5	49.3	1811	27.1	46	12.9

Table 5. Analysis of variance of grain yields (Kg/Ha) in Experiment II.

Source	DF	SS	MS	F
BETWEEN	1	3584771	3584771	2.44 NS
WITHIN	6	8799709	1466618	
TOTAL	7	12384480		

NS. Non significant at less than 10% level of probability.

Table 6. Analysis of variance of the harvest index values in Experiment II.

Source	DF	SS	MS	F
BETWEEN	1	57.8	57.8	2.63 NS
WITHIN	6	131.8	21.9	
TOTAL	7	189.6		

NS. Non significant at less than 10% level of probability.

Table 7. Tiller Contribution to Yields

	# of tiller heads per m^2	# grains/ panicle in main	# grains/ panicle in tillers	weight of 1000 grains (gm) in main	weight of 1000 grains (gm) in tillers	yield contributed by tillers (%)
Exp. I						
NF-5	5.1	1482	663	32.7	36.1	15
NF-4	4.4	1111	582	34.5	32.8	15
NF-3	13.9*	530	445	35.9	32.9	43
NF-2	16.4*	289	403	34.1	31.6	61
NF-1	18.4*	175	378	32.3	29.2	68
NF-5	4.5	1754	1010	31.1	34.2	18
NF-4	4.5	1539	914	32.3	32.9	17
NF-3	5.6*	731	323	35.4	33.7	17
NF-2	12.5*	475	281	33.7	30.5	37
NF-1	12.5*	236	248	30.9	29.1	48
Exp. II						
F-NI	1.5	1868	942	26.5	28.7	6
F-1	3.6	2029	876	24.9	39.3	17

*These tillers were new branch heads.

V. SUMMARY AND CONCLUSIONS

Two experiments (I and II) with Sorghum bicolor (L.) Moench, "Pioneer 846" were conducted on the University Farm at Davis during the season of 1977. The soil in Davis is deep with a high water holding capacity. Experiment I consisted of two large line source sprinkler plots in which one of the plots was irrigated every 10 to 14 days (NF regime) and the other was irrigated every other day (HF regime). However, the same seasonal amount of water was applied in analogous treatments of both regimes. In Experiment I the subsoil was very dry at planting time, thus the continuous and variable amount of applied water across the line source sprinkler, allowed a gradual development of none to severe water stress. Five locations across each side of the line sources were selected as treatments. Experiment II was conducted in an adjacent area where the soil had a fully charged profile. In this experiment the treatments were irrigated every week (I) and nonirrigated (NI). All treatments in Experiment I had water stress prior to the start of differential irrigation because of the dry subsoil conditions.

Applied water was measured for each irrigation in both experiments. Soil water content throughout the profile was measured several times during the growing season in both experiments. Plant responses such as main stem leaf area index, ground cover, leaf water potential and leaf diffusive resistance were monitored at frequent intervals in Experiment I. Dry matter accumulation, yields and yield components were also measured in both experiments.

The following conclusions can be made:

1) The line source sprinkler method is an excellent téchnique to obtain a continuous gradient of applied water. There was no significant differences between the seasonal water applied in analogous treatments of HF and NF regimes.

2) Main stem LAI an indicator of vegetative growth, was drastically affected by the different treatments in the Experiment I. Maximum values were 4.5 and 4 for treatments HF-5 and NF-5. In contrast, the maximum values for HF-1 and NF-1 were only 1.6 and 1.9.

3) There was a very close linear relationship between main stem LAI and percent ground cover for HF and NF regimes in the period from day 28 to day 64.

4) The canopy architecture appeared to be different for the HF and NF regimes. Plants of the HF regime seemed to have more erect leaves than those of the NF regime. For any given value of main stem LAI, ground cover was higher for the NF regime than for the HF regime.

5) Adaptation to water stress as indicated by a shift in the relative water content - leaf water potential curve, occured in all the treatments of Experiment I. However the leaf area development, percent ground cover,

dry matter accumulation and yields were drastically reduced in the severe water stressed treatments.

6) Severe water stress affected and even totally killed the panicle of main stems. This happened in treatments 1 and 2 of Experiment I. However, new branch tillers appeared which developed new heads. These new branch panicles reached physiological maturity much later in the season.

7) Moderate water stress induced early maturity in the sorghum as compared to lack of stress and severe stress.

8) Linear relations were found between total dry matter production and total seasonal evapotranspiration in both HF and NF regimes. The slopes of the two lines were significantly different, indicating that the total dry matter accumulation at high values of ET was similar in both regimes. The total dry matter was significantly less in the HF regime as compared with the NF regime at low values of ET.

9) Similar results were found in the relationship between grain yield and total seasonal evapotranspiration. Again the lines HF and NF differed in shape. The same production level was obtained in both irrigation regimes at high values of total seasonal ET (approximating maximum ET). However, at low seasonal ET values, the grain yield of the HF regime was less than analogous treatments in the NF regime.

10) Grain yield of the irrigated and non-irrigated treatment of Experiment II was 797 and 663 gm/m^2 respectively. However this difference was not statistically significant.

11) The yield response functions (grain yield versus total seasonal ET) found for HF and NF regimes differed markedly from the equation obtained at Davis by Stewart _et al_. (1975). This may be due to the wet soil profile at planting time in Stewart's experiment and the dry subsoil at planting time in this study.

    When the seasonal ET was decreased by water stress, it appears that higher grain yields are obtained if the water can be stored in the soil at planting time. The NI treatment of Experiment II, which had a fully charged profile at planting time, had a seasonal ET of 40.9 cm and a grain yield of 663 gm/m^2. However, for the same level of ET with dry subsoil (treatments HF-2 and NF-2) the yields were much smaller; 303 gm/m^2 in HF-2 and 337 gm/m^2 in NF-2.

12) Yield contribution by tillers was very important in both irrigation regimes and the percentage of yield contribution by tillers increased as water stress increased in severity. For example the grain yield contributed by tillers in NF-5 and HF-5 was only 15 and 18%, respectively. In contrast, yield contributed by tillers was 68% and 48% in NF-1 and HF-1 respectively.

13) Harvest index was maximum in treatments HF-5 and NF-5 (52 and 50%) and was decreased as the severity of water stress increased. Harvest index of HF-1 and NF-1 was only of 31 and 35% respectively.

14) At low values of ET, it can be concluded that grain yield and water use efficiency will be higher in the NF regime than in the HF regime. Therefore no advantage was found for the deficit high frequency irrigation regime in grain sorghum.

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