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Dennis Scott NeSmith

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Joe T. Ritchie
Major professor

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GROWTH RESPONSES OF CORN (ZEA MAYS L.) TO INTERMITTENT SOIL WATER DEFICITS

By

Dennis Scott NeSmith

A DISSERTATION

Submitted to
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ABSTRACT

GROWTH RESPONSES OF CORN (*ZEA MAYS* L.) TO INTERMITTENT SOIL WATER DEFICITS

By

Dennis Scott NeSmith

An increased understanding of corn responses to intermittent water deficits is a prerequisite to achieving goals of maintaining production and protecting the environment in humid regions where supplemental irrigation is used. A rain shelter was employed to impose periodic drought on corn at various growth stages in a field environment in Michigan, and whole plant responses were examined. Results indicated yield losses due to 18 to 21 day water deficits on a sandy soil were 15 % to 25 % when the water shortage occurred during pre-anthesis growth, were as great as 90 % when the deficit occurred during anthesis, and were 25 % to 40 % when the deficit occurred during the grain filling period. A notable correlation between water absorption from the upper 0.25 m of soil and plant extension growth was observed. Reduction in extension growth resulted in reduced size of leaves, internodes, and ears that were expanding during the deficit period, and the smallness was primarily attributable to decreased growth rate rather than shortened duration of growth. Above ground biomass accumulation was less under deficit conditions at all growth stages and was largely attributable to reduced production of leaf area or increased

loss of green leaf area due to early senescence. Limited data indicated leaf rolling, alteration in light interception, and increased root growth at deeper soil depths also contributed to the decline in above ground crop growth rate. Tasseling, silking, and beginning grain fill were delayed by pre-anthesis water deficits. Water shortages during anthesis caused as much as 80 % barren plants. The period of time from just before anthesis until beginning linear grain filling was determined to be critical in obtaining substantial kernel set. Maximizing grain number per unit area was important in maintaining favorable yields, as little compensation in grain weight was observed for plants with lower numbers of kernels. Water deficits during grain filling reduced the duration of linear filling more than the rate. Grain size distributions demonstrated deficit plants had a larger percentage of grains weighing less than 100 mg $seed^{-1}$ than did irrigated plants.

ACKNOWLEDGEMENTS

I would like to extend a sincere appreciation to the many people that have been involved in the various processes leading up to this event in my life. First, there is my advisor Dr. Joe T. Ritchie. He has allowed me opportunities for personal and professional growth I feel I could have obtained few places. He has often remained at arms length, but that was so that I could learn the needed independence it will take to set off on a scientific career of my own. However, he has always been willing to take the time to listen to my ideas as well as my gripes and grievances. I am certain that having him as a mentor will enhance my scientific endeavors for many years to come. Thanks Dr. Ritchie.

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challenges through the past few years. I appreciate their leading me to Christ at an early age most of all. The relationship with Him has been my source of strength, love, and wisdom, all of which I needed to complete this task, or any other which I may encounter. He is my Rock.

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INTRODUCTION

Record yields of important agronomic crops are three to seven times greater than those obtained on average, even in more developed agricultural regions (Boyer, 1982; Ritchie, 1983). Diseases and insects account for only a small fraction of the deviation from the high yields, whereas physicochemical problems make up 70 % of the difference (Boyer, 1982). Among the environmental factors responsible for drastic crop yield reductions, drought, or water deficit conditions, is the main one. Boyer and McPherson (1975) stated that no other factor limits grain yield so extensively and unpredictably. Water deficits are not confined to dry regions. Decker (1983) reminded that drought is not a rare event even in humid regions, and Ritchie (1983) viewed an important avenue for world wide improvement of crop productivity was through reduction of short drought periods in humid regions.

Decker (1983) suggested three ways of defining drought with a definition based on; 1) climatic expectation, 2) long term impact of "dry" weather such as reservoir water levels or yields of major crops, and 3) dryness of agricultural soils using a pre-set value relating to plant available water. The first two definitions have been used in a broad sense to describe production limitations of rather large agricultural regions, however, as Ritchie (1983) pointed out these definitions are restricted in making resource and management decisions. The third definition approaches that needed for decisions on state, county, or even individual grower levels, yet it is important only as related to weather and yields. Functional crop models attempt to incorporate all three aspects such that management and resource decisions can be made on any desired level. However, these models are useful only if they can predict yields reasonably well for a diversity of environmental conditions. This requires the support of continued research into the mechanisms of how plants respond to water deficits.

Solving production limitations due to water deficiencies in more humid regions is not as simple as a mass change to irrigated agriculture in these regions, especially in the United States. Ritchie (1983) reminded that principles of humid region irrigation are different than those of drier regions. He suggested that technology has to be sought that minimizes excess water movement through the soil which lends to chemical leaching, while maintaining a favorable nutrient and water supply in the root zone. While economic incentives have dominated U.S. production agriculture in the past, an age where this may no longer be true is likely eminent. There is a growing concern for the environment as well as maintaining production, and this poses great challenges. Boyer (1982) remarked, "Responding effectively to mounting world food demands, economic pressures, and the need for conservation are dilemmas for farmers and legislators alike." One could add that pressure has been put on agricultural scientists as well to seek ways of maintaining this balance.

Michigan is a state which holds potential for increased crop production with supplemental irrigation. According to Lucas and Vitosh (1978), Michigan has the lowest summer rainfall of any state east of the Mississippi River. They reasoned there is about a 40 % probability of at least a mild drought occurrence during the months of June, July, and August. Their definition used for drought incorporated definitions one and three of Decker (1983) as discussed previously. Soils ranging in texture from sandy to sandy loam were depicted by Lucas and Vitosh (1978) as running out of water in 4 to 14 days under crop production. They indicated 75 % of the plant available water in the upper 0.9 m of soil as the threshold depletion value. Corn grain yields were estimated to increase as much as 90 % to 300 % under irrigated conditions on these soils.

Algozin et al. (1988) reported about 162,000 hectares of irrigated cropland in Michigan with about 50 % of this being dedicated to corn production. Their work analyzed irrigation strategies based on yield, as well as water use and energy consumption. Based on a somewhat crude definition of water use efficiency (WUE) which is defined as unit of economical yield per unit of water applied (Bolton, 1981), the results of Algozin et al. (1988) demonstrated that irrigation application rates of 6 mm, 13 mm, and 25 mm per application had WUE values of 69, 65, and 59 kg mm^{-1}, respectively, for the supplemental water. Therefore, the smaller volume but more frequent irrigation applications were the most efficient in terms of water and energy as opposed to traditional applications of 25 mm or more. While this analysis was based on simulated results using a crop model, their results were within the range of real values which they reported.

The aim of the scenario presented by Algozin et al. (1988) was to encourage irrigation scheduling on the basis of profit and efficiency instead of maximum yields. Field research often leans toward the latter point, therefore, there exists the need for exploring yield compromises in exchange for reduced applications of water. Begg and Turner (1976) discussed several important aspects to consider when studying water deficit effects on plants, and these would fit well in to the planning of irrigation strategies as well. An increased understanding of crop water deficits is a prerequisite to achieving the previously mentioned goals of maintaining production and resources. One of the most important factors to consider is the crop growth stage. Ludlow and Muchow (1988) stated that management and cultivar selection should match crop phenology with expected water supply in the most efficient way. They presented several avenues to explore in improving crop production per unit of given water under conditions prone to either terminal or intermittent drought. Those given for intermittent drought regions included leaf growth, water extraction, developmental patterns, and hybrid differences under deficit conditions.

Shaw (1983) reviewed yield reductions of corn due to water deficits. A general concept presented showed potential yield reductions due to a water shortage were as much as 3 % per day of stress when it occurred 30 days either side of silking. A more critical time from a few days prior to silking to 10 to 12 days past could result in yield losses as great as 8 % per day of stress. These broad concepts lend areas of focus for discerning crop water needs, however, it is difficult to incorporate these ideas into the more careful management strategies that have been presented in the preceding discussion. Begg and Turner (1976) suggested that sensitivity of crops to stress at any growth stage varies and depends on degree, duration, and timing of the stress.

More detailed investigations as to whole plant responses to water deficits at different growth stages are needed, especially at the field level. Several investigations in controlled environments with container grown plants have been used for this purpose also. Much of our understanding of plant water relations has evolved from container experiments, however, the information gained must eventually be proven useful under field environments. Ritchie (1973) emphasized differences between container grown plants and those in the field. He viewed that a major difference between the two environments was that of an unrealistic rooting volume for container plants. Begg and Turner (1976) supported this idea as well. They surmised that water deficits developed so rapidly when containers were used that plant adaption to stresses could not occur as it might in the field. Also, Shaw (1983) indicated that under field conditions fertility stress is often combined with water deficit conditions as nutrients are concentrated in the surface soil layers which are often dry.

The objective of this research was to investigate whole plant responses of corn to intermittent water deficits at different stages of growth under field conditions. An auxiliary goal is to utilize the results to lend understanding and improvement to the prediction of corn performance under deficit conditions using crop models. The integration of this knowledge with that of experiments being conducted by others will help in developing the needed decision and management tools to achieve sustainable, productive, and profitable farming of corn in more humid regions such as Michigan.

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CHAPTER 1

PRE-ANTHESIS SOIL WATER DEFICIT EFFECT ON CORN (*ZEA MAYS* L.). I. VEGETATIVE GROWTH AND DEVELOPMENT

ABSTRACT

An increased interest in scheduling irrigation in more humid regions in order to conserve water and prevent ground water contamination while maintaining favorable crop production lends to the necessity of determining effects of intermittent water deficits on crop growth. A plausible growth stage for reduced irrigation applications is pre-anthesis. Research was conducted in Michigan during 1988 and 1989 utilizing a rain shelter to control water regimes in a field environment. Objectives were to determine immediate and subsequent responses of corn to periods of soil water deficit prior to anthesis. An 18 to 21 day period without water on a sandy soil was initiated as the 8th or 9th leaf emerged from the whorl of plants for two corn hybrids. Results of vegetative growth and development reported here indicated plant extension growth was highly correlated with water absorption from the upper 0.25 m of soil. When relative water absorption (actual divided by potential maximum) from the surface soil layer fell to 85 % to 90 %, relative plant extension growth of deficit plants declined linearly reaching zero at 25 % to 30 % relative water absorption. The reduction in extension growth resulted in delayed leaf tip emergence, reduced leaf area, and shortened internodes. Height to the top leaf ligule was determined to be a much less laborious plant measurement than individual leaf measurements, and it proved to be just as useful in evaluating extension growth and leaf area to some degree. Additional results on reproductive growth and development and on biomass and nitrogen accumulation and partitioning are presented in companion papers.

INTRODUCTION

There has been an increasing interest in scheduling irrigation applications in order to conserve water and to prevent excess water movement through the soil which might lend to ground water contamination. This has been especially true in more humid regions where irrigation is supplemental, and the soil profile is often fully recharged at the beginning of the growing season. A corn growth stage plausible for reduced water applications is pre-anthesis, as vegetative water deficits have been found to be less detrimental to final yield than flowering and grain filling water deficits (Claassen and Shaw, 1970; Denmead and Shaw, 1960; Grant et al., 1989; Robins and Domingo, 1953). Nevertheless, leaf and stem elongation have been determined to be among the most sensitive plant processes to shortages of water (Hsiao, 1973), and these processes have been shown to be reduced as plant water status declines (Acevedo et al., 1979; Boyer, 1970; Michelena and Boyer, 1982; Sharp and Davies, 1979). If the goal of reducing irrigation applications is to be met, pre-anthesis water deficits need to be examined more carefully to circumscribe the overall influence on plant growth and yield, and to improve the predictability of this influence.

Agronomically, soil water has been a frequently measured parameter. Grant et al. (1989) indicated that the status of soil water was more predictable and obtainable than that of plants on a field level, and Ludlow (1987) suggested that the lack of a unique relationship between plant water potentials and physiological processes has led to the use of soil water status to simulate shoot performance in many crop growth models. Recent experiments have demonstrated stomatal conductance and leaf and stem elongation were reduced in response to soil drying before there was any appreciable influence on shoot water status (Blackman and Davies, 1985; Davies et al., 1986; Gollan et al., 1986; Schulze, 1986). Additional information on the dynamics of soil water and its influence on plant growth processes in the field is needed.

Field water deficit experiments are difficult to conduct in humid regions due to the untimeliness of rain. This is especially true when the study of drought during a specific growth stage is desired. Rain shelters have aided in reducing the risk of rain interfering with water deficit experiments (Foale et al., 1986; Upchurch et al., 1983). This, along with controlled water applications, can provide judicious scheduling of crop water supply (NeSmith et al., 1990). The objectives of this research were to utilize a rain shelter to determine the immediate and subsequent effects of corn growth and development in response to a pre-anthesis soil water deficit in a field environment. Results of vegetative growth and development are reported here, while results of reproductive growth and development, and of biomass and nitrogen accumulation and partitioning are reported in companion papers.

MATERIALS AND METHODS

This research was conducted during 1988 and 1989 at the Kellogg Biological Research Station near Kalamazoo, Michigan, USA. Corn was grown in an area that could be covered by a rain shelter. This facility has been described elsewhere by Martin et al. (1988). The soil was a Spinks sand (sandy, mixed, mesic Psammentic Hapludalf). Figure 1.1 illustrates the water content of the soil profile after near saturation

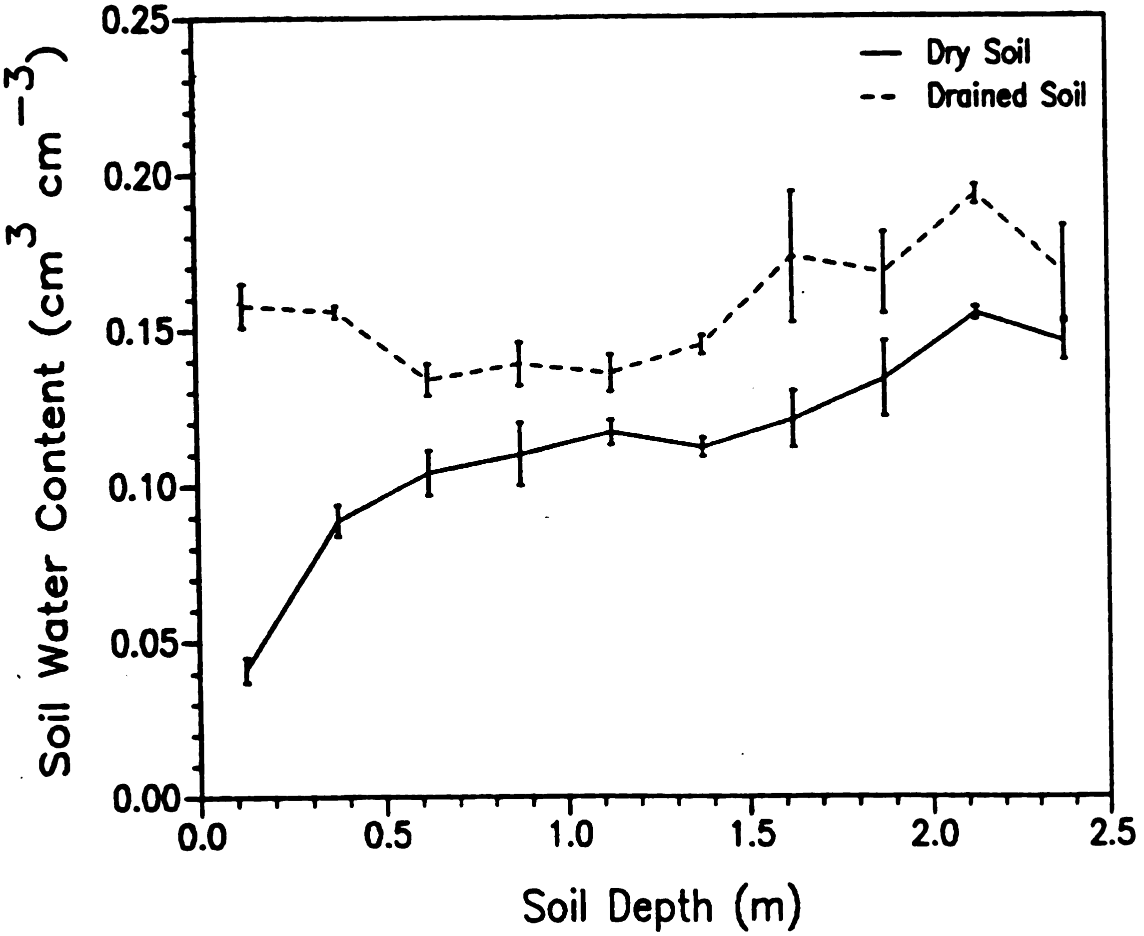

Figure 1.1. Soil water content of a Spinks soil at different depths after saturation followed by three days drainage and after more than forty days of drying by a corn crop.

followed by three days of drainage and after more than forty days of drying by a corn crop with no additions of water. The rain shelter did not cover plots from September to April each year, and as a result the soil water profile was near the drained equilibrium status at the beginning of the growing season because of snow and rain.

Due to limited space at the rain shelter site, the first year experiment consisted of a single replication for each treatment. A completely randomized split-plot experimental design was used in which water regime was the main plot and corn cultivar was the sub-plot. Main plot size was 4.3 m x 6.2 m. Pioneer corn hybrids 3540 and 3475 were planted at a higher than desired density on 5 May (day of year, DOY, 126) in 0.71 m rows at a depth of 0.05 m. These hybrids were chosen because there had been some observed differences between them in response to drought during certain years but not others. Part of this investigation was to determine potential reasons for such variability. Emergence occurred on 15 May, and plants were thinned to a population of 7.9 plants m^{-2} on 25 May. Fertilizer applications were 150 kg ha^{-1} K on 20 April, 60 kg ha^{-1} N on 25 May, 300 kg ha^{-1} P and 160 kg ha^{-1} N on 6 June, and 75 kg ha^{-1} N on 15 July.

In 1989, the experiment was enlarged to include two replications for each treatment. There were two planting dates. The reason for this was that there was a difference in leaf number of one leaf between the two cultivars during 1988, as well as a two to three day difference in tasseling and silking. It was hypothesized that this could be linked to some of the differences in observed responses to drought, as plants would have been at different developmental stages (e.g. hybrid 3475 flowered 2 to 3 days before hybrid 3540). It was planned that around 50 degree days (°Cd) would elapse between the first and second planting dates to provide a thermal time separation so that the two genotypes would end their vegetative growth nearer the same time. This was to provide hybrid comparisons of plants nearer in development (i.e. the second planting date of hybrid 3475 would be similar in development to the first planting date of hybrid 3540). Water deficits were imposed at the same time for both planting dates. Plot size, row width, and seeding depth were the same as in 1988. Main plots were water regime and planting date, and again sub-plots were corn cultivars. Planting dates were 3 May (DOY 123, this will be referred to as P1 indicating first planting) and 17 May (DOY 137, this will be referred to as P2 indicating second planting) which were separated by 64 °Cd (Figure 1.2). Emergence occurred on 18 May and 25 May, and plants were thinned on 26 May and 30 May for P1 and P2, respectively. Fertilizer was applied at planting at a rate of 63 kg ha^{-1} N, 230 kg ha^{-1} P, and 63 kg ha^{-1} K. Additional fertilizer applications for P1 and P2 were 96 kg ha^{-1} N on 1 June, 53 kg ha^{-1} N on 23 June, and 45 kg ha^{-1} N on 20 July. Weeds were controlled manually during both years.

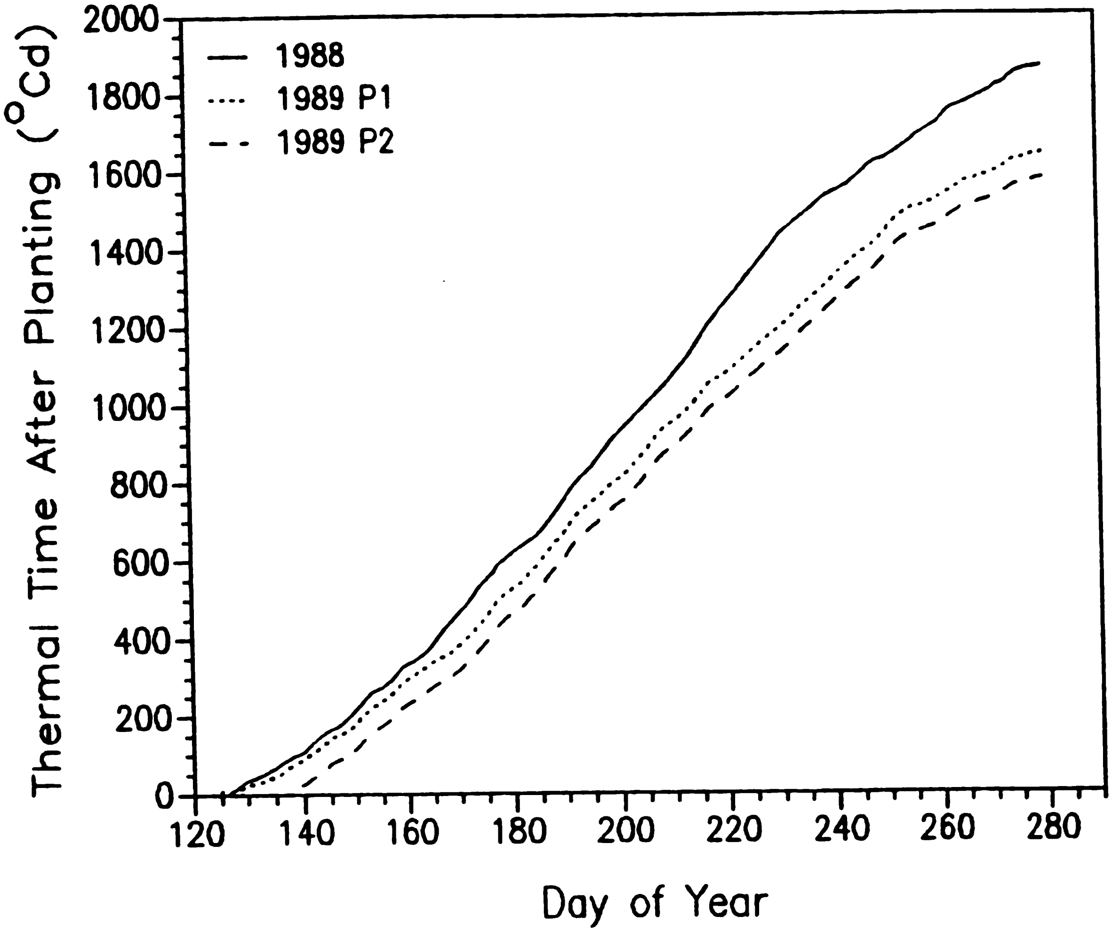

Figure 1.2. Thermal time accumulation during 1988 and 1989. There were two planting dates (P1 and P2) during 1989. Units were calculated using 8 °C as base temperature.

Water regimes were similar for both years. There were two treatments, an irrigated control (I) and a pre-anthesis water deficit (PAD). Water applications were the same for treatments except during the deficit period (Figures 1.3a and 1.3b). The PAD began near the appearance of the tenth leaf tip and ended before tassel emergence of the irrigated control. The deficit was 21 days (300 °Cd) in 1988 and 18 days (265 °Cd) in 1989.

Sample plants for nondestructive measurements of leaf area and extension growth were selected one month after planting. Eight and four plants per plot were tagged and monitored throughout the growing season during the first and second year, respectively. During both years leaf extension was determined by measuring the growth of upper leaves that did not have a visible ligule. Relative leaf extension was calculated for the water deficit plants by dividing their extension rate by that of the control plants. Height from the soil surface to the top leaf ligule was measured several times weekly. Relative extension was also calculated from this measurement for water deficit plants by dividing by the rate of control plants. The PAD P2 plants during 1989 were compared to P2 control plants, as there was a treatment in another experiment with the same planting date which was irrigated until after silking. Final internode lengths were measured on plants at the end of the growing season.

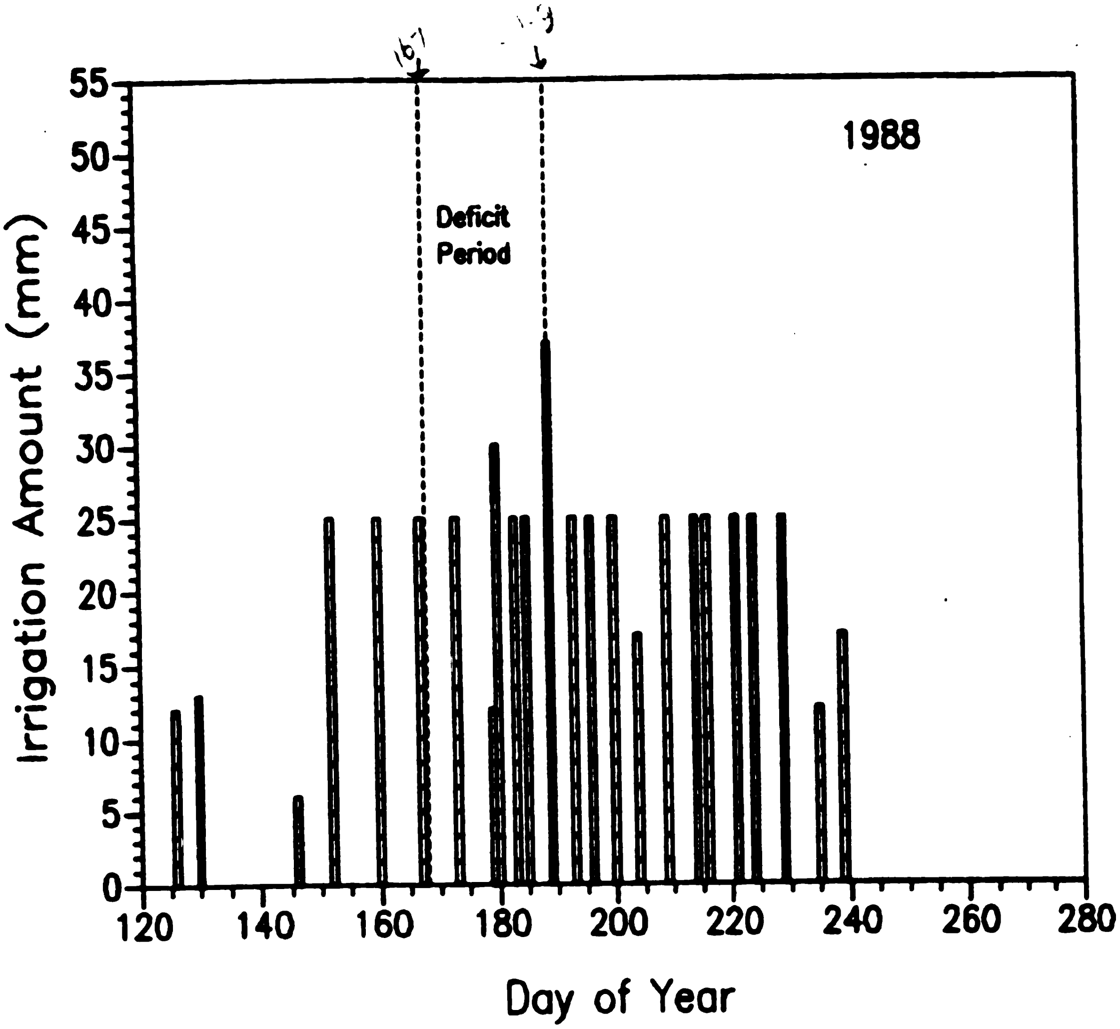

Figure 1.3a. Irrigation amounts applied to treatments during 1988. The region between vertical dashed lines represents the period when no water was applied to pre-anthesis deficit treatments.

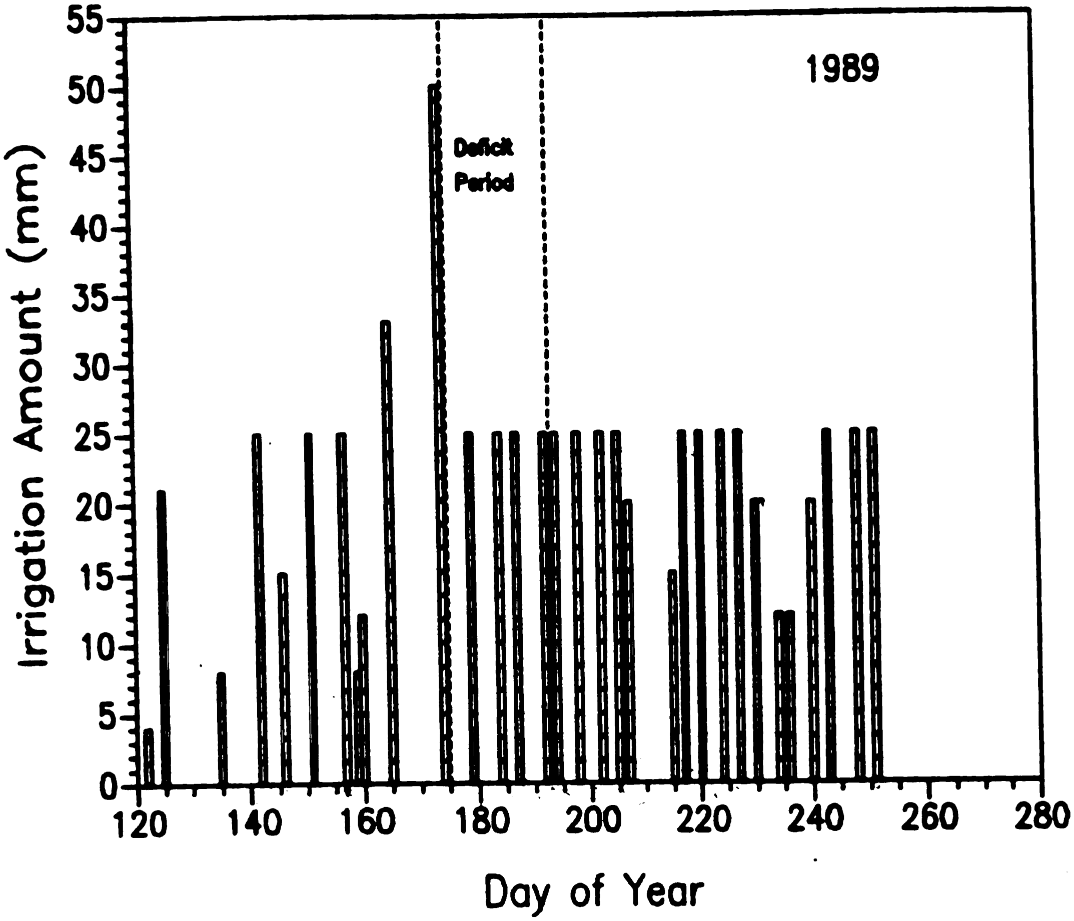

Figure 1.3b. Irrigation amounts applied to treatments during 1989. The region between vertical dashed lines represents the period when no water was applied to pre-anthesis deficit treatments.

During 1988, leaf appearance was determined by recording when a respective leaf tip was visible. In 1989, visible leaf tip number was recorded four to six times weekly for all the sample plants, and these values were averaged and plotted as a function of thermal time. Leaf ligule appearance rate was assessed similarly during the second year. Leaf area was determined two or three times weekly during 1989, beginning with the fourth leaf. Leaf length, taken as the distance from the uppermost leaf ligule to the tip of a growing leaf, was multiplied by the maximum exposed leaf width, and 75 % of this product was assumed to approximate the area of an individual leaf (see Johnson and Tanner, 1972; Linvill et al., 1978). Leaf area was considered maximum when its respective leaf ligule appeared.

Soil water content was measured both years using the neutron scattering technique. Sampling was in 0.25 m increments to a depth of 1.5 m. There was one access tube in the center row of each sub-plot the first year and two the second. In 1988, weekly measurements did not begin until after the deficit treatment had been imposed. However, in 1989 measurements began shortly after planting and were taken one or two times weekly until near physiological maturity of the crop. The water content during the 1989 deficit period was plotted and a line fitted through the data for each sampled depth. The slope of this line was taken as water absorption rate, with the assumption that upward soil water flux was negligible.

RESULTS AND DISCUSSION

Figures 1.4a and 1.4b depict the water content of the 1.5 m soil profile each year in units of equivalent depth. The soil water data were averaged for both hybrids as there were no detectable differences between them. Similar patterns of profile drying occurred during the two years for deficit treatments, except that the soil was drier at the end of the deficit period in 1988. This was primarily attributable to a longer deficit period during the first year. Irrigated control plots were maintained at a favorable water content both years.

Plant extension growth declined in response to the soil water deficits for the two hybrids similarly both years (Figures 1.5a through 1.5c). A measurable decrease in extension of PAD plants was obtained in less than five days after withholding water, indicating the sensitivity of this process to shortages of soil water. The assessment of relative extension growth from leaf length and from the height to the top leaf ligule gave comparable results. After irrigation resumed, extension rate of PAD plants rapidly returned to that of I plants. Continued comparisons were not valid after the deficit period because I plant extension

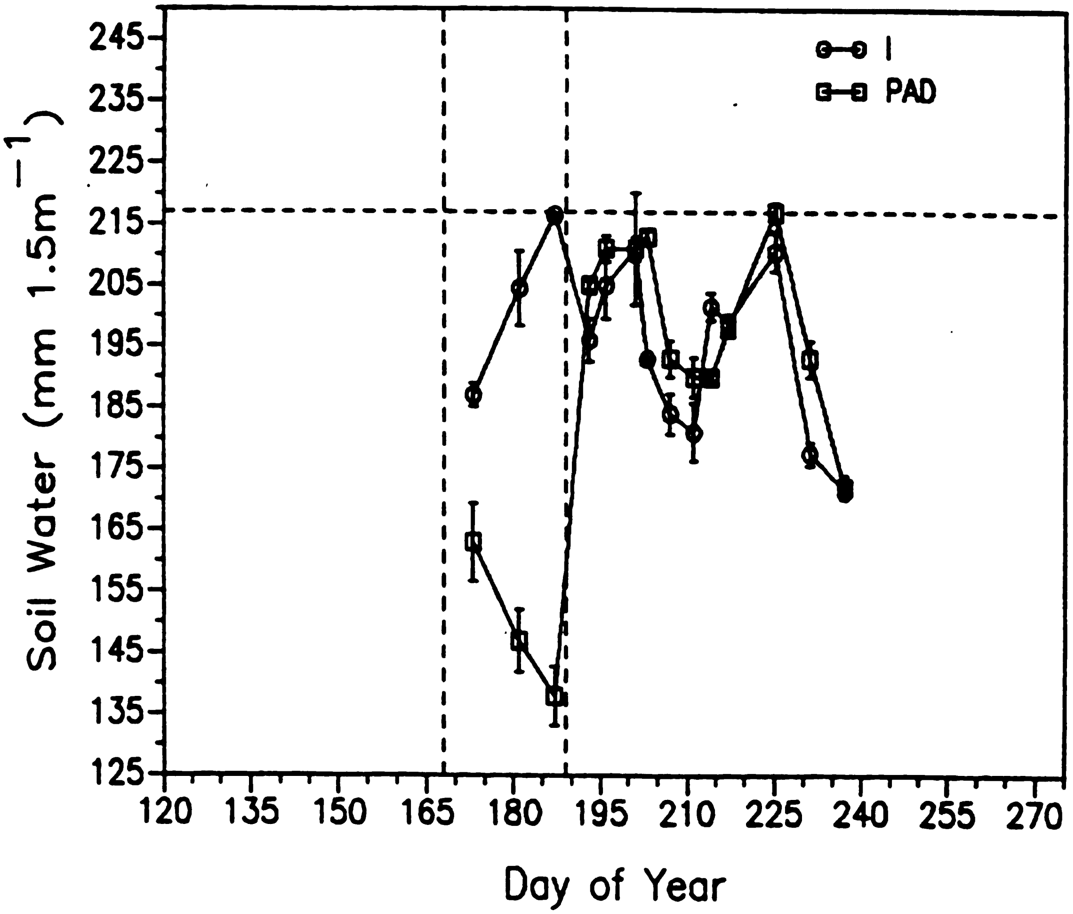

Figure 1.4a. Soil water content of the 1.5 m profile during 1988. Values are equivalent depth water. The horizontal dashed line represents the estimated drained upper limit of soil water, and the region between the vertical dashed lines depicts the deficit period.

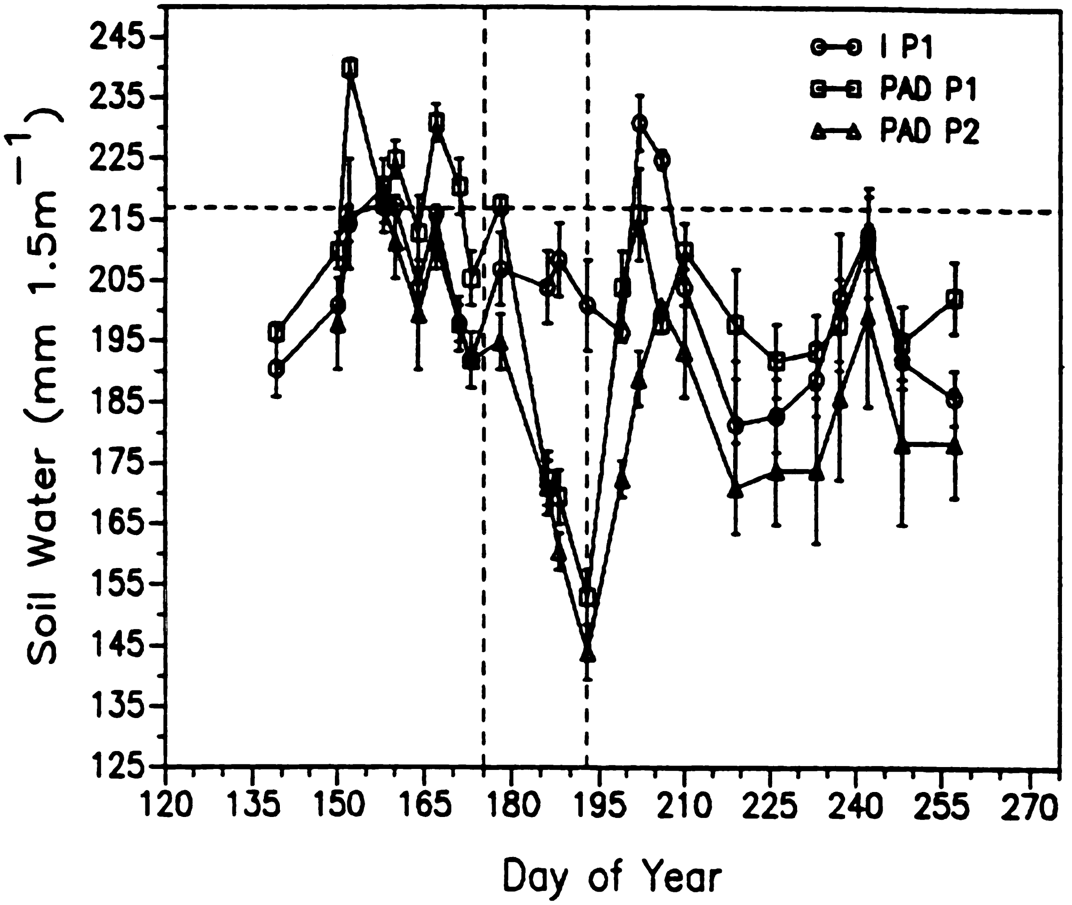

Figure 1.4b. Soil water content of the 1.5 m profile during 1989. Values are equivalent depth water. The horizontal dashed line represents the estimated drained upper limit of soil water, and the region between the vertical dashed lines depicts the deficit period.

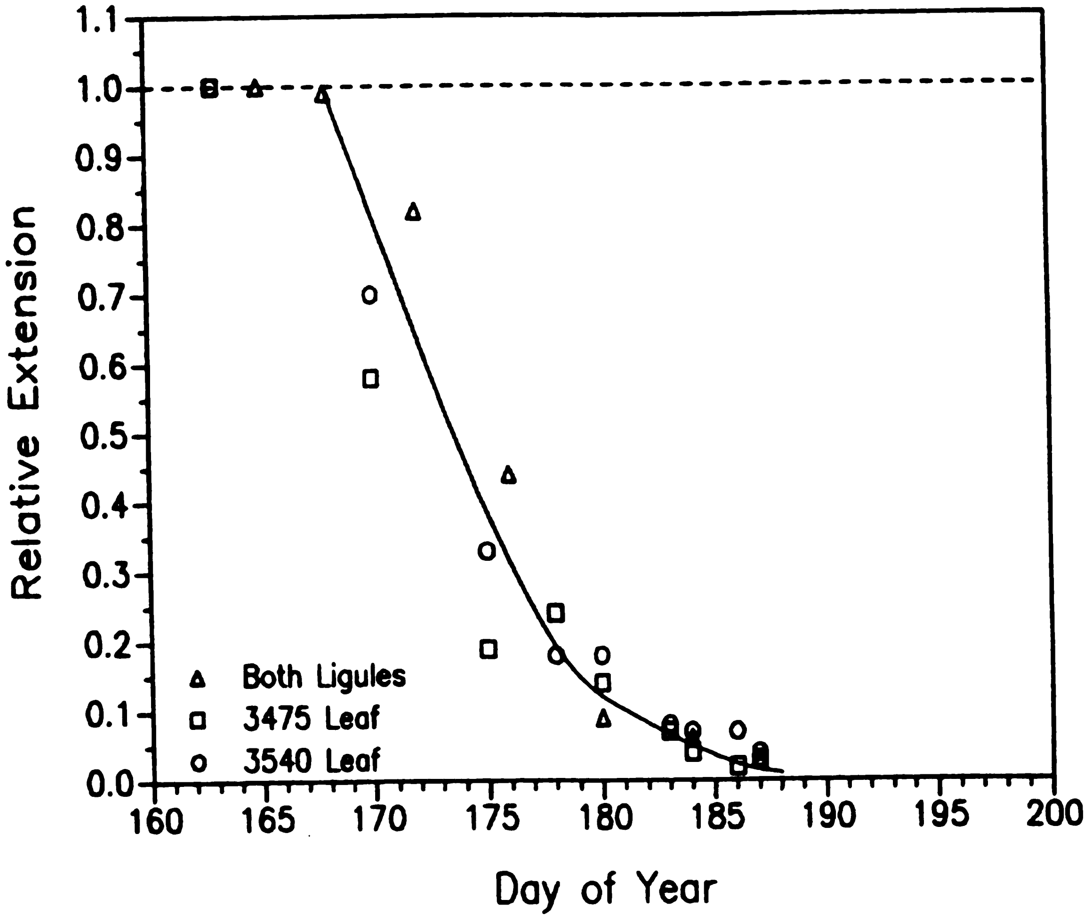

Figure 1.5a. Relative extension growth of pre-anthesis deficit plants during 1988 for hybrids 3540 and 3475 as determined from leaves and from the height to the top leaf ligule.

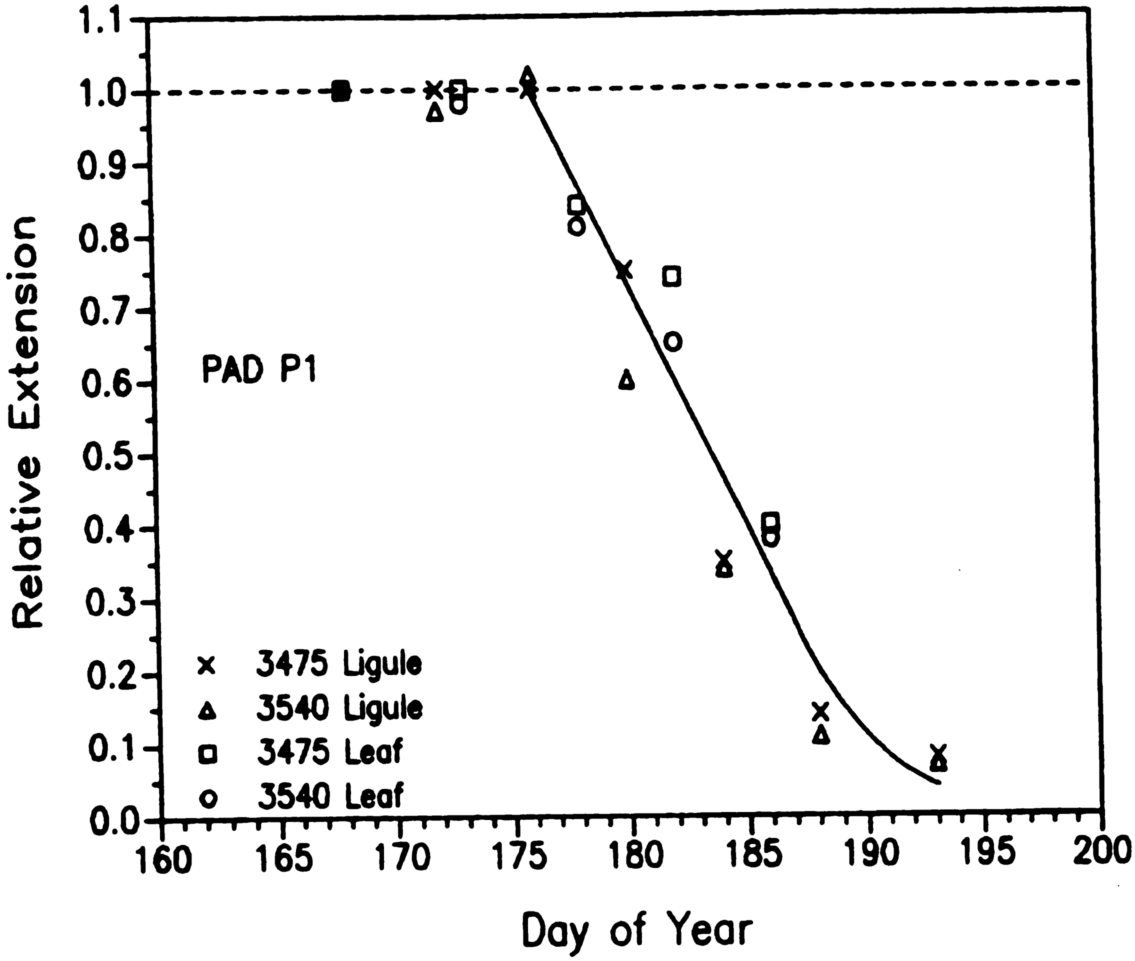

Figure 1.5b. Relative extension growth of pre-anthesis deficit plants of the first planting date during 1989 for hybrids 3540 and 3475 as determined from leaves and from the height to the top leaf ligule.

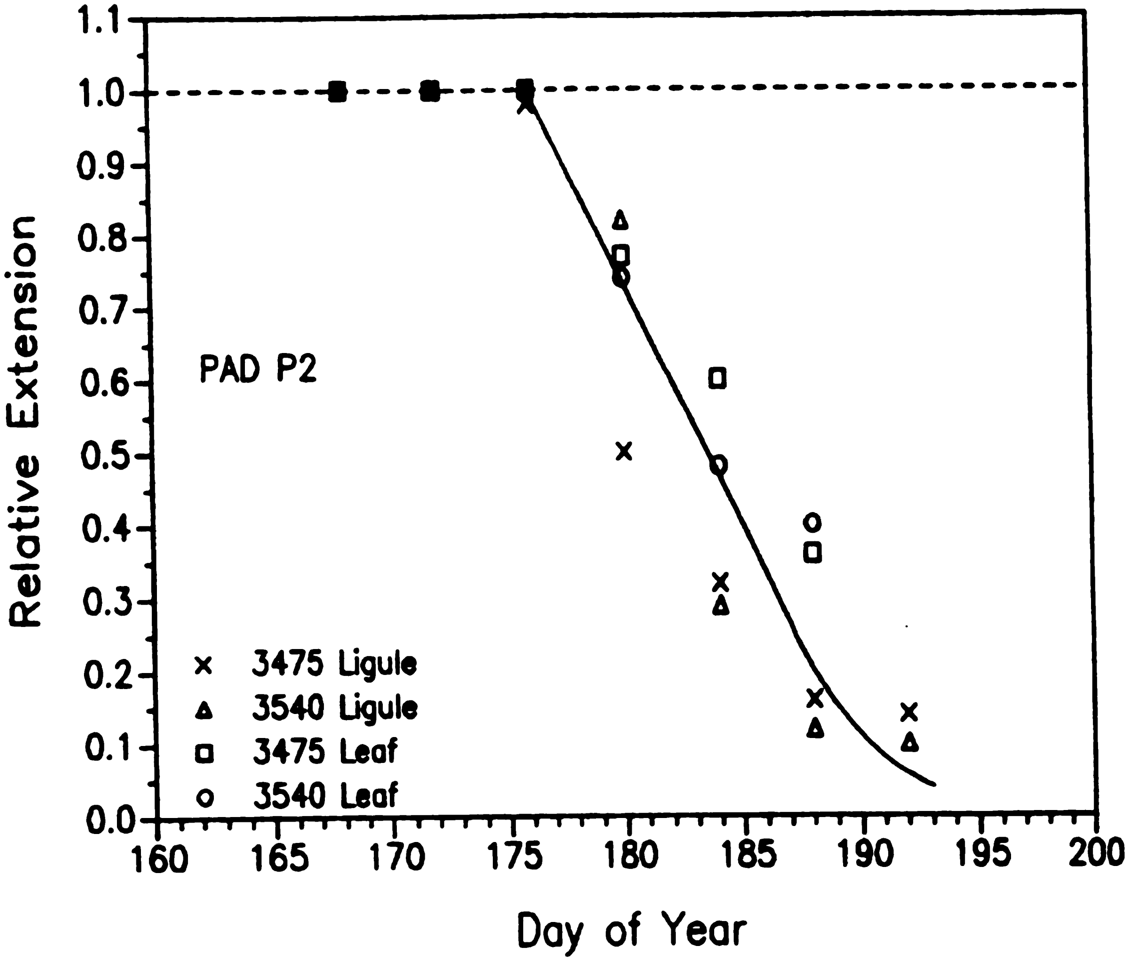

Figure 1.5c. Relative extension growth of pre-anthesis deficit plants of the second planting date during 1989 for hybrids 3540 and 3475 as determined from leaves and from the height to the top leaf ligule.

growth had began to decline due to the approach of vegetative maturity.

Water absorption rates at different soil depths during the 1989 deficit period are depicted for PAD P1 plants and PAD P2 plants in Figures 1.6a and 1.6b and Figures 1.7a and 1.7b, respectively. Shortly after the deficit began there was a rather rapid decline in water absorption rate in the upper 0.25 m of soil, while there was a marked increase followed by a continuous decrease at soil depths from 1.0 m to 1.5 m for both planting dates. Water absorption at depths between 0.25 m and 1.0 m remained nearly steady until DOY 187. After this, there was generally a decline in water absorption rate at depths between 0.25 m and 0.75 m, while there was an increase at the depth from 0.75 m to 1.0 m. These changing water absorption rates followed changes in root growth as reported by several researchers which indicated decreased surface rooting and increased root proliferation at lower soil depths in response to water deficits (Blum and Ritchie, 1984; Davies et al., 1986; Hoogenboom et al., 1987; Sharp and Davies, 1979). Taylor and Klepper (1973) noted an increased effectiveness of deeper roots of maize as upper soil layers dried out. A companion paper includes root growth data of the current experiment (NeSmith et al., 1990).

Figure 1.8 depicts the relationship between relative extension growth and water absorption rates at different depths for PAD P1 plants during the deficit period of 1989.

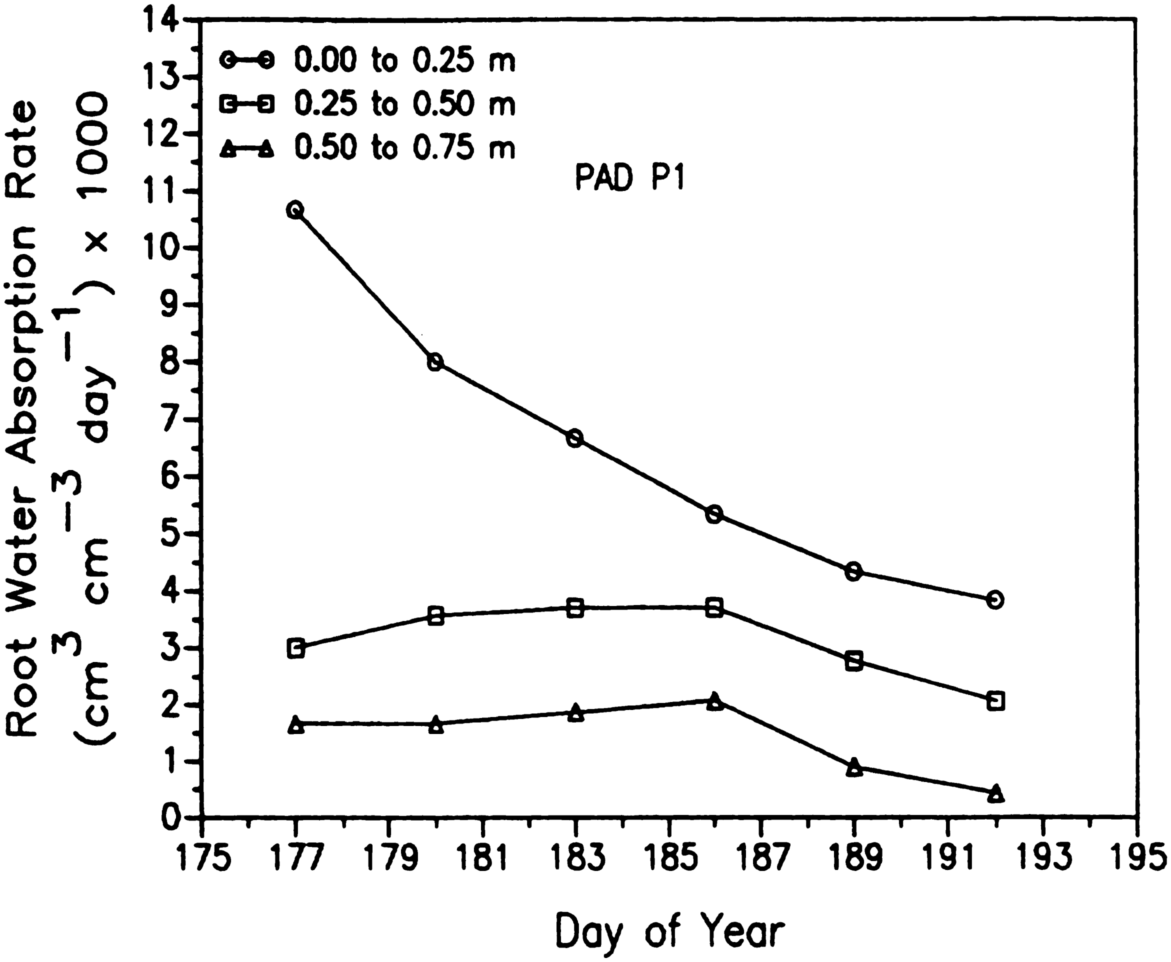

Figure 1.6a. Water absorption rates at depths of 0.00 to 0.25 m, 0.25 to 0.50 m, and 0.50 to 0.75 m during the deficit period for the pre-anthesis deficit, first planting date treatment during 1989.

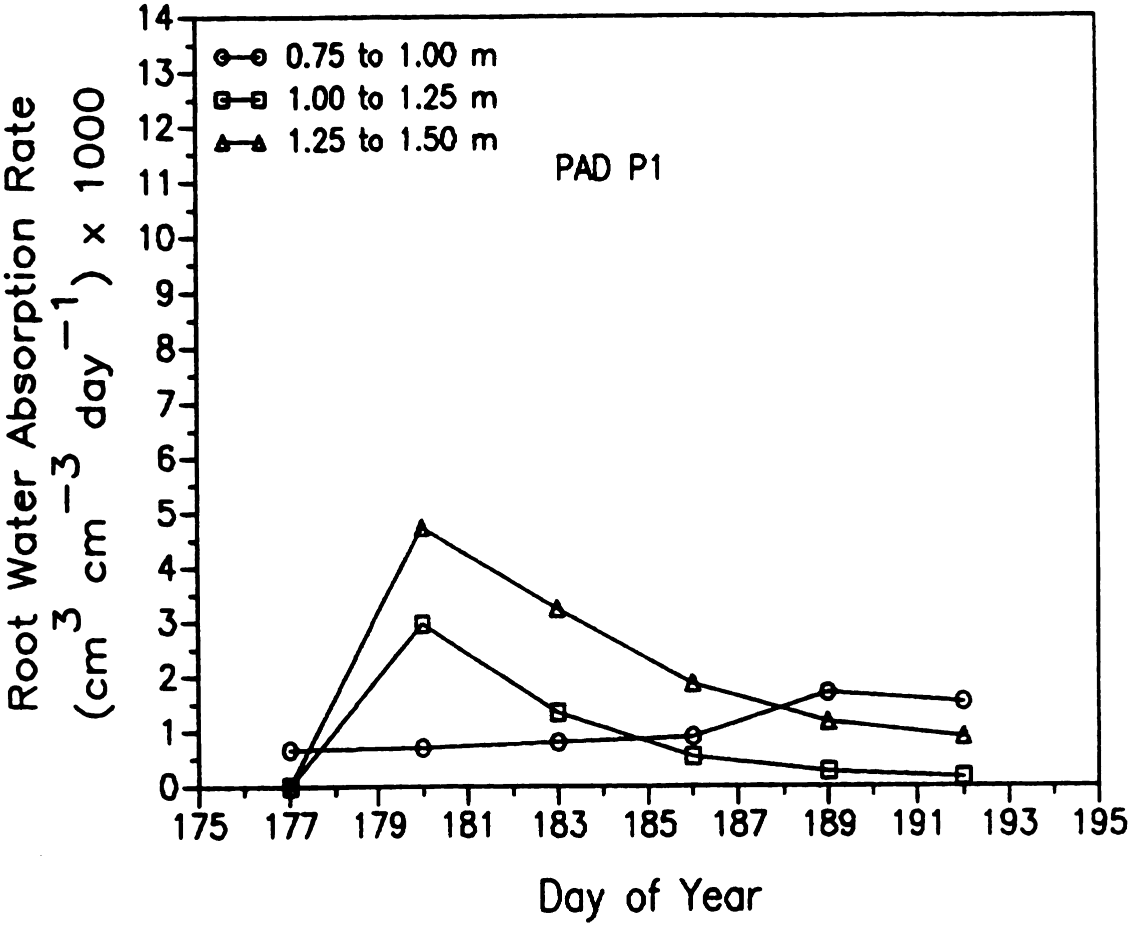

Figure 1.6b. Water absorption rates at depths of 0.75 to 1.00 m, 1.00 to 1.25 m, and 1.25 to 1.50 m during the deficit period for the pre-anthesis deficit, first planting date treatment during 1989.

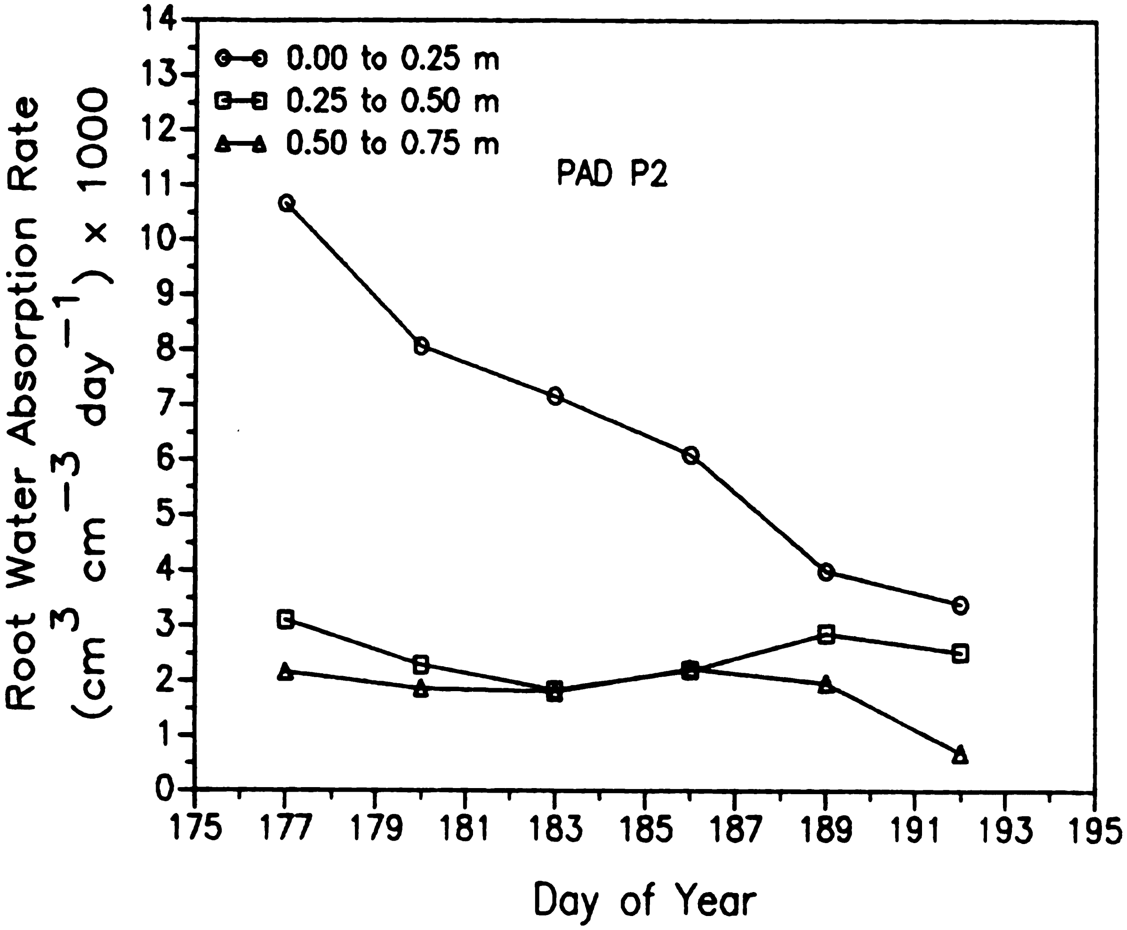

Figure 1.7a. Water absorption rates at depths of 0.00 to 0.25 m, 0.25 to 0.50 m, and 0.50 to 0.75 m during the deficit period for the pre-anthesis deficit, second planting date treatment during 1989.

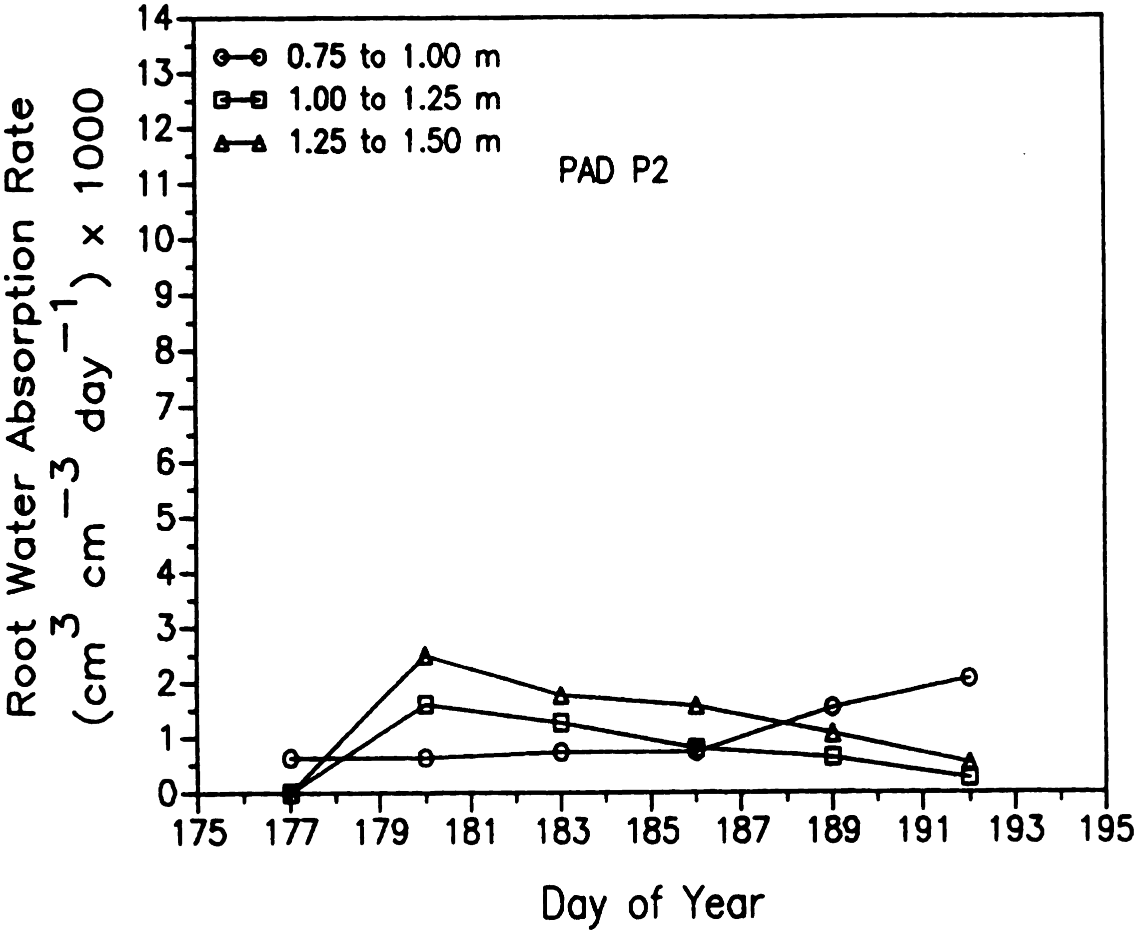

Figure 1.7b. Water absorption rates at depths of 0.75 to 1.00 m, 1.00 to 1.25 m, and 1.25 to 1.50 m during the deficit period for the pre-anthesis deficit, second planting date treatment during 1989.

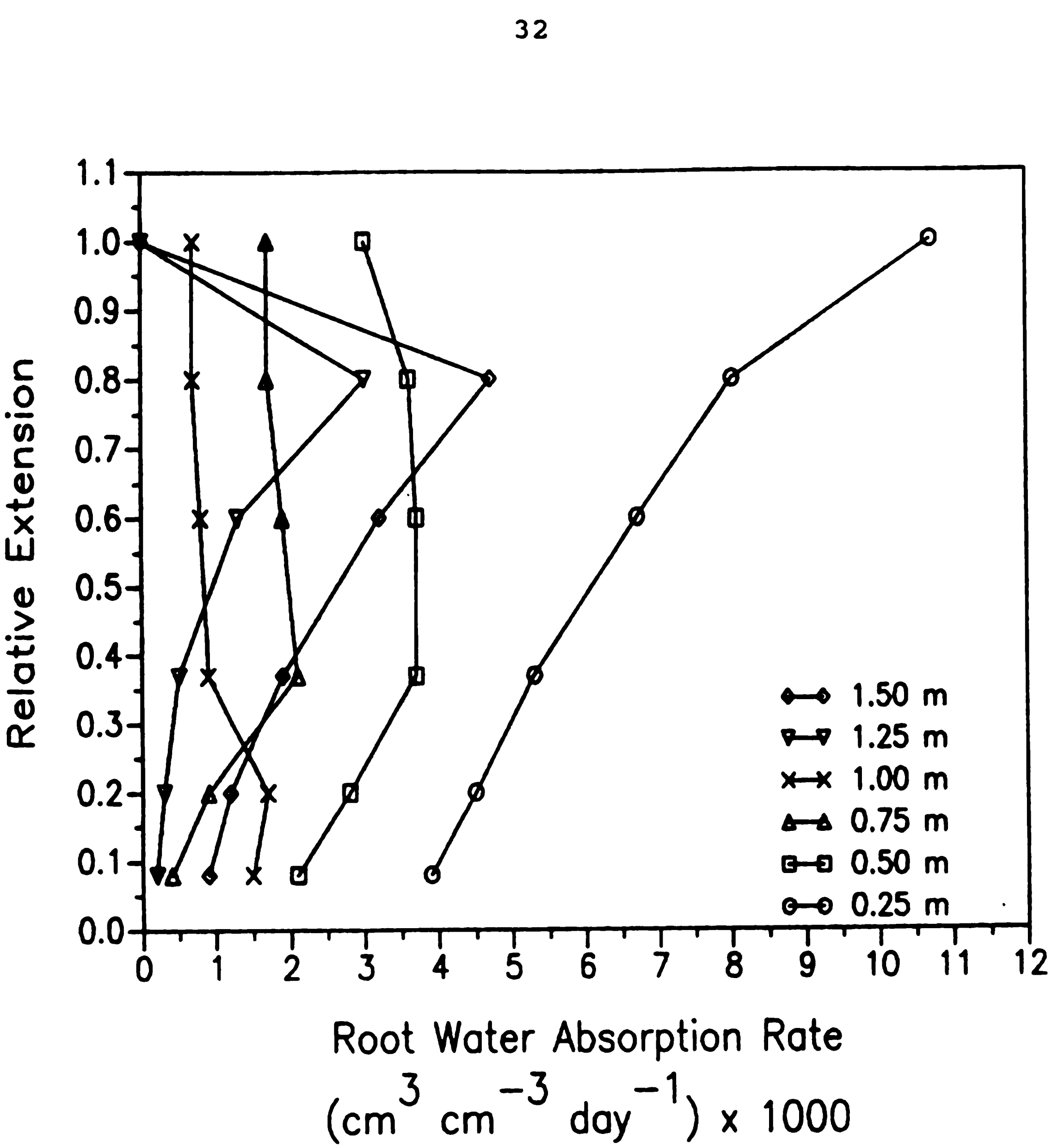

Figure 1.8. Relative extension growth of pre-anthesis deficit, first planting date plants as a function of water absorption rate at different depths during 1989.

There was little correlation with any depth other than the 0.0 m to 0.25 m increment. Combinations of the first two depths and all depths did not correlate better than the first depth alone. Relative water absorption rate was calculated by dividing the respective rate by the maximum rate measured. Relative extension growth for PAD plants from both years was plotted as a function of the relative water absorption rate from the 0.00 m to 0.25 m soil layer (Figure 1.9). Relative extension growth declined linearly when relative water absorption fell to 0.85 to 0.90 and approached zero at relative water absorption values of 0.25 to 0.30. Rosenthal et al. (1987) studied relative extension rates of container grown cotton and grain sorghum leaves in response to decreases in plant available water (PAW). They observed rapid, near linear decreases in extension growth as PAW of the entire soil volume fell from 50 % to 0 %.

Calculations of total absorption from the 1.5 m profile demonstrated there was enough water to meet transpiration demand at least until DOY 183, and probably beyond this from water below the 1.5 m depth (Figures 1.10a and 1.10b). Therefore, the influence of soil drying on extension growth was not due to insufficient water for transpiration. Other investigators have shown that leaf growth was decreased under deficit conditions before any appreciable influence on transpiration was observed (Meyer and Green, 1980; Rosenthal et al., 1987).

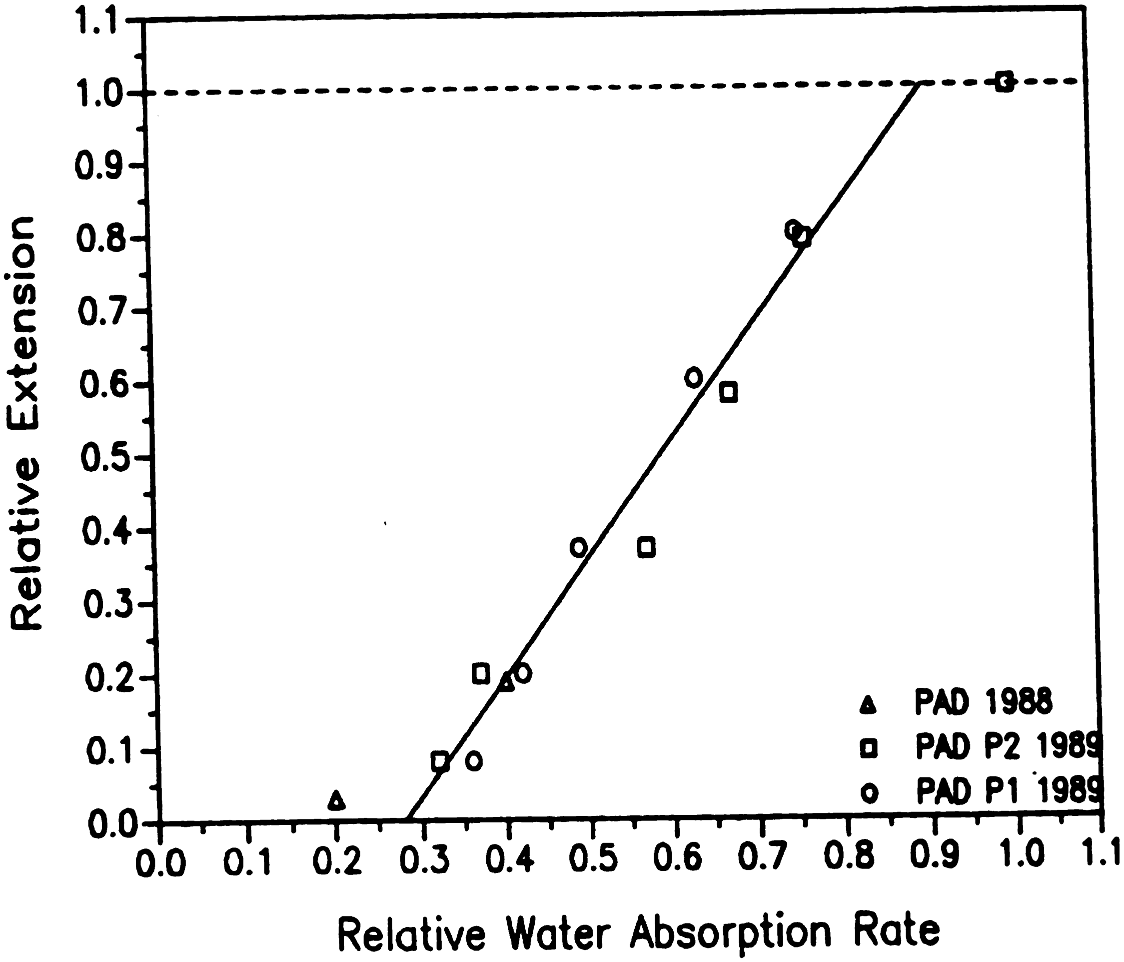

Figure 1.9. Relative extension growth of pre-anthesis deficit plants as a function of relative water absorption rate at the 0.00 m to 0.25 m soil depth during 1988 and 1989.

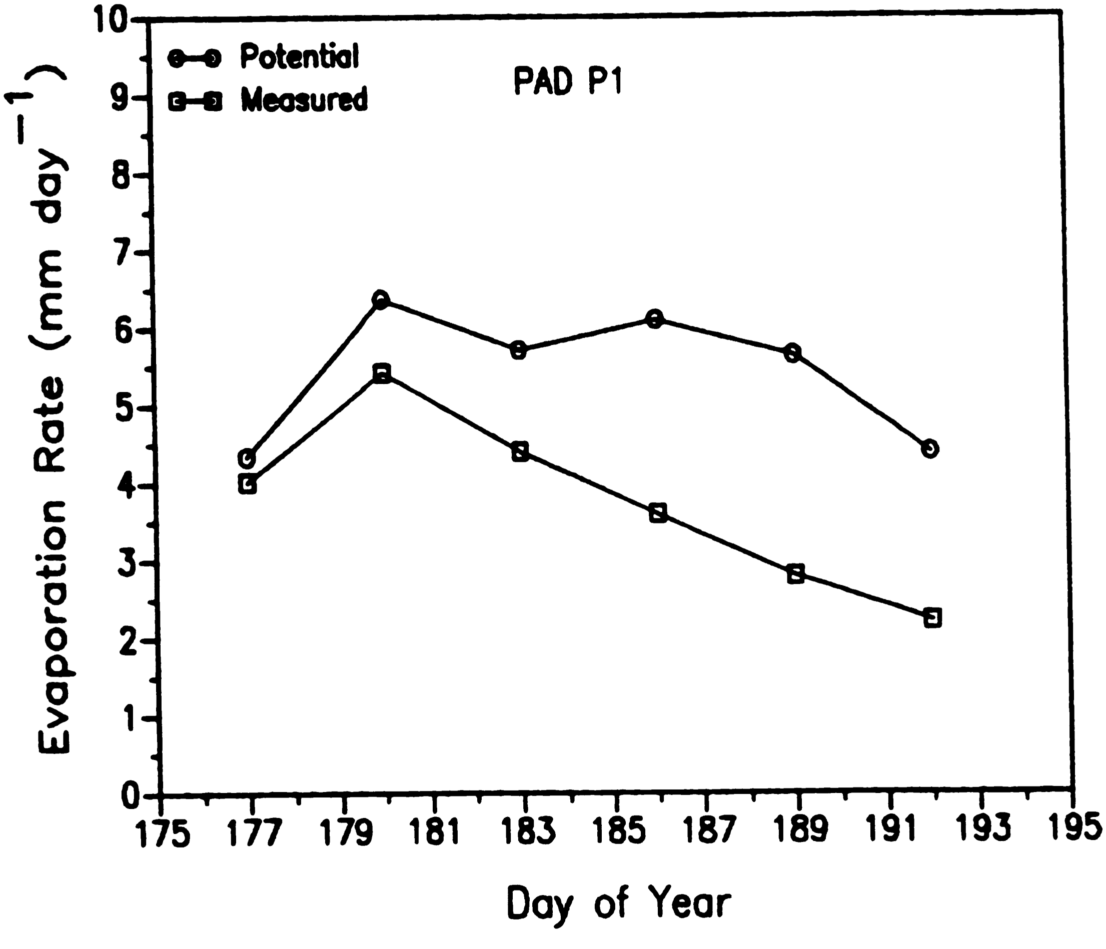

Figure 1.10a. Potential evaporation and measured total water absorption from the 1.5 m soil profile during the deficit period for the pre-anthesis deficit, first planting date treatment during 1989.

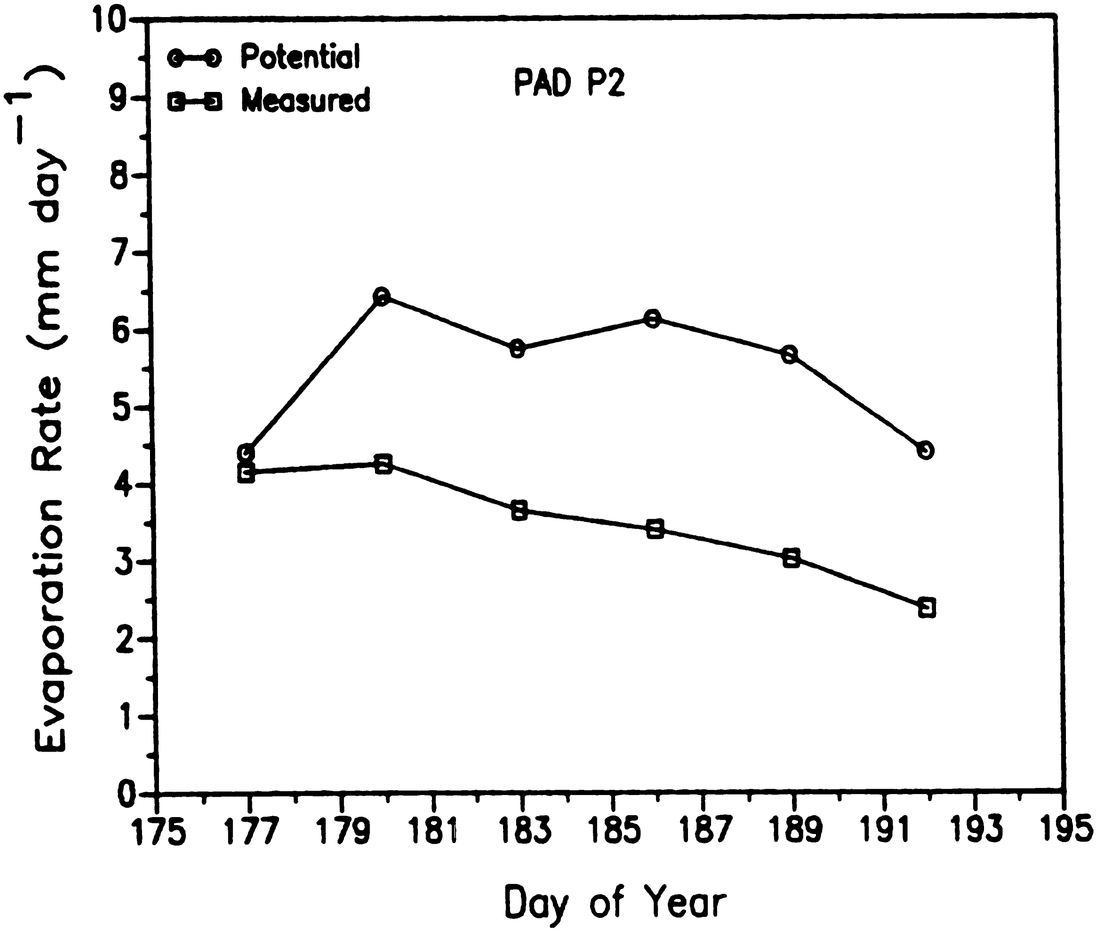

Figure 1.10b. Potential evaporation and measured total water absorption from the 1.5 m soil profile during the deficit period for the pre-anthesis deficit, second planting date treatment during 1989.

The idea of a root-to-shoot signal in response to soil drying has been the subject of several recent research reports and reviews (Blackman and Davies, 1979; Davies et al., 1986; Gollan et al., 1986; Schulze, 1986; Turner, 1986). The exact signal responsible for modified shoot behavior has not been identified, however, candidates have included abscissic acid and cytokinins as well as other unknown growth substances. Davies et al. (1986) indicated that further investigations were needed in this area, as soil drying can reduce root supply of many substances, including plant nutrients. They proposed a complex signal involving several chemical compounds. The current study seems to support the idea of a signaled response of soil surface drying. Results of nitrogen uptake presented in a companion paper (NeSmith et al., 1990) indicated this may have been linked to some of the growth reductions reported here.

According to Barlow (1986), under severe water deficit conditions expansion growth of plants ceases and osmotic adjustment serves to ensure survival of meristematic tissue. He proposed this plant adaption to the stress as a means by which young leaves remain viable while suppressing growth. This osmotic adjustment and halting of growth would require continued water absorption. The relationship between extension growth and water absorption in Figure 1.9 tends to support this, as extrapolation indicated extension growth would have ceased before water absorption.

The influence of the reduced leaf extension rates during 1989 on leaf area expansion is depicted in Figure 1.11. There were no treatment differences between hybrids, and results for only one hybrid (Pioneer 3540) are presented. Observed decreases of PAD P1 and PAD P2 treatments began between DOY 182 and DOY 185. After resuming irrigation of the PAD treatment, leaf area expansion rate increased rapidly, but the slope was less than that of the I treatment. The result was irreversibly reduced leaf area of PAD plants.

Figure 1.12 delineates leaf growth (measured as the leaf emerged from the whorl) for a single leaf growing before, during, and after the PAD during 1989. Growth was plotted as a function of thermal time to normalize the two planting dates. These data indicated that duration of growth was altered only slightly by the water deficit, whereas, growth rate was reduced considerably more as evident by the expansion rate of leaf 14 which was growing during the deficit. This suggests that "windows of time" exist for growth of individual plant organs which are primarily a function of thermal time. The delayed appearance of leaf 17 for PAD treatments depicted in Figure 1.12 indicated that the reduction in expansion rate for this leaf occurred while the blade was growing inside the leaf sheathes or whorl of the plant.

Final leaf size during 1989 and final internode lengths during both years are depicted in Figures 1.13a through 1.13c. All leaves after leaf 10 for the PAD P2 treatment and leaf 11

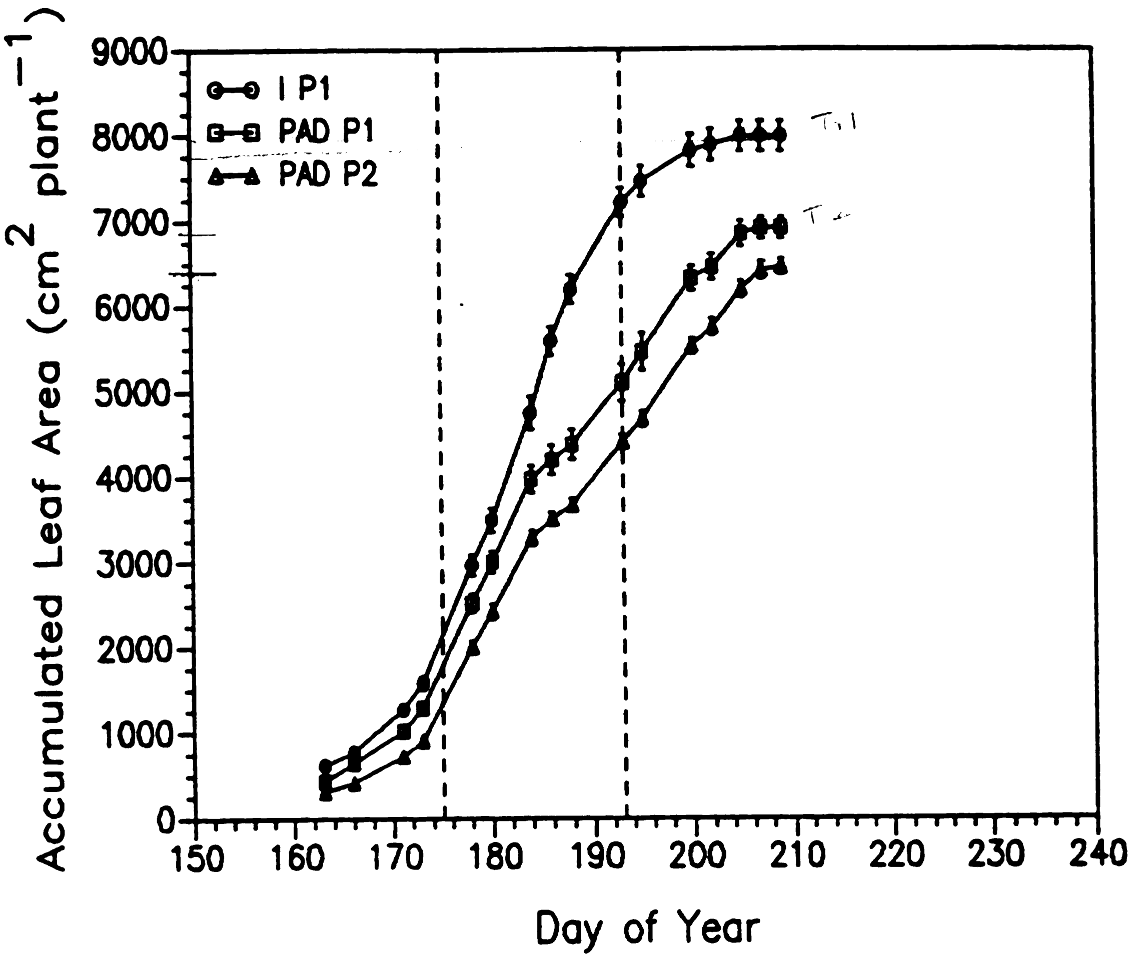

Figure 1.11. Leaf area accumulation for all treatments of hybrid 3540 during 1989. The region between the vertical dashed lines depicts the deficit period.

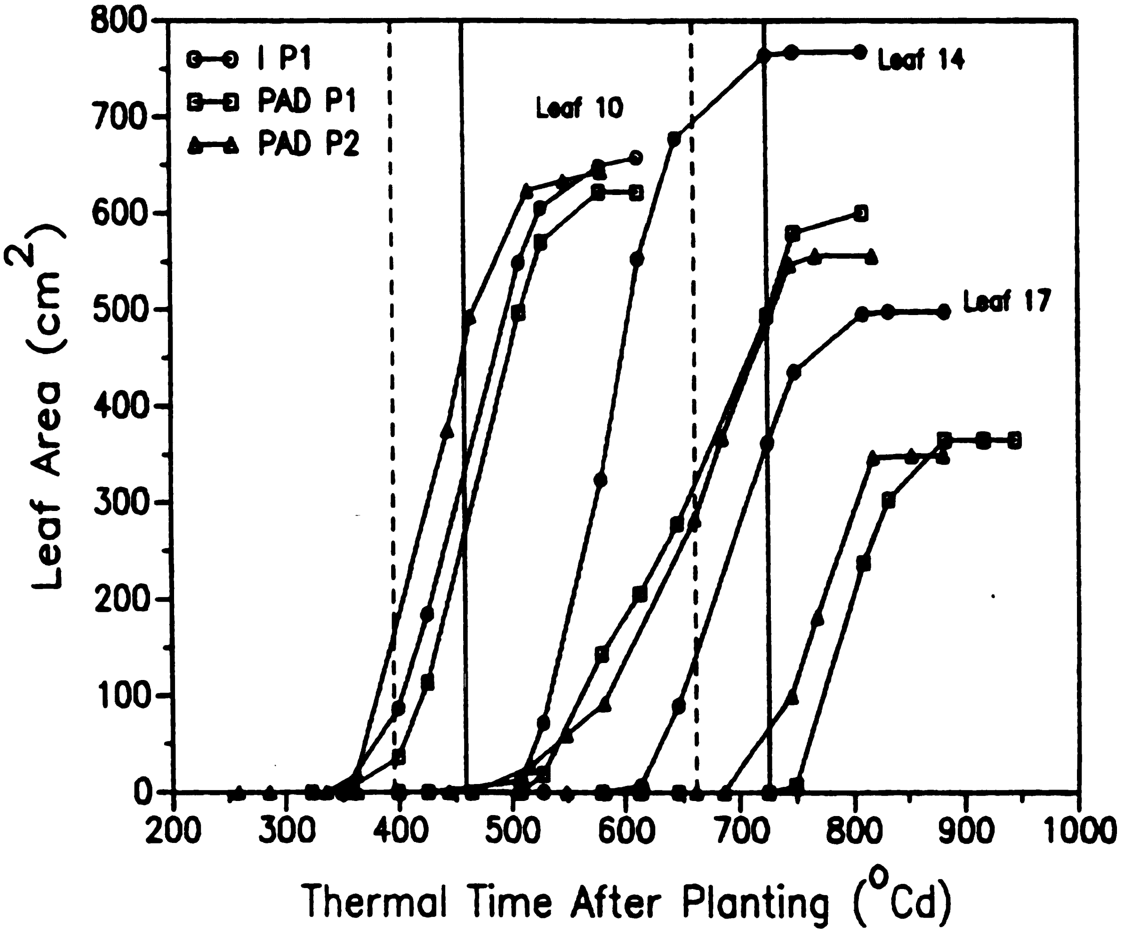

Figure 1.12. Growth of individual leaves for all treatments of hybrid 3540 during 1989 before (leaf 10), during (leaf 14), and after (leaf 17) the pre-anthesis deficit as a function of thermal time after planting. The region between vertical dashed lines represents the thermal time of the pre-anthesis deficit of the second planting date, and the region between the vertical solid lines represents the thermal time of the pre-anthesis deficit of the first planting date.

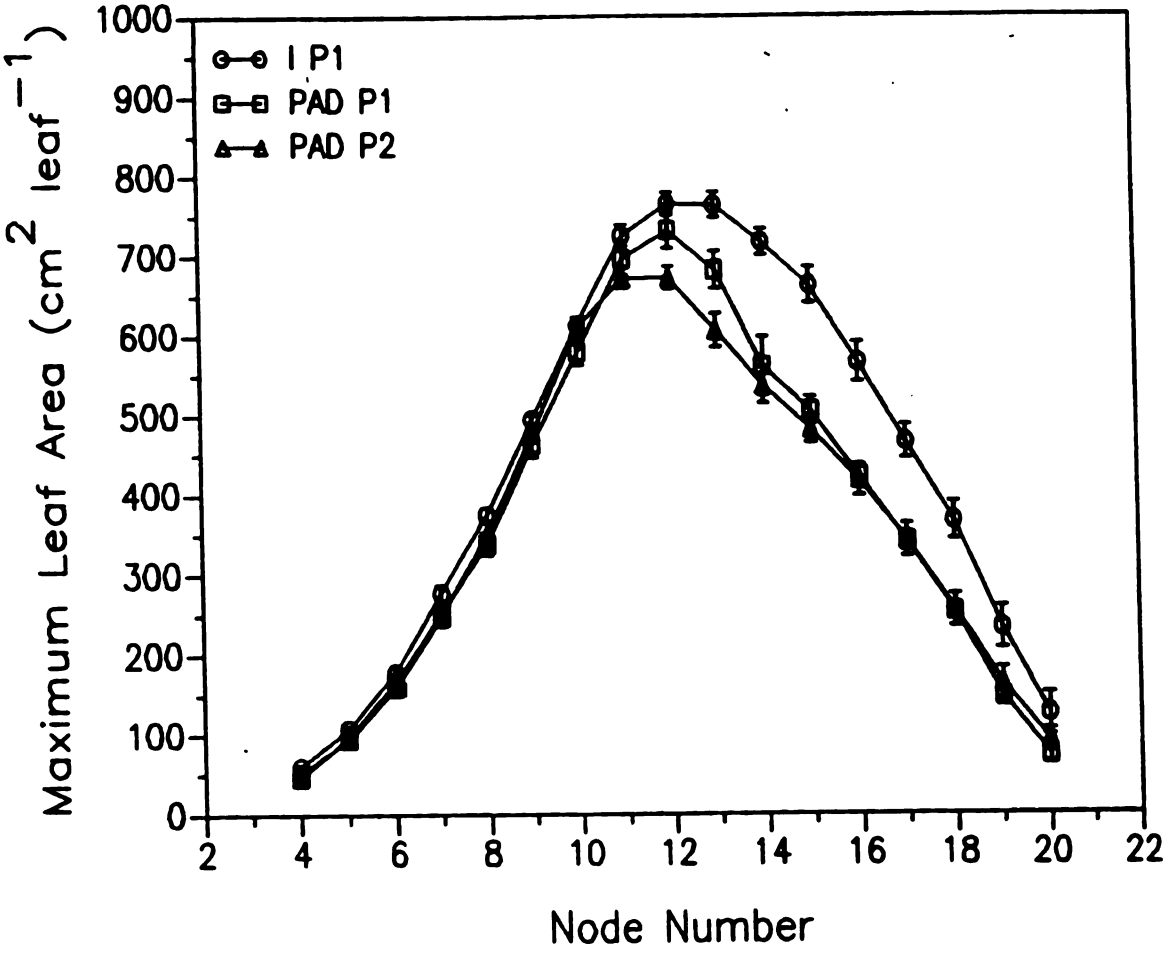

Figure 1.13a. Maximum area of individual leaves for all treatments of hybrid 3540 during 1989.

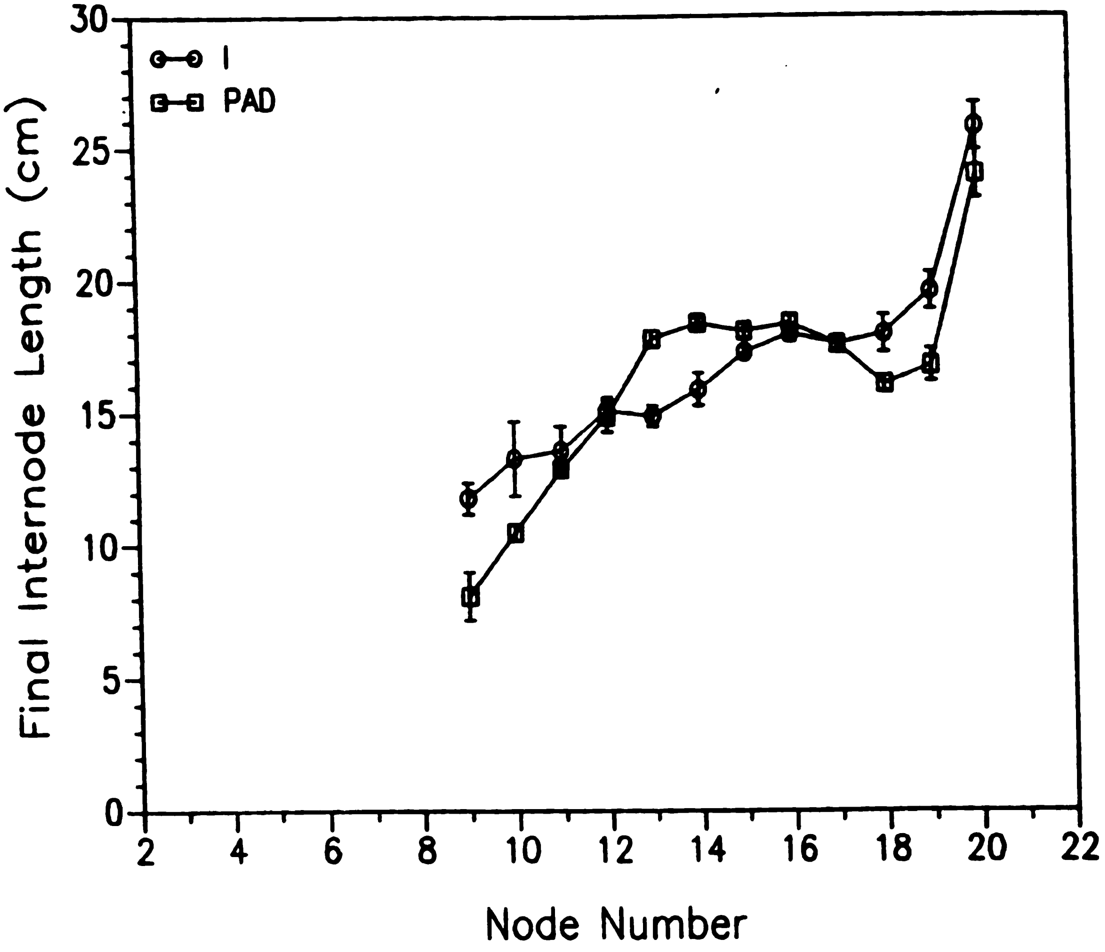

Figure 1.13b. Final internode lengths for all treatments of hybrid 3540 during 1988.

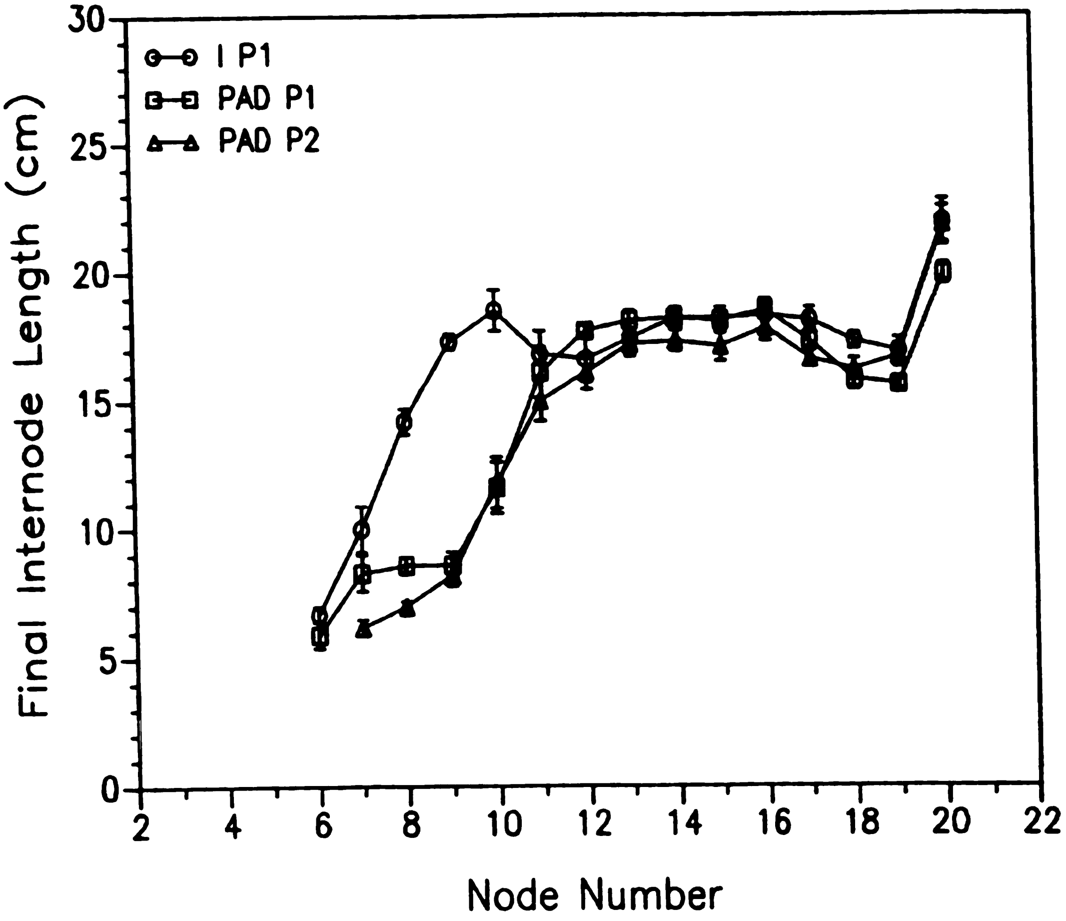

Figure 1.13c. Final internode lengths for all treatments of hybrid 3540 during 1989.

for the PAD P1 treatment were smaller than the I P1 treatment during 1989, although, the difference for the final leaf was negligible. Internodes above number 11 were not reduced by the water deficits, and in fact some compensation growth was apparent. While the fact that more leaves were growing during the deficit period than internodes caused some of the difference between these two plant components, there also may be different and more flexible windows of time for internode expansion than those of leaves.

Acevedo et al. (1971) found that a mild deficit did not influence final leaf size of corn, rather it simply postponed growth. On the other hand, Jordan (1983) presented similar results for sorghum leaves in response to a water deficit as those observed in the current study for corn leaves. He also reported a reduction in leaf number, suggesting that water deficits before floral initiation may reduce final leaf number. Ritchie and Hanway (1984) indicated floral initiation occurs in corn around stage V5 (fifth leaf ligule present). There was no difference in leaf numbers in the present study probably because floral initiation was completed before the PAD treatments were imposed.

The linear response of leaf appearance to temperature is well documented in the absence of stress (Hesketh and Warrington, 1989; Tollenaar et al., 1979; Warrington and Kanemasu, 1983). Figures 1.14a through 1.14c portray leaf tip appearance during both years and leaf ligule appearance

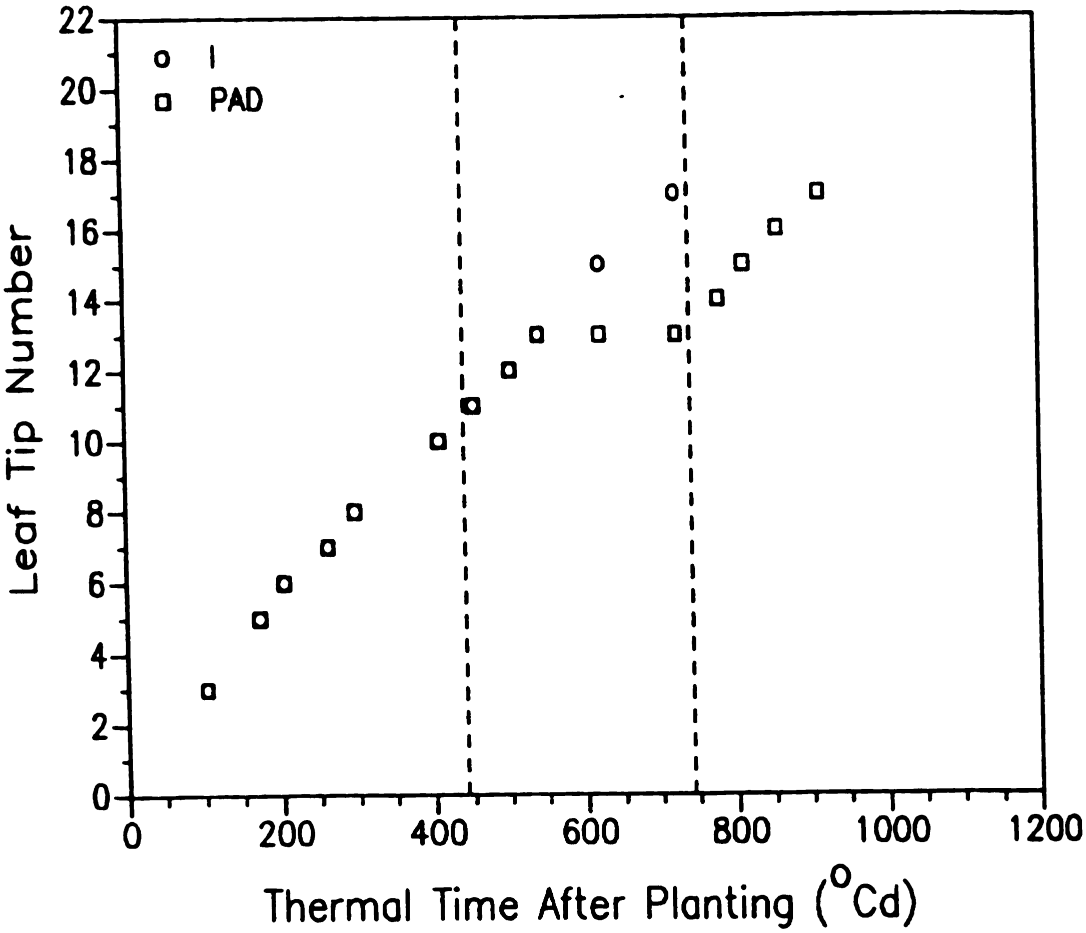

Figure 1.14a. Leaf tip number for all treatments of hybrid 3540 during 1988 as a function of thermal time after planting. The region between vertical dashed lines represents the thermal time of the pre-anthesis deficit treatment.

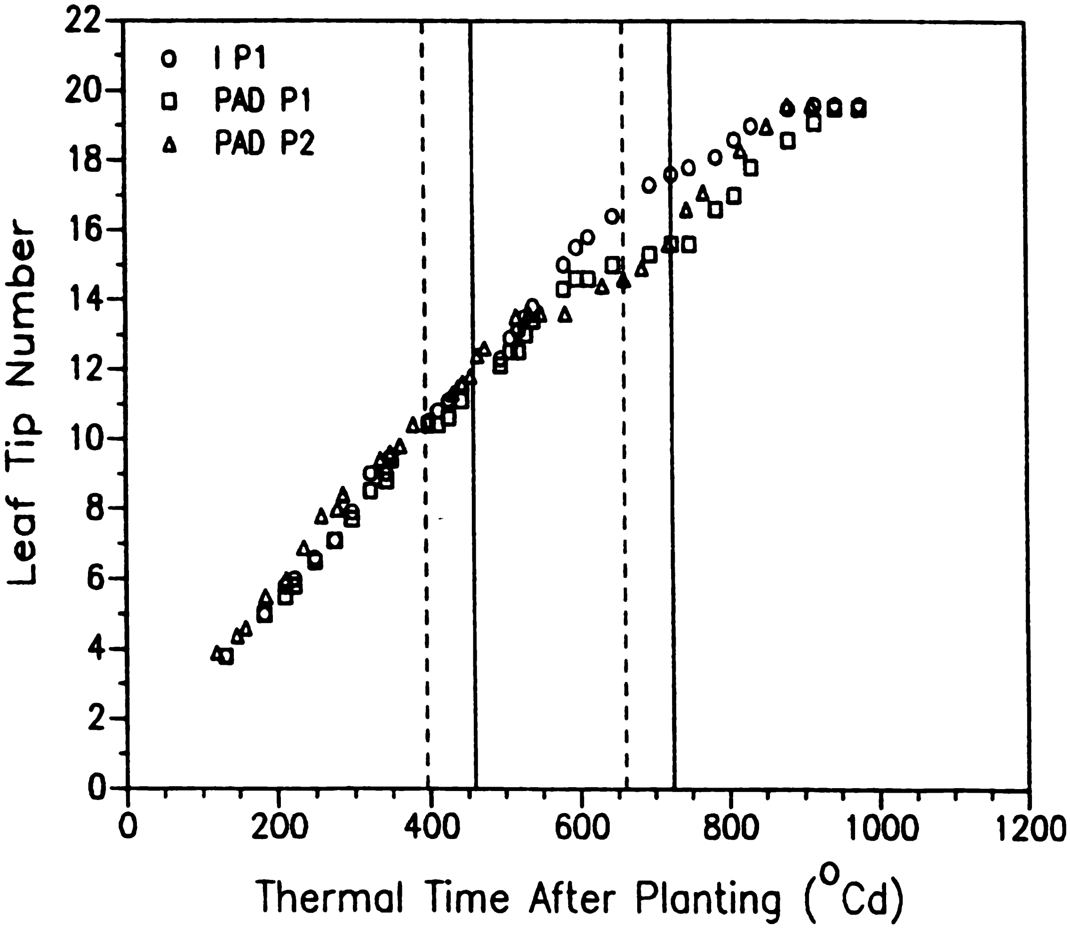

Figure 1.14b. Leaf tip number for all treatments of hybrid 3540 during 1989 as a function of thermal time after planting. The region between vertical dashed lines represents the thermal time for the pre-anthesis deficit of the second planting date, and the region between vertical solid lines represents the thermal time for the pre-anthesis deficit of the first planting date.

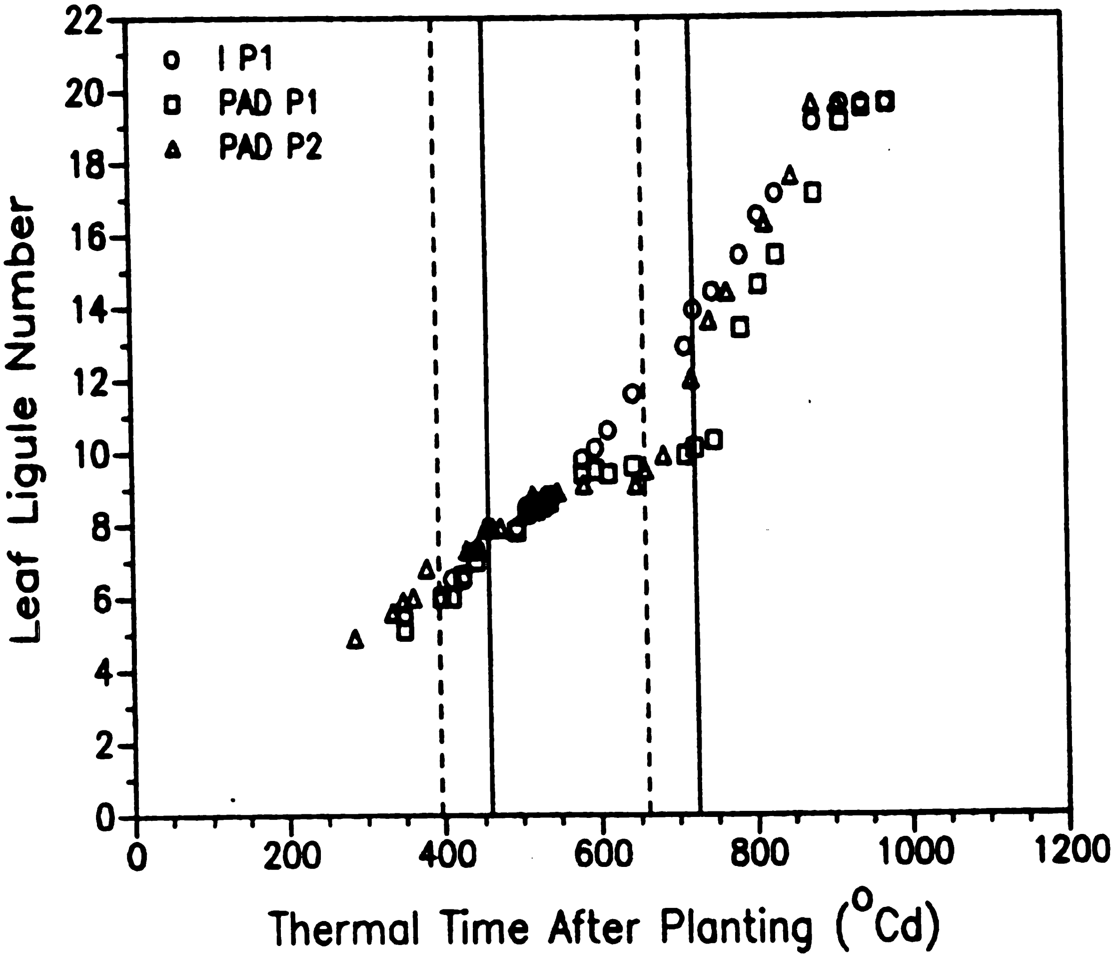

Figure 1.14c. Leaf ligule number for all treatments of hybrid 3540 during 1989 as a function of thermal time after planting. The region between vertical dashed lines represents the thermal time for the pre-anthesis deficit of the second planting date, and the region between vertical solid lines represents the thermal time for the pre-anthesis deficit of the first planting date.

during 1989. A linear response to thermal time was observed for all treatments until 500 to 550 °Cd. Treatments experiencing water deficits began to deviate at this point, which corresponded to the real time (see Figure 1.2) at which extension growth began to decrease. After irrigation resumed, leaf appearance returned to the same rate as it was prior to the deficit. Leaf tip and ligule appearance responded similarly to the shortage of water.

Measurement of individual leaf growth is time consuming for a large number of plants. However, extension growth has potential value in evaluating crop water needs, especially in irrigation scheduling. An alternative to measuring whole leaf growth was examined in this study. Figures 1.15a and 1.15b portray dynamics of height to the top leaf ligule for all treatments during 1988 and 1989. This measurement can be made rapidly on several plants. The time at which values for deficit plants began to deviate from those of control plants was similar to that found with leaf expansion measurements. The relationship between height to the top leaf ligule and accumulated leaf area is illustrated in Figure 1.16 for a combination of planting dates, water regimes, and cultivars from the 1989 experiment. While the absolute value of the ligule measurement may be of little consequence, a correlation with leaf growth and leaf area development was possible. Also, as described previously, relative extension growth was easily determined from the ligule heights.

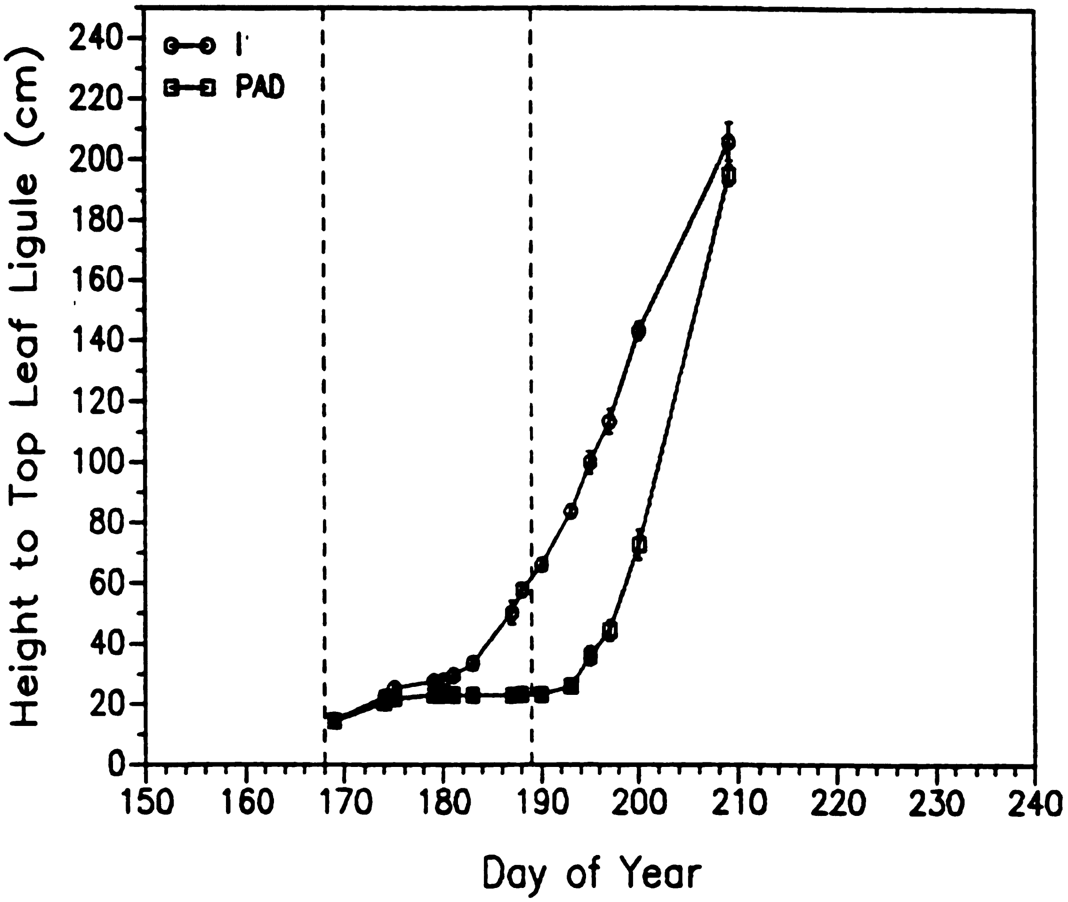

Figure 1.15a. Height to the top leaf ligule for all treatments of hybrid 3540 during 1988. The region between the vertical dashed lines depicts the deficit period.

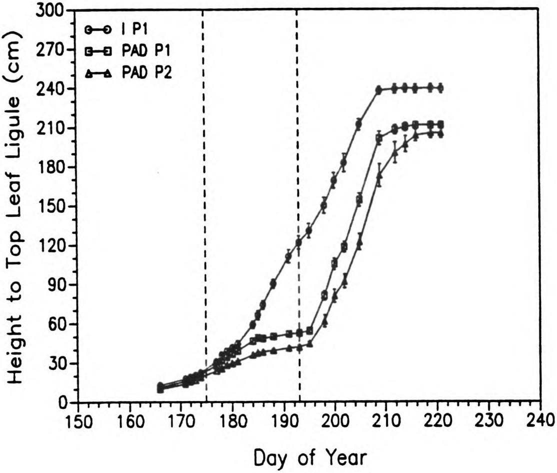

Figure 1.15b. Height to the top leaf ligule for all treatments of hybrid 3540 during 1989. The region between the vertical dashed lines depicts the deficit period.

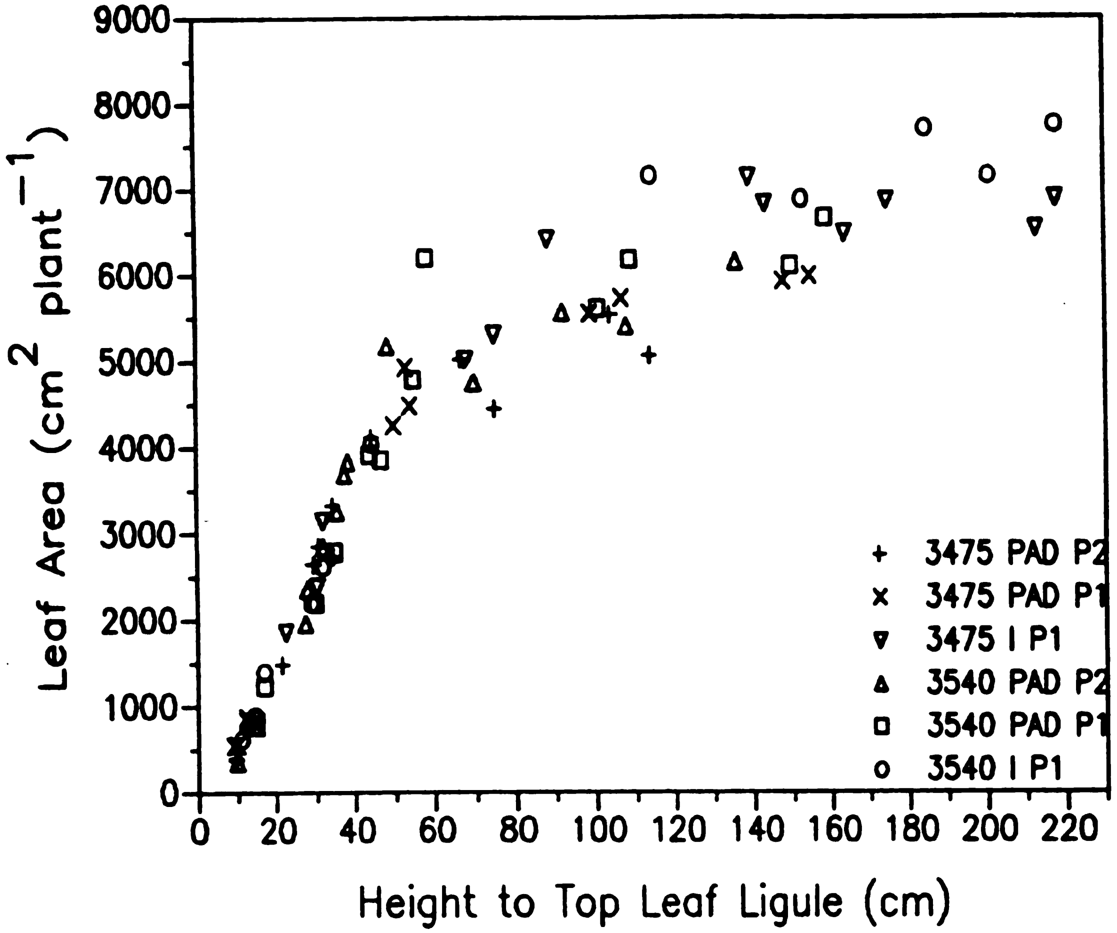

Figure 1.16. Plant leaf area as a function of height to top leaf ligule for a combination of cultivars, planting dates, and water regimes during 1989.

In summary, results have indicated water absorption rate in the surface soil was strongly correlated with plant extension growth. Reductions in extension growth caused by soil water deficits resulted in small leaves and shortened internodes as the effects were irreversible. Leaf appearance was modified under deficit conditions from the generally reported linear response to temperature. The use of height to the top leaf ligule in evaluating plant extension growth was effective and has advantages over the more tedious leaf measurements.

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CHAPTER 2

PRE-ANTHESIS SOIL WATER DEFICIT EFFECT ON CORN (ZEA MAYS L.). II. REPRODUCTIVE GROWTH AND DEVELOPMENT

ABSTRACT

Water deficits during the flowering and pollination period of determinate species such as corn are often devastating to crop yields, however, those occurring prior to anthesis generally have the greatest impact on leaf and stem growth. An increased interest in irrigation water savings through reduced applications contributes to the need for further understanding of how intermittent water deficits effect the whole crop. Research was conducted during 1988 and 1989 in Michigan utilizing a rain shelter to impose a pre-anthesis soil water deficit on two corn hybrids under field conditions to determine the immediate and subsequent responses of the crop to the paucity of water. Planting dates and hybrids provided a range in developmental patterns. Treatments consisted of an irrigated control and an 18 to 21 day water deficit which was ended a week or more prior to

tassel emergence of control plants. Results demonstrated that tassel and silk emergence as well as beginning grain fill were delayed 2 to 3 days for water deficient plants. Intact ear size was reduced under deficit conditions, as were yields by 15 % to 25 %. Grain number was the component most responsible for yield loss, however, examination of grain size distribution revealed a higher percentage of seeds weighing less than 100 mg were present on ears of water deficit plants. The impact of the water shortages on vegetative growth and development and on biomass and nitrogen accumulation and partitioning are presented in companion papers.

INTRODUCTION

Water deficits during or shortly after anthesis are considered to be among the most devastating to crop yields, especially for determinate species such as corn (Begg and Turner, 1976). The reduction in yield depends on the severity and duration of the deficit (Robins and Domingo, 1953). The primary component responsible for yield decreases during this growth stage has been found to be grain number (Claassen and Shaw, 1970b; Grant et al., 1989), and this has been attributed, in part, to poor synchronization in emergence of male and female flower components (Hall et al., 1982; Herrero and Johnson, 1981).

Pre-anthesis water deficits have been shown to reduce leaf growth substantially (Acevedo et al., 1971; Boyer, 1970; Rosenthal et al., 1987; Van Volkenburgh and Boyer, 1985). The ensuing effects on reproduction and yield were not reported for these experiments. Hall et al. (1981) found that a water shortage just prior to tasseling reduced leaf area 13 %, delayed silk emergence six days, and reduced yields 50 % as compared to irrigated plants. Claassen and Shaw (1970a and 1970b) included a pre-anthesis deficit treatment in their experiment and observed leaf dry weight decreases followed by yield reductions of 12 % to 15 %. Grant et al. (1989) reported no yield loss due to a soil water deficit during vegetative growth.

Water savings through reduced irrigation do not seem feasible during the flowering period in corn, however, there may be savings potential before anthesis. An increased understanding of the impact of water shortages on plant growth and yield during this growth stage is needed. An experiment was conducted to examine immediate and subsequent effects of corn growth and development in response to pre-anthesis soil water deficits in a field environment. Results of reproductive growth and development are reported here, while results of vegetative growth and development, and of biomass and nitrogen accumulation and partitioning are reported in companion papers.

MATERIALS AND METHODS

Corn was grown in an area that could be covered by a rain shelter at the Kellogg Biological Station near Kalamazoo, MI, USA, during 1988 and 1989. There were two irrigation treatments, an irrigated control (I) and a pre-anthesis deficit (PAD), and two cultivars, Pioneer hybrids 3540 and 3475, during both years. Additionally, there were two planting dates in 1989 (P1 and P2). Treatments and experimental establishment were further described in a companion paper (NeSmith et al., 1990). The deficit period during 1988 was from day of year (DOY) 168 to DOY 189, and during 1989 it was from DOY 175 to DOY 193.

Silking measurements were made on eight sample plants per plot during 1988, and tasseling and silking measurements were made on ten random plants per plot in 1989. Tasseling was declared when the tassel tip was clearly visible emerging from the whorl of the plant, and silking was determined as the day when there were any visible silks for a respective plant. Recordings were made every two or three days, and percentages of the population were calculated.

A compounded measurement of elongation of husks, shanks, and ears (referred to as intact ear length) was determined for eight and four sample plants per plot during the first and second year, respectively. During 1988, a point of reference was marked on a stem at the node just above where an ear was attached to the plant. During 1989, the point of reference was the node at which the respective ear was attached. Length was determined by recording the distance between the reference point and the tip of the visible husk.

During 1989 single kernels were taken from two plants per sub-plot twice weekly after grain filling began. Husks were gently pulled back on sample ears, and five individual kernels were removed from the center portion using a small knife and were placed in an envelope. After oven drying at 60 °C, weight was determined for each grain individually. After each sampling, ears were covered by the husks which were then held in place with a rubber band. The same plants were used for all the sampling dates.

Single ears were harvested both years from which yield, grain numbers, and final grain weight were determined. On 19 September 1988, four plants were harvested in each plot, and on 27 September 1989, twenty plants were harvested. Ears were placed in an oven at 60 °C for four days. After drying, grain was removed from each ear manually and was weighed and counted. During 1989, grain size distribution was determined for a sub-sample of ears. This was accomplished by weighing individual kernels of an 80 cm^3 (ca. 200 kernels) sample from single ears. These kernels were categorized in 50 mg increments for three ears of each plot.

RESULTS AND DISCUSSION

Results of a companion paper (cited previously) describing vegetative growth and water absorption rates demonstrated that leaf extension rate was reduced in response to the PAD treatments, resulting in decreased leaf area and delayed emergence of leaves from the whorl of the plant that continued after irrigation resumed. The influence of the deficit was not on leaves only, however. Figures 2.1a and 2.1b depict tasseling for Pioneer hybrids 3540 and 3475 during 1989, and Figures 2.2a through 2.2c portray silking for the hybrids during both years. Pioneer 3475 flowered about two days before 3540, and this was attributable to a developmental difference of one leaf between the hybrids. There was a delay in appearance of tassels and silks of PAD plants during both years. The two hybrids were affected similarly, with generally a three to four day difference between the I and PAD treatments. The second planting date during 1989 provided a more extensive range of flowering dates. It was hypothesized that plants further away from the time of flowering when the PAD was imposed would be affected less by the treatment. This was not the result, however, as tassel and silk appearance of plants from the PAD P2 treatments were delayed similar to the PAD P1 treatment. There was a trend for PAD plants in general to take longer to reach 100 % tasseling once it began, indicating an increased variation among stressed plants.

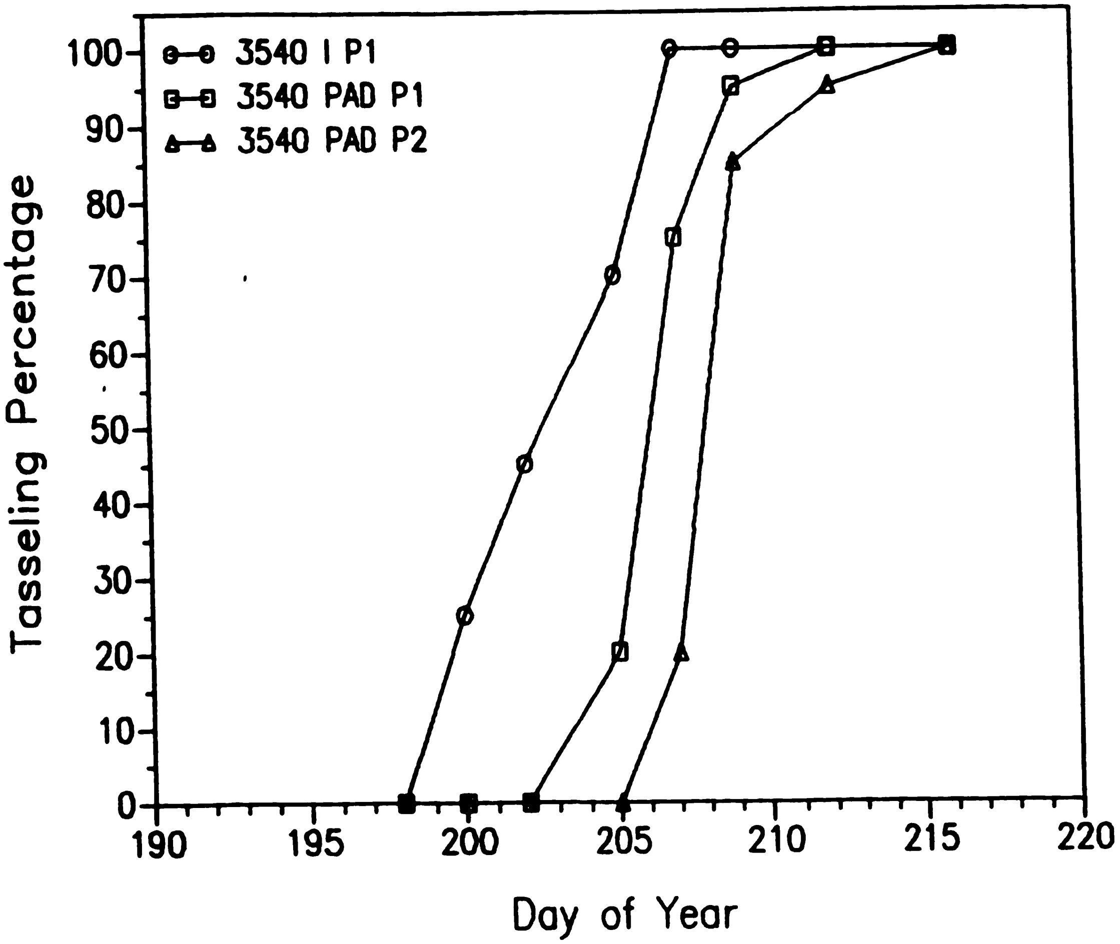

Figure 2.1a. Tasseling percentage of treatments as a function of time for hybrid 3540 during 1989.

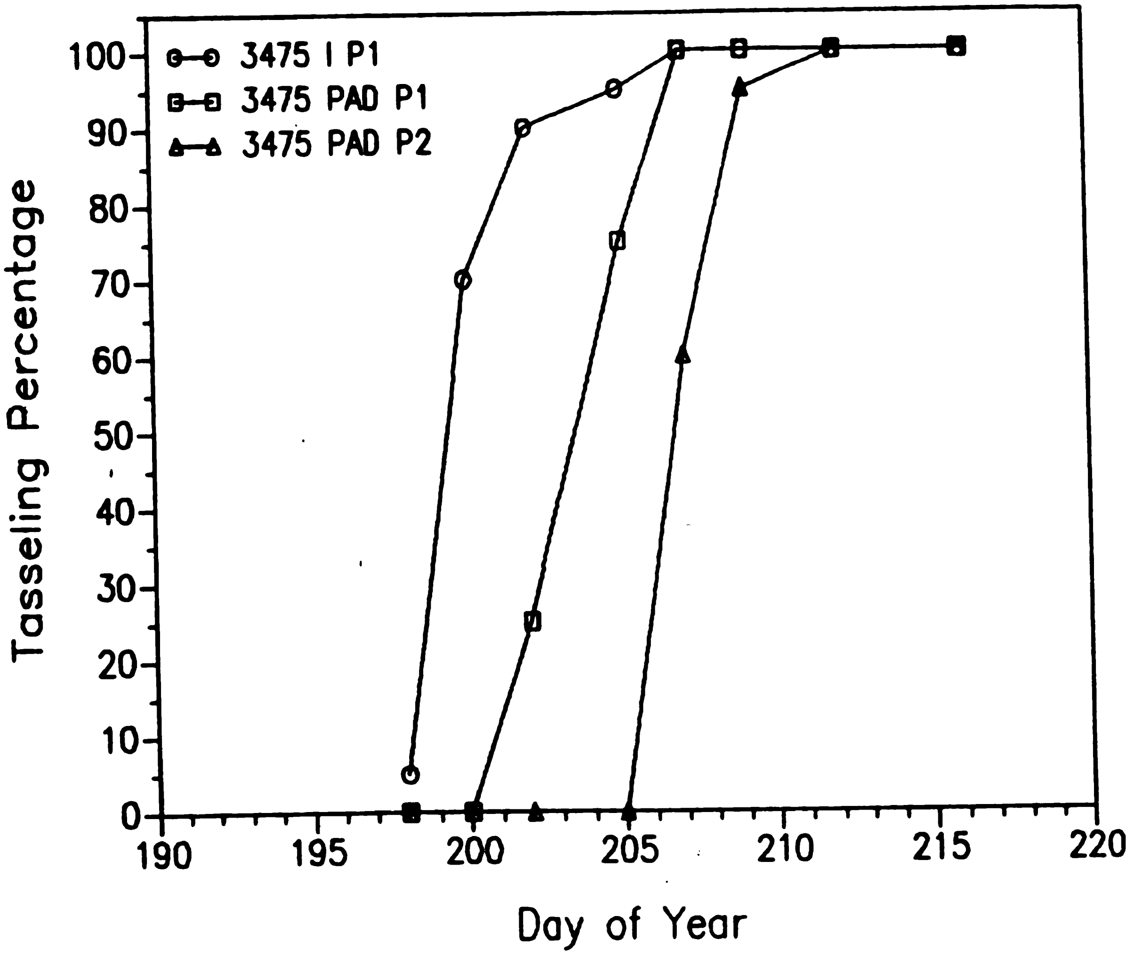

Figure 2.1b. Tasseling percentage of treatments as a function of time for hybrid 3475 during 1989.

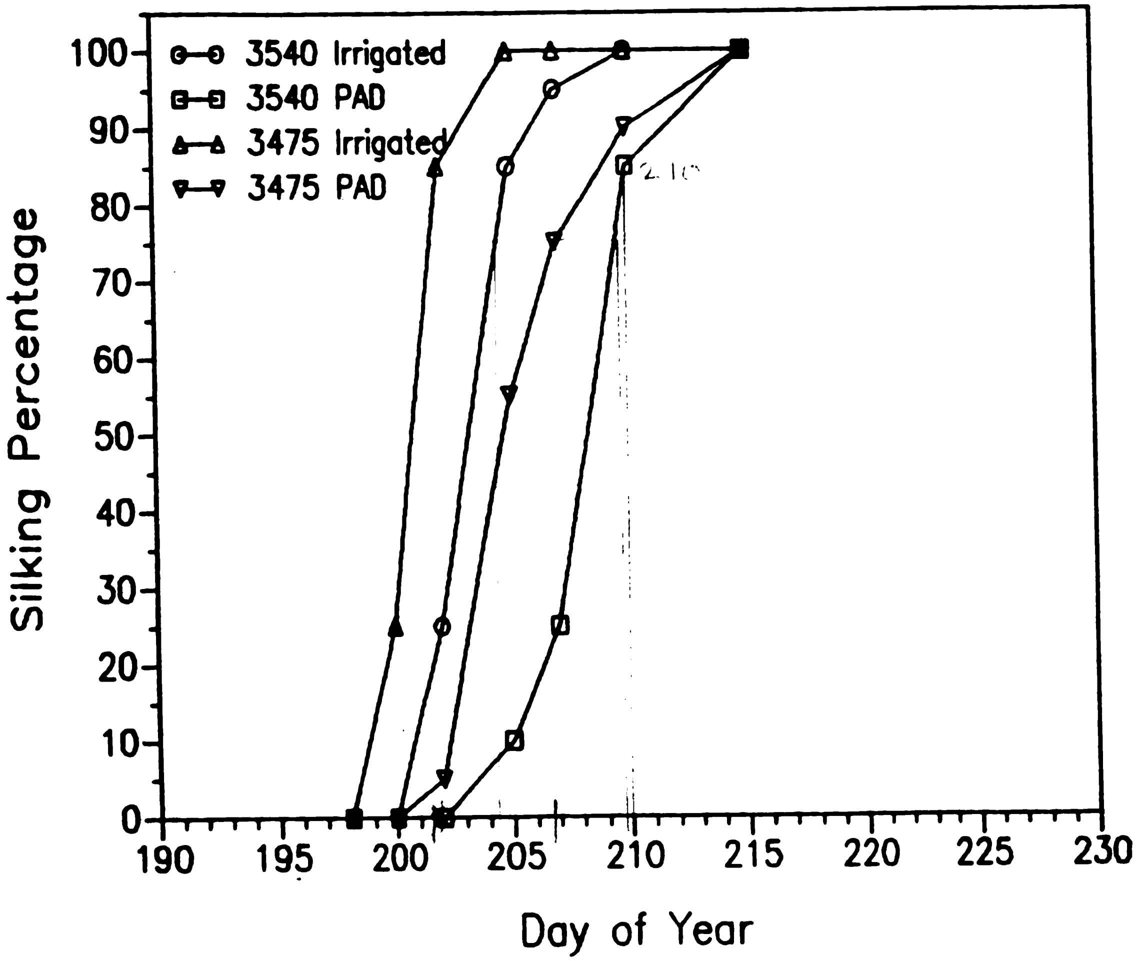

Figure 2.2a. Silking percentage of treatments as a function of time for both hybrids during 1988

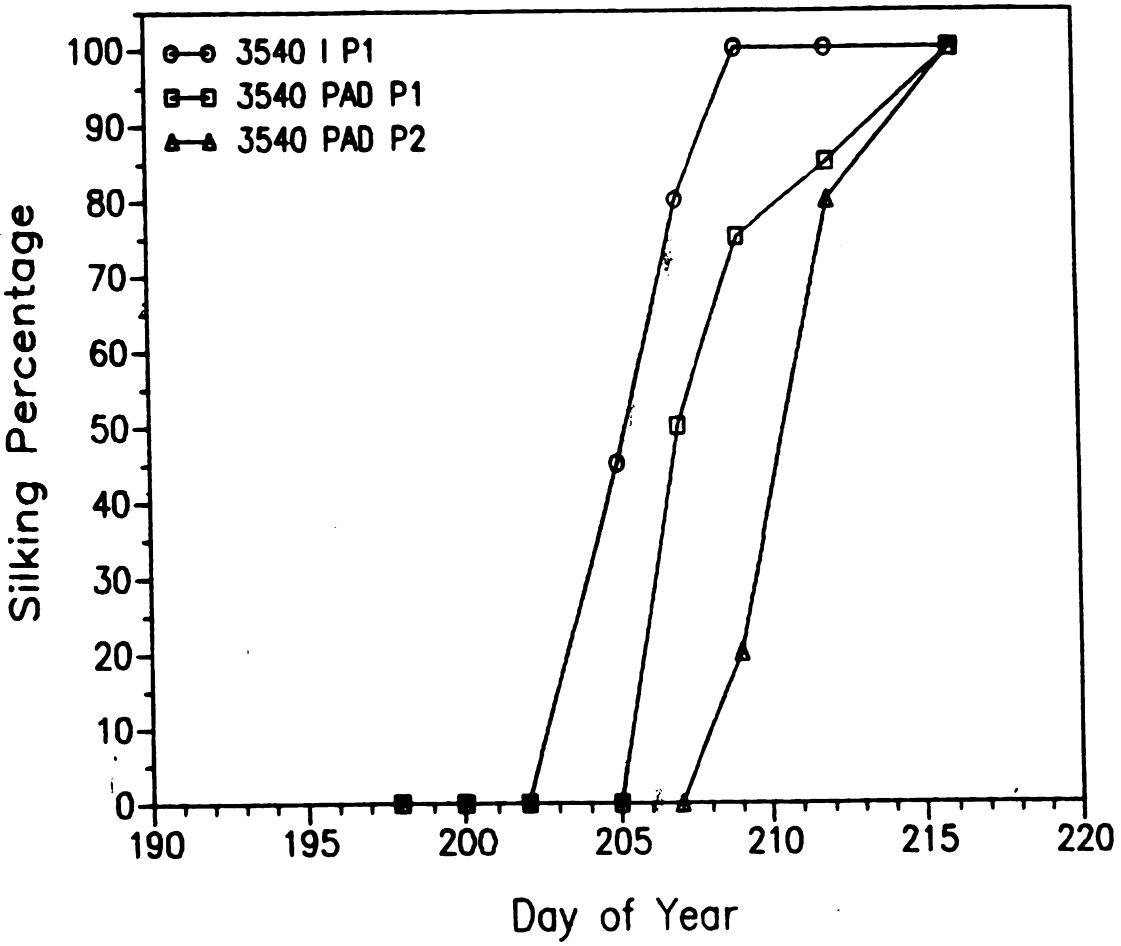

Figure 2.2b. Silking percentage of treatments as a function of time for hybrid 3540 during 1989.

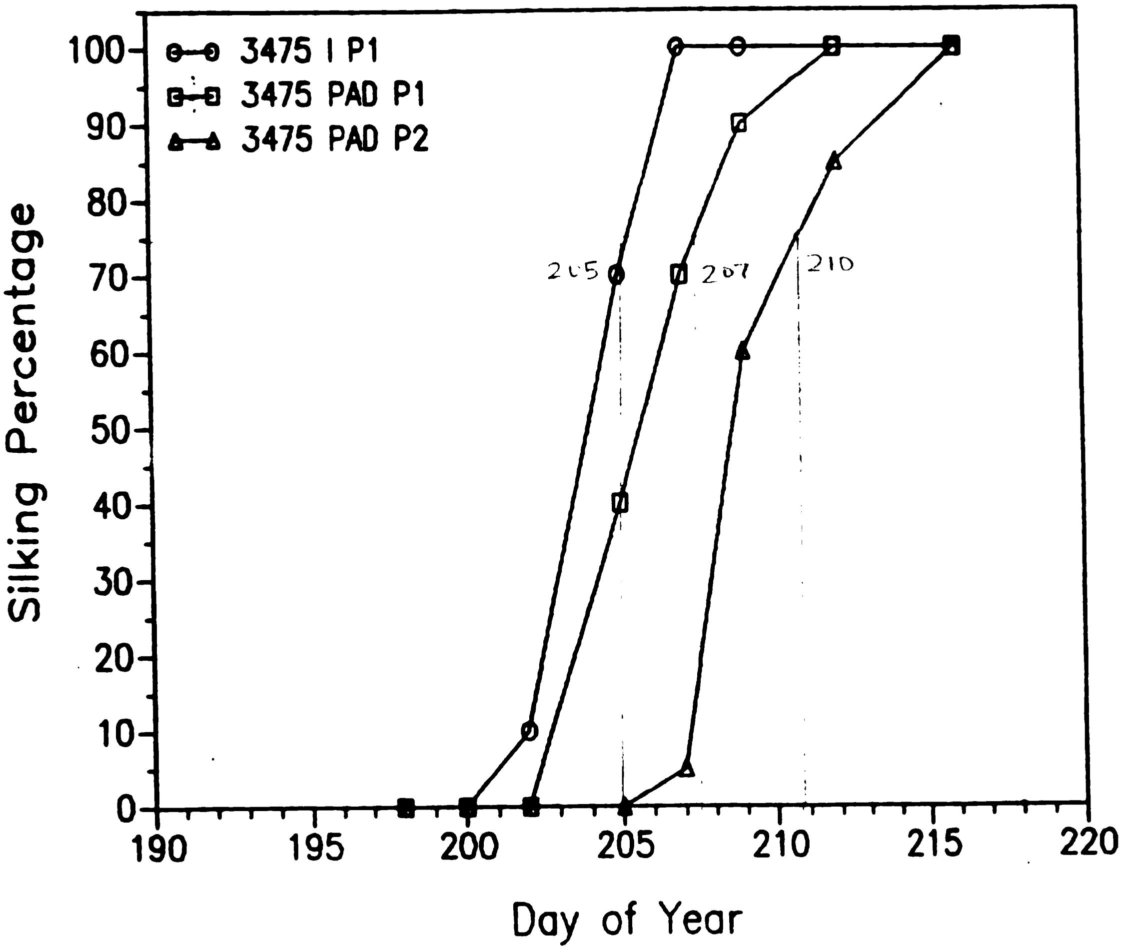

Figure 2.2c. Silking percentage of treatments as a function of time for hybrid 3475 during 1989.

Tassel and silk emergence were delayed for deficit plants in the current study even though irrigation had resumed a week or more before tassel emergence of control plants. Other researchers have reported delayed silk emergence of one to eight days as a result of a water deficit during, or a few days prior to, anthesis (Grant et al., 1989; Herrero and Johnson, 1981; Hall et al., 1981; Robins and Domingo, 1953; Vincent and Woolley, 1972). Unpublished data of the current authors have shown that tassel and silk emergence can be delayed as much as fourteen days on a sandy soil by such deficits. Poor synchronization in emergence of male and female reproductive components occurred in several of the aforementioned experiments. This was not observed in the current study, as there was generally the same time separation between tasseling and silking of PAD plants and I plants.

Figures 2.3a through 2.3c delineate intact ear length for treatments during 1988 and 1989. There was a postponed appearance of ears for PAD plants which was proportional to delays previously described for leaves, tassels, and silks. Ritchie and Hanway (1984) indicated that ear shoots are formed around stage V5 (fifth ligule visible). The deficits of the current study occurred well after this growth stage and should not have influenced ear initiation. The smaller ears of PAD plants were a result of reduced growth rate rather than a shortened duration of growth. According to Ritchie and

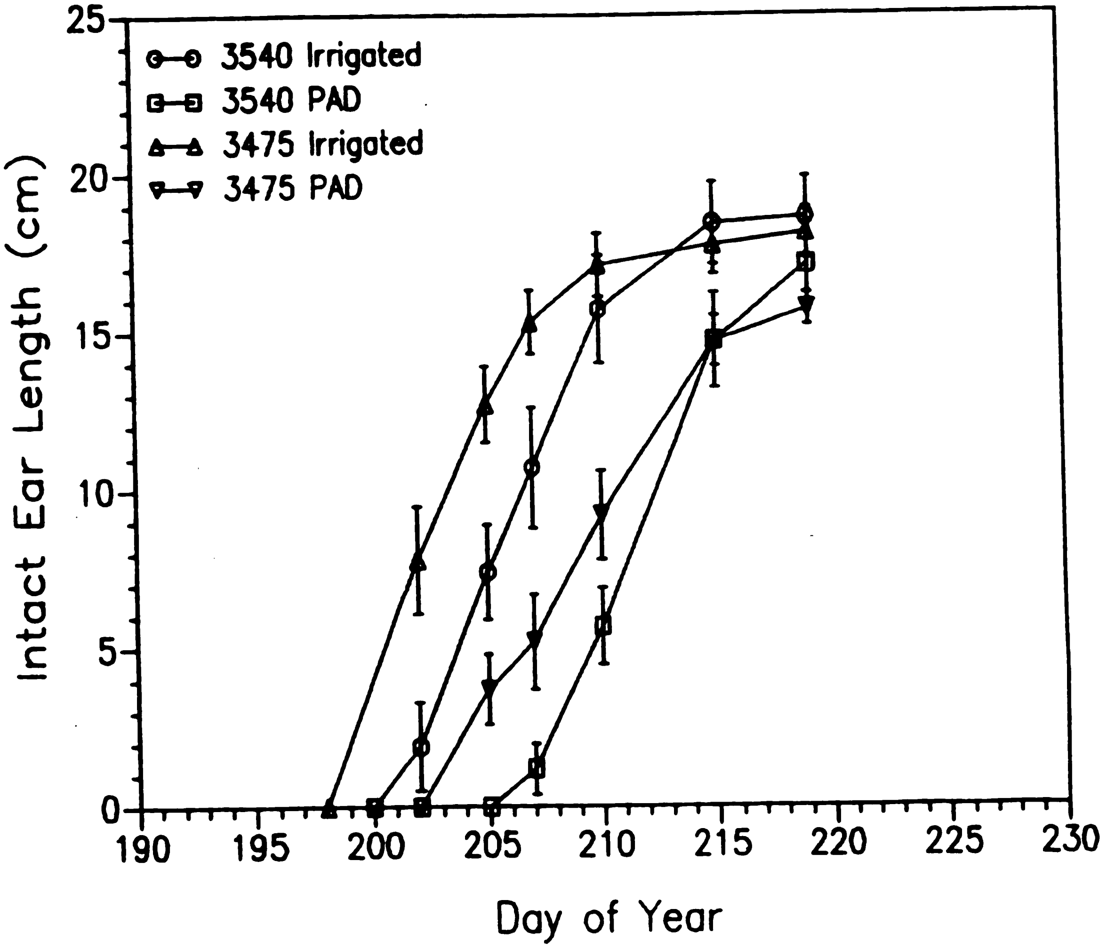

Figure 2.3a. Intact ear length of treatments for both hybrids during 1988.

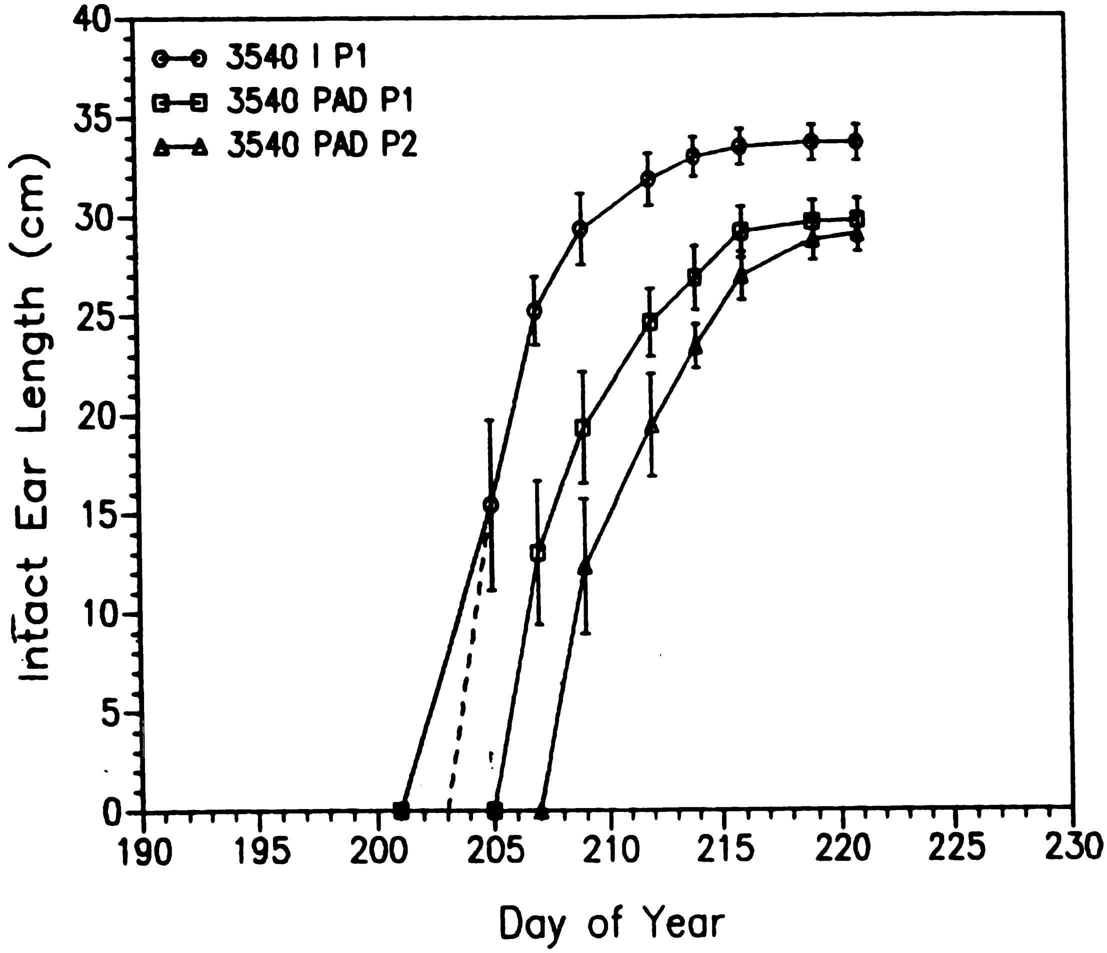

Figure 2.3b. Intact ear length of treatments for hybrid 3540 during 1989. The dashed line represents the probable beginning date of ear appearance for the respective treatment.

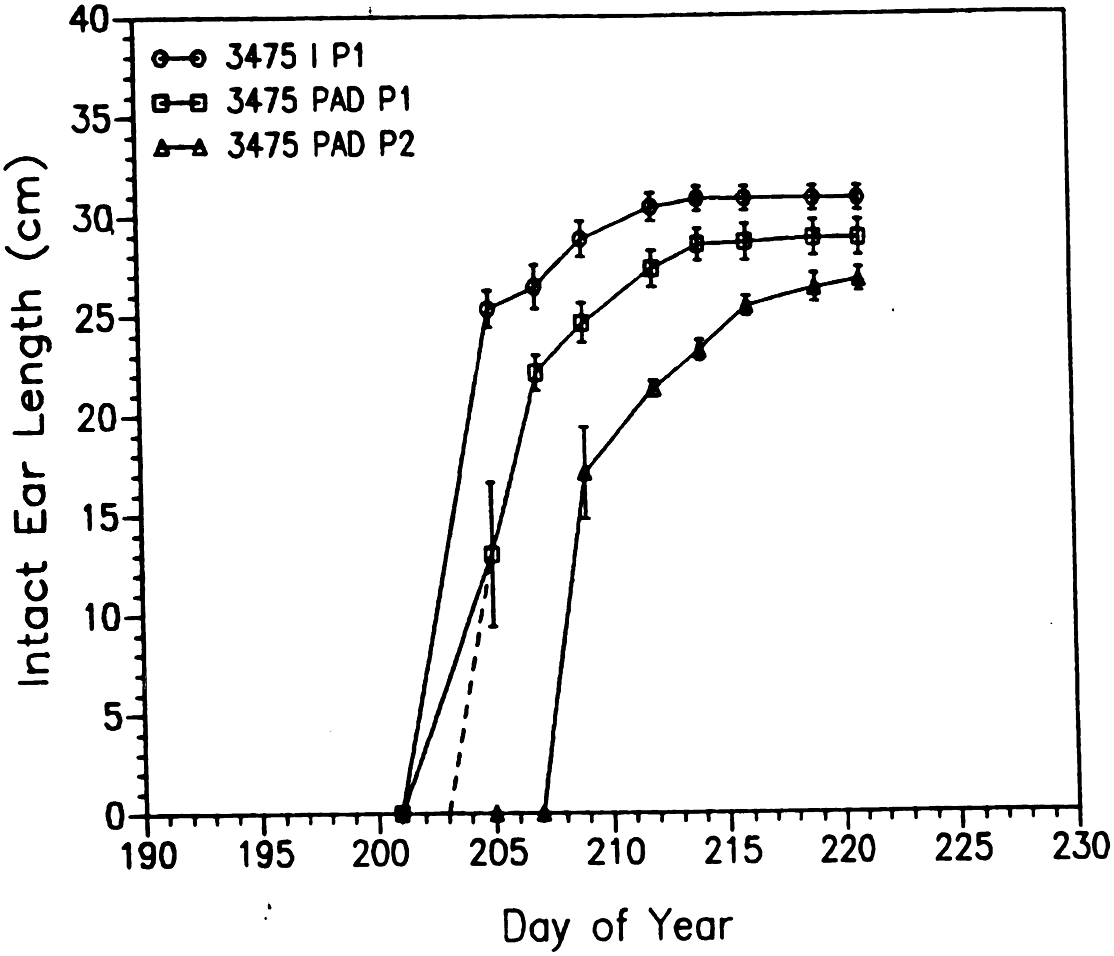

Figure 2.3c. Intact ear length of treatments for hybrid 3475 during 1989. The dashed line represents the probable beginning date of ear appearance for the respective treatment.

Hanway (1984) water and nutrient deficiencies at growth stage V12 (twelfth ligule visible) can result in reduced ear size.

Figures 2.4a and 2.4b portray single grain weight for all treatments of the current experiment during 1989. There was a delay in beginning grain filling of three to four days for PAD plants which was similar to postponements in other developmental events such as leaf appearance and flowering. The linear phase of grain filling tended to end at the same time regardless of treatment, resulting in a slightly shortened grain filling period for the PAD plants. There was no apparent influence on the rate of grain filling for hybrid 3475 due to the PAD, however, there was an observed increase in the rate for hybrid 3540. Several investigators have studied the influence of a variety of post-flowering stresses on grain filling (Barnett and Pearce, 1983; Frey, 1981; Jones and Simmons, 1983; Tollenaar and Daynard, 1978), but the impact of stress prior to flowering on subsequent grain filling has not been as widely reported. Lorens et al. (1987) observed a seed growth rate decrease of 7 % for one hybrid and an increase of 2 % for another in response to a vegetative water deficit. They also calculated slight differences in effective grain filling period in response to the paucity of water.

Reported yield decreases due to pre-anthesis water shortages range from no reduction to over 70 % loss (Claassen and Shaw, 1970b; Grant et al., 1989; Hall et al., 1981;

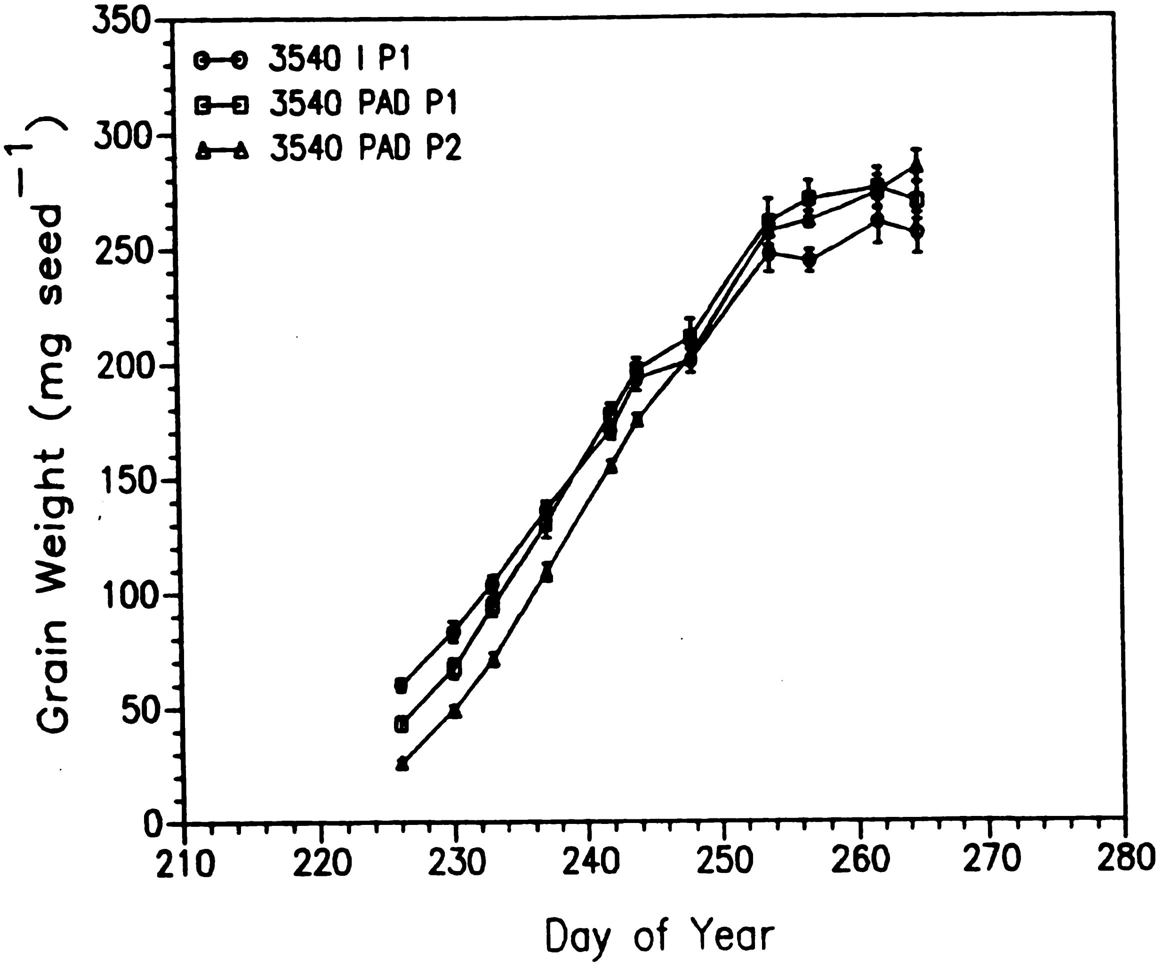

Figure 2.4a. Grain filling as measured by single kernel samples for treatments of hybrid 3540 during 1989.

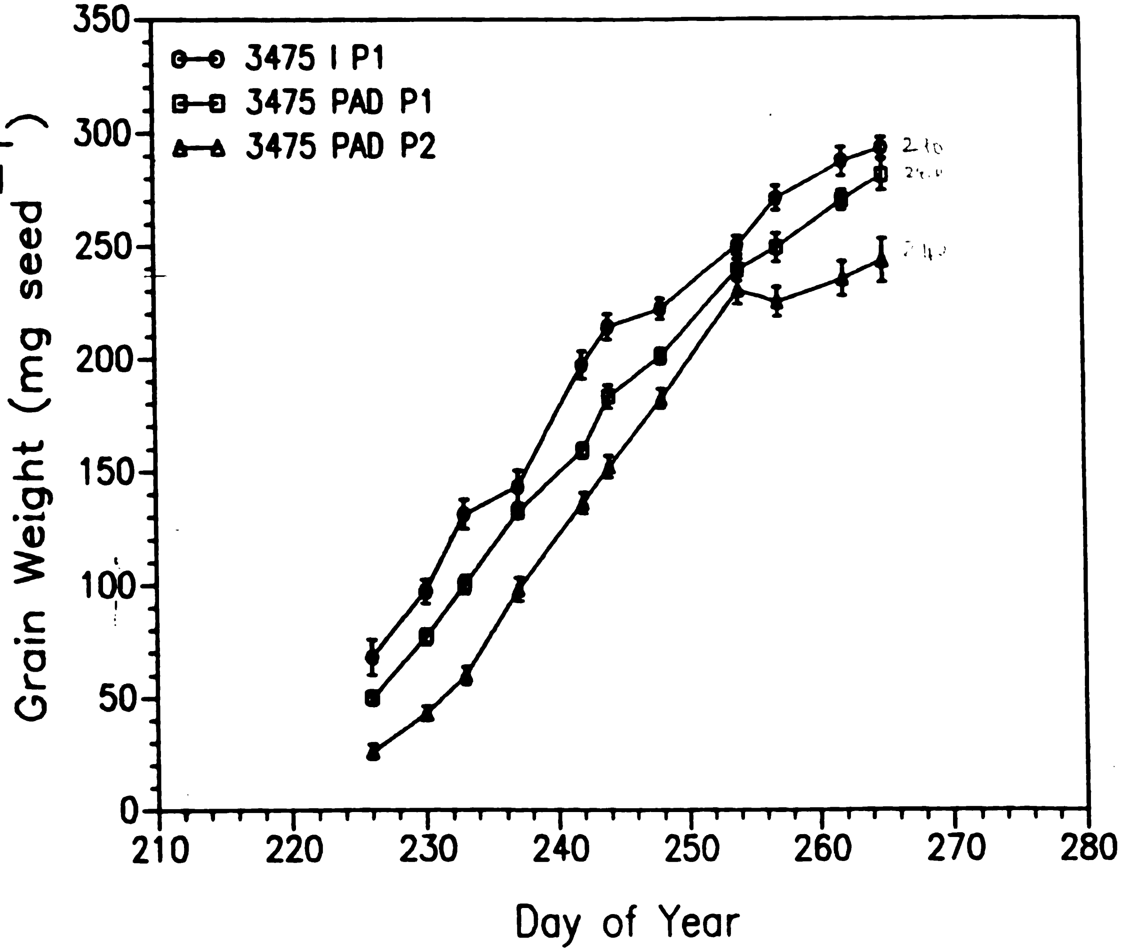

Figure 2.4b. Grain filling as measured by single kernel samples for treatments of hybrid 3475 during 1989.

Lorens et al., 1987). This variation is attributable to differences in deficit severity and timing in the various experiments. Results of the current study generally showed a yield reduction of 15 % to 25 % in response to PAD treatments for hybrids and years overall (Figures 2.5a through 2.5c). The component most responsible for yield decrease was grain number. This agreed with findings of Claassen and Shaw (1970b), Hall et al. (1981), and Lorens et al. (1987).

Grant et al. (1989) observed no influence of pre-anthesis water deficits on grain number and indicated the interval of sensitivity to this yield component began some time after silking. Kiniry and Ritchie (1985) concluded that such a post-silking interval was the time when grain number was most responsive to stresses, however, their data revealed that reductions could be caused as early as thirty days prior to flowering depending on the hybrid. Sadras et al. (1985) constructed a model in which kernel set was not affected by stress if it was relieved five days or more prior to pollination. The data from 1989 of the current study did not indicate largest reductions in grain number for plants nearest flowering when deficits were imposed, instead the opposite was found. Grain numbers were 12 %, 14 %, 14 %, and 18 % less than control plants for 3475 PAD P1, 3540 PAD P1, 3475 PAD P2, and 3540 PAD P2 treatments, respectively.

Reduction in grain weight caused by PAD treatments was observed, but there were varying responses. Hybrid 3475

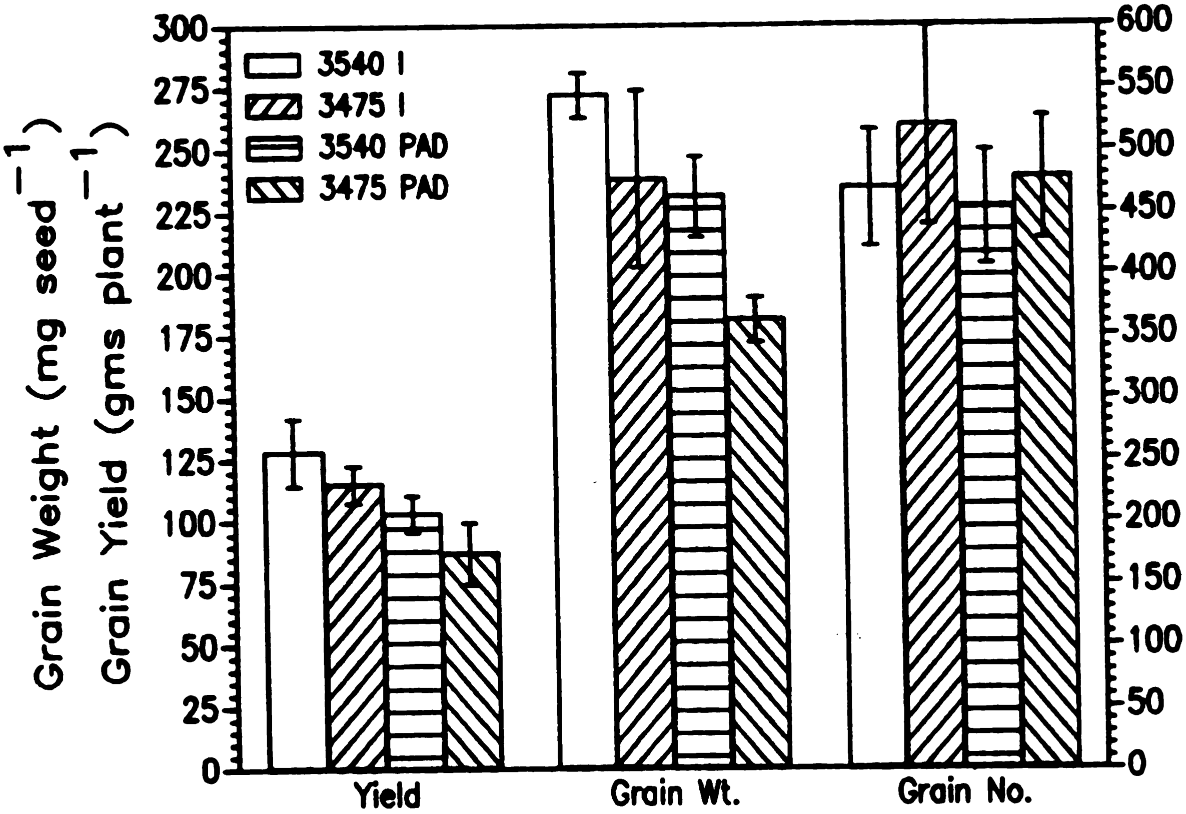

Figure 2.5a. Grain yields, final grain weight, and grain number for treatments of both hybrids during 1988.

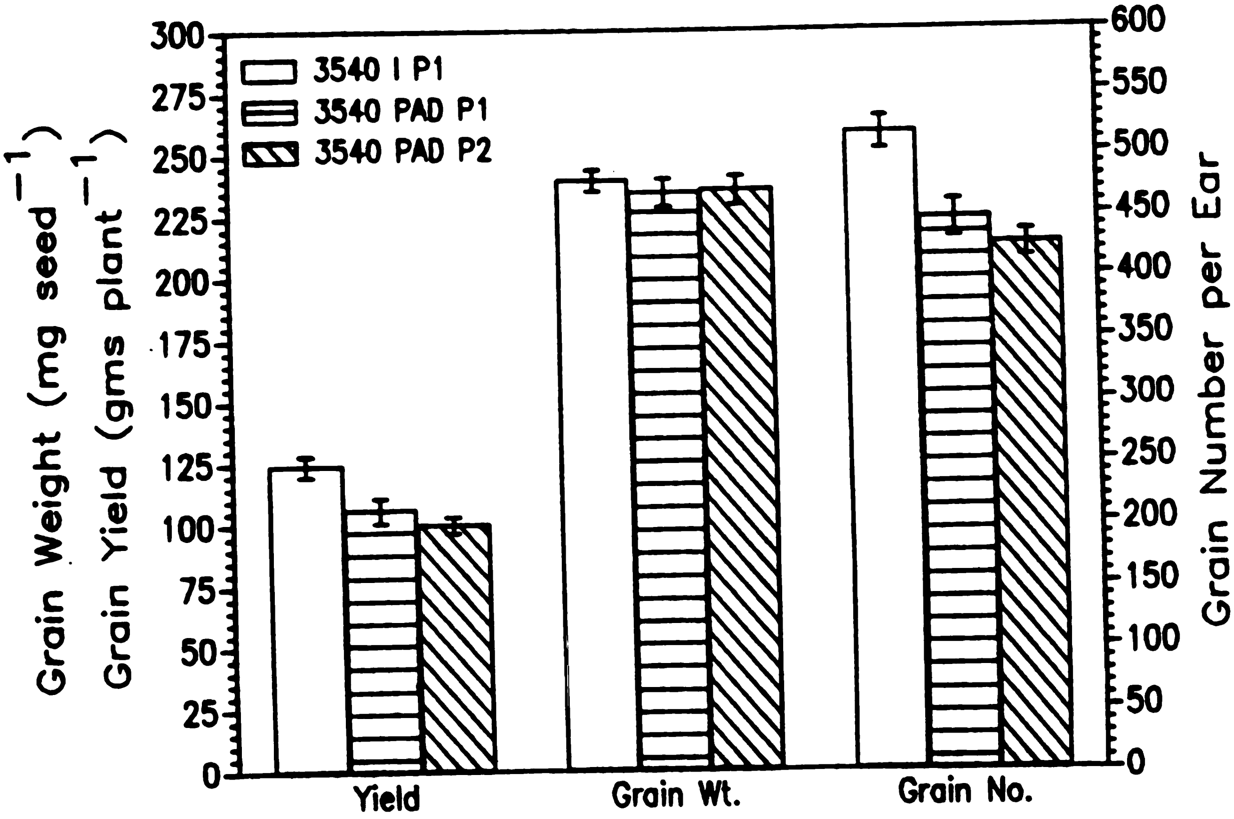

Figure 2.5b. Grain yields, final grain weight, and grain number for treatments of hybrid 3540 during 1989.

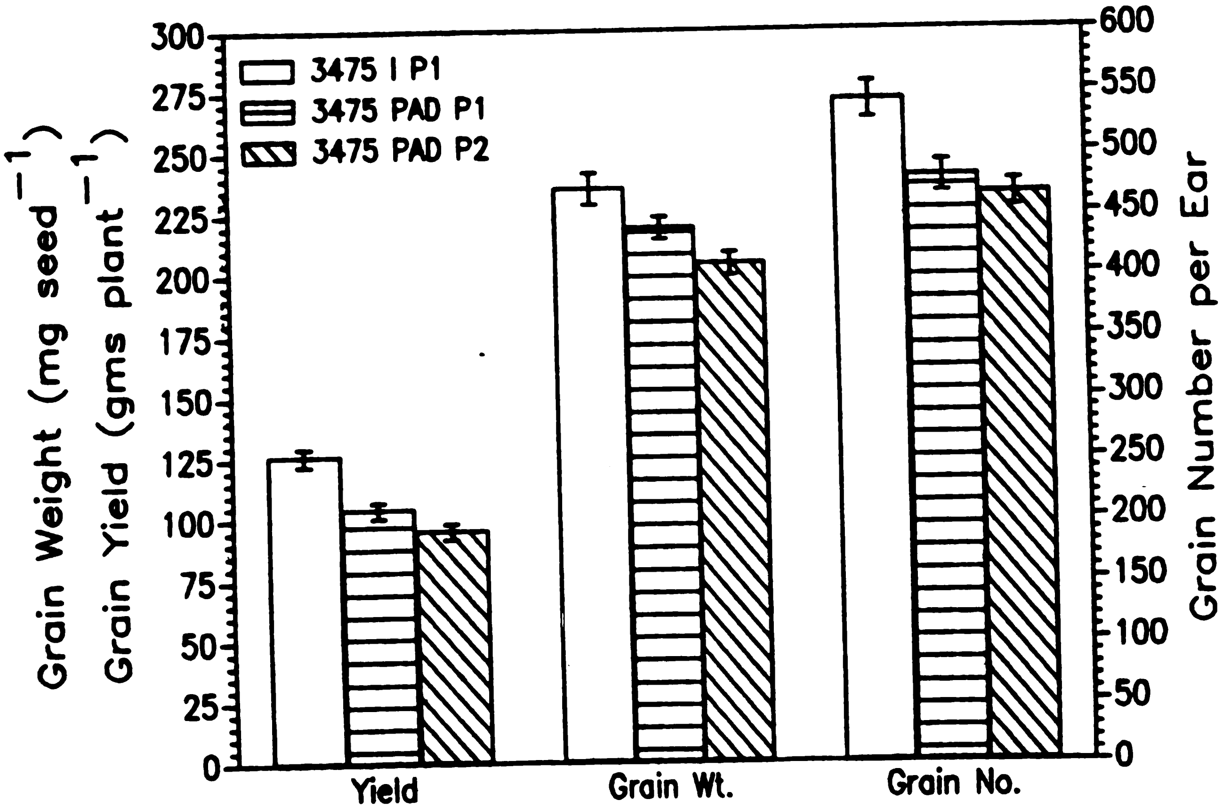

Figure 2.5c. Grain yields, final grain weight, and grain number for treatments of hybrid 3475 during 1989.

appeared more sensitive to reductions in this yield component than hybrid 3540. Generally, grain weight is determined by weighing a large sample of seed and then dividing by the number. This assumes an equal distribution of seed size among treatments. Figures 2.6a through 2.6f demonstrate dissimilar seed size distributions occurred among treatments during 1989. PAD plants had a greater proportion of seeds under 100 mg than I plants. If seeds weighing less than 100 mg were discarded, distributions and average grain weight were the same for treatments. These small seeds added little to the total ear weight and would probably not have been retained in mechanical harvesting.

Claassen and Shaw (1970b) demonstrated that grain weight was reduced during a vegetative water deficit when all kernels were considered. However, when they adjusted for small, less developed seeds they calculated no difference in weight. The criteria they used for classifying seeds was diameter. Seed diameter can be useful, but the variation in shape of kernels among hybrids may pose problems. Separating seeds on a weight basis in the current investigation was laborious, however, this method was determined to be less biased. Furthermore, weight is generally considered when modeling grain growth.

The data from this experiment and that of Claassen and Shaw (1970b) indicate that a threshold seed size needs to be developed for determining effective yield components. This lack of a standard may be a source of variability among

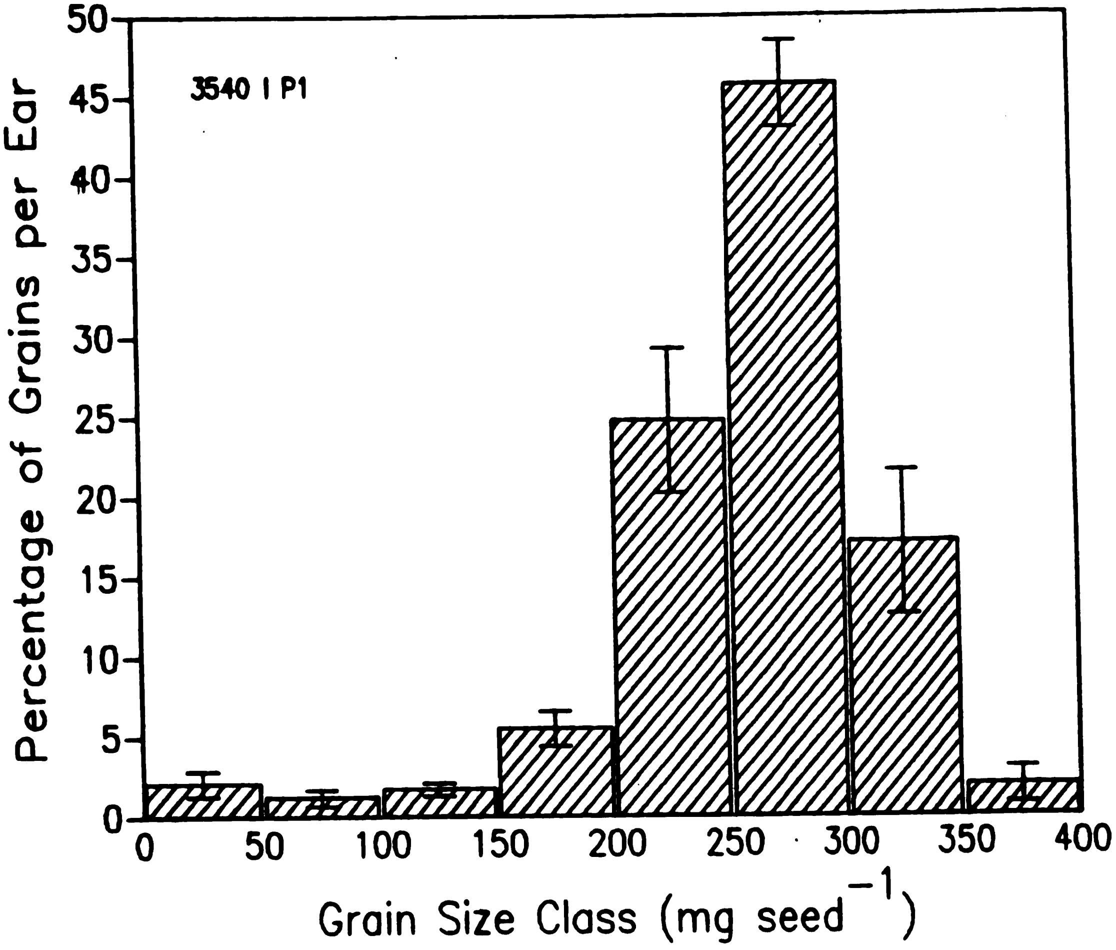

Figure 2.6a. Grain size distribution of single ears at harvest for the hybrid 3540 I P1 treatment during 1989.

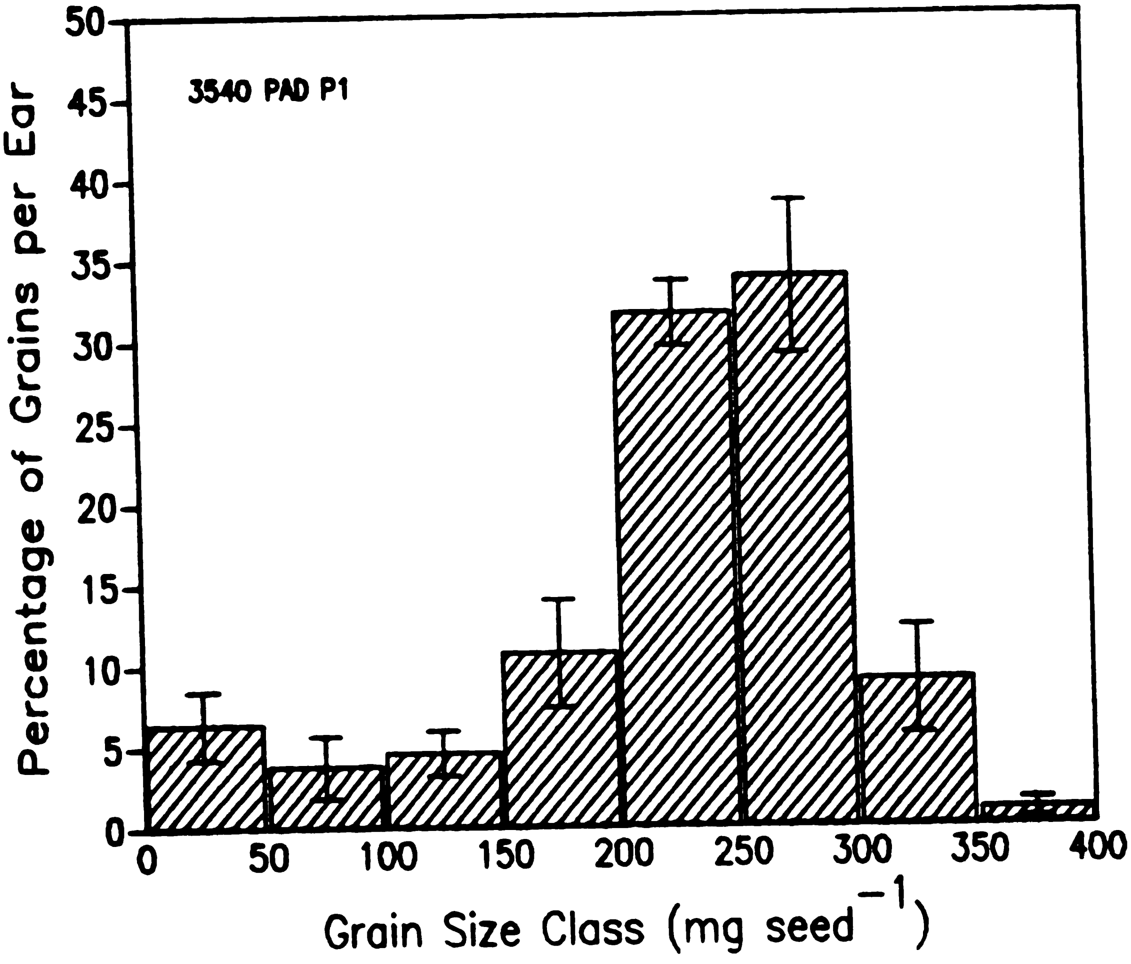

Figure 2.6b. Grain size distribution of single ears at harvest for the hybrid 3540 PAD P1 treatment during 1989.

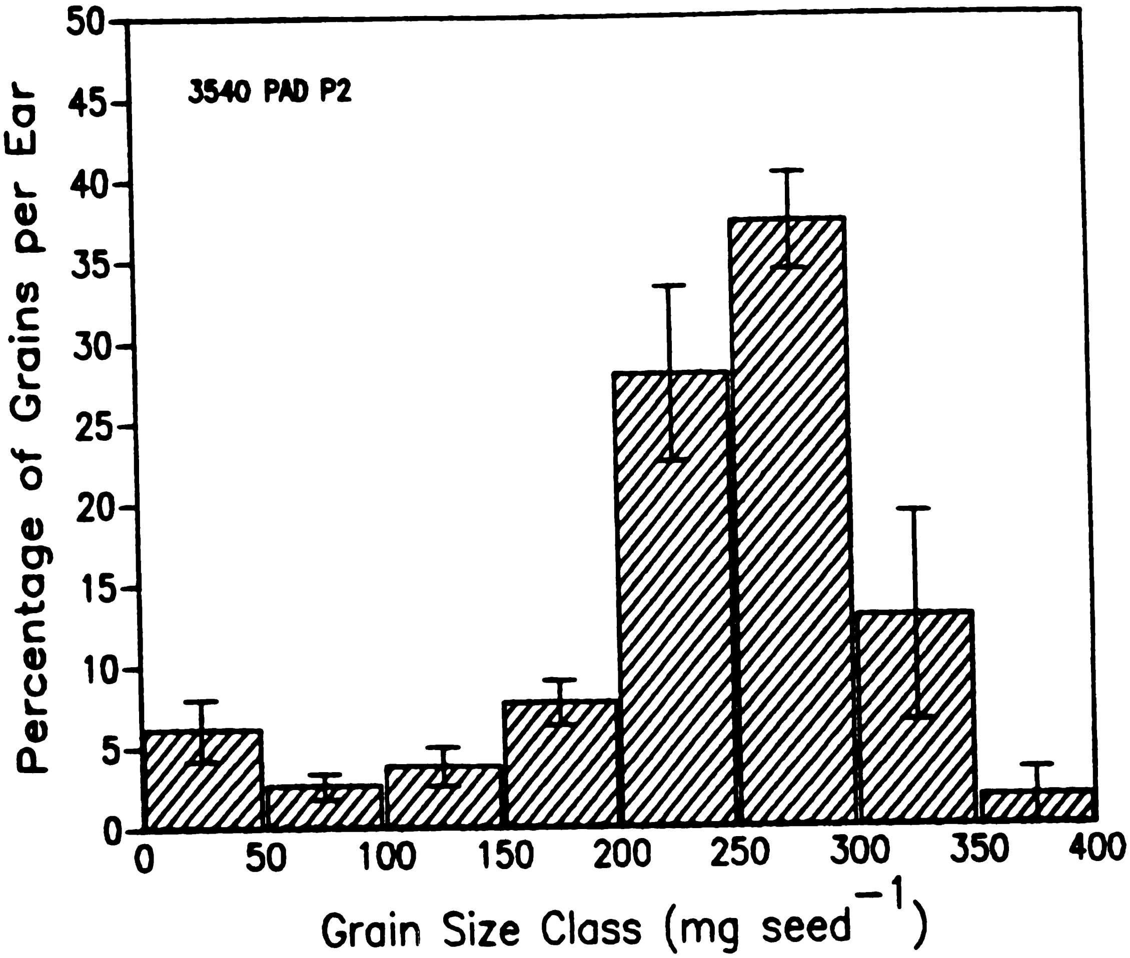

Figure 2.6c. Grain size distribution of single ears at harvest for the hybrid 3540 PAD P2 treatment during 1989.

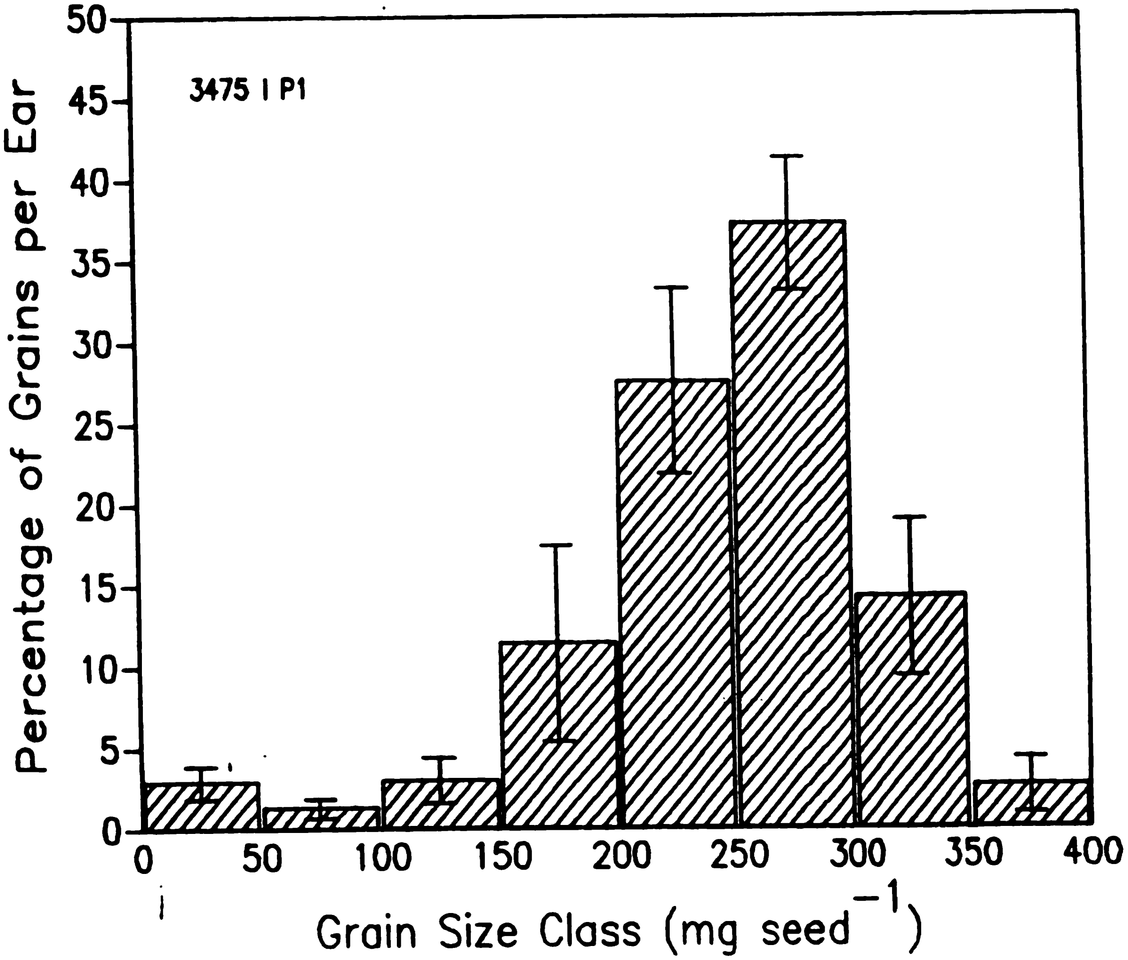

Figure 2.6d. Grain size distribution of single ears at harvest for the hybrid 3475 I P1 treatment during 1989.

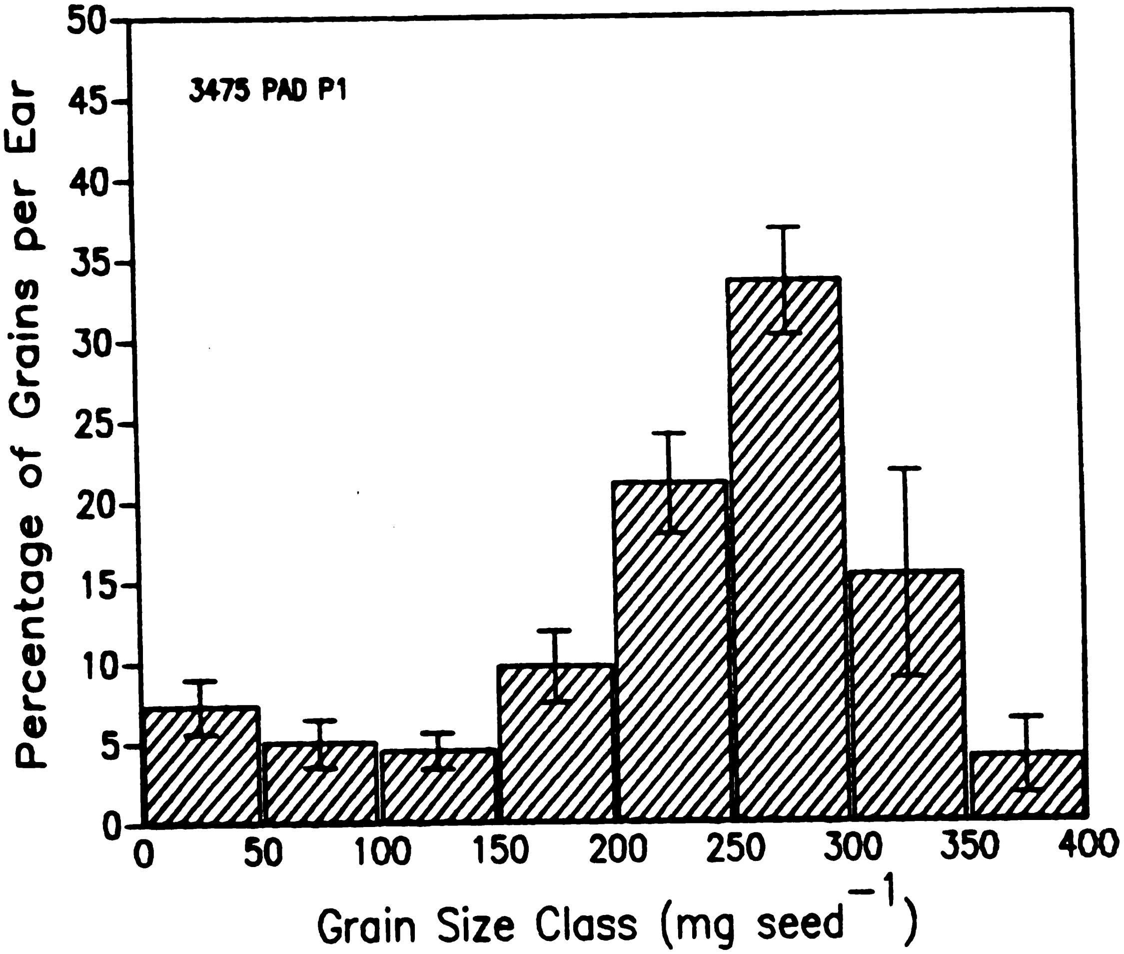

Figure 2.6e. Grain size distribution of single ears at harvest for the hybrid 3475 PAD P1 treatment during 1989.

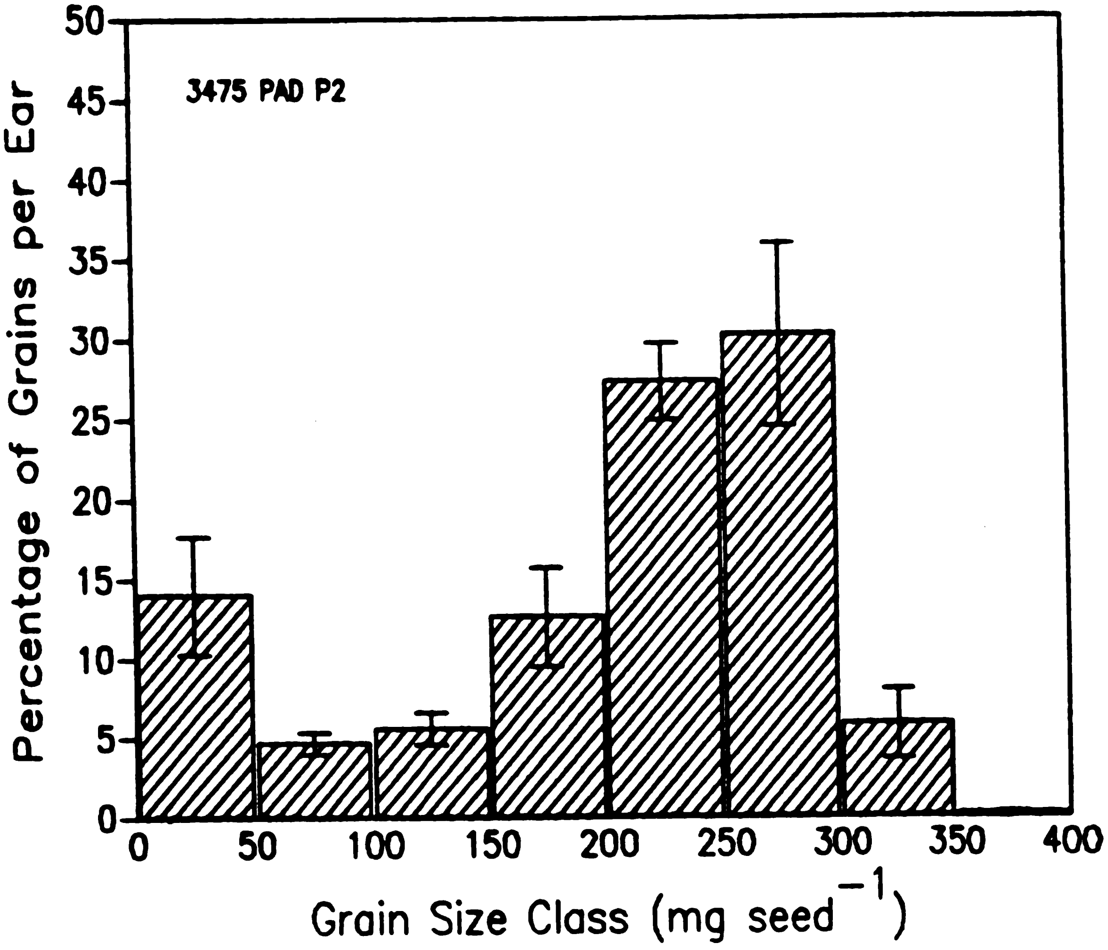

Figure 2.6f. Grain size distribution of single ears at harvest for the hybrid 3475 PAD P2 treatment during 1989.

research reports which differ in the yield component most sensitive to stresses. If all kernels are regarded weight may be biased, and if certain ones are discarded grain number may not be represented accurately. These factors need to be considered when developing crop models that reliably predict yield components.

In summary, results have shown that tassel emergence, silk emergence, and beginning grain fill were delayed by pre-anthesis water deficits even though irrigation resumed at least a week prior to flowering of control plants. There was no apparent synchronization problems between tassels and silks. Intact ear size was reduced due to the water shortages. Yields of deficit plants were 15 % to 25 % less than irrigated plants. Grain number was the yield component most reduced when mechanically harvestable seeds were considered, although, examination of grain size distributions revealed a higher percentage of seeds less than 100 mg were present on ears of water deficient plants.

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CHAPTER 3

PRE-ANTHESIS SOIL WATER DEFICIT EFFECT ON CORN (ZEA MAYS L.). III. BIOMASS AND NITROGEN ACCUMULATION AND PARTITIONING

ABSTRACT

Biomass accumulation and nitrogen uptake patterns in corn are similar. Usually 65 % to 70 % of the total season nitrogen is taken up by the mid-silking growth stage, hence, interruption or alteration of pre-anthesis nitrogen acquisition is potentially detrimental to dry matter production and yield. Research was conducted during 1988 and 1989 in Michigan utilizing a rain shelter to impose an intermittent water deficit on corn in a field environment prior to anthesis. Biomass accumulation and partitioning results indicated an 18 to 21 day water deficit during vegetative growth reduced above ground dry matter production of deficit plants 35 % to 45 % as compared to irrigated control plants. The greatest reduction was at the end of the deficit period which was a week or more prior to tassel emergence of control plants. Examination of crop growth rate revealed there was a reduction for water deficit plants as great as 65 %. Reduced leaf area as well as leaf rolling was the major causal factor of the crop growth rate differences, although, increased partitioning to roots of deficit plants was observed as well. There were proportional reductions in dry weight of all above ground plant organs of deficit plants. Assessment of above ground nitrogen status 10 to 12 days past silking revealed little difference in the percentage of this element among treatments, although, absolute uptake was less. Subsequent evaluation of grain nitrogen revealed similar results. Results of vegetative and reproductive growth and development are presented in companion papers.

INTRODUCTION

Plant nitrogen status is important agronomically and has received considerable attention among experimenters. Hanson and Hitz (1983) divided nitrogen economy into two phases, the acquisition phase and the reallocation phase, with some overlap between phases. They indicated the acquisition phase was nearly completed for oats shortly after anthesis. Researchers have shown that 50 % to 90 % of corn's total nitrogen was acquired by flowering, with most reports indicating it was in the range of 70 % (Friedrich et al., 1979; Hanway, 1962b; Karlen et al., 1987; Tsai et al., 1984; Wolfe et al., 1988). Hanway (1962b) found that grain contained 65 % of the total nitrogen at harvest, and that this was equal to the amount of nitrogen taken up at silking. In an experiment with ^{15} N, Friedrich and Schrader (1979) concluded that almost the entire amount of grain nitrogen was that acquired prior to silking. In fact, post silking nitrogen deprivation did not reduce grain nitrogen content even though the capacity for uptake still existed.

Interruption or alteration of pre-anthesis nitrogen uptake can decrease biomass and grain yield significantly because dry matter production and nitrogen uptake patterns are similar (Hanway, 1962a and 1962b; Hanway and Russell, 1969). Verasan and Phillips (1978) reported plant dry weight and nutrient accumulation were highly correlated with evapotranspiration. Similar responses have been observed for plants deprived of either water or nitrogen, which include delayed flowering and reductions in leaf extension, leaf area, biomass production, and yield (Claassen and Shaw, 1970; Denmead and Shaw, 1960; Greenwood, 1976; Hall et al., 1981; Hanway, 1962a; Lorens et al., 1987; Radin and Boyer, 1982; Wolfe et al.,1988). Kevlen (1981) discussed research in which plant growth reductions seemingly caused by water shortage were corrected by nitrogen applications deeper in the soil, indicating that surface drying had reduced nitrogen uptake. Rhoads (1984) reviewed some interactions of water and nitrogen stresses and suggested that water deficits reduce nitrogen use efficiency.

The objective of this research was to utilize a rain shelter to impose a soil water deficit prior to anthesis to determine immediate and subsequent effects on corn growth and development under field conditions. Vegetative and reproductive growth and development responses have been presented by the current authors in companion papers. Results of biomass production, growth analysis, leaf area index, root growth, and plant nitrogen status are presented here.

MATERIALS AND METHODS

Corn was grown in an area that could be covered by a rain shelter at the Kellogg Biological Station near Kalamazoo, MI, USA, during 1988 and 1989. There were two irrigation treatments, an irrigated control (I) and a pre-anthesis deficit (PAD), and two cultivars, Pioneer hybrids 3540 and 3475, during both years. Planting date in 1988 was 5 May (DOY 126). In 1989, there were two planting dates referred to as P1 and P2, which were 3 May (DOY 123) and 17 May (DOY 137), respectively. Plants were thinned to a population of 7.9 plants m^{-2} at the fourth leaf stage. Row spacing was 0.71 m. The deficit period was from DOY 168 to DOY 189 and from DOY 175 to DOY 193 during 1988 and 1989, respectively. Additional description of treatments and experimental establishment was in a companion paper (NeSmith et al., 1990a).

Biomass for the above ground portion of the plants was determined several times during the growing season each year by a combination of nondestructive estimates and destructive sampling. Biomass (BIOM) for 1988 was estimated from height to the top leaf ligule (LIG) for the period from DOY 168 to DOY 200 using the following equation which was fitted from sampling in 1989:

$$\text{BIOM} = 16.2 + 0.46(\text{LIG}); \quad r^2 = .84 \qquad [1]$$

$$(30 \text{ cm} < \text{LIG} < 160 \text{ cm})$$

After DOY 200, biomass was determined by harvesting four plants per treatment and oven drying them at 60 °C until no further weight loss occurred.

During 1989, leaf and stem biomass (LFBIOM and STMBIOM) were estimated from plant leaf area (PLA) and height to the top leaf ligule (LIG) for the period from DOY 166 to DOY 187 using the following equations fitted from sampling in 1989:

$$\text{LFBIOM} = 6.15 \times 10^{-3}(\text{PLA}) - 2.83; \quad r^2 = 0.94 \qquad [2]$$

$$(2000 \text{ cm}^2 \text{ plant}^{-1} < \text{PLA} < 7000 \text{ cm}^2 \text{ plant}^{-1})$$

$$\text{STMBIOM} = 3.02 \times 10^{-1}(\text{LIG}) + 0.89; \quad r^2 = 0.87 \qquad [3]$$

$$(30 \text{ cm} < \text{LIG} < 160 \text{ cm})$$

Leaf biomass was for visible blades and sheathes only. The stem biomass included leaves which had not emerged from the whorl of the plant, as well as internodes. Beginning DOY 195, biomass was obtained by harvesting four plants per treatment and oven drying as in 1988. Individual plants were separated into leaves (including sheath), stems (including tassel), husks-silks-cobs, and grain on each sampling date the second year.

Additionally for 1989, crop growth rate (CGR) was calculated from the derivative of smooth fitted lines to biomass data (see Brown, 1984; Radford, 1967), and leaf area index (LAI) was estimated from leaf length, width, and senescence measurements (see Johnson and Tanner, 1972; Linvill et al., 1978). Net assimilation rate (NAR) was computed by dividing CGR by LAI on a given day. CGR, LAI, and NAR were calculated on a land area basis. Leaf rolling was assessed between 1100 h and 1200 h on DOY 186 through DOY 188. These were clear days with little or no wind. Measurements were made on leaves 10, 11, and 12. The rolled width was measured first, followed by the fully open width.

During 1988, root observations were made using a minirhizotron system similar to that described by Upchurch and Ritchie (1984), with modifications as described by Ferguson and Smucker (1989). There were six observation tubes installed in each plot at a 45° angle. Root images were recorded with a VHS video recording system to a vertical depth of 1 m on three dates occurring before, during, and after the water deficit period. Root observations were averaged for each 0.1 m vertical depth increment.

During 1989, nitrogen content of plants sampled on 31 July (DOY 212) was determined by micro-Kjeldahl procedures for leaves, stems, and ears. There was no appreciable grain on this date, so the whole ear (husks, cob, silks) was aggregated as a single sample. Nitrogen content of grain only was determined for DOY 227, DOY 249, and harvest (DOY 270) plant samples.

RESULTS AND DISCUSSION

There were no appreciable differences between hybrids in the data presented here, and the averaging of them did not influence statistical significance. Therefore, results for hybrid 3540 only are discussed. Figures 3.1a and 3.1b depict above ground biomass for treatments during 1988 and 1989, and Figures 3.2a and 3.2b show solar radiation for the first and second year, respectively. The accumulation curves for irrigated plants was similar to typical curves as described by Hanway (1962a). The PAD plants deviated from this pattern during the deficit period and never recovered fully after irrigation had resumed. Maximum biomass reduction of PAD plants as compared to I plants during 1988 occurred at the end of the deficit period, and it was 35 %. At harvest PAD

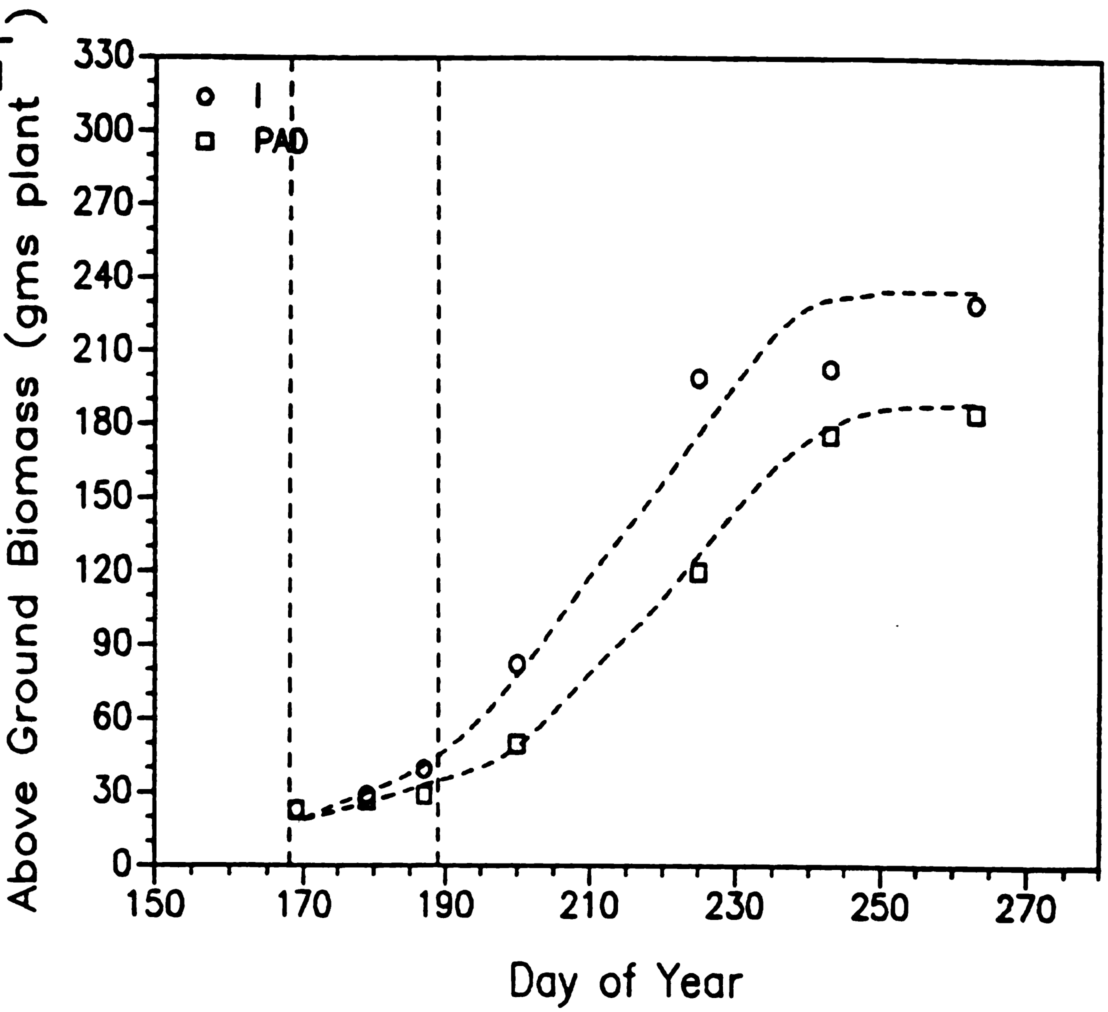

Figure 3.1a. Above ground biomass for treatments during 1988. The region between the vertical dashed lines depicts the deficit period.

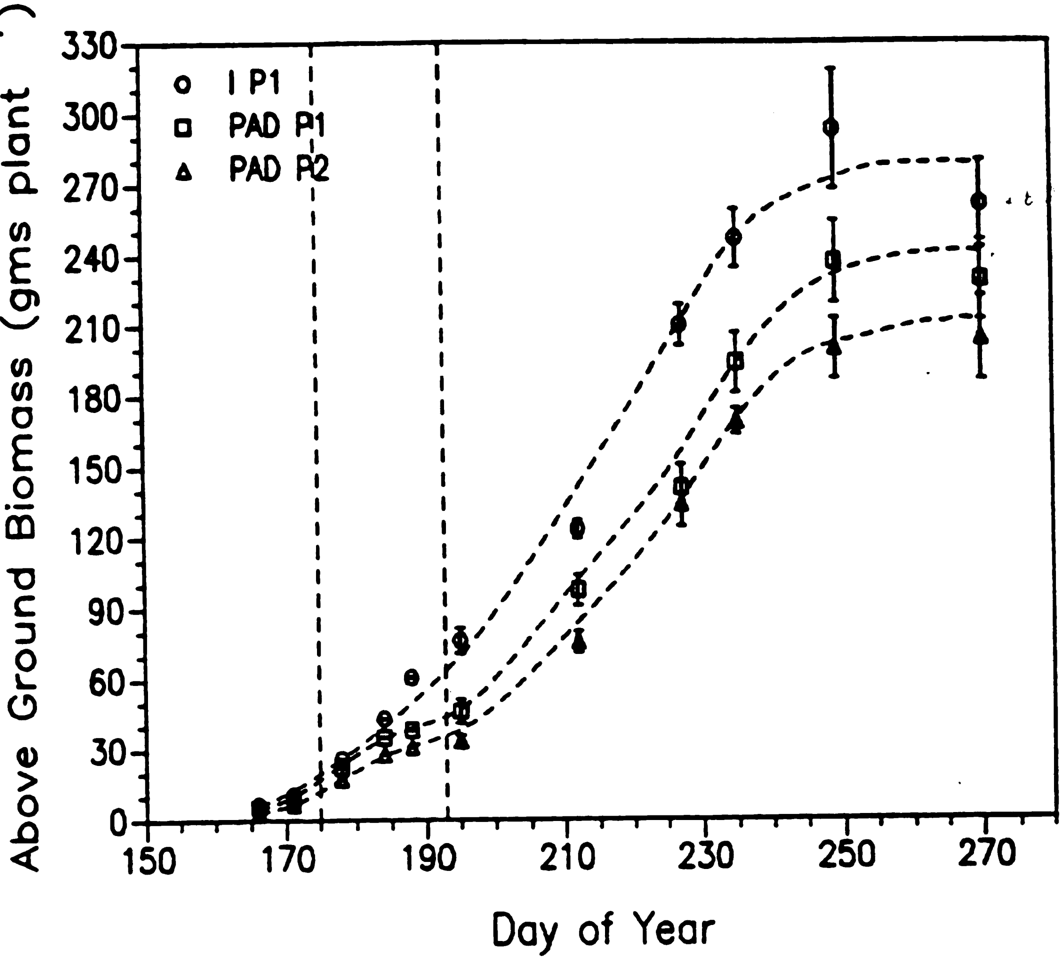

Figure 3.1b. Above ground biomass for treatments during 1989. The region between the vertical dashed lines depicts the deficit period.

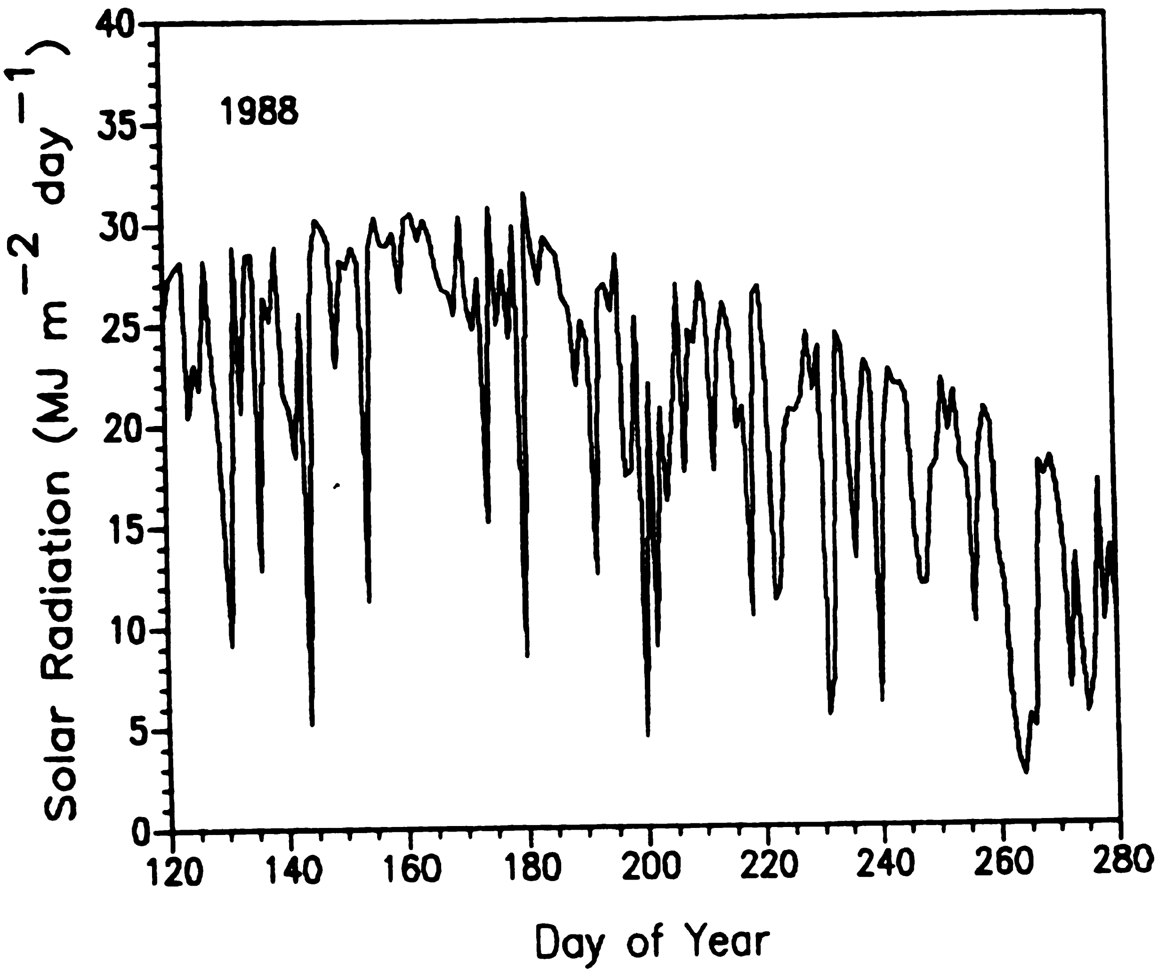

Figure 3.2a. Daily solar radiation at the research site during 1988.

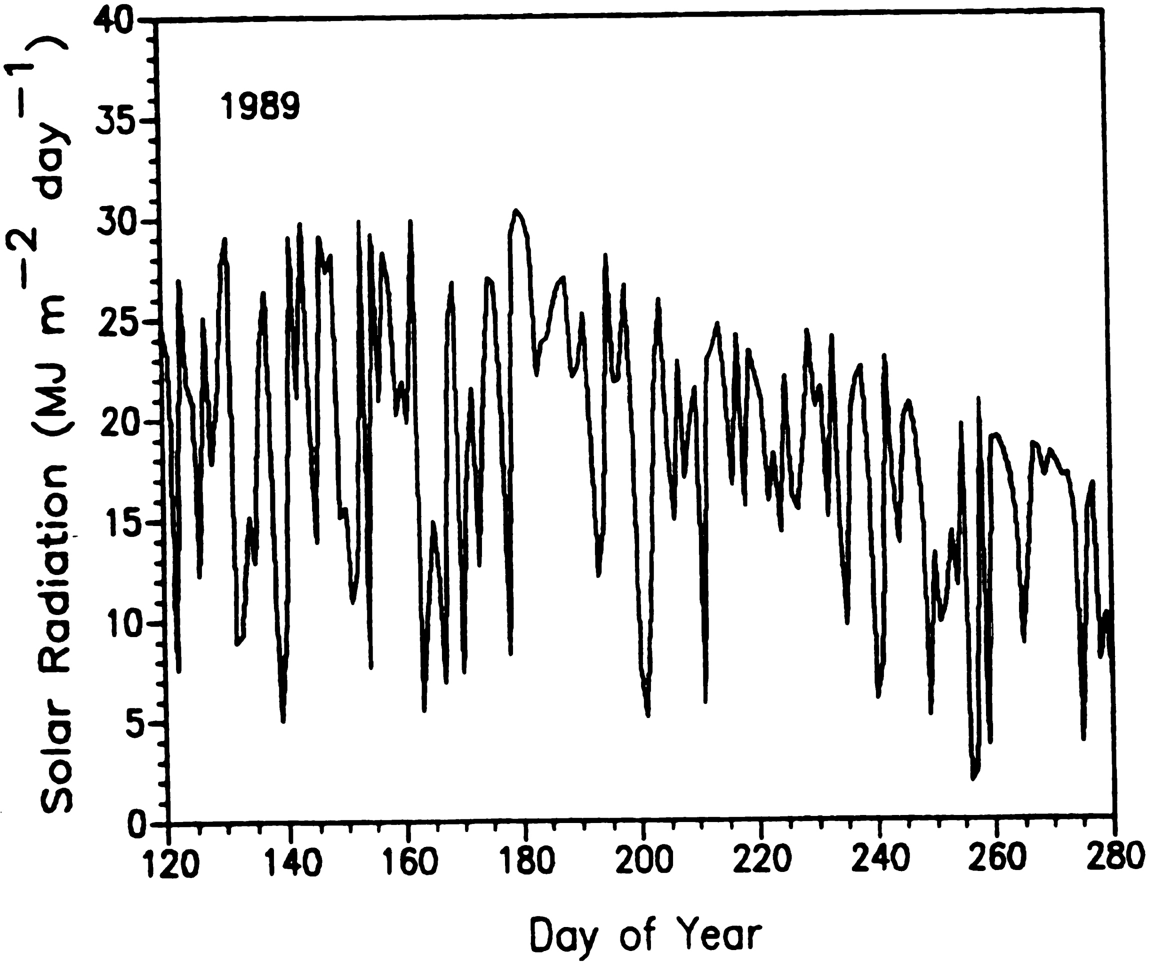

Figure 3.2b. Daily solar radiation at the research site during 1989.

biomass was 20 % less than I plants. During 1989, maximum biomass reduction as compared to the I P1 treatment was again at the end of the deficit period and was 32 % and 45 % for the PAD P1 and PAD P2 treatments, respectively. At harvest PAD P1 plants had 14 % less biomass than I P1 plants, and PAD P2 plants had 25 % less. These results were in the range of reductions found by other experimenters in response to pre-anthesis water deficits.

Claassen and Shaw (1970) reported 15 % to 17 % less dry matter at harvest caused by water deficits during vegetative growth, and Lorens et al. (1987) observed 25 % to 30 % less. Results of Grant et al. (1989) and Hall et al. (1981) indicated 12 % and 38 % biomass reductions, respectively, at harvest. Wolfe et al. (1988) found a 40 % reduction in total biomass on a two year average for nonirrigated corn as compared to irrigated. Their results also showed a similar biomass reduction for plants which received irrigation but no nitrogen.

Figures 3.3a through 3.3d portray the distribution of biomass to the various above ground portions of the plant during 1989. There was a trend at the end of the deficit period for stem weight to be reduced more than leaf weight for PAD plants of both planting dates. Reductions at harvest, however, were proportional for the different components, indicating no significant influence of the PAD treatments on above ground biomass partitioning. Stem weight and

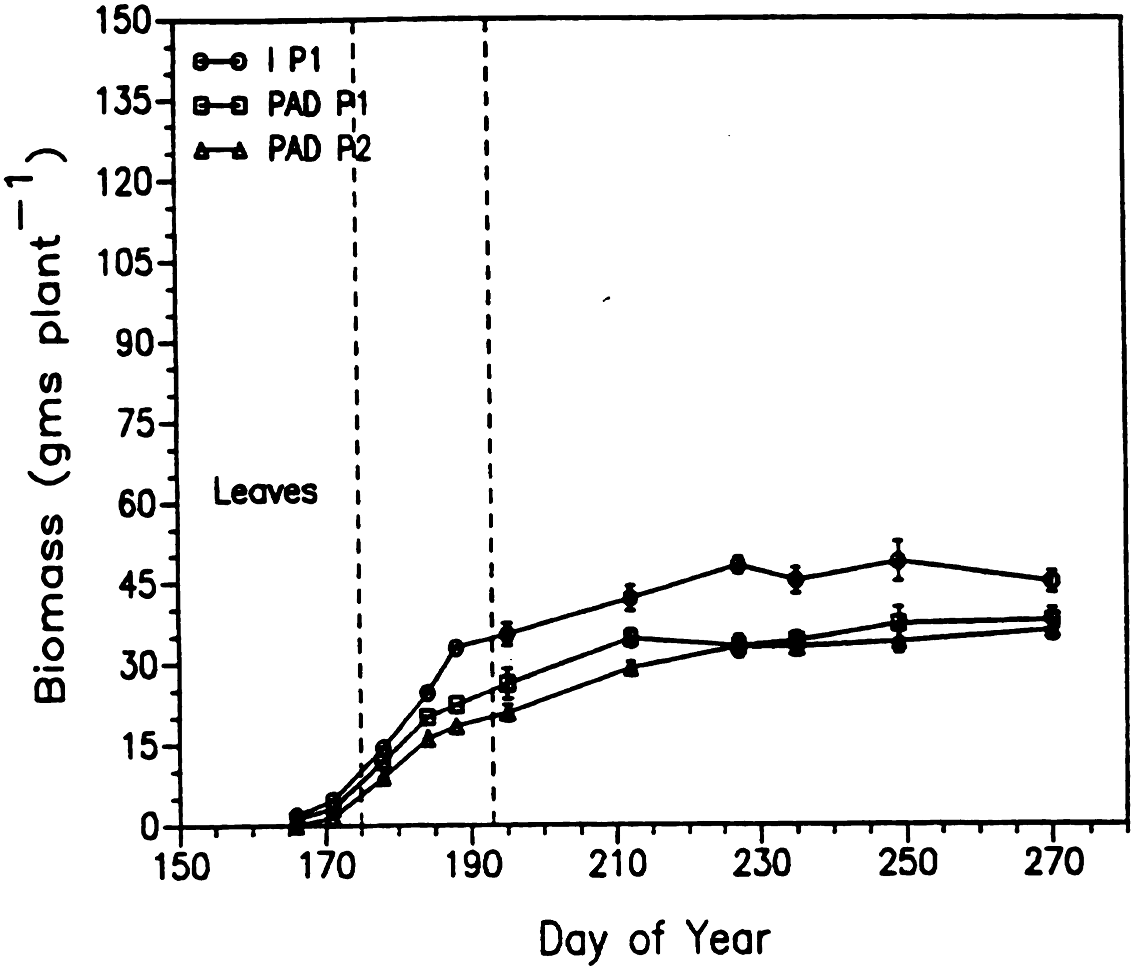

Figure 3.3a. Leaf biomass for treatments during 1989. The weight includes sheathes. The region between the vertical dashed lines depicts the deficit period.

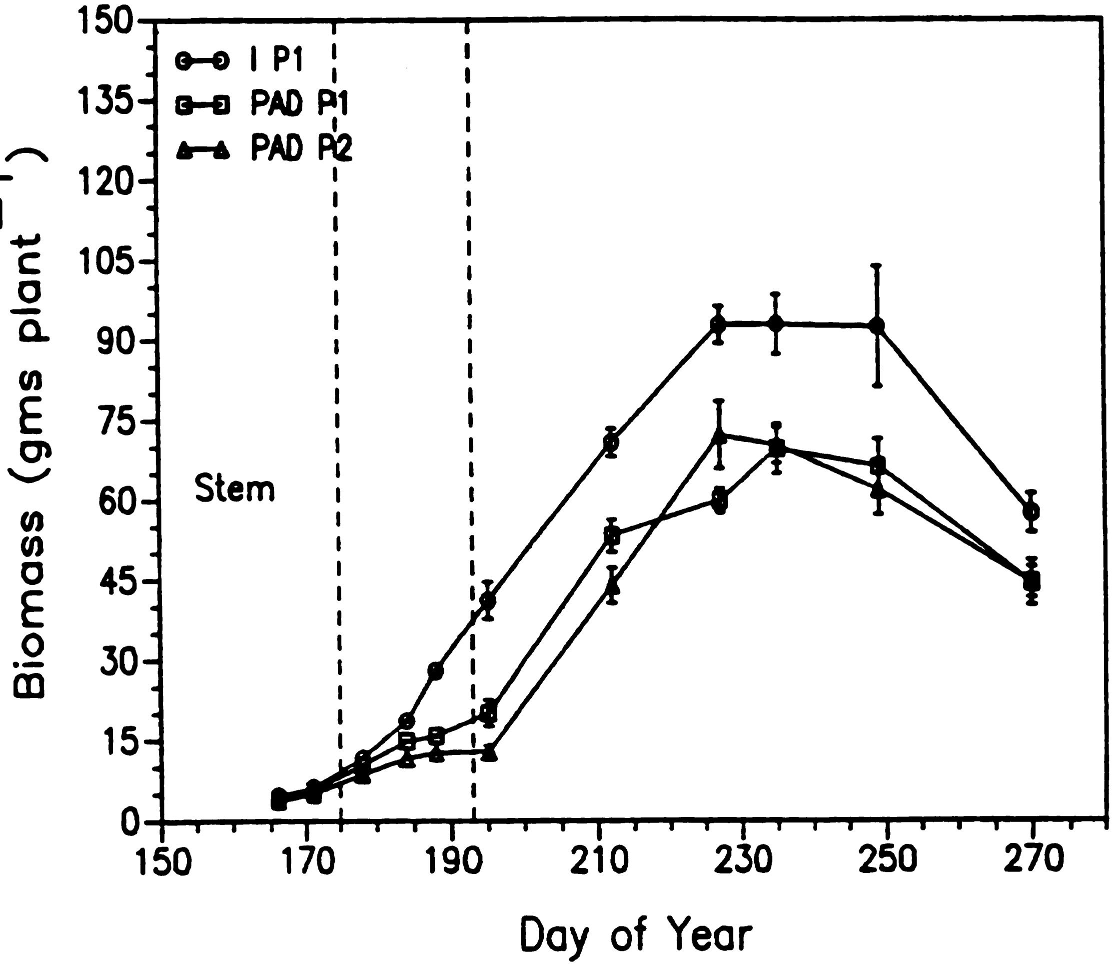

Figure 3.3b. Stem biomass for treatments during 1989. The weight includes the tassel. The region between the vertical dashed lines depicts the deficit period.

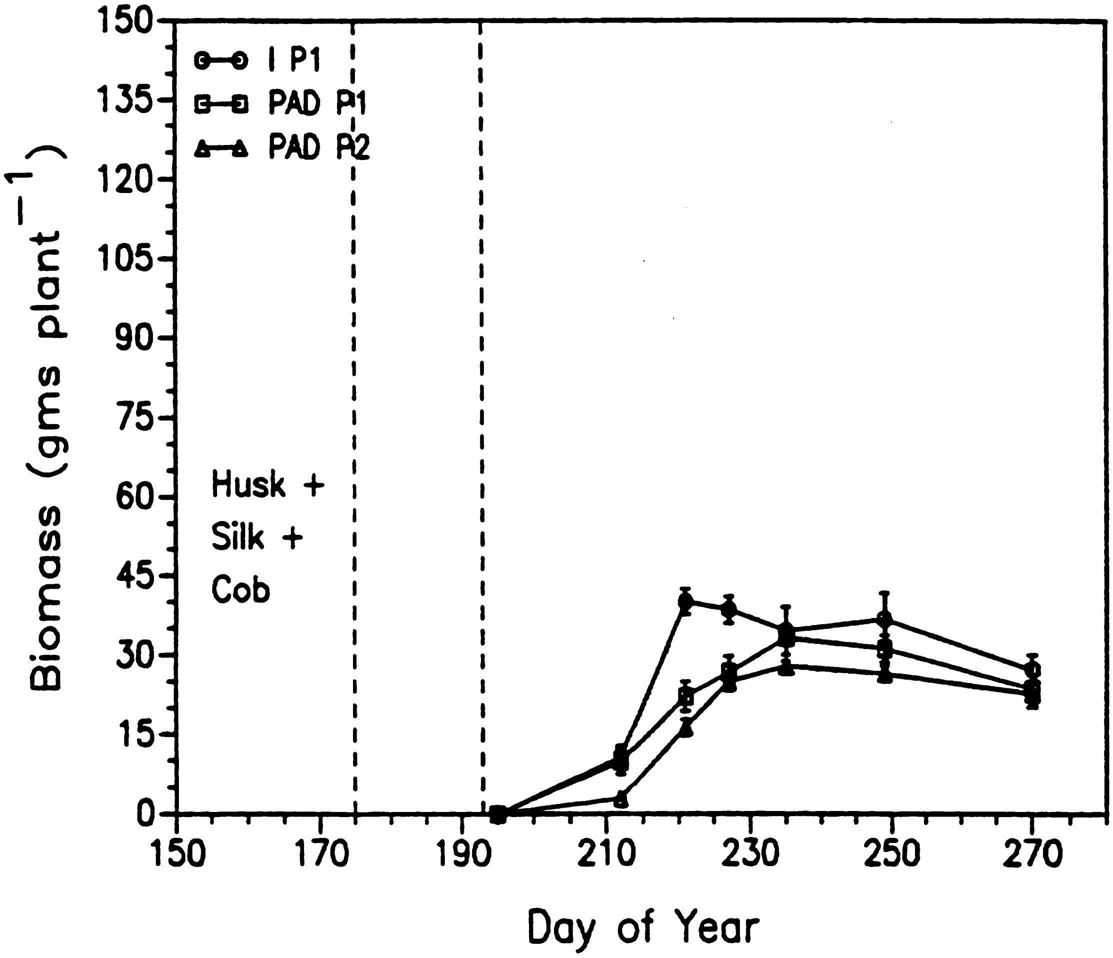

Figure 3.3c. Husk, silk, and cob biomass for treatments during 1989. The region between the vertical dashed lines depicts the deficit period.

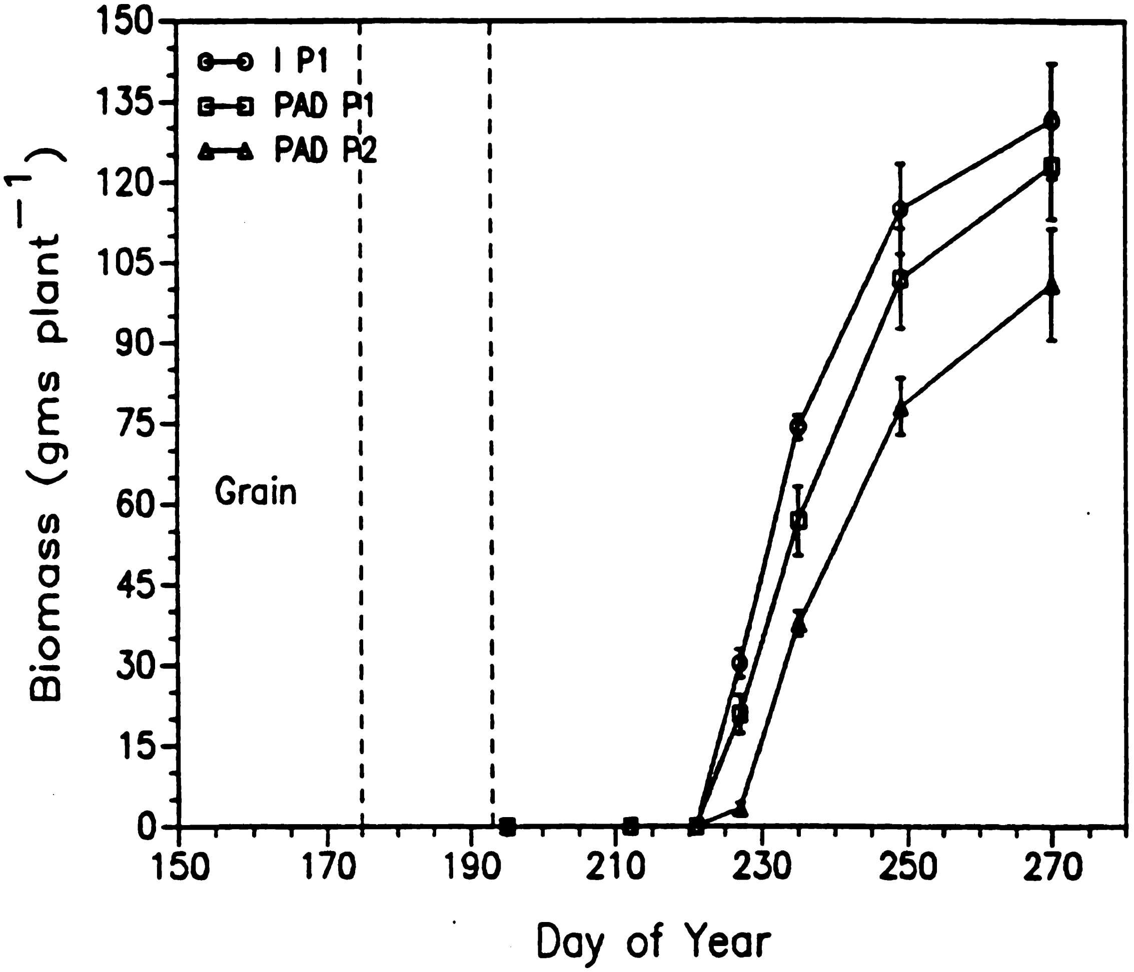

Figure 3.3d. Grain biomass for treatments during 1989. The region between the vertical dashed lines depicts the deficit period.

husk-silk-cob weight declined for all treatments near the end of the growing season, whereas leaf weight remained fairly constant. In general, harvest percentages of total above ground biomass were 17 %, 22%, 11%, and 50 % for leaves, stems, husk-silk-cobs, and grain, respectively, for all treatments. Hall et al. (1981) also found no effect of pre-anthesis water deficits on post silking above ground dry matter partitioning as compared to fully irrigated plants. These results suggest that all plant parts are reduced in size by a soil water deficit that occurs before anthesis.

Figure 3.4 illustrates crop growth rate (CGR) during 1989 for the current study. There was a maximum reduction in CGR of 55 % and 65 % near the end of the deficit period for PAD P1 and PAD P2 plants, respectively, compared to the control. After irrigation resumed, CGR for PAD P1 plants remained 18 % less than I P1 plants, and CGR for PAD P2 plants remained 26 % less until DOY 230. This marked the end of the linear biomass accumulation period. In comparison to these results, Lorens et al. (1987) observed a 12 % to 15 % reduction in CGR during the linear biomass accumulation period caused by a 12 day water deficiency.

Examination of CGR alone did not define the cause of biomass reductions. McCree (1986) indicated that leaf expansion reductions due to stress were important for whole-plant carbon balance. Details of leaf growth for the current study were discussed in a companion paper, however, Figure 3.5

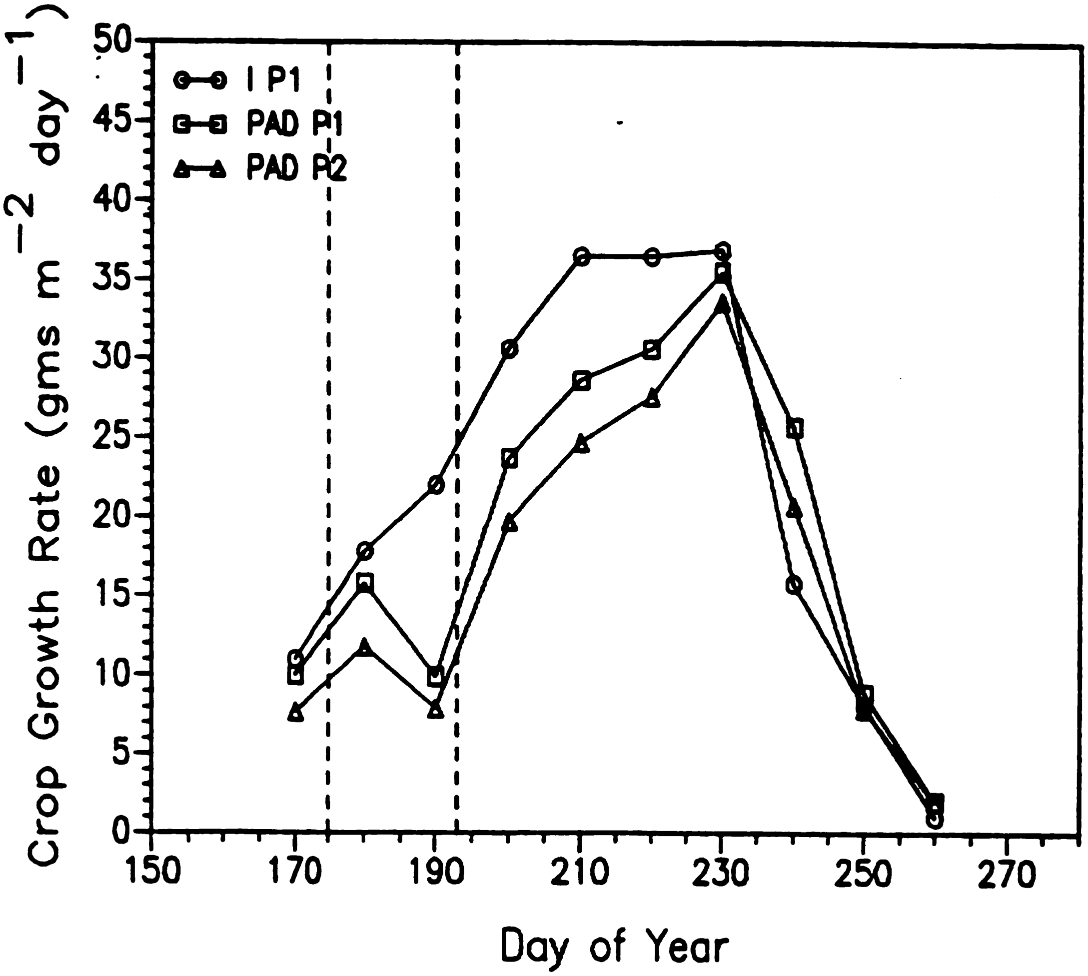

Figure 3.4. Above ground crop growth rate (CGR) for treatments during 1989. The region between the vertical dashed lines depicts the deficit period.

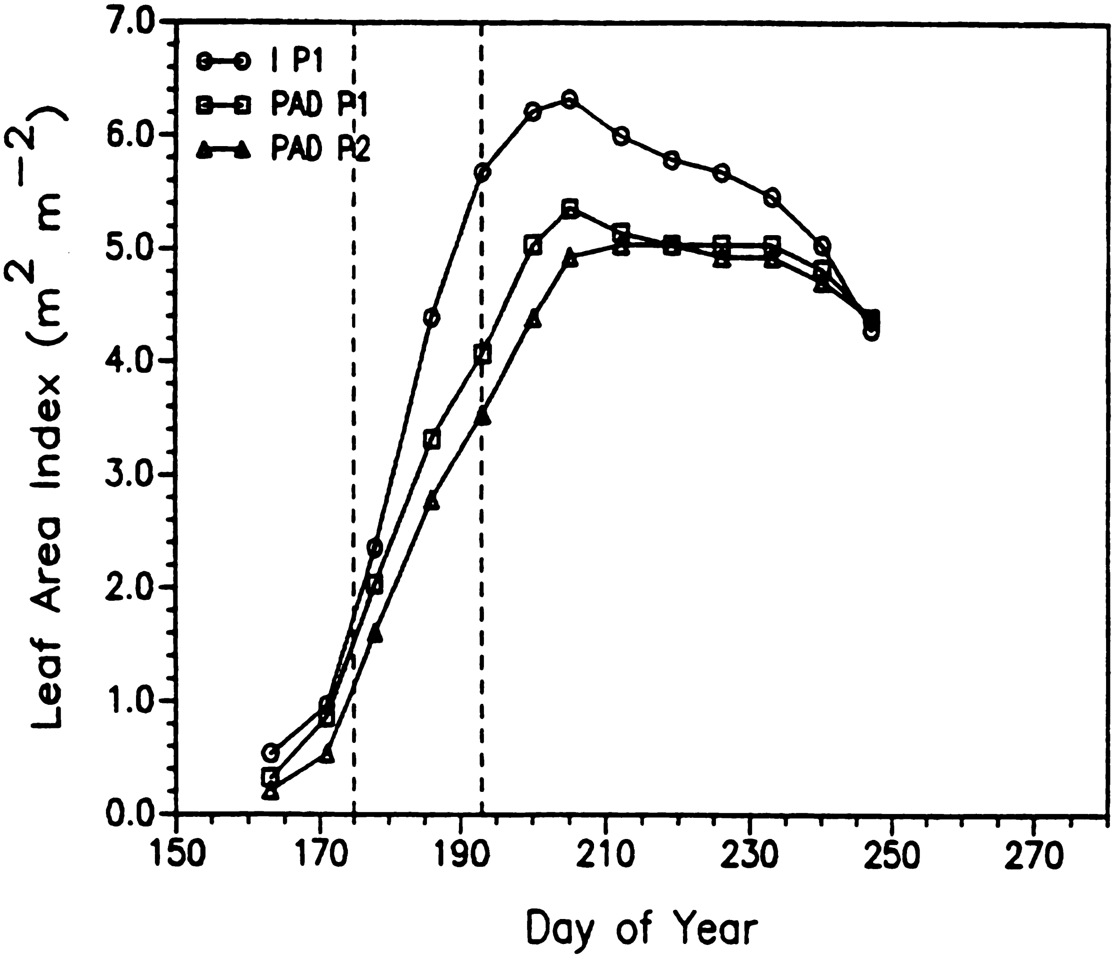

Figure 3.5. Leaf area index (LAI) for treatments during 1989. The region between the vertical dashed lines depicts the deficit period.

delineates leaf area index (LAI) for the treatments during 1989. There was a marked difference caused by the PAD treatments, and this remained after irrigation had resumed. Senescence was not different due to the deficit period, in fact, PAD plants seemed to maintain green leaf area longer late in the season. Hall et al. (1981) and Lorens et al. (1987) reported leaf area reductions of 13 % and 35 %, respectively, due to vegetative water deficits. In addition to water deficit influence on leaf area, Greenwood (1976) proposed that leaf growth in monocots was a sensitive indicator of nitrogen deficiency. Wolfe et al. (1988) observed 30 % reductions in green leaf area over two years for water deficit and nitrogen deficit plants alike.

Net assimilation rate (NAR) accounts for differences in crop growth rate due to leaf area. Figure 3.6 illustrates NAR for treatments during 1989. Whereas maximum CGR reductions were 55 % to 65 % for PAD plants as compared to the control, maximum NAR reductions were only 40 % to 45 % near the end of the deficit period. Also, after irrigation resumed there was little difference between NAR among treatments. Radin (1983) reported a 25 % decrease in NAR for barley resulting from decreased leaf area. The lack of leaf area in that experiment was caused by a reduction in nitrogen accumulation rate rather than by a water shortage.

While NAR assessment in the current study explained some of the differences in above ground biomass accumulation, there

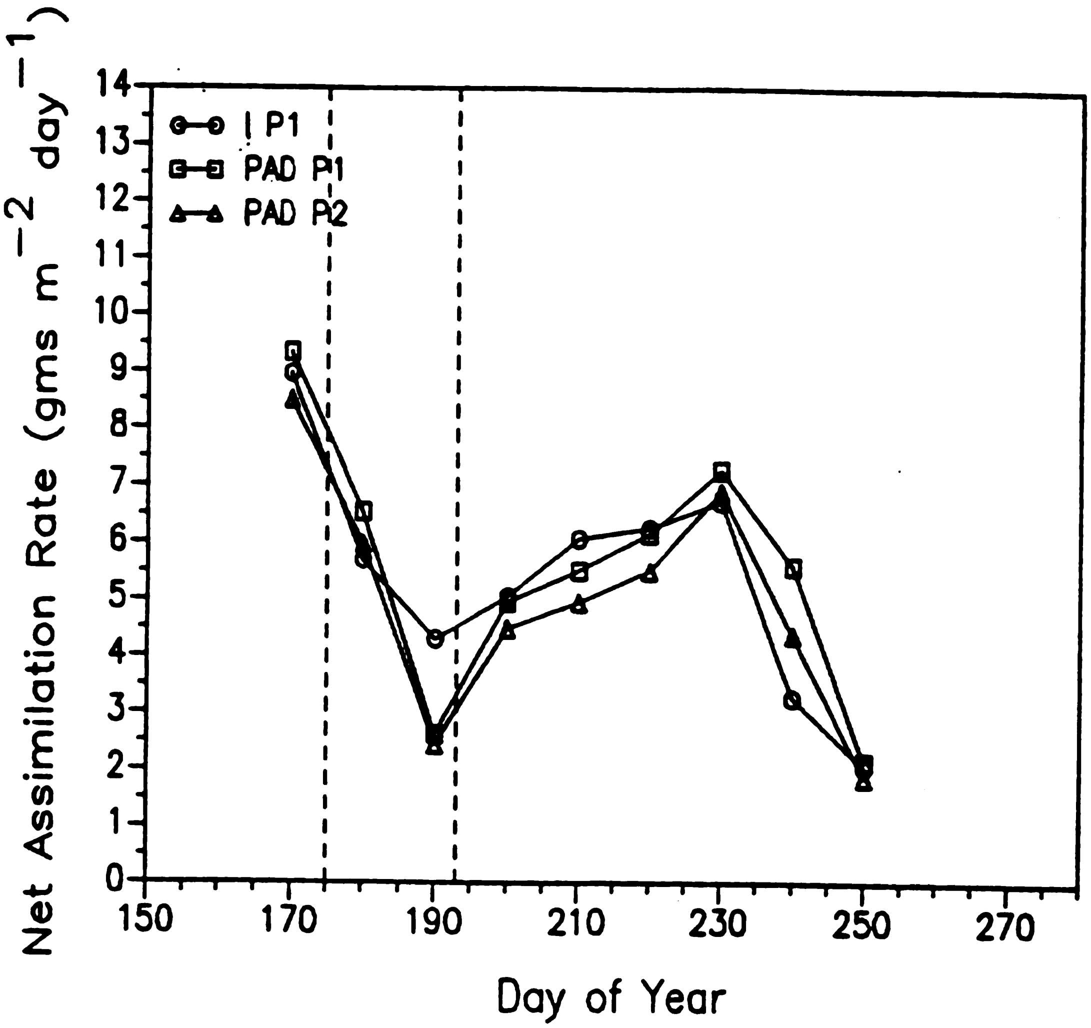

Figure 3.6. Above ground net assimilation rate (NAR) for treatments during 1989. The region between the vertical dashed lines depicts the deficit period.

was still a substantial reduction in this value for PAD treatments. This would seem to suggest a reduced photosynthetic capacity for the water deficit plants, however, this was not believed to be the case. Figures 3.7a and 3.7b show leaf rolling on three successive clear days for the PAD plants during the deficit of 1989. The rolled width was on average 50 % to 60 % less than the fully open width. All leaves were not measured, but if one assumes an overall rolling of 40 %, and also takes into account the change in leaf angle, then the "effective LAI" would have been considerably less than that measured. This could have accounted for the difference in NAR values without loss in photosynthetic capacity. A midday light interception assessment on 7 July (DOY 188) indicated 25 % to 30 % of the light measured above the canopy was intercepted by PAD plants as compared to 65 % to 70 % by I P1 plants. Jordan (1983) cited a light interception value of 52 % for water deficit sorghum plants as compared to 96 % for irrigated plants. He discussed the beneficial role of leaf rolling as being twofold: (i) less radiation load due to smaller exposed leaf area, and (ii) less transpiring surface. He indicated more research was needed to quantify the influence on crop growth.

The effects of above ground biomass production have been considered thus far. Figures 3.8a through 3.8c depict root growth before (DOY 166), during (DOY 182), and after (DOY 203) the water deficit period during 1988. A decrease in root

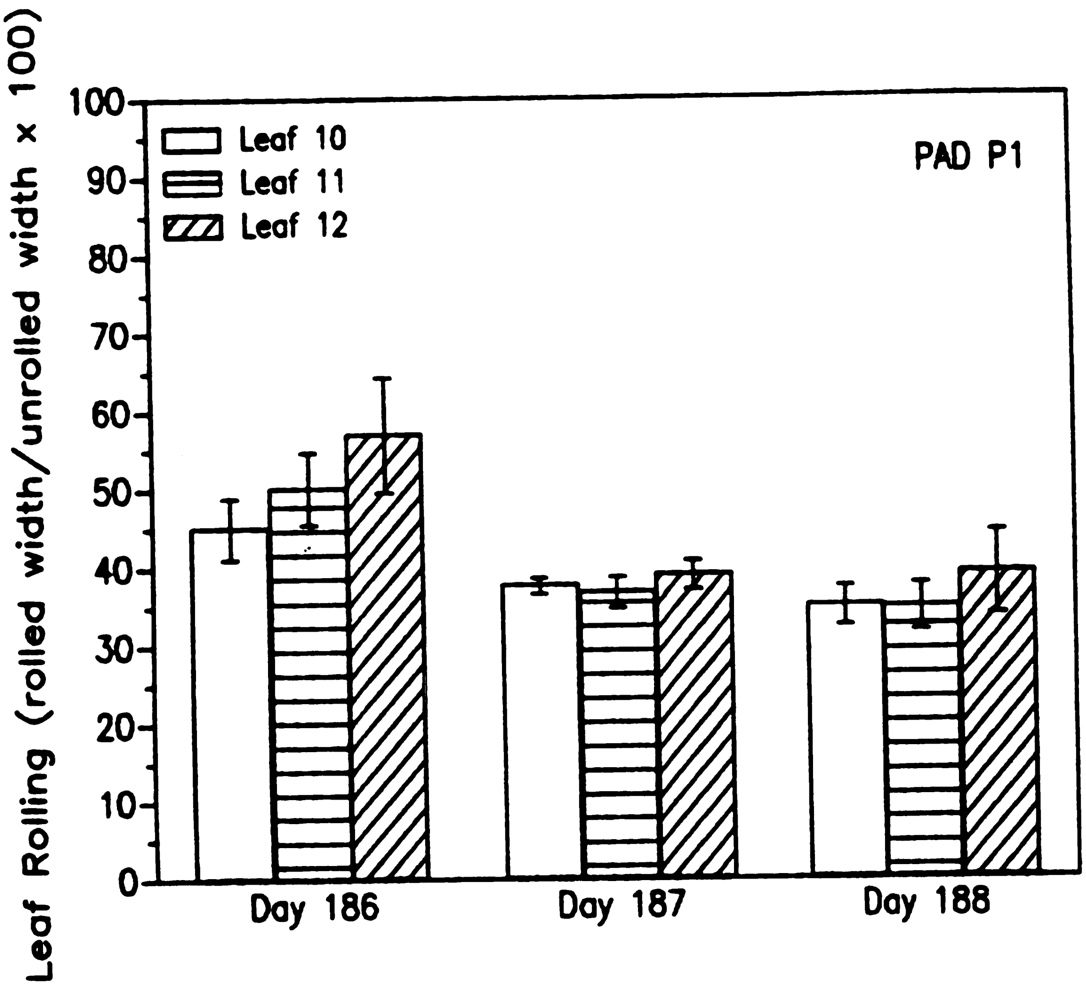

Figure 3.7a. Leaf rolling for leaves 10, 11, and 12 of pre-anthesis deficit plants of the first planting date during 1989.

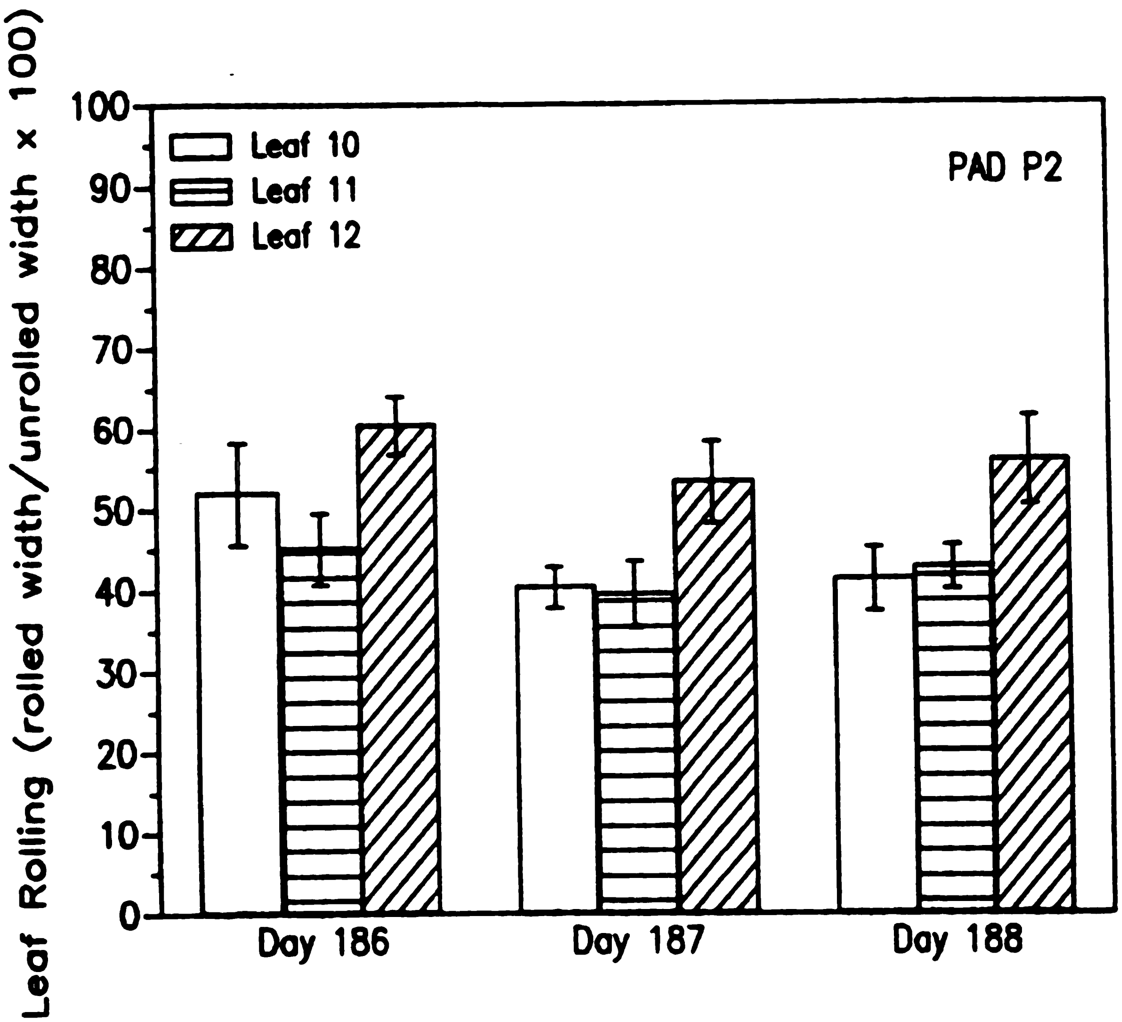

Figure 3.7b. Leaf rolling for leaves 10, 11, and 12 of pre-anthesis deficit plants of the second planting date during 1989.

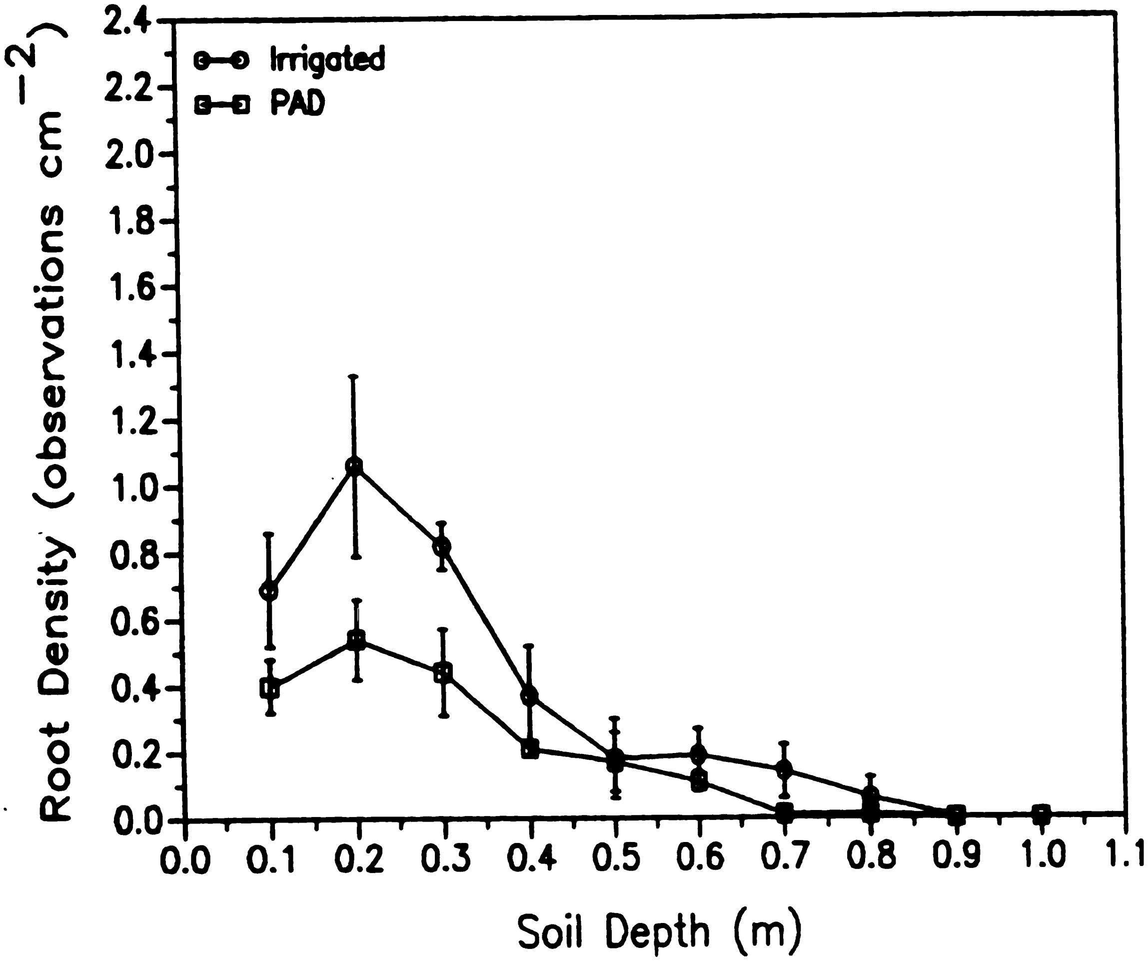

Figure 3.8a. Minirhizotron root observations for irrigated and pre-anthesis deficit plants on DOY 166 in 1988. This was before the deficit period.

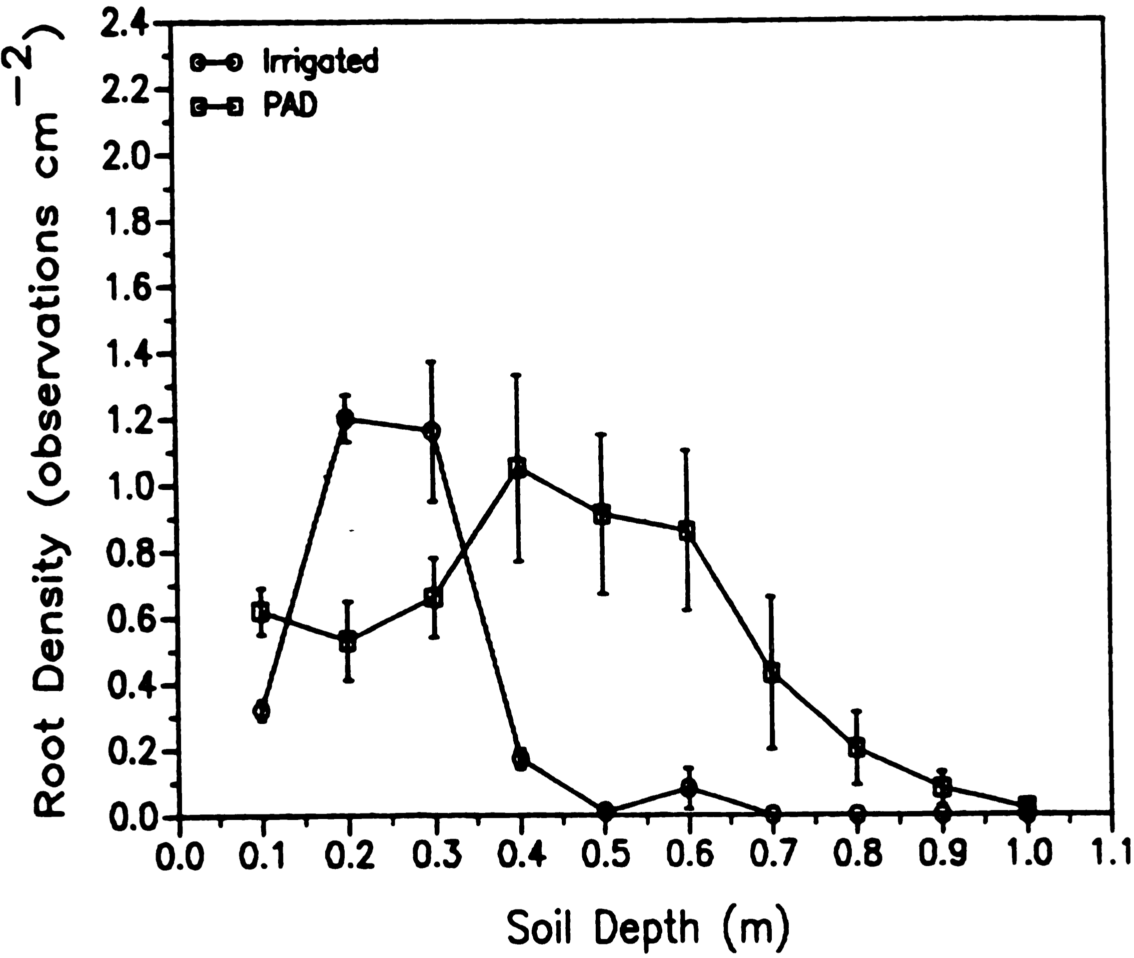

Figure 3.8b. Minirhizotron root observations for irrigated and pre-anthesis deficit plants on DOY 182 in 1988. This was during the deficit period.

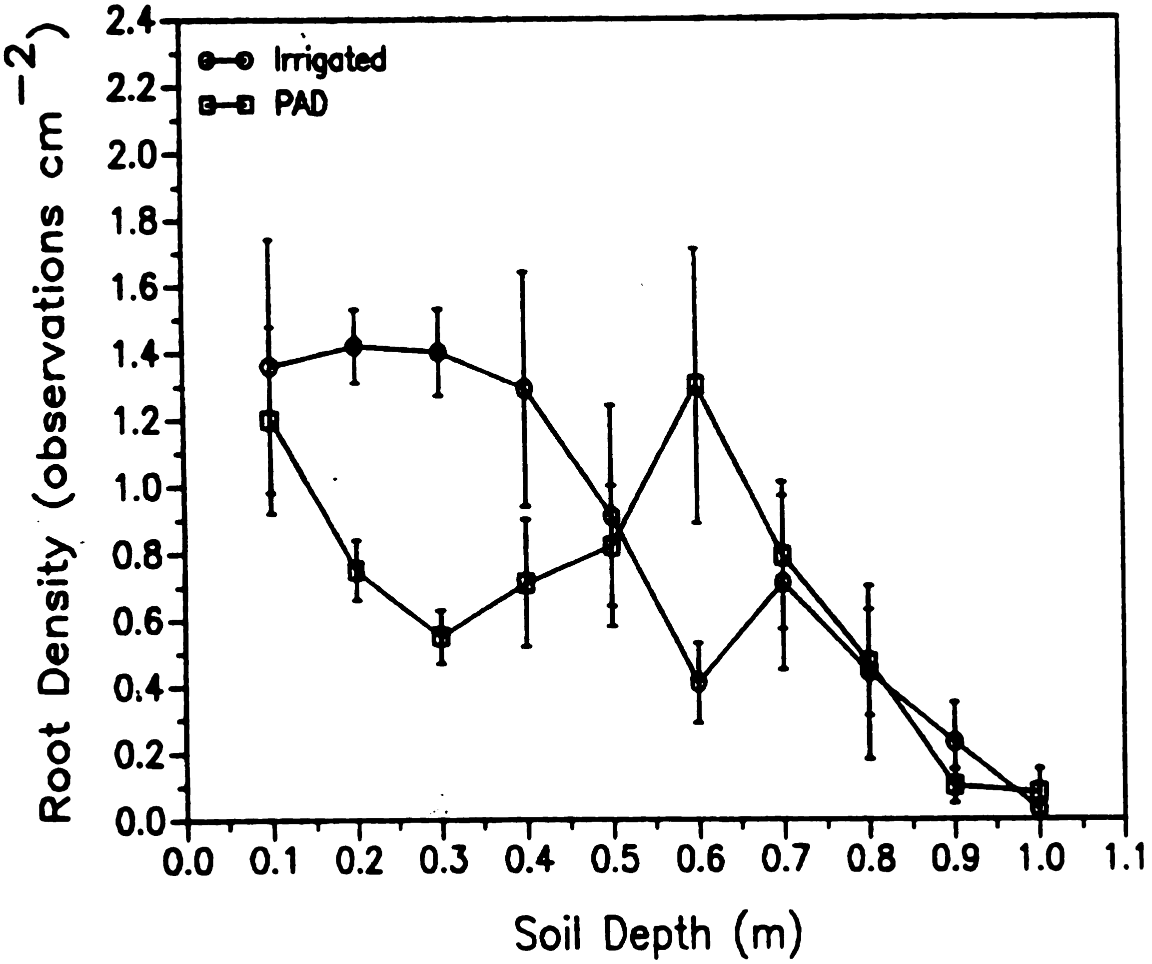

Figure 3.8c. Minirhizotron root observations for irrigated and pre-anthesis deficit plants on DOY 203 in 1988. This was after the deficit period.

observations in the upper 0.3 m of soil was present during the deficit period, along with a substantial increase in roots from 0.4 m to 0.8 m for PAD plants. Examination of the whole profile indicated a net increase in root observations for the PAD plants overall during the deficit period as compared to I plants. Thus, a greater percentage of carbon was allocated to the root system during the deficit period. This could have accounted for some of the observed differences in above ground biomass accumulation reported earlier. After the deficit period the root distribution became more similar, although, the PAD treatment still had less roots from 0.2 m to 0.3 m.

Increased root proliferation at deeper depths and decreases in the surface soil in response to water deficits has been observed by several researchers, including unpublished data of the current authors. Hoogenboom et al. (1987) demonstrated nonirrigated soybeans produced more roots at depths of 0.6 m to 1.4 m than irrigated soybeans. Mayaki et al. (1976) reported both soybeans and corn produced more roots from 0.9 m to 1.5 m under nonirrigated conditions than under irrigated conditions. They observed a 70 % reduction in corn yield with only a 25 % reduction in total root weight. Thus, the shoot to root ratio was not the same under water deficit conditions. Further, Sharp and Davies (1979) confirmed a rapid decrease in leaf extension with a simultaneous increase in root length and dry weight in response to a water shortage. These various results suggest that reports on shoot to root ratios for corn by Foth (1962) and Fairey and Daynard (1978) under more normal conditions cannot be used to estimate whole plant carbon balance under a diversity of environments and stress conditions.

Data presented thus far have indicated similar responses of water deficit plants and those experiencing nitrogen shortages. These factors cannot be considered independently, especially under field conditions. Sanchez et al. (1982) indicated that the whole-plant nitrogen uptake was sensitive to water deficits. The reduced surface rooting and water uptake under deficit conditions as described in the current study and companion papers should have had an influence on the nitrogen status of plants. Observations by the current authors over several years in the field have indicated plants suffering from pre-anthesis water deficits were also suffering from nitrogen problems. Invariably, after irrigation resumed plants would remain pale-yellow for three to four days as though there were nitrogen deficiencies. In order to evaluate this, plants were sampled in 1989 for nitrogen content on 31 July (DOY 212), which was about a week after anthesis of irrigated plants. In addition, grain nitrogen uptake was monitored through three subsequent samplings.

Figures 3.9 and 3.10 depict whole-plant nitrogen and grain nitrogen, respectively, for all treatments. There was no significant difference in percent nitrogen for the treatments other than. An exception was grain nitrogen of

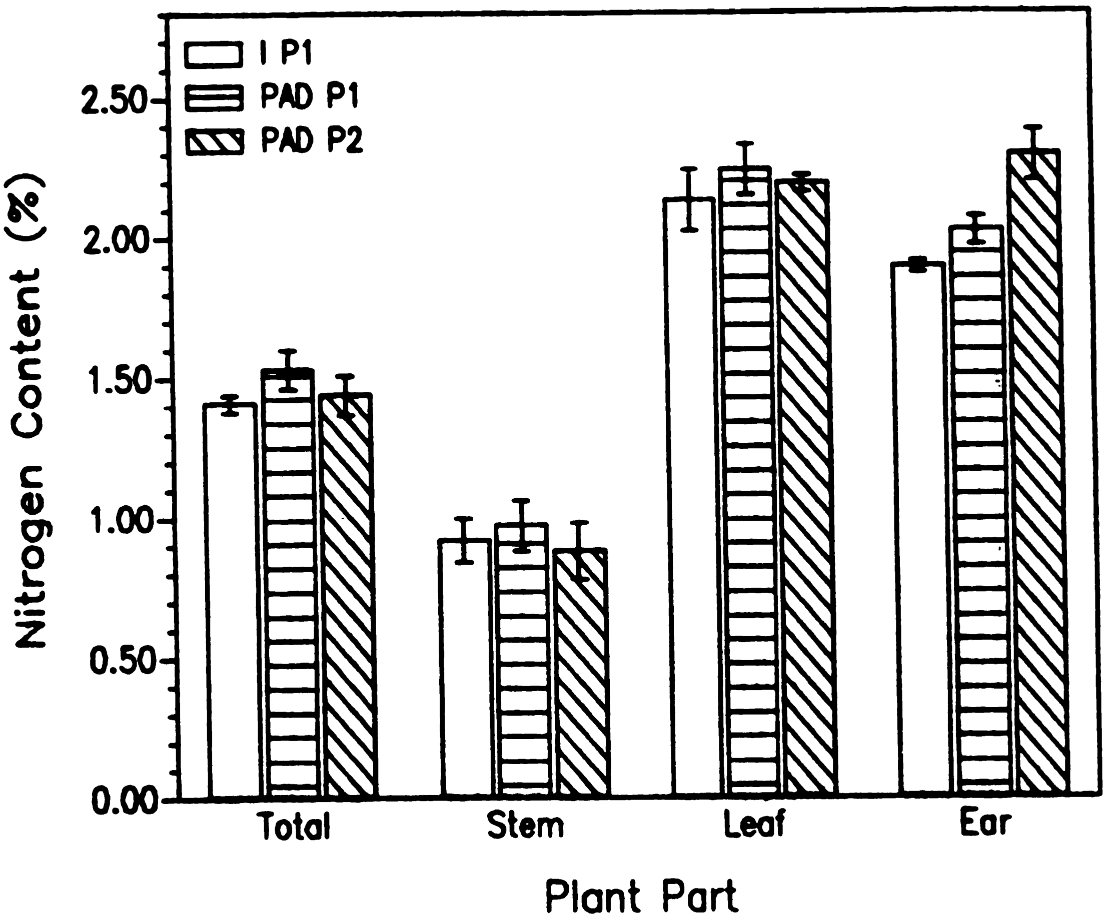

Figure 3.9. Above ground plant nitrogen content (%) and distribution in leaves, stems, and ears for all treatments on DOY 212 in 1989.

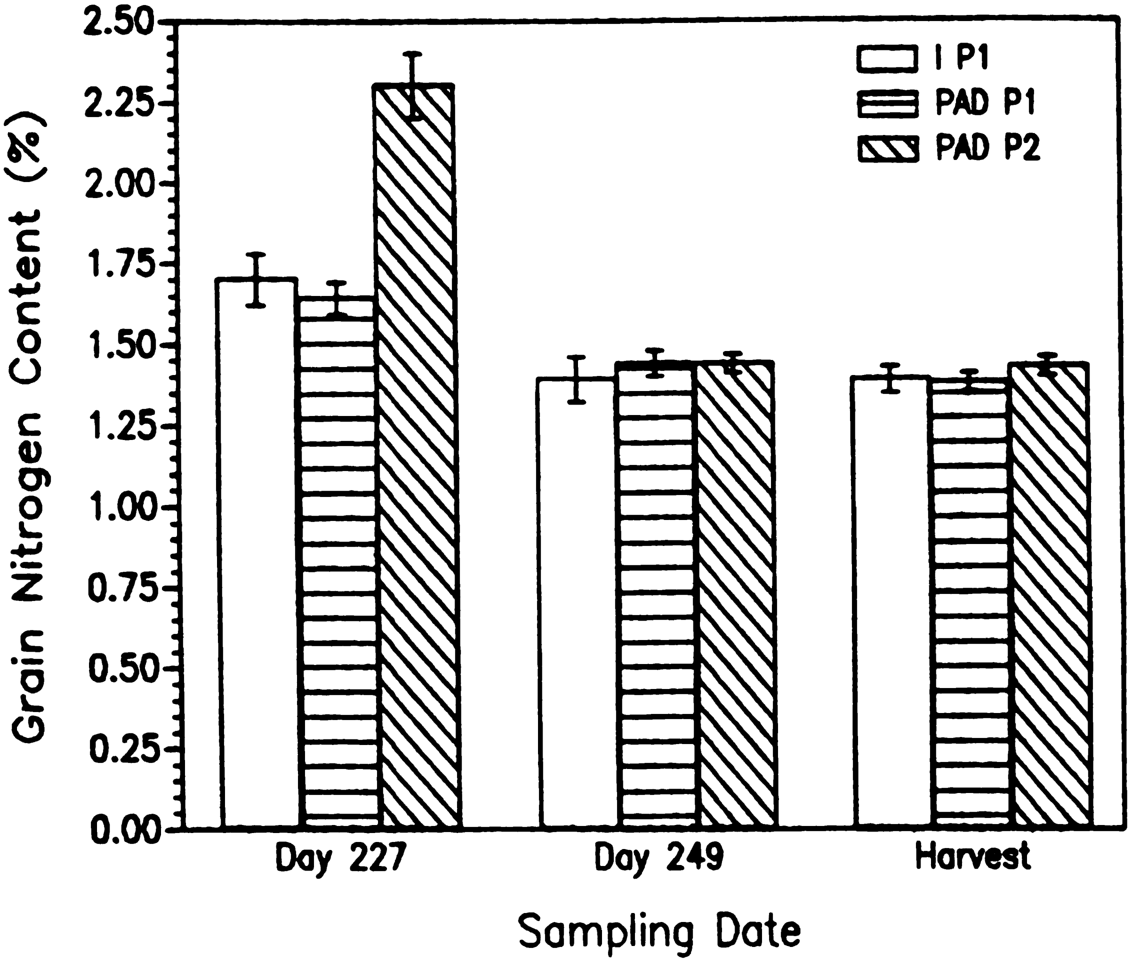

Figure 3.10. Grain nitrogen content (%) on DOY 227, DOY 249, and at harvest (DOY 270) for all treatments in 1989.

PAD P2 plants on DOY 227. Grain for this treatment on this date was small and not very developed as PAD P2 plants were the latest flowering (see NeSmith et al., 1990b). Therefore, nitrogen constituted a greater percentage of the grain dry weight. Total nitrogen by weight was dissimilar for treatments as it was proportional to the differences in biomass. The final amount of grain nitrogen (on a weight basis) was similar to that amount in the above ground portion of the plant when sampled on DOY 212. The exception was the PAD P2 treatment, which apparently had additional uptake that was to become grain nitrogen under this treatment. Again, this was the latest flowering treatment. These results compare to those of Hanway (1962b) and Friedrich and Schrader (1979) who reported that the nitrogen amount in the grain at harvest was nearly that present shortly after silking.

Wolfe et al. (1988) observed no difference in nitrogen uptake at anthesis and at the end of the growing season for water deficient and nitrogen deficient plants, although, both were different from plants which received adequate water and nitrogen. Davies et al. (1986) postulated an interactive effect between nutrient supply and root cytokinin supply on shoot growth rate. These results and those of the current study indicate that a major influence of pre-anthesis water deficits may be on the nitrogen uptake of plants, and that this has resulting effects on biomass production. Dry weight was proportional to the amount of nitrogen and so was yield and grain number as reported in a companion paper.

Hawkins and Cooper (1981) concluded from examination of several sets of data that grain number, and thus yield, of corn was determined by pre-flowering growth rate. They indicated that a static value of plant size was also correlated with grain number, however, they argued that the dynamic process of grain number determination would not be linked to such a fixed value. They further postulated that a mechanism yet determined was responsible for the influence of biomass accumulation on grain number. The current results suggest that nutrient uptake and status of plants may be linked to such a mechanism. The quantification here is not enough to merit a conclusion as to this. Additional research on water deficit influence on nutrition of plants is needed, especially in the area of nitrogen acquisition and how pre-anthesis water deficits influence this.

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CHAPTER 4

EFFECTS OF SOIL WATER DEFICITS DURING ANTHESIS ON FIELD GROWN CORN (*ZEA MAYS* L.)

ABSTRACT

Water deficits during flowering and pollination are the most devastating to yields, especially those of determinate crops such as corn. The objective of this research was to gain a clearer understanding of how intermittent soil water deficits influence emergence of tassels and silks and what the resulting effects on yield and yield components were. A rain shelter was utilized to provide timely water deficits in a field environment during 1987 and 1988 on a sandy soil in Michigan. Yield reductions in excess of 90 % occurred when a water deficit spanned the interval from floral component emergence to beginning grain fill. Delayed emergence of tassels and silks greater than two weeks was observed for some water deficit plants. Water deficit treatments that impacted plant extension growth such that emergence of tassels was delayed until irrigation resumed were less detrimental than

deficits treatments in which there was tassel exposure. Grain number was the yield component consistently reduced by the intermittent water deficits, and there was both reductions and increases in grain weight depending on the deficit severity and timing.

INTRODUCTION

Water deficits during or shortly after anthesis are considered to be among the most devastating to grain yields, especially for determinate species such as corn (Begg and Turner, 1976). Consistent observations of yield reductions in excess of 50 % have been reported for several experiments using plants grown in containers, and grain number has been the primary component affected (Claassen and Shaw, 1970; Denmead and Shaw, 1960; Grant et al., 1989; Hall et al., 1981). The lack of grain number due to water shortages during flowering has been attributed, in part, to poor synchronization in emergence of male and female flower components (Freier et al., 1984; Hall et al., 1982; Herrero and Johnson, 1981).

Field water deficit experiments are difficult to conduct in more humid regions due to the untimeliness of rain. However, field research is needed in order to verify responses of crops grown in container systems. Rain shelters along with controlled water applications can reduce precipitation interferences and provide judicious scheduling of crop water supply in field environments (Foale et al., 1986; NeSmith et al., 1989; Upchurch et al., 1983). The objective of the experiments reported here was to utilize a rain shelter to impose soil water deficits during anthesis of corn and determine the influence on flowering, yield, and yield components.

MATERIALS AND METHODS

This research was conducted during 1987 and 1988 at the Kellogg Biological Research Station near Kalamazoo, Michigan, USA. Corn was grown in an area that could be covered by a rain shelter when needed. This facility has been described elsewhere by Martin et al. (1988). The soil was a Spinks sand (sandy, mixed, mesic Psammentic Hapludalf). Figure 4.1 illustrates the water content of the soil profile after near saturation followed by three days of drainage and after more than forty days of drying by a corn crop with no additions of water. The rain shelter did not cover plots from September to April each year, and as a result the soil water profile was near the drained status at the beginning of the growing season because of snow and rain.

During 1987 a completely randomized experimental design with two replications was used. Great Lakes hybrid 599 was planted in 4.3 m x 6.2 m plots on 12 May (day of year,

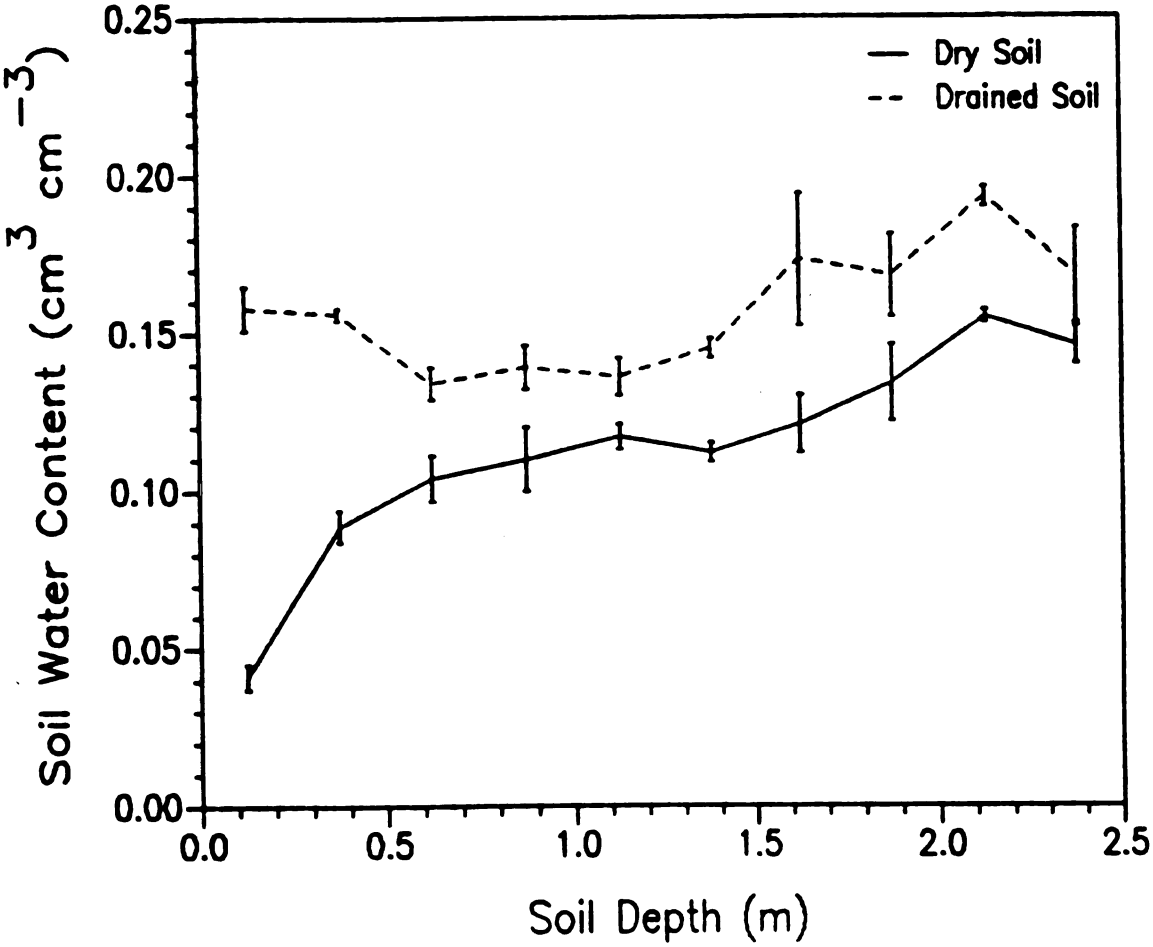

Figure 4.1. Soil water content of a Spinks soil at different depths after saturation followed by three days drainage and after more than forty days of drying by a corn crop.

DOY 132) in 0.71 m rows at a depth of 0.05 m. The plants emerged on 17 May and were thinned two weeks later to a population of 8.3 plants m^{-2}. Fertilizer applied at planting was at a rate of 15 kg ha^{-1} N, 60 kg ha^{-1} K, and 15 kg ha^{-1} P. Additional nitrogen was applied at a rate of 120 kg ha^{-1} N and 90 kg ha^{-1} N on 24 June and 1 July, respectively. Irrigation regimes of the various treatments were as follows:

Treatment 1 - Irrigated as depicted in Figure 4.2.
Treatment 2 - Not irrigated between 11 July (DOY 192) and 23 July (DOY 204).
Treatment 3 - Not irrigated between 11 July (DOY 192) and 30 July (211).
Treatment 4 - Not irrigated between 11 July (DOY 192) and 17 August (DOY 229).

Treatments 2 through 4 received an initial 40 mm of water when irrigation resumed. Other than this one application the irrigation schedule of treatment 1 was followed for these treatments except during the deficit period. On 5 October, 1987 a 6.5 m^2 area was harvested for each plot. Plants with and without ears were counted to determine barrenness. Yield was calculated on a per plant basis from a composite sample, and yield components were determined from a subsample of ears. These ears were oven dried at 60 °C and grain was removed manually, after which it was weighed and grain number was counted.

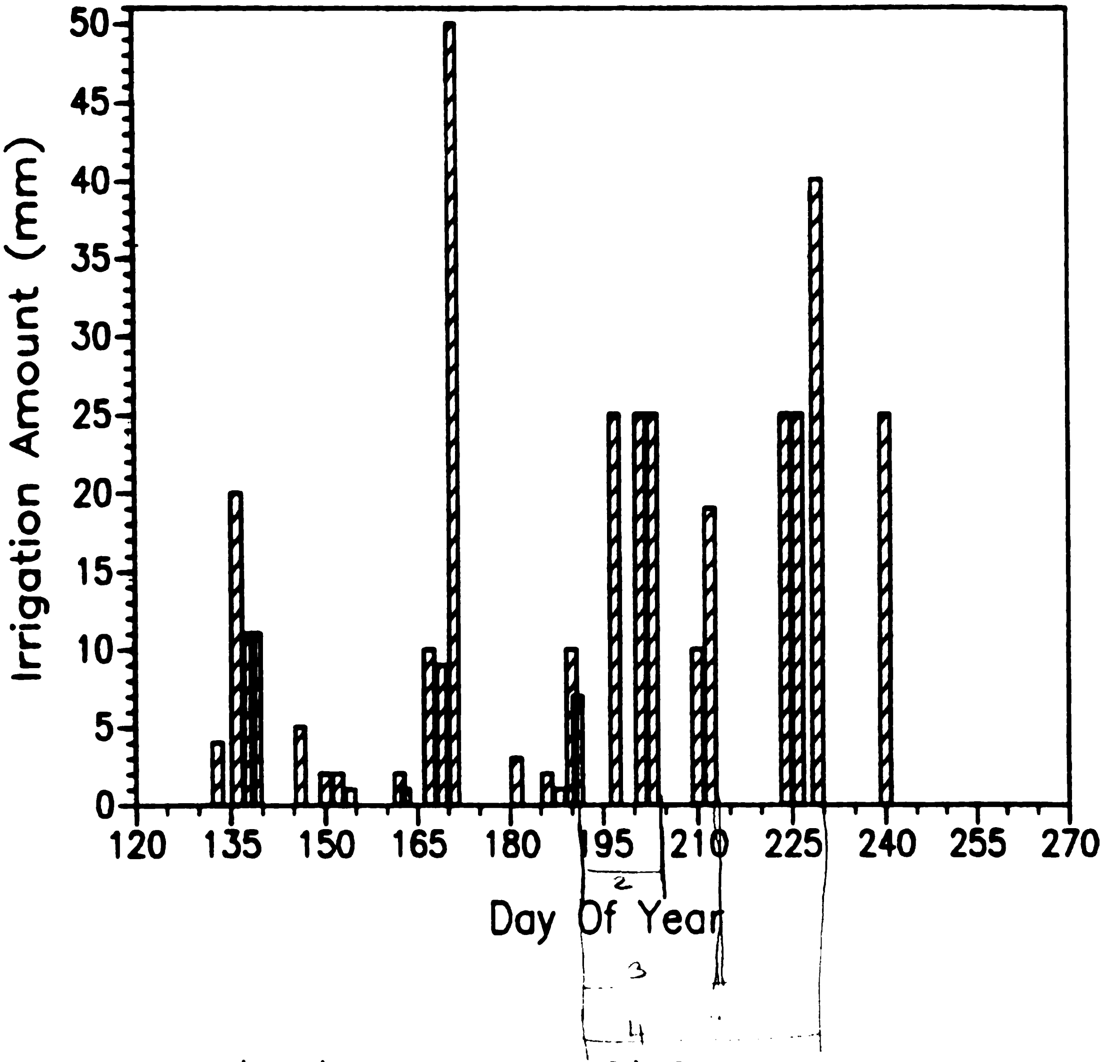

Figure 4.2. Irrigation amounts applied to treatment 1 during 1987.

During 1988 a completely randomized split-plot experimental design with one replication was used in which water regime was the main plot and corn cultivar was the sub-plot. Main plot size was 4.3 m x 6.2 m. Pioneer corn hybrids 3540 and 3475 were planted at a higher than desired density on 5 May (day of year, DOY, 126) in 0.71 m rows at a depth of 0.05 m. These hybrids were chosen because there had been some observed differences between them in response to drought during certain years but not others. Part of this investigation was to determine potential reasons for such variability. Emergence occurred on 15 May, and plants were thinned to a population of 7.9 plants m^{-2} on 25 May. Fertilizer applications were 150 kg ha^{-1} K on 20 April, 60 kg ha^{-1} N on 25 May, 300 kg ha^{-1} P and 160 kg ha^{-1} N on 6 June, and 75 kg ha^{-1} N on 15 July. There were two water regimes, an irrigated control (I) and a flowering water deficit (FD). Water applications were the same for treatments except during the deficit period (Figure 4.3).

Plant measurements during 1988 included silking determination which was made on eight sample plants per plot. Silking was declared as the day when there were any visible silks for a respective plant. A compound measurement of elongation of husks, shanks, and ears (referred to as intact ear length) was determined for the eight sample plants. A point of reference was marked on a stem at the node just above where an ear was attached to the plant, and length was

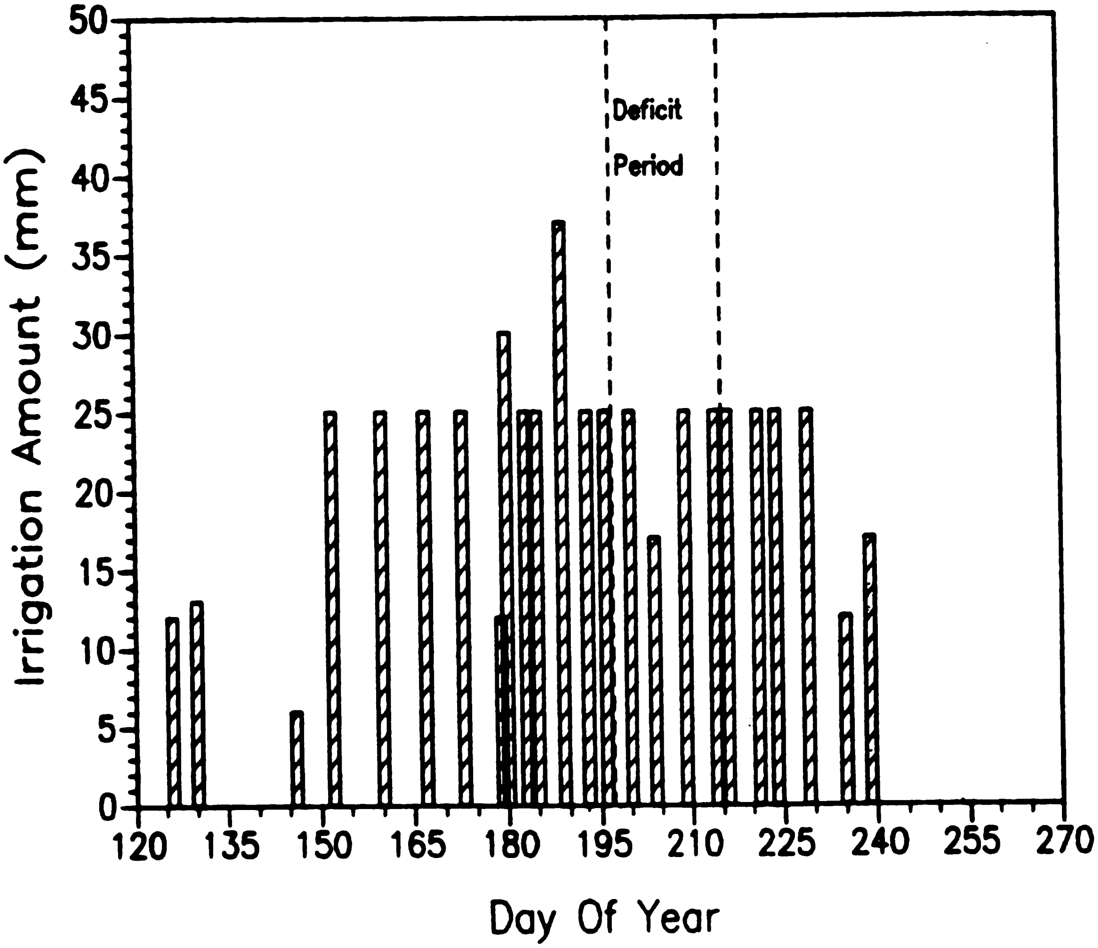

Figure 4.3. Irrigation amounts applied to treatments during 1988. The region between vertical dashed lines represents the period when no water was applied to flowering deficit (FD) treatment.

determined by recording the distance between the reference point and the tip of the visible husk. On 19 September 1988, four plants were harvested in each sub-plot from which yield, grain number, grain weight, and harvest index were determined. Ears and plants were separated and were placed in an oven at 60 °C for four days. After drying, grain was removed from each ear manually and was weighed and grain number counted. Barren plant number was determined in each plot from the entire population.

Soil water content was measured during 1988 using the neutron scattering technique. Sampling was in 0.25 m increments to a depth of 1.5 m, and there was one access tube in the center row of each sub-plot. Measurements began during mid-vegetative growth and were taken one or two times weekly. The water content during the deficit period was plotted and a line fitted through the data for each sampled depth. The slope of this line was taken as water absorption rate, assuming negligible flow.

RESULTS AND DISCUSSION

Table 4.1 depicts results from the 1987 experiment. The water deficits began just before tassel emergence of treatment 1 plants. Cessation of extension growth of deficit plants caused delayed tassel and silk emergence. When irrigation resumed for treatments 2 and 3 emergence of tassels and silks

Table 4.1. Silking date, yield, grain number, grain weight, and percent barren plants for treatments during 1987.

	Treatment Number			
	1	2	3	4
75 % Silking (Day of Year)	201	207	213	--- +
Yield * (gms plant^{-1})	88 (7.7)**	69 (7.5)	46 (6.4)	26 (8.8)
Grain Number per Ear	452 (33.7)	362 (25.8)	194 (24.9)	105 (18.4)
Grain Weight (mg seed^{-1})	194 (6.6)	190 (9.6)	238 (12.8)	244 (52.1)
Barren Plants (%)	7	8	4	80
Yield Based on Land Area *** (kg ha^{-1})	8039	6235	4338	511

\+ This treatment never achieved 75 % silking.

* Only plants with ears were used to calculate.

** Values in parenthesis () are standard errors of means with n = 10 except treatment 4 where n = 6.

*** Calculated as 15.5 % moisture.

occurred within 2 to 3 days. Treatment 4 was under deficit conditions long enough that only a few plants eventually flowered prior to resuming irrigation. When irrigation resumed for treatment 4 tassels and silks emerged rapidly as with other treatments, yet there was little pollen produced by the tassels of these plants. Less than 50 % of the treatment 4 plants produced any silks. Delayed silk emergence of 1 to 8 days has been reported by other researchers in response to water deficits during or just prior to anthesis (Grant et al., 1989; Herrero and Johnson, 1981; Hall et. al., 1981; Robins and Domingo, 1953; Vincent and Woolley, 1972). As with the current study, the length of the delay in these experiments depended on the duration and degree of the deficit.

Although treatment 1 was irrigated the most, it did not receive as much water as it needed due to problems with the irrigation system. Therefore, its yield was less than that observed for this and other cultivars under well-watered conditions in other years. Irrigated corn yields have averaged around 110 gms plant^{-1} on this soil at the plant population and fertilizer rates used. Yield losses due to delayed flowering can be determined from these data, however. Reductions in yields for treatments 2 and 3 on a per plant basis were 22 % and 47 %, respectively, as compared to treatment 1. This corresponded to 6 and 12 day delays in silking for these treatments. Treatment 4 resulted in 80 %

barren plants, and even those with ears had drastic yield reductions. Calculations on a land area basis for treatment 4 showed more than a 90 % reduction in yield as compared to treatment 1.

Grain numbers during 1987 were reduced for the deficit treatments relatively proportional to the delayed flowering. This was not the case with grain weights. Average grain weights for treatment 2 was not different than that of treatment 1, however, treatments 3 and 4 had increased weights of 25 %. The increased weights for the late flowering treatments were somewhat of a compensation for the excessively low grain numbers. These results agree with those of several aforementioned investigations in that grain number was the most affected parameter by the water deficits.

Results from the 1988 experiment differed somewhat from those of the 1987 experiment. The water deficits hastened beginning silk emergence slightly for both hybrids, however, 3540 FD plants did not exceed 75 % silk emergence until irrigation resumed (Figure 4.4). These influences on silking were due to the developmental stage at which deficits caused stress in the FD plants. The plants for 1988 overall were closer to anthesis when the deficit began than were those in 1987, and hybrid 3475 was closer to anthesis than hybrid 3540 when the deficit began in 1988.

Intact ear measurements demonstrated results similar to that of silking data for 1988 (Figure 4.5). Ear growth was

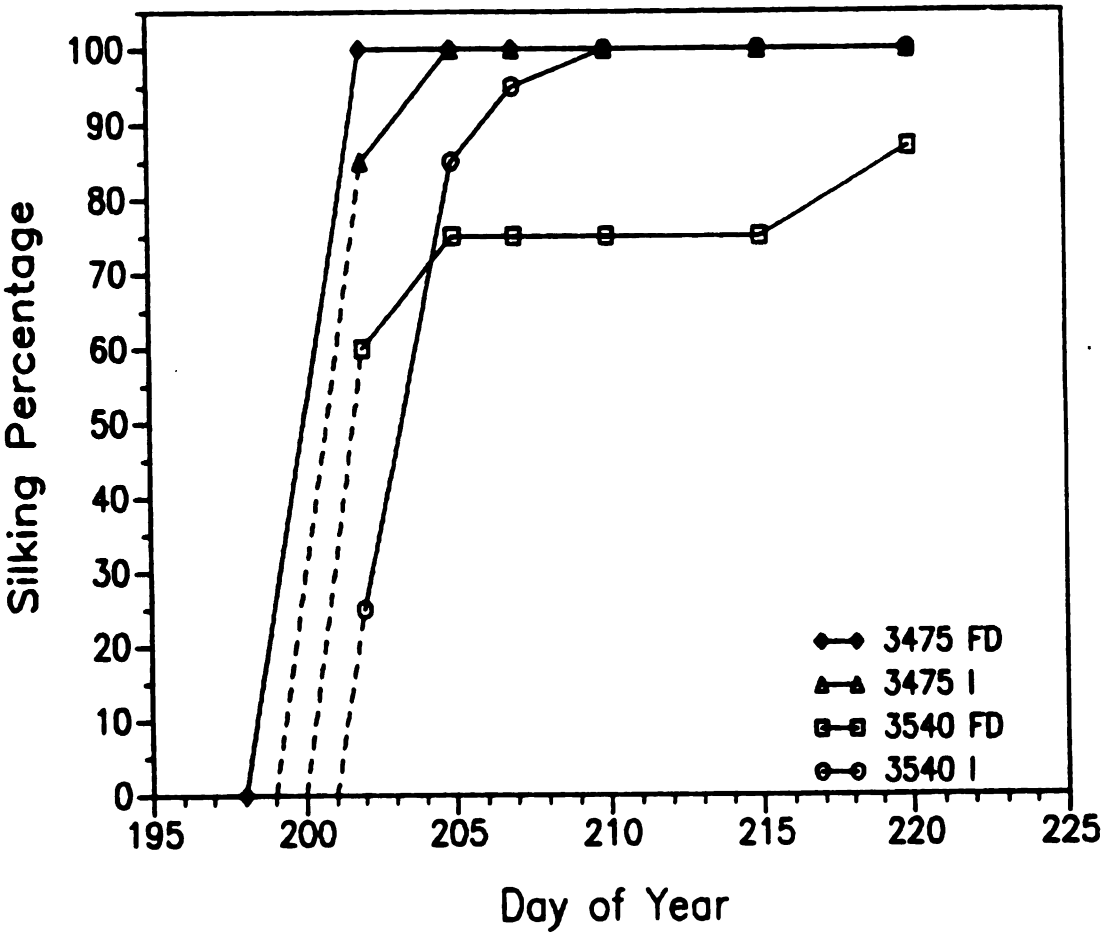

Figure 4.4. Silking percentage of treatments as a function of time during 1988.

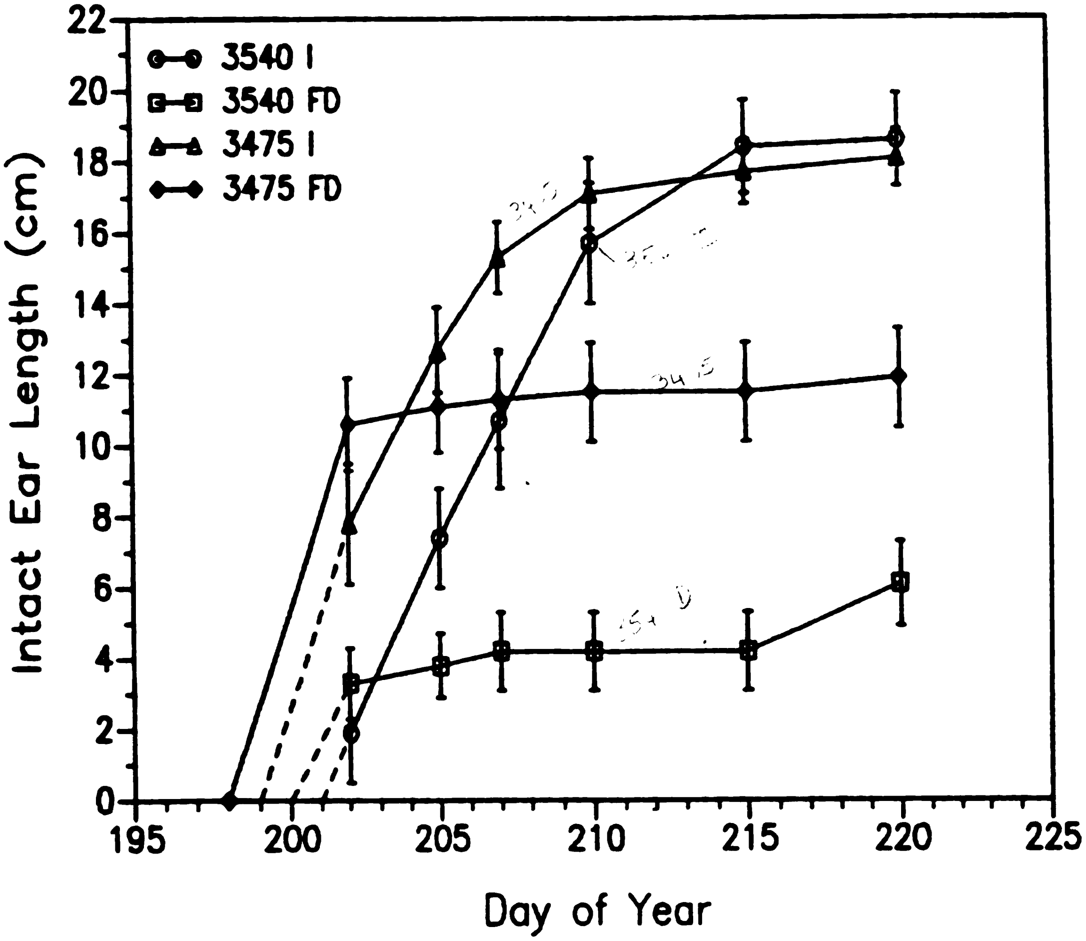

Figure 4.5. Intact ear length of treatments as a function of time during 1988.

greater for 3475 FD plants than for 3540 FD plants as the latter treatment was just beginning rapid ear elongation when the water shortage caused extension growth reductions. These results indicate the importance of considering developmental stage of the plants in conducting water deficit experiments, especially when comparing different cultivars. It is imperative that even slight differences in development be accounted for.

Water absorption rates at different soil depths for FD treatments during the deficit period of 1988 are depicted in Figures 4.6a and 4.6b. There was a rapid decline in water absorption rate at the 0.00 m to 0.25 m depth paired with a slight increase at the 0.25 m to 0.50 m depth shortly after water was withheld. Water absorption rates at the other measured depths remained nearly constant. Figure 4.7 demonstrates that transpiration was sustained by water absorption from the upper 1.5 m of soil until around DOY 203. The magnitude of the water deficit can be determined by comparing these results with those of another experiment (NeSmith et al., 1990) in which plant extension growth essentially ceased when the surface soil water absorption rate reached a value of 3 (water absorption rate units).

Table 4.2 depicts harvest data for the 1988 experiment. The harvest index values reflected there were large plants with small ears under deficit conditions indicating there was no appreciable influence on vegetative growth. Yield

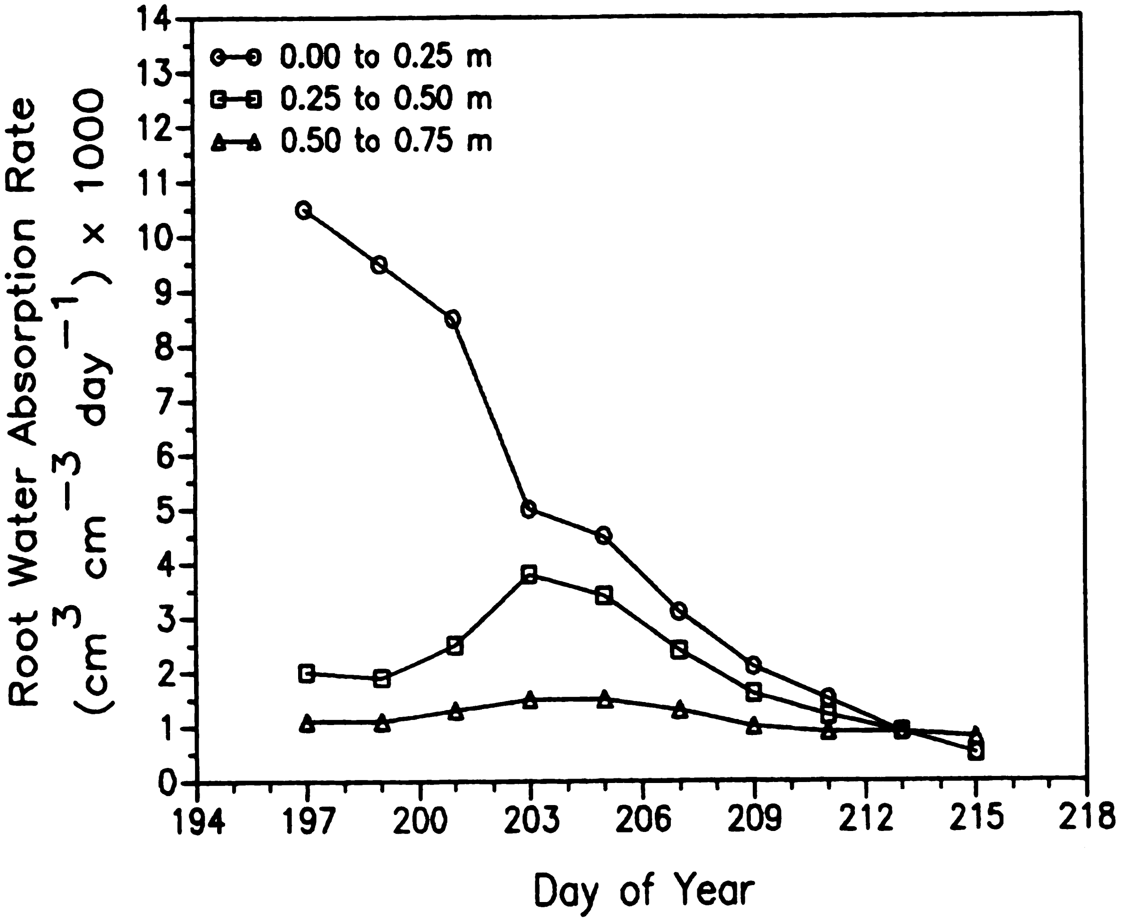

Figure 4.6a. Water absorption rates at depths of 0.00 to 0.25 m, 0.25 to 0.50 m, and 0.50 to 0.75 m during the deficit period for the flowering deficit treatment during 1988.

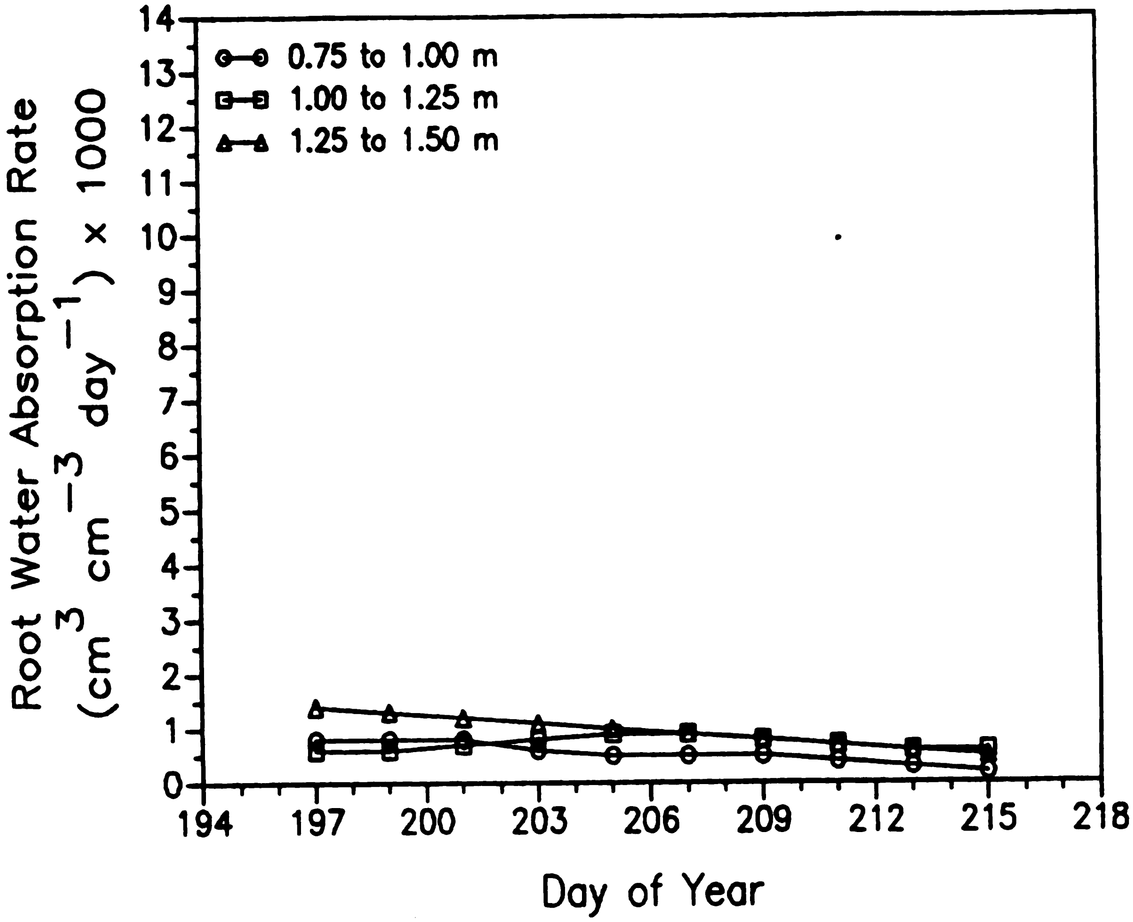

Figure 4.6b. Water absorption rates at depths of 0.75 to 1.00 m, 1.00 to 1.25 m, and 1.25 to 1.50 m during the deficit period for the flowering deficit treatment during 1988.

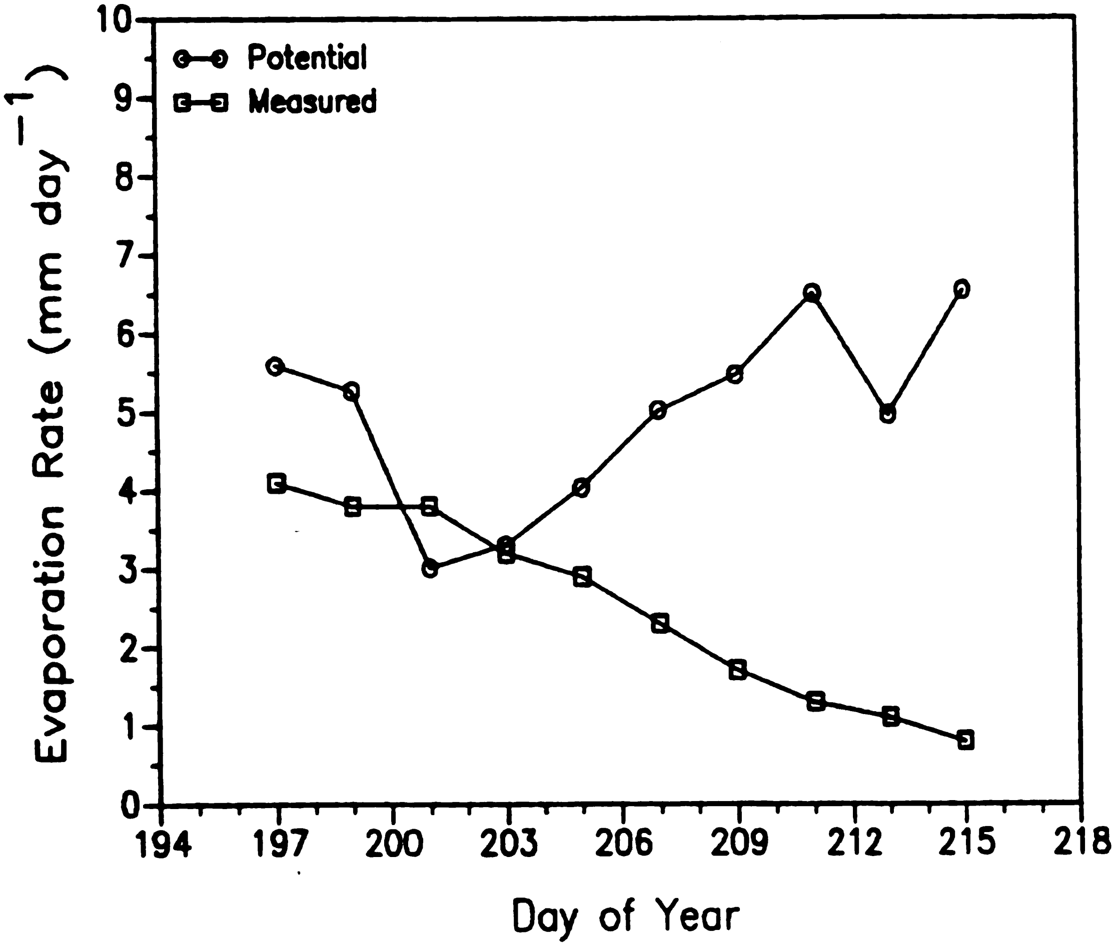

Figure 4.7. Potential evaporation and measured total water absorption from the 1.5 m soil profile during the deficit period for the flowering deficit treatment during 1988.

Table 4.2. Grain yield, grain number, grain weight, percent barren plants, and harvest index for treatments during 1988.

	Treatments			
	3540 I	3540 FD	3475 I	3475 FD
Grain Yield ($gms\ plant^{-1}$)	128 (11.9)*	29** (10.0)	115 (6.4)	38** (11.1)
Grain Number per Ear	469 (40.4)	176** (58.6)	519 (69.4)	287** (86.1)
Grain Weight ($mg\ seed^{-1}$)	272 (8.0)	165** (14.5)	222 (31.0)	133** (22.1)
Barren Plants (%)	0	15	0	40
Yield Based on Land Area ($kg\ ha^{-1}$) ***	11,967	2305	10,751	2132
Harvest Index	0.56	0.24**	0.53	0.32**

* Values in parenthesis () are standard errors of means with n = 4.

** Only plants with ears were used in this calculation.

*** Calculated as 15.5 % moisture.

reductions for FD treatments as compared to their respective controls were similar to the reductions caused by treatment 4 during 1987. On an area basis yields were 80 % less for the FD treatments. Both grain number and average grain weight were reduced. This was due to the deficit extending into the grain filling period which has been shown to be a time when grain weights are most reduced by stress (Grant et al., 1989; Jurgens et al., 1978; NeSmith and Ritchie, 1990; Westgate and Boyer, 1985).

Evaluation of results from these two experiments indicate that flowering is indeed a critical time in which to avoid water deficits. However, there were more drastic effects on plants when deficits were experienced during the time when tassels and silks were exposed, or when emergence of these was delayed for more than two weeks. If deficits were prior to emergence of tassel and silks such that these were delayed, there was some benefit. This may be linked to increased pollen survival under deficit conditions if the tassel is not exposed to atmospheric conditions. Further research in this area would be beneficial.

In summary, results have shown that yield reductions in excess of 90 % can be caused by water deficits in a field environment during the flowering period in corn. Delayed emergence of tassels and silks in excess of two weeks was observed. Grain number was the most reduced yield component when water shortages were confined to the fertilization and kernel setting period, however, if the deficit was extended into the grain filling period average grain weight was reduced as well. Results indicate that managing irrigation in a manner that would obtain maximum kernel set through avoidance of water deficits is necessary to maintain favorable yields as grain weight compensation is insufficient to off-set loss of grain numbers.

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CHAPTER 5

CORN (ZEA MAYS L.) RESPONSE TO AN INTERMITTENT SOIL WATER DEFICIT DURING GRAIN FILLING

ABSTRACT

Grain filling is an important growth period to the economical yield of many crops including corn. Rate and duration of filling are the two basic components determining final grain weight, and any alteration of these can be detrimental to final yield. Research was conducted during 1989 in Michigan utilizing a large rain shelter to impose an intermittent soil water deficit during the grain filling period of two commercially grown corn hybrids. Objectives were to determine the influence on crop and grain growth, rate and duration of grain filling, grain numbers, grain size distribution, and final yield as compared to an irrigated control. Two planting dates and two hybrids provided a range in the development stage at which deficits were imposed. Results demonstrated deficit plants had less green leaf area during grain filling, along with reduced crop and grain growth. Crop growth rate was reduced as much as 67 %, whereas grain growth rate reductions were only about 30 % for deficit plants as compared to irrigated control plants. Continuous single grain samples showed duration of the linear grain filling phase was shortened by as much as 8 days due to the water shortages depending on the hybrid and planting date. One hybrid had reductions in rate of single grain filling of 14 % to 24 % and the other was unaffected for this parameter. Yield reductions were observed by all treatments experiencing water deficits and were as great as 40 % loss. Examination of grain size distributions showed a larger percentage of seeds weighing less than 100 mg were on ears of deficit plants along with fewer seeds in the range greater than 200 mg. Percent nitrogen of the grain was not affected by the paucity of water, but absolute grain nitrogen was. These results lend to the importance of managing crop water supply through irrigation when available in order to avoid water deficits from flowering until linear grain filling so that maximum kernel numbers can be achieved.

INTRODUCTION

The period of grain filling is important to the overall economic yield of grain crops. Johnson and Tanner (1972b) described three distinct stages in the grain filling process of corn following pollination. These stages were i) a lag period at the beginning, ii) a linear dry matter accumulation period, and iii) a leveling off period as maturity approached. The second stage is commonly referred to as the effective grain filling period and is considered the most important to final yield. Duncan (1975) suggested that a simple way to think of grain yield was to view it as a product of the rate of photosynthesis during the grain filling period multiplied by the duration of the period, plus the change in labile reserves, with grain sink as the upper limit. He pointed out that this was not entirely correct when the periods of slow growth (lag and leveling off stages) were considered. In any case, factors influencing rate, duration, or kernel capacity impact grain yield.

Several investigations have centered on whether source (current and stored photosynthates) or sink (kernel number and filling capacity) limit yield the most during the grain filling period with mixed results reported (Barnett and Pearce, 1983; Egharevba et al., 1976; Frey, 1981; Hanway, 1969; Jones and Simmons, 1983; Tollenaar and Daynard, 1978a and 1978c). In a review on the subject Tollenaar (1977) indicated that both sink and source limitations occur and that combinations of genotypes and environmental conditions determines the dominant one. An important environmental factor at any crop growth stage is water supply.

Denmead and Shaw (1960) reported a soil water shortage during the grain filling period caused a 21 % decrease in yield, and Claassen and Shaw (1970) observed a 30 % yield reduction in response to a water deficit three weeks after silking. Jurgens et al. (1978) imposed a terminal drought stress 10 days after silking and noticed a 58 % yield reduction with 48 % of the loss due to lower grain weight. Westgate and Boyer (1985) withheld water from plants at early grain filling (lag stage) and at mid-grain filling and found yield decreases of 82 % and 36 % for the treatments, respectively. Grain weight and number were reduced by the early deficit, whereas only grain weight was reduced by the mid-grain fill deficit. Grant et al. (1989) determined that water shortages 16 to 22 days after silking decreased grain yield 65 % with a 13 % decrease in grain number and a 48 % decrease in grain weight. When the deficit occurred 22 to 26 days after silking, yield reductions were 47 % and were attributable entirely to lower grain weight. These various experiments were with container grown plants and generally one cultivar was monitored.

In a field experiment with a single cultivar, Robins and Domingo (1953) observed a 31 % decrease in yield for a treatment in which no irrigation was applied after tasseling when compared to one which received three post-anthesis irrigation applications. Investigations involving defoliation of plants in the field during or shortly after silking have shown that yields were often reduced similarly to the aforementioned container water deficit experiments with components responsible being grain size and/or grain number depending on the hybrid as well as timing and severity of leaf removal (Barnett and Pearce, 1983; Egharevba et al., 1976; Frey, 1981; Hanway, 1969; Tollenaar and Daynard 1978c). Grain weight reduction due to defoliation stress has been attributed to decreased rate of filling, shortened duration of filling, and combinations of both (Hanway, 1969; Jones and Simmons, 1983; Tollenaar and Daynard, 1978c). Decreased grain numbers have been determined to result from cessation of development of fertilized kernels caused by stress during the early stages of grain filling (Frey, 1981; Kiniry and Ritchie, 1985).

Field water deficit experiments are difficult to conduct in humid regions due to the untimeliness of rain. This is especially true when drought during a specific growth stage is desired. Rain shelters, which reduce the risk of precipitation interferences, and controlled water applications can provide judicious scheduling of crop water supply in field environments (Foale et al., 1986; NeSmith et al., 1989; Upchurch et al., 1983). The objective of this experiment was to utilize a rain shelter to impose an intermittent soil water deficit during grain filling of corn and to determine what influence there was on crop and grain growth rate, rate and duration of grain filling, grain numbers, grain size distribution, and final yield. Two hybrids and two planting dates provided a range of times during grain filling when drought occurred.

MATERIALS AND METHODS

This research was conducted during 1989 at the Kellogg Biological Research Station near Kalamazoo, Michigan, USA. Corn was grown in an area that could be covered by a rain shelter. This facility has been described elsewhere by Martin et al. (1988). The soil was a Spinks sand (sandy, mixed, mesic Psammentic Hapludalf). Figure 5.1 illustrates the water content of the soil profile after near saturation followed by three days of drainage and after more than forty days of drying by a corn crop with no additions of water. The rain shelter did not cover plots from September to April each year, and as a result the soil water profile was near the drained status at the beginning of the growing season because of snow and rain.

A completely randomized split-plot experimental design was used in which water regime and planting date was the main plot and corn cultivar was the sub-plot. There were two replications of each treatment. Pioneer corn hybrids 3540 and 3475 were used in this investigation because there had been some observed differences between them in response to drought during certain years but not others. There were two planting dates. The reason for this was that there was a difference in leaf number of one leaf between the two cultivars during a 1988 experiment. It was hypothesized that this could be linked to some of the differences in observed responses to

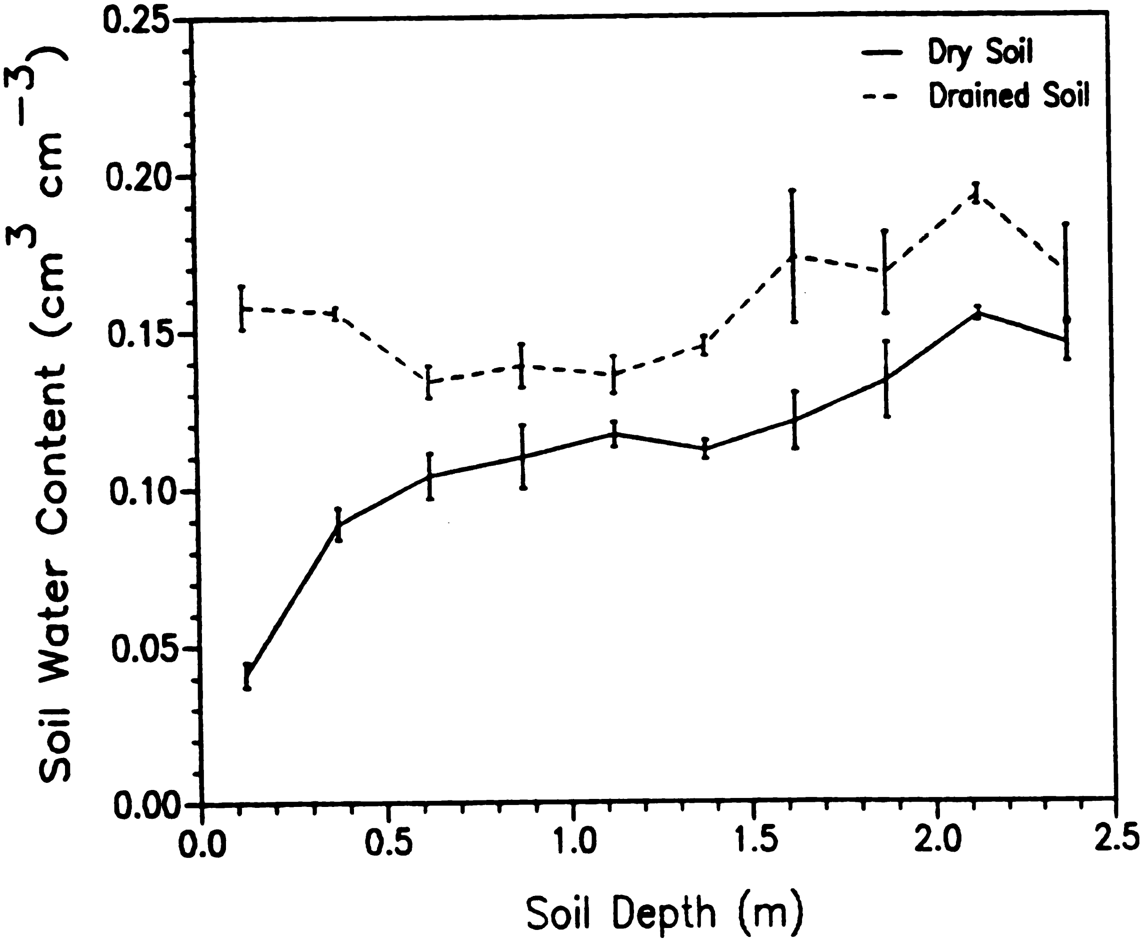

Figure 5.1. Soil water content of a Spinks soil at different depths after saturation followed by three days drainage and after more than forty days of drying by a corn crop.

drought, as plants would have been at different developmental stages during a water deficit period (e.g. hybrid 3475 flowered 2 to 3 days before hybrid 3540). It was planned that 50 degree days (°Cd) would elapse between the first and second planting dates to provide a thermal time separation in order to have hybrid comparisons of plants nearer in development (i.e. the second planting date of hybrid 3475 would be similar in tasseling and silking to the first planting date of hybrid 3540). Water deficits were imposed at the same time for both planting dates.

Plot size was 4.3 m x 6.2 m, row width was 0.71 m, and seeding depth was 0.05 m. Planting dates were 3 May (DOY 123, this will be referred to as P1 indicating first planting) and 17 May (DOY 137, this will be referred to as P2 indicating second planting) which were separated by 64 °Cd (Figure 5.2). Emergence occurred on 18 May and 25 May, and plants were thinned on 26 May and 30 May for P1 and P2, respectively to a population of 7.9 plants m^{-2}. Fertilizer was applied at a rate of 63 kg ha^{-1} N, 230 kg ha^{-1} P, and 63 kg ha^{-1} K at planting. Additional fertilizer applications for P1 and P2 were 96 kg ha^{-1} N on 1 June, 53 kg ha^{-1} N on 23 June, and 45 kg ha^{-1} N on 20 July. Weeds were controlled manually. There were two water regimes, an irrigated control (I) and a grain filling water deficit (GFD). Water applications were the same for treatments except during the deficit period (Figure 5.3). The GFD began on DOY 217 and ended on DOY 236. This

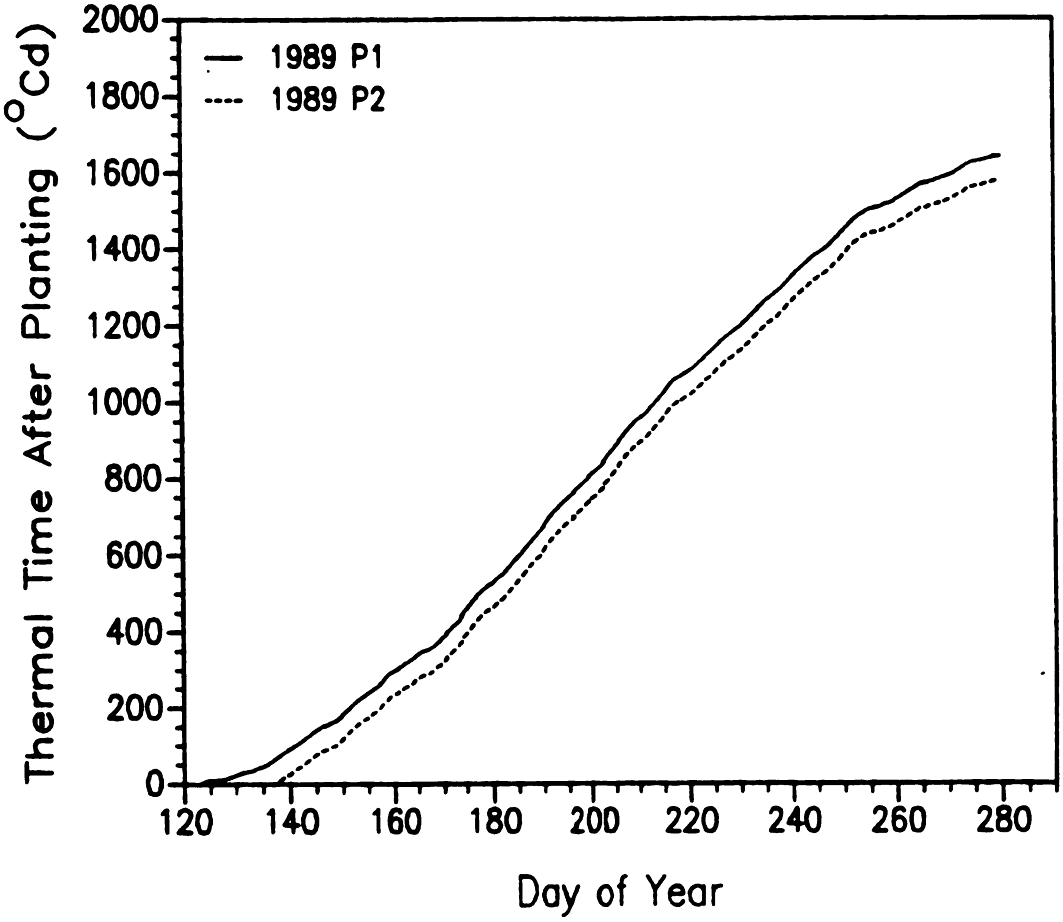

Figure 5.2. Thermal time accumulation during 1989. There were two planting dates (P1 and P2). Units were calculated using 8 °C as base temperature.

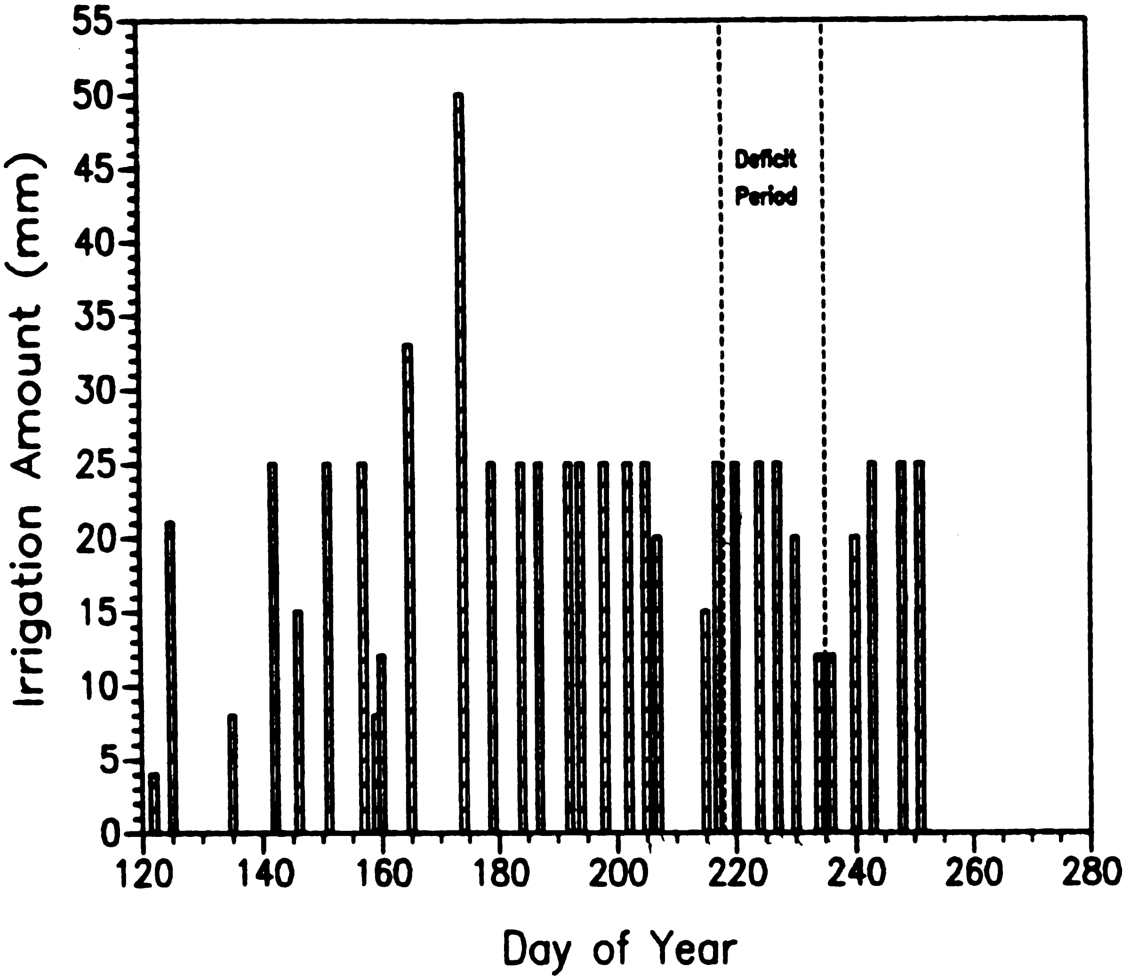

Figure 5.3. Irrigation amounts applied to treatments. The region between vertical dashed lines represents the period when no water was applied to grain filling deficit (GFD) treatments.

corresponded to 1055 °Cd and 1273 °Cd for the first planting date and to 991 °Cd and 1209 °Cd for the second planting date.

Four sample plants per plot were selected for nondestructive measurements one month after planting. Leaf area was determined two or three times weekly beginning with the fourth leaf. Leaf length, taken as the distance from the uppermost leaf ligule to the tip of a growing leaf, was multiplied by the maximum exposed leaf width, and 75 % of this product was assumed to approximate the area of an individual leaf (see Johnson and Tanner, 1972a; Linvill et al., 1978). Leaf area was considered maximum when its respective leaf ligule appeared. Silking was determined on ten random plants every two or three days until it was complete. Silking was declared for a respective plant when any silks were visible.

Biomass for the above ground portion of the plants was determined several times during the growing season by a combination of nondestructive estimates and destructive sampling. Leaf and stem biomass (LFBIOM and STMBIOM) were calculated from plant leaf area (PLA) and height to top leaf ligule (LIG) for the period from DOY 166 to DOY 187 using the following equations:

$$\text{LFBIOM} = 6.15 \times 10^{-3}(\text{PLA}) - 2.83; \quad r^2 = 0.94 \qquad [1]$$

$$\text{STMBIOM} = 3.02 \times 10^{-1}(\text{LIG}) + 0.89; \quad r^2 = 0.87 \qquad [2]$$

Leaf biomass was for visible blades and sheathes only. The stem biomass included leaves which had not emerged from the whorl of the plant, as well as internodes. Beginning DOY 195, biomass was obtained by harvesting four plants per treatment and oven drying them at 60 °C until no further weight loss occurred (usually 4 to 5 days). Prior to drying individual plants were separated into leaves (blade and sheath included), stems, husks-silks-cobs, and grain on each sampling date. Crop growth rate (CGR) and grain growth rate (GGR) were calculated from the derivative of smooth fitted lines. Nitrogen content of plants sampled on 31 July (DOY 212) was determined by micro-Kjeldahl procedures for leaves, stems, and ears. There was no appreciable grain on this date, so the whole ear (husks, cob, silks) was aggregated. Nitrogen content of grain only was determined for DOY 227, DOY 249, and harvest (DOY 270) plant samples.

Grain filling was monitored by sampling single kernels from two plants per sub-plot twice weekly. Husks were gently pulled back on sample ears, and five individual kernels were removed from the center portion using a small knife and were placed in an envelope. After oven drying at 60 °C, weight was determined for each grain individually. After each sampling, ears were covered by the husks which were then held in place with a rubber band. The same plants were used for all the sampling dates. This procedure was similar to a method described by Tollenaar and Daynard (1978b). They determined that there was no significant effect of husk and kernel removal on the dry matter accumulation of remaining kernels.

On 27 September twenty ears per plot were harvested, and yield, grain number, and final grain weight were determined for each one. Ears were placed in an oven for four days at 60 °C. After drying, grain was removed from each ear manually and was weighed and counted. Grain size distribution was determined for a sub-sample of ears. This was accomplished by weighing individual kernels of an 80 cm^3 (ca. 200 kernels) sample from single ears. These kernels were categorized in 50 mg increments for three ears of each plot.

Soil water content was measured using the neutron scattering technique. Sampling was in 0.25 m increments to a depth of 1.5 m. There were two access tubes in the center row of each sub-plot. Measurements began shortly after planting and were taken one or two times weekly until near physiological maturity of the crop. The water content during the deficit period was plotted and a line fitted through the data for each sampled depth. Water absorption rate was determined from the slope of the fitted line.

RESULTS AND DISCUSSION

Table 5.1 gives dates and degree days of 50 % and 75 % silking for the various treatments. There was a range of four days among the planting dates and hybrids. Water was withheld

Table 5.1. Day of year (DOY) and thermal time after planting (°Cd) when 50 % and 75 % silking occurred for treatments.

Treatment	50 % Silking		75 % Silking	
	--DOY--	--°Cd--	--DOY--	--°Cd--
3540 I P1	205	882	207	917
3540 GFD P1	206	899	207	917
3540 GFD P2	208	869	209	881
3475 I P1	204	864	205	882
3475 GFD P1	205	882	206	899
3475 GFD P2	207	853	208	869

after DOY 217 which was 9 to 12 days after 50 % silking. All treatments had reached 100 % silking by this date. The soil profile was at a substantial water content when irrigation ceased, so stress did not occur for several days.

Soil water content differences were not detected between hybrids, therefore these data were averaged. Figures 5.4a and 5.4b and Figures 5.5a and 5.5b depict water absorption rate for the GFD P1 and GFD P2, respectively, during the deficit period. Water content of the irrigated treatment was favorable throughout the experiment. Water absorption was occurring at all depths at the beginning of the deficit which indicated roots were distributed throughout the 1.5 m soil profile. A rather rapid decrease in water absorption from the 0.00 m to 0.25 m depth occurred around DOY 223 for deficit plants of both planting dates. This was generally coupled with increased water absorption rate at depths below 0.50 m.

Water absorption from the 1.5 m profile of GFD treatments was sufficient to meet transpiration requirements of plants until at least DOY 227 (Figure 5.6). This was near the time when LAI of GFD plants began to decline rapidly due to senescence (Figures 5.7a and 5.7b). If the LAI decline, leaf rolling, and potential water absorption at depths below 1.5 m were considered, transpiration was probably maintained longer. Other research by the current authors with corn on this soil revealed that when water absorption rate in the 0.00 m to 0.25 m layer of soil reached values of 3.0 to

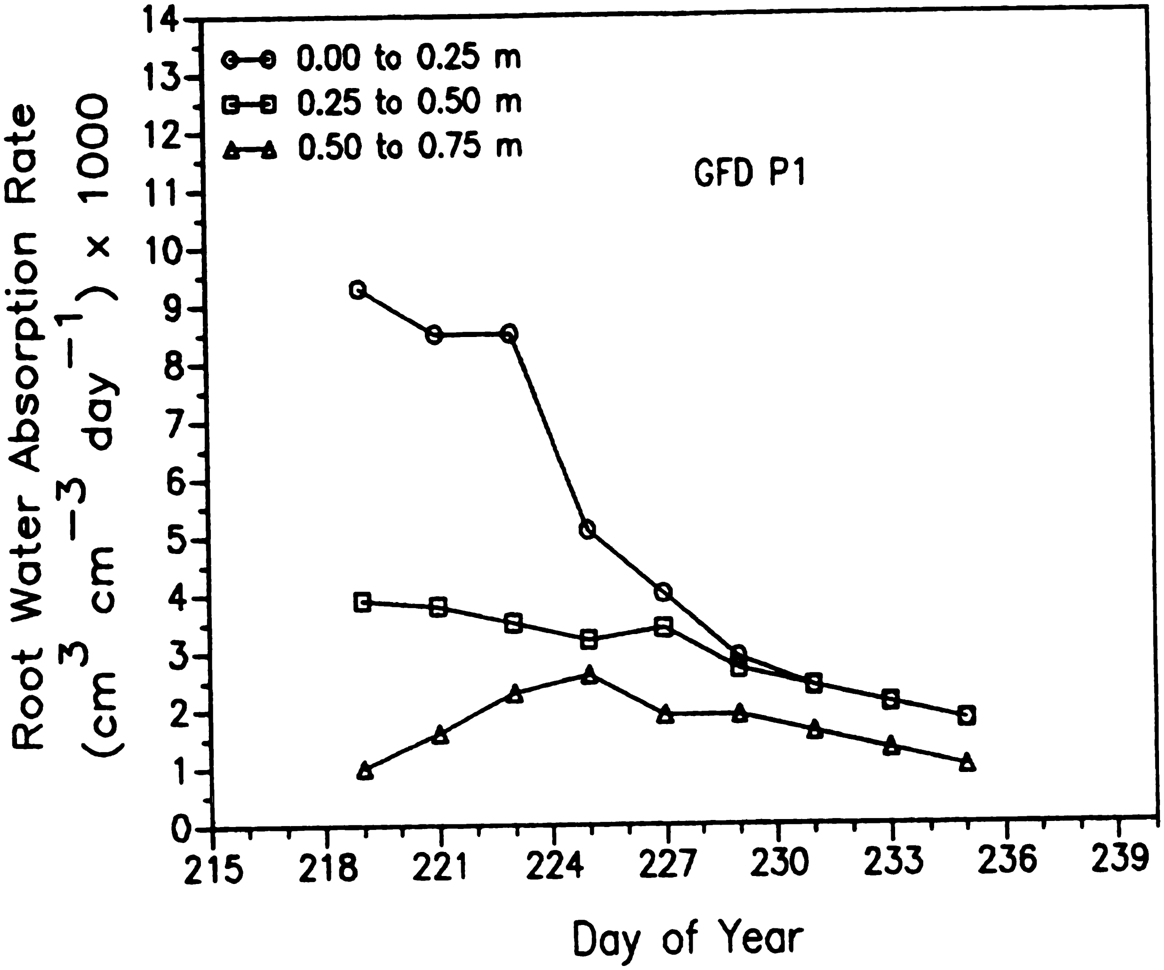

Figure 5.4a. Water absorption rates at depths of 0.00 to 0.25 m, 0.25 to 0.50 m, and 0.50 to 0.75 m during the deficit period for the grain filling deficit, first planting date treatment.

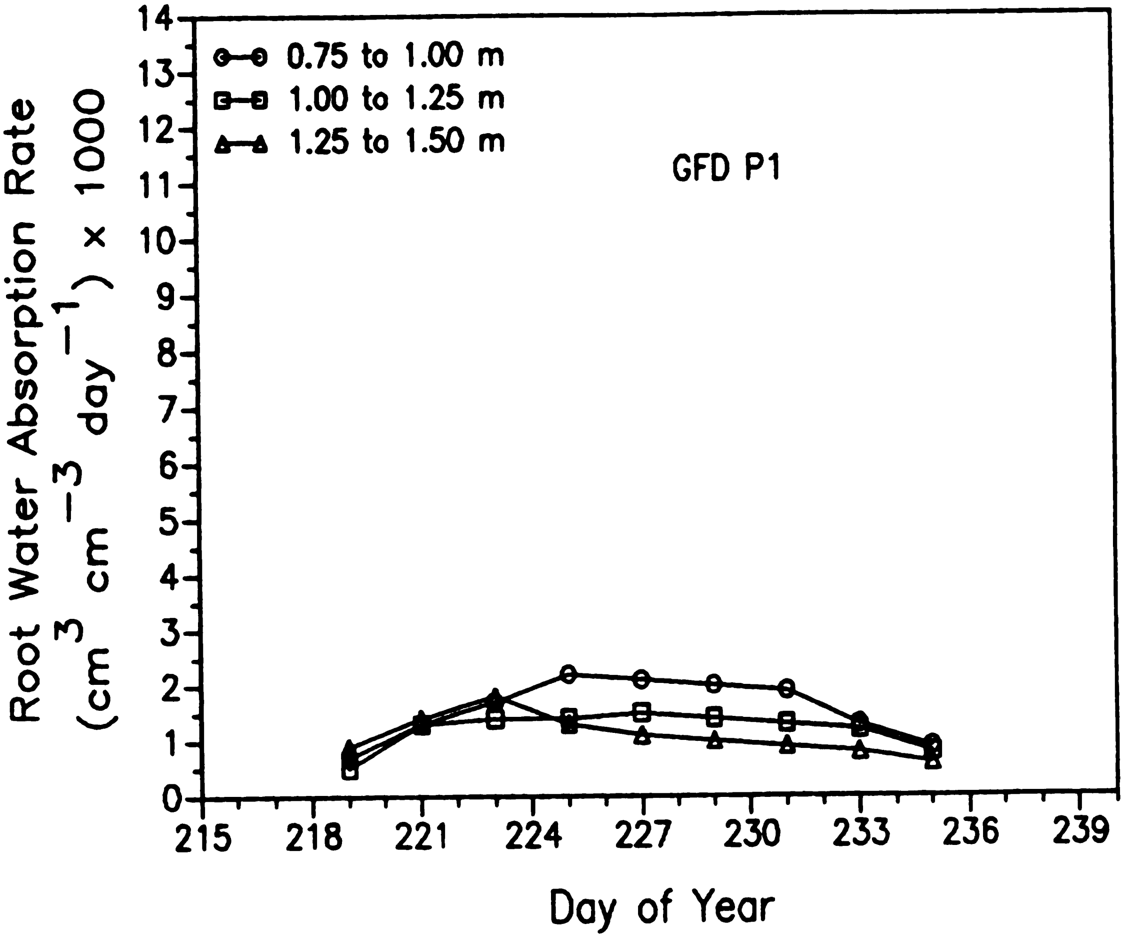

Figure 5.4b. Water absorption rates at depths of 0.75 to 1.00 m, 1.00 to 1.25 m, and 1.25 to 1.50 m during the deficit period for the grain filling deficit, first planting date treatment.

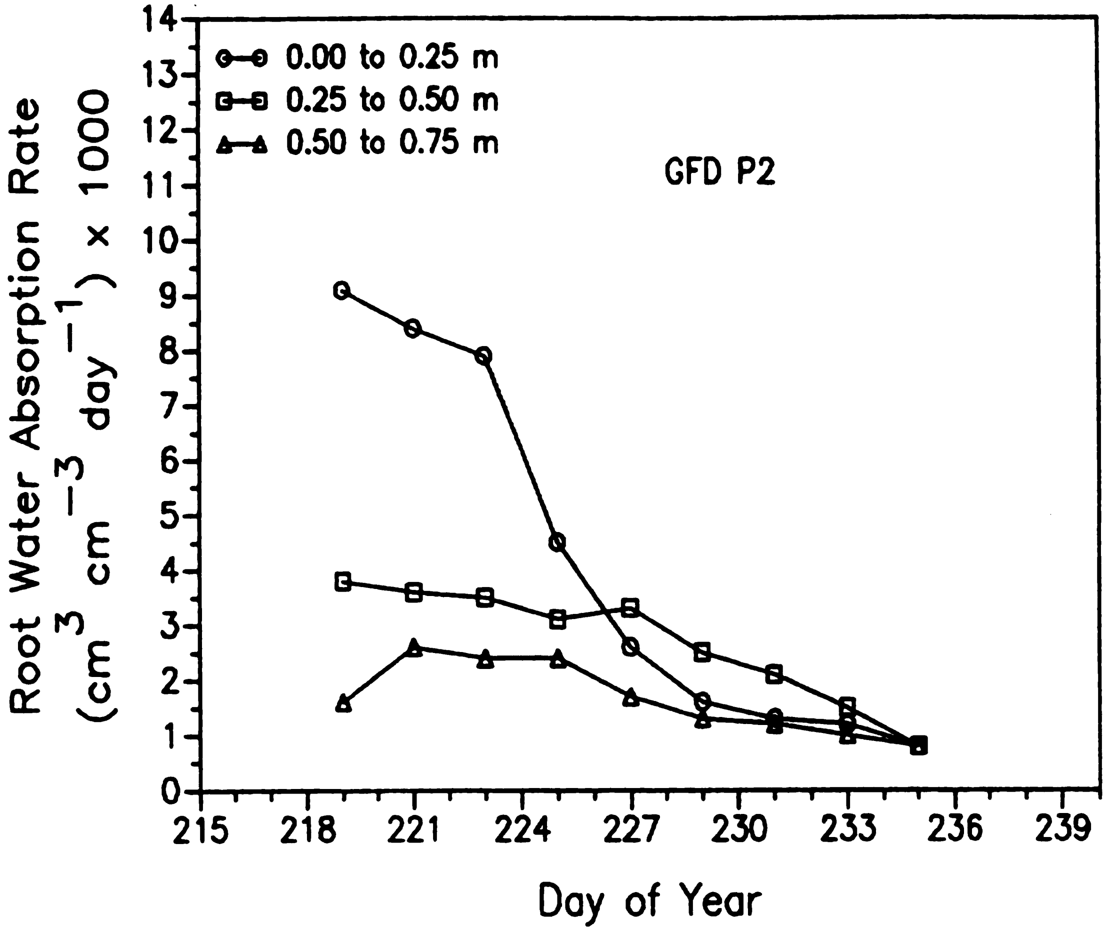

Figure 5.5a. Water absorption rates at depths of 0.00 to 0.25 m, 0.25 to 0.50 m, and 0.50 to 0.75 m during the deficit period for the grain filling deficit, second planting date treatment.

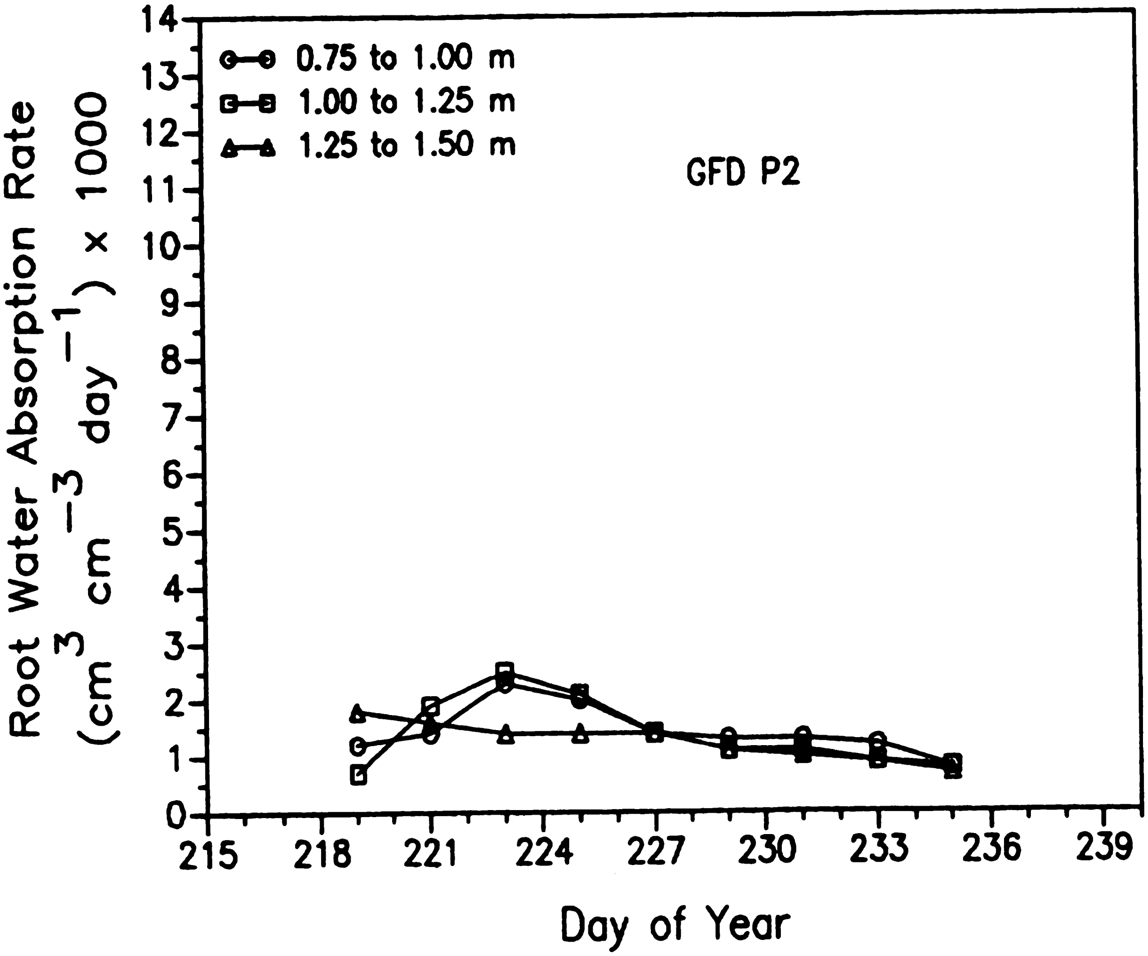

Figure 5.5b. Water absorption rates at depths of 0.75 to 1.00 m, 1.00 to 1.25 m, and 1.25 to 1.50 m during the deficit period for the grain filling deficit, second planting date treatment.

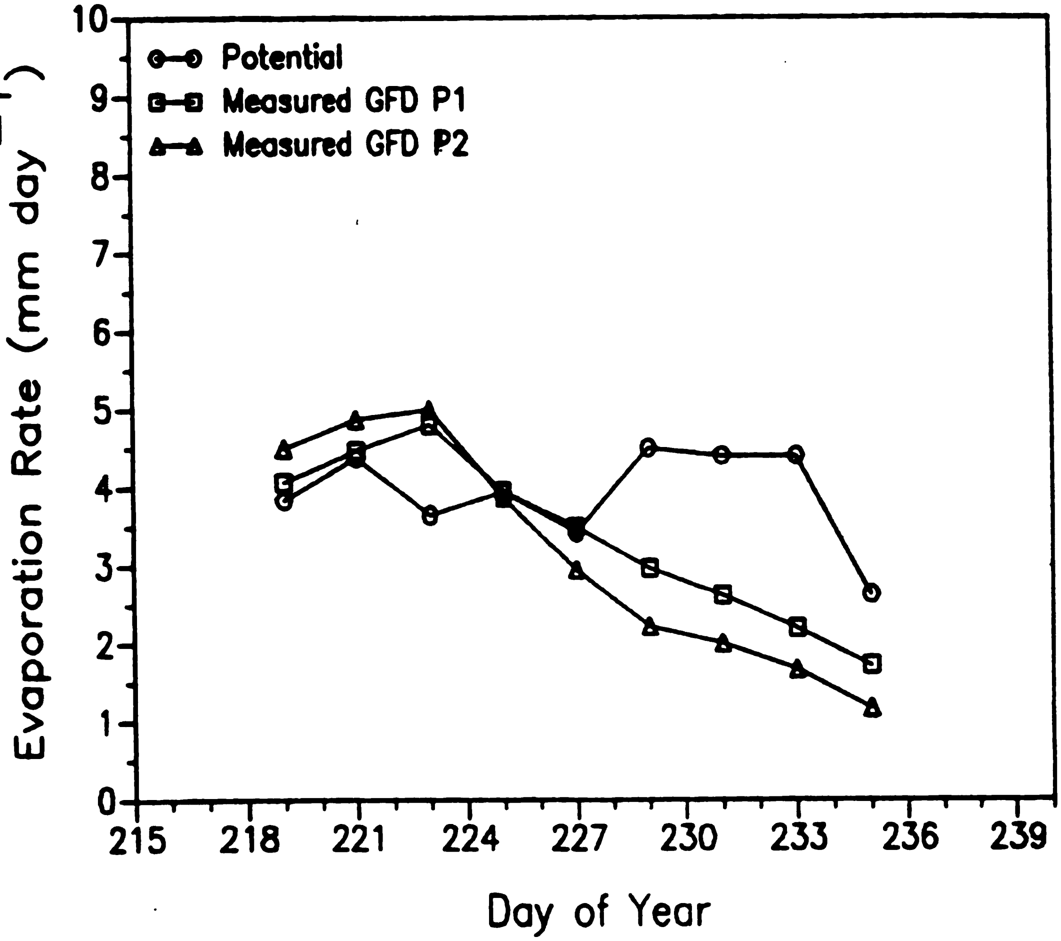

Figure 5.6. Potential evaporation and measured total water absorption from the 1.5 m soil profile during the deficit period for the grain filling deficit treatments.

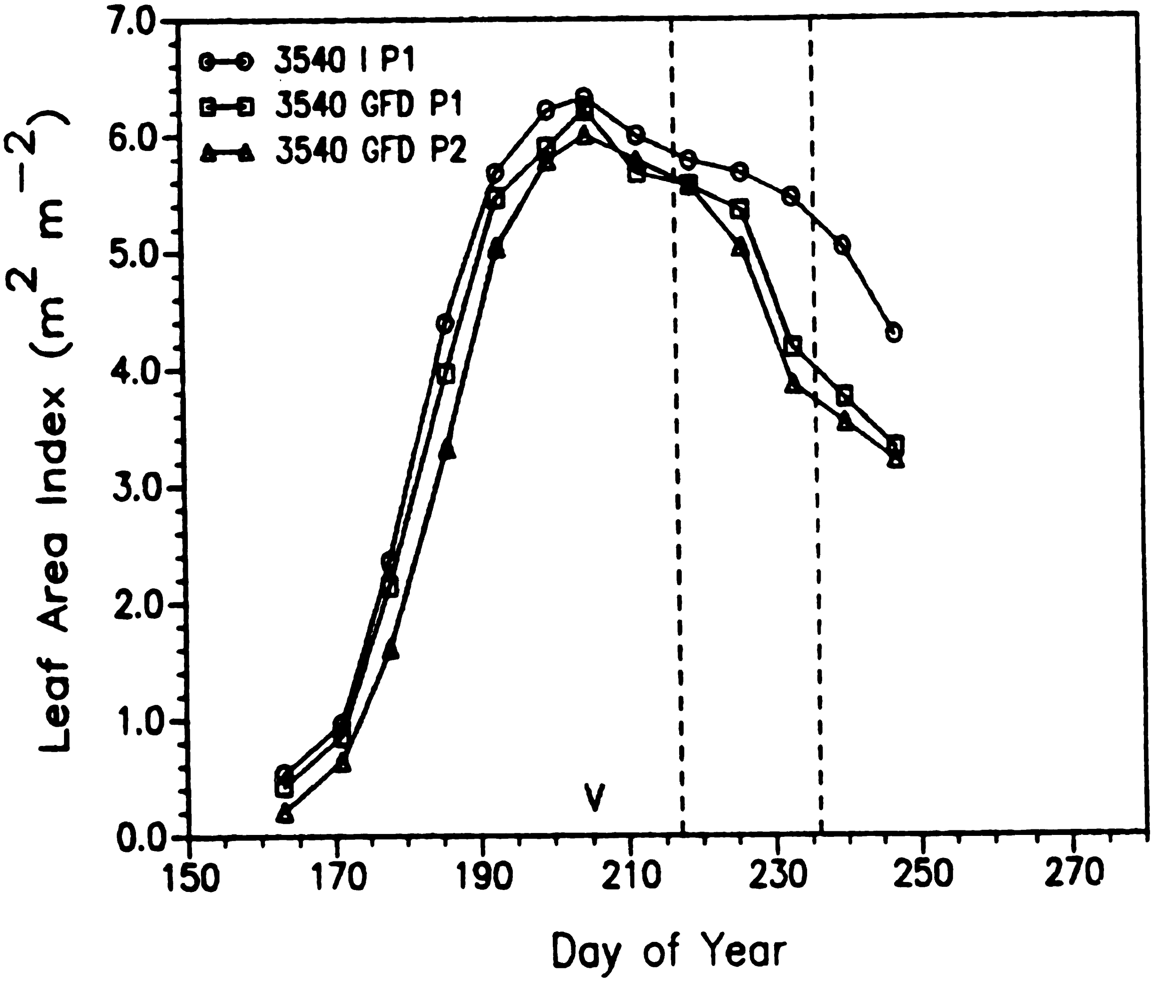

Figure 5.7a. Leaf area index (LAI) for treatments of hybrid 3540. The region between the vertical dashed lines represent the water deficit period, and the V marks silking date of irrigated control.

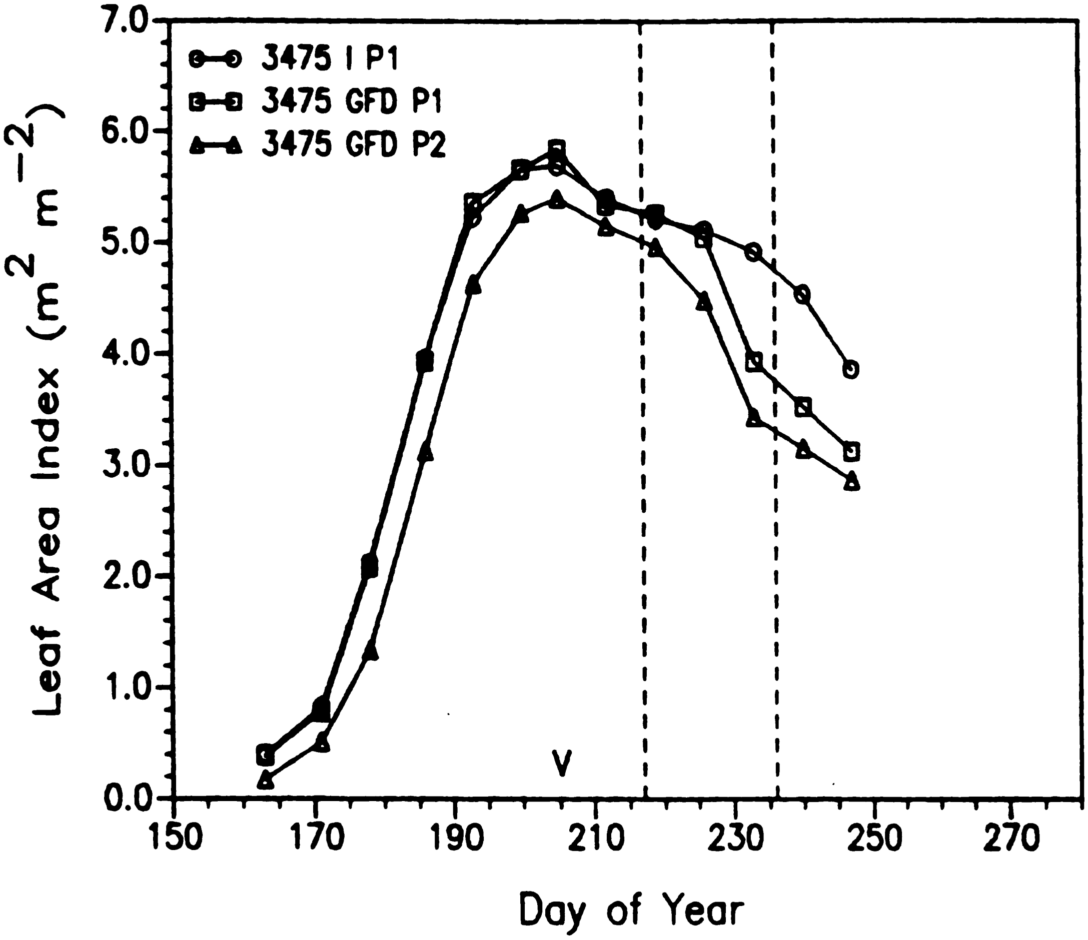

Figure 5.7b. Leaf area index (LAI) for treatments of hybrid 3475. The region between the vertical dashed lines represent the water deficit period, and the V marks silking date of irrigated control.

3.5 (absorption units) plant extension growth essentially ceased (NeSmith et al., 1990). The magnitude of the stress in this experiment can be discerned as water absorption rate in the upper soil layer was between values of 1.0 and 2.0 (absorption units) by the end of the deficit period.

Above ground biomass accumulation began to decline for GFD plants as compared to I plants about the same time LAI declined rapidly (Figures 5.8a and 5.8b). Hybrid 3540 had more leaf area and greater biomass overall than hybrid 3475. The reduction in biomass was more apparent from the crop growth rate (CGR) calculations (Figures 5.9a and 5.9b). Maximum CGR reductions of GFD plants were near DOY 231 as the I plants were still growing substantially. The decrease in CGR at this time was 63 % to 67 % for all GFD treatments except 3475 GFD P1 which only had a reduction of 46 %. The corresponding decrease in LAI of deficit plants was 20 % to 25 % for P1 plants and 30 % for P2 plants, indicating that leaf area loss could not account totally for reductions in biomass production. This would seem to suggest an effect on photosynthesis in the deficit plants.

Several previous reports have indicated that dry matter accumulation ceased due to impairment of photosynthesis under water deficit conditions during grain filling (Jurgens et al., 1978; McPherson and Boyer, 1977; Westgate and Boyer, 1985). This compares the with work of Frey (1981) in which a 20 % to 30 % reduction in CGR was observed when 50 % defoliation was

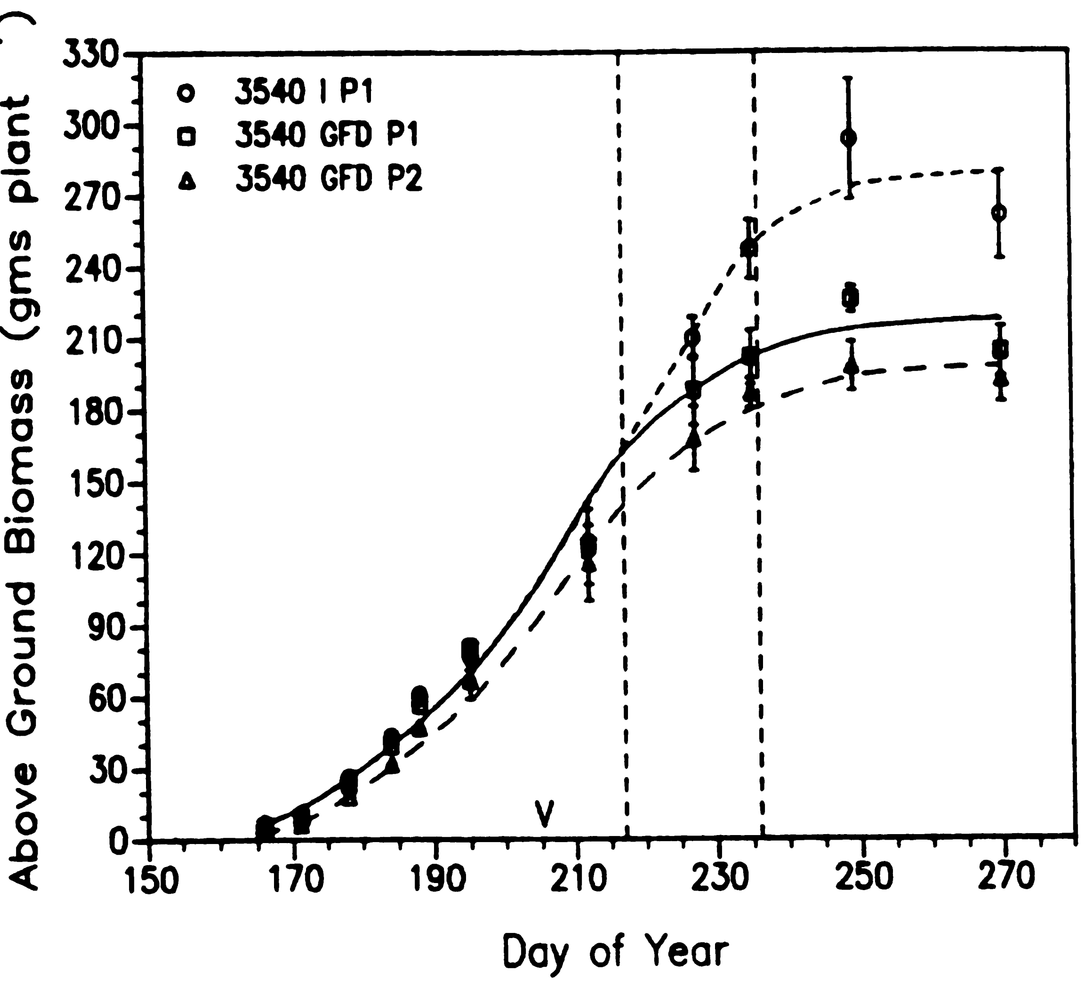

Figure 5.8a. Above ground biomass for treatments of hybrid 3540. The region between the vertical dashed lines represents the water deficit period, and the V marks silking date of irrigated control.

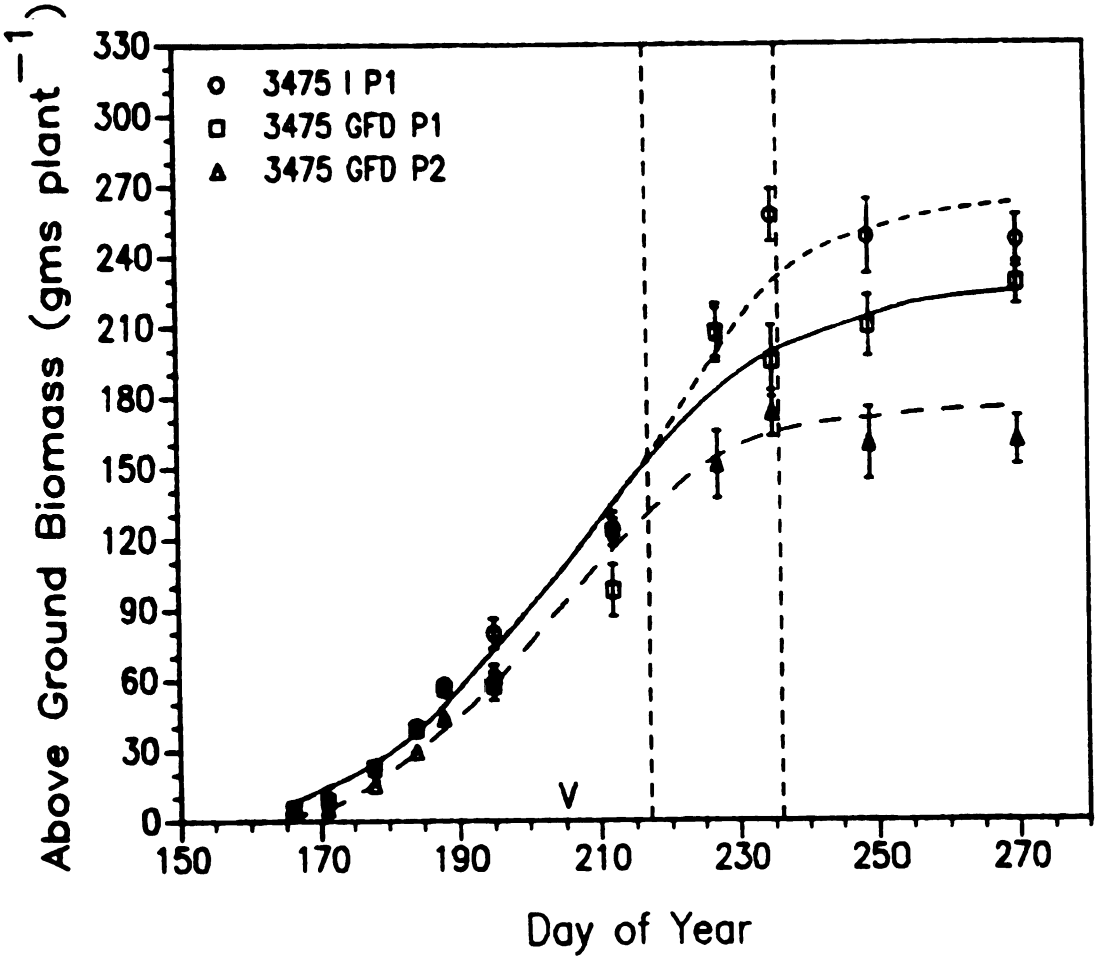

Figure 5.8b. Above ground biomass for treatments of hybrid 3475. The region between the vertical dashed lines represents the water deficit period, and the V marks silking date of irrigated control.

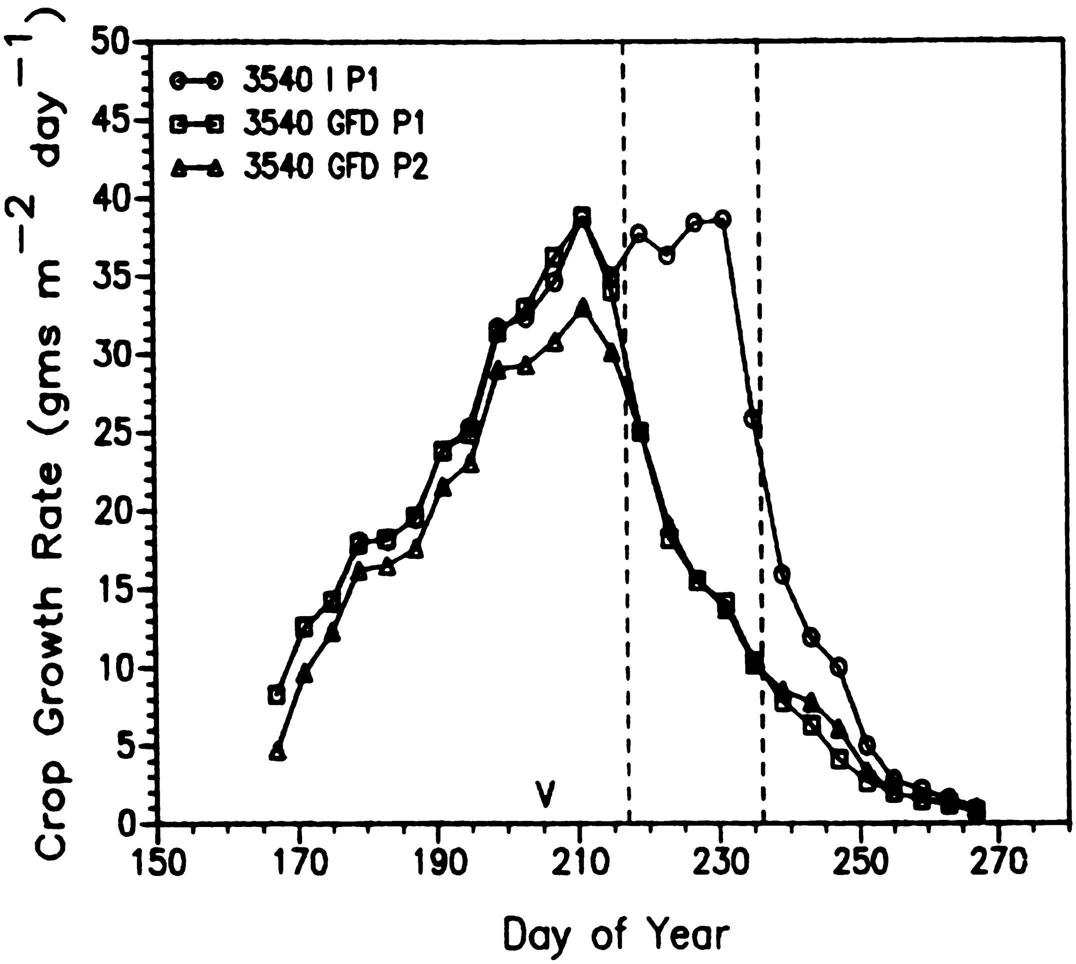

Figure 5.9a. Above ground crop growth rate (CGR) for treatments of hybrid 3540. The region between the vertical dashed lines represents the water deficit period, and the V marks silking date of irrigated control.

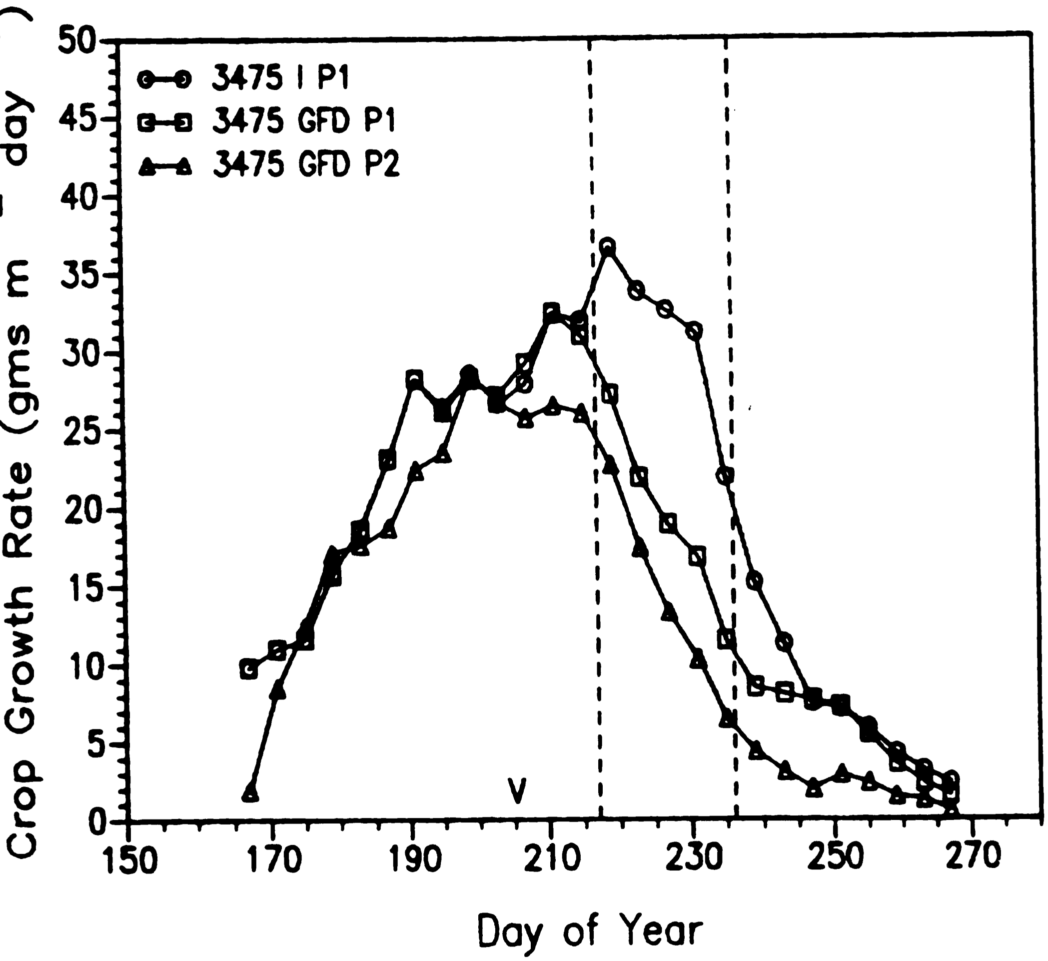

Figure 5.9b. Above ground crop growth rate (CGR) for treatments of hybrid 3475. The region between the vertical dashed lines represents the water deficit period, and the V marks silking date of irrigated control.

performed on plants at mid-silking. Recovery of deficit plants in the current experiment after irrigation resumed was difficult to determine because I plants had started to decrease CGR sharply due to approaching maturity.

The influence of the water deficit was less pronounced for grain dry matter accumulation, although, marked differences occurred (Figures 5.10a and 5.10b). Examination of grain growth rates (GGR) indicated that maximum reductions of GFD plants as compared to I plants occurred around DOY 235 and were 27 % to 29 % for all treatments except 3475 GFD P2 which was decreased by over 50 % (Figures 5.11a and 5.11b). These data indicated that translocation of stored assimilates was less influenced by the water deficits than was current assimilation. This agrees with results of McPherson and Boyer (1977) and Westgate and Boyer (1985).

Nitrogen content of plants after silking and of grain on three subsequent dates is given in Table 5.2. Data were somewhat variable, but there was no discernable effect of treatments on the percent of nitrogen in the grain. This would support the hypothesis of continued translocation under deficit conditions. Research has shown that nearly all grain nitrogen is that which is accumulated prior to anthesis and that deprivation of nitrogen during grain filling has little effect on grain nitrogen content (Friedrich et al., 1979; Friedrich and Schrader, 1979; Hanway, 1962). Therefore, even though drying of the surface soil layer during the water

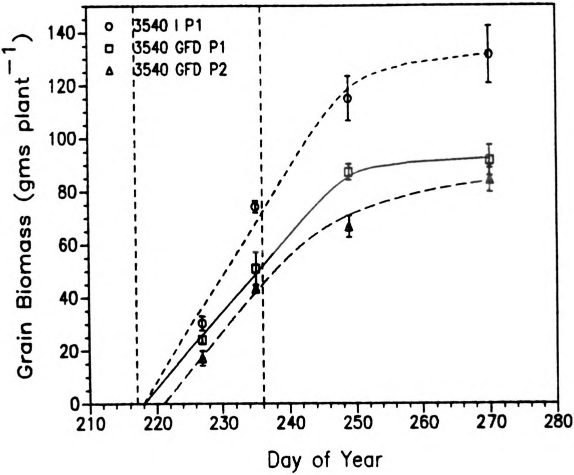

Figure 5.10a. Grain biomass for treatments of hybrid 3540. The region between the vertical dashed lines represents the water deficit period.

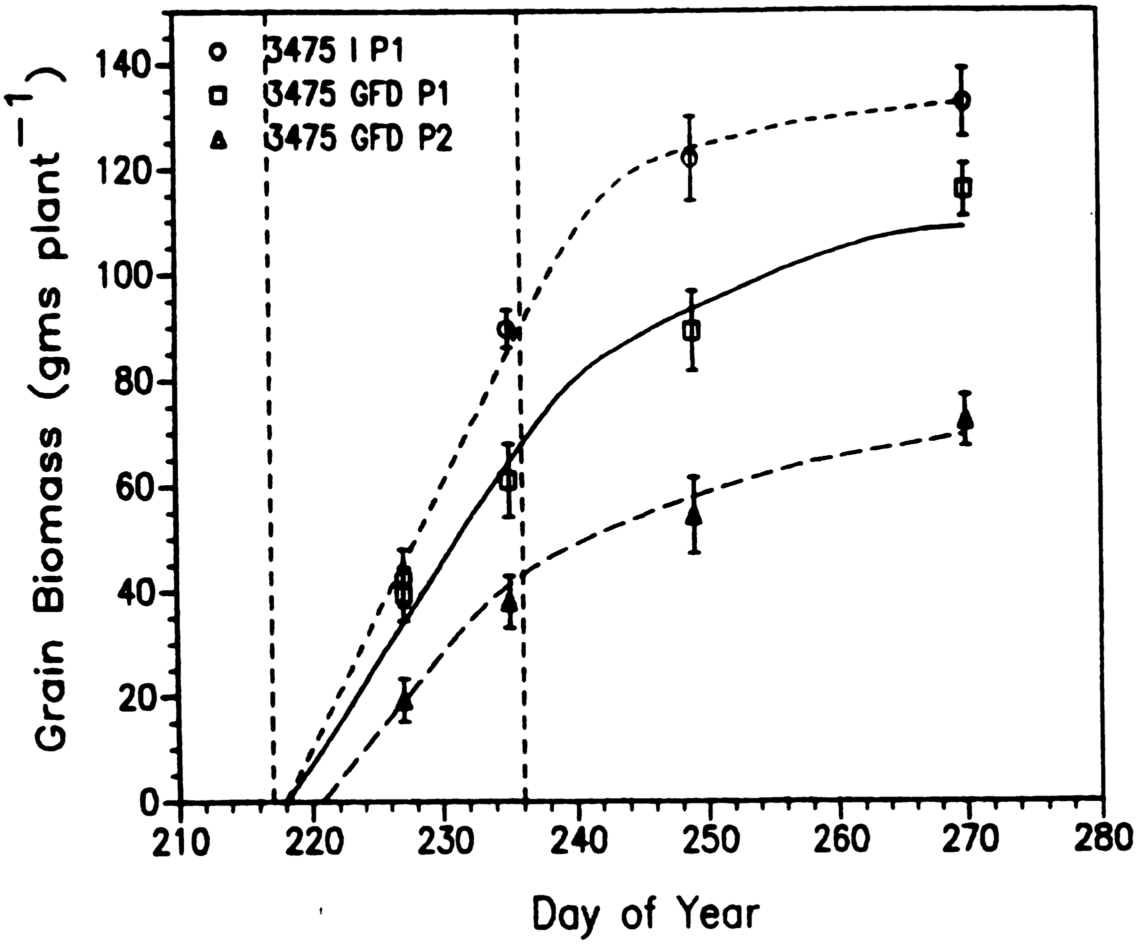

Figure 5.10b. Grain biomass for treatments of hybrid 3475. The region between the vertical dashed lines represents the water deficit period.

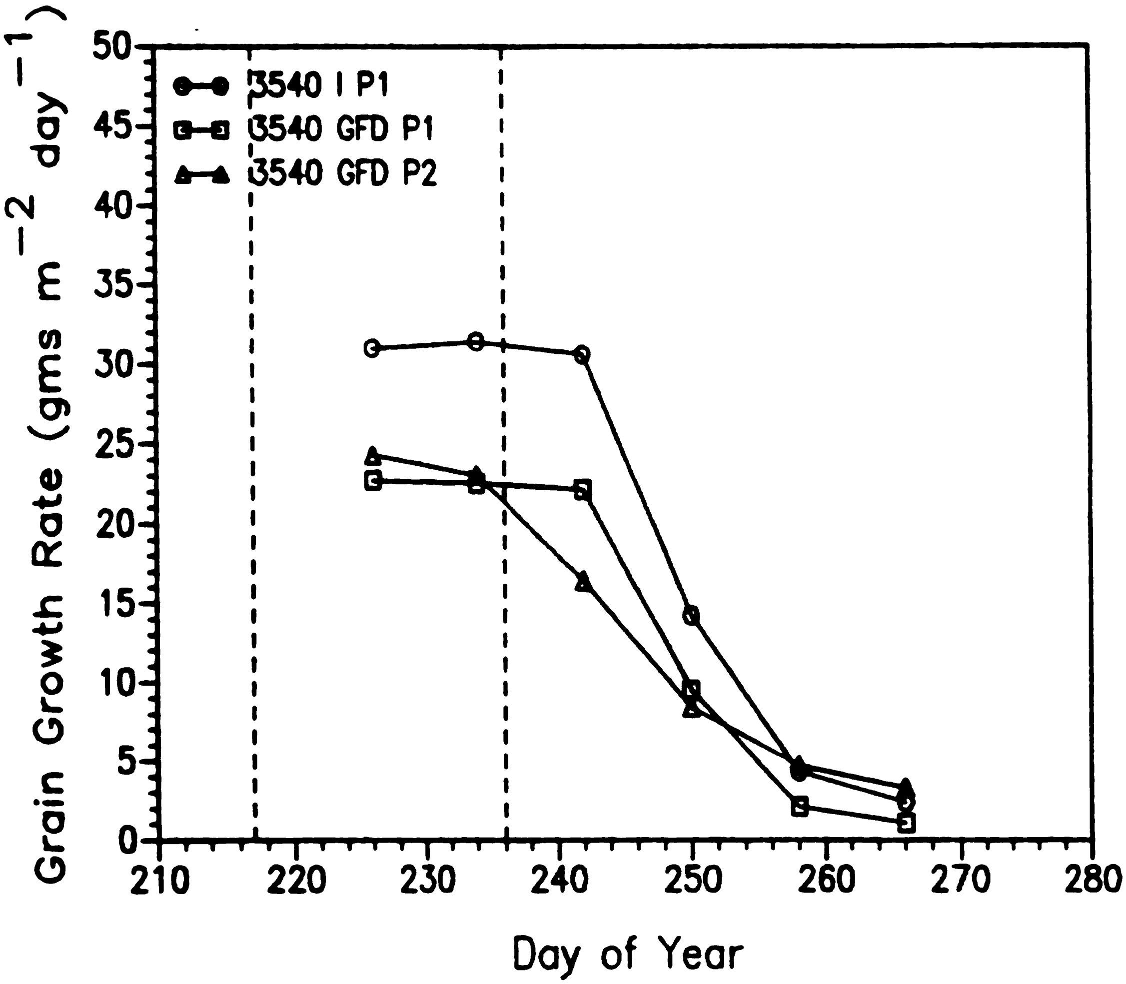

Figure 5.11a. Whole plant grain growth rate (GGR) for treatments of hybrid 3540. The region between the vertical dashed lines represents the water deficit period.

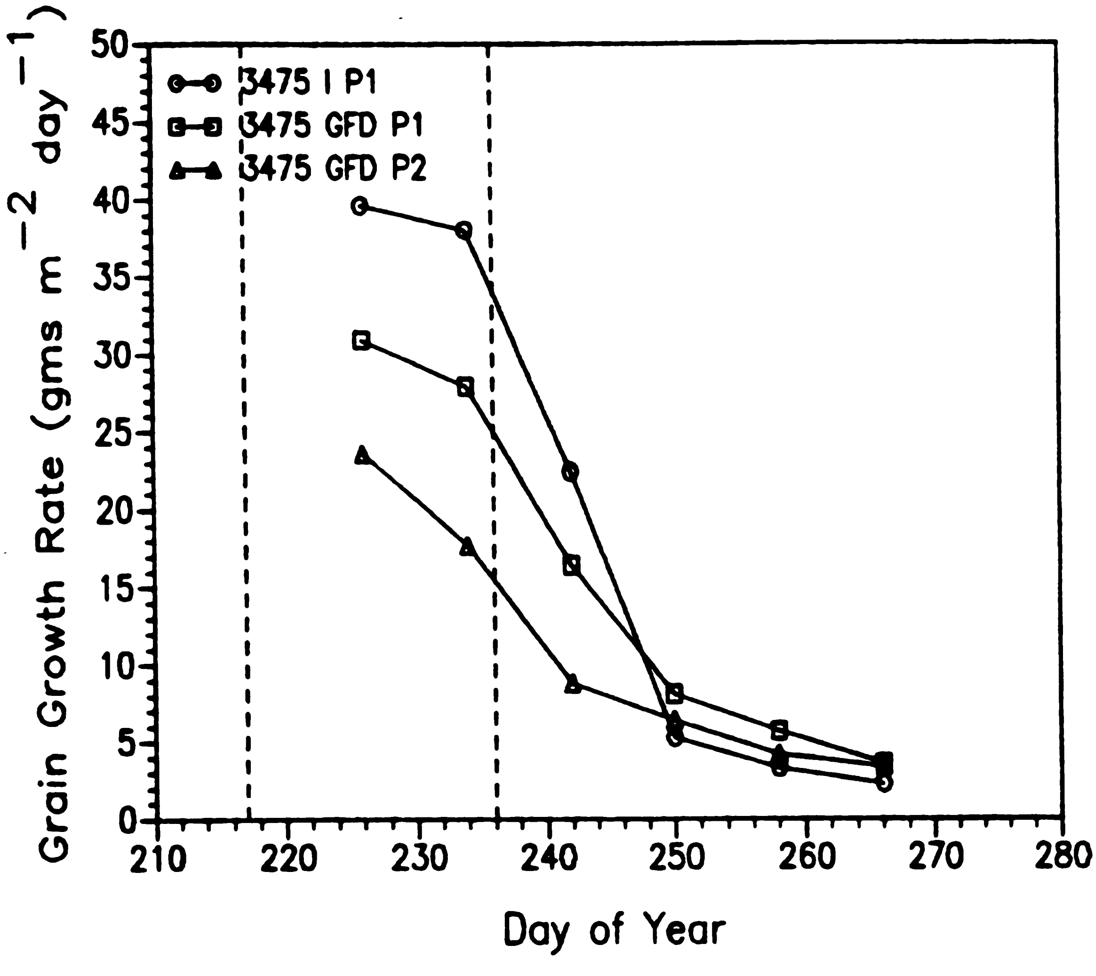

Figure 5.11b. Whole plant grain growth rate (GGR) for treatments of hybrid 3475. The region between the vertical dashed lines represents the water deficit period.

Table 5.2. Nitrogen content of whole plants excluding roots on July 31 (DOY 212) and of grain only on August 15 (DOY 227), September 6 (DOY 249), and September 27 (DOY 270).

	Whole Plant	Grain		
Treatment	DOY 212	DOY 227	DOY 249	DOY 270
	%			
3540 I P1	1.41 (.03)*	1.70 (.08)	1.39 (.07)	1.39 (.04)
3540 GFD P1	1.23 (.02)	1.76 (.04)	1.47 (.08)	1.40 (.05)
3540 GFD P2	1.29 (.08)	1.81 (.07)	1.35 (.05)	1.41 (.01)
3475 I P1	1.25 (.07)	1.72 (.09)	1.23 (.03)	1.35 (.04)
3475 GFD P1	1.28 (.06)	1.59 (.02)	1.31 (.07)	1.28 (.02)
3475 GFD P2	1.32 (.09)	1.92 (.04)	1.40 (.02)	1.39 (.03)

* Values in parenthesis () are standard errors of treatment means where n = 4.

shortage could have potentially influenced nutrient uptake, this would not have necessarily reduced transport of nitrogen to the grain.

A comparison to determine simplistically to what extent translocation contributed to grain filling in the different hybrids and treatments is through the ratio of CGR to GGR (Figures 5.12a and 5.12b). The days represented were during the linear grain filling period. A value greater than one (CGR > GGR) indicates that photosynthesis exceeded that required by the growing grain, and a value less than one (CGR < GGR) indicates that current assimilation did not meet the grain growth requirement. This ratio does not consider root growth or plant respiration. All GFD plants had ratios less than one, but there was little difference between hybrids in response to the deficit. These results compare with those of Jurgens et al. (1978) which indicated that a terminal water deficit during grain filling resulted in grain accumulating 2.7 times as much dry matter as the entire shoot. Irrigated plants of the hybrids in the current study were different in that hybrid 3540 maintained a higher ratio than hybrid 3475. The significance of this is difficult to determine since yields (presented later) were not different for the irrigated hybrids. However, this suggests that this ratio, or some modification, might be useful in selecting hybrids in a breeding program.

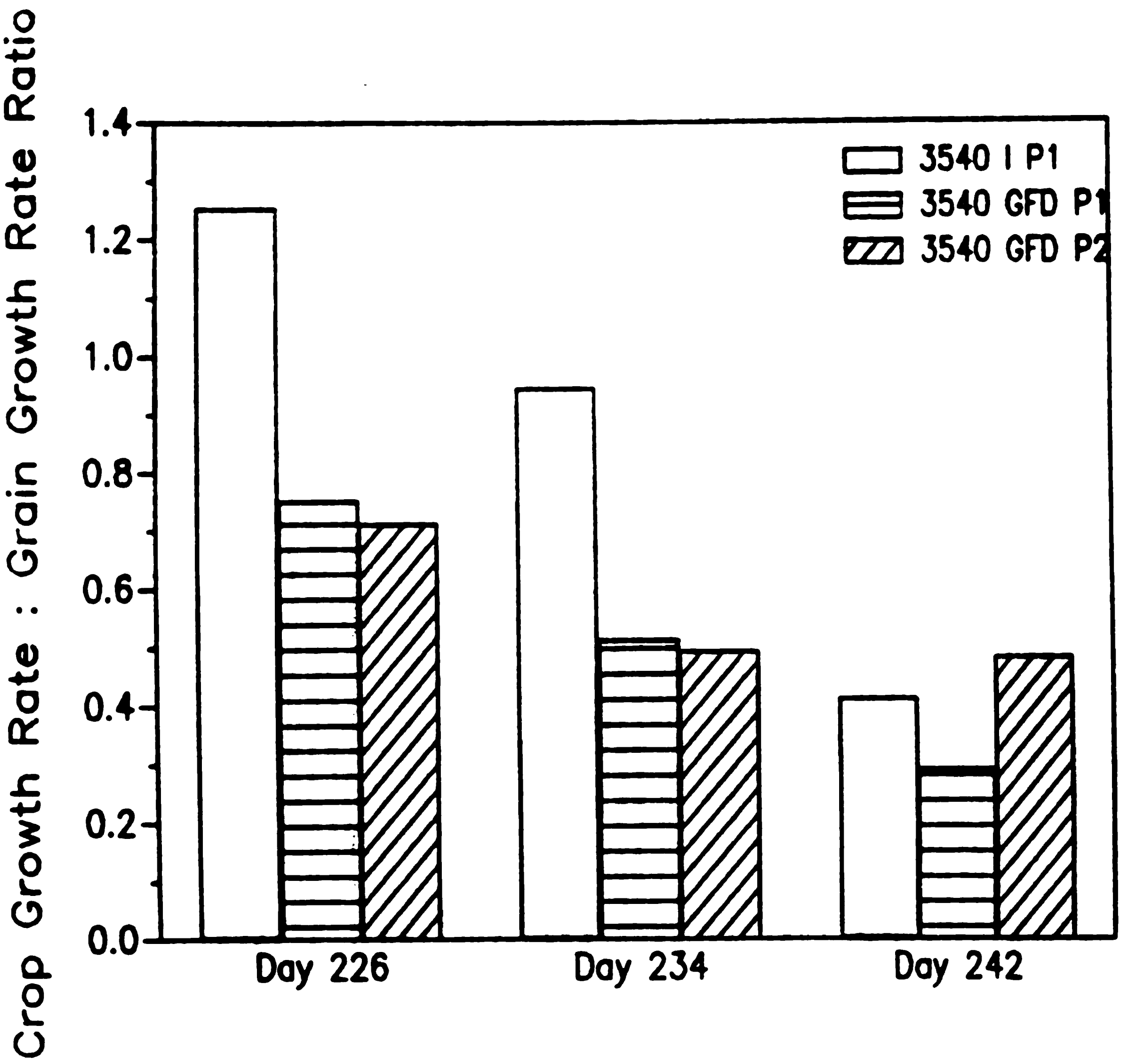

Figure 5.12a. Crop growth rate (CGR) to grain growth rate (GGR) ratios for treatments of hybrid 3540 during linear grain filling.

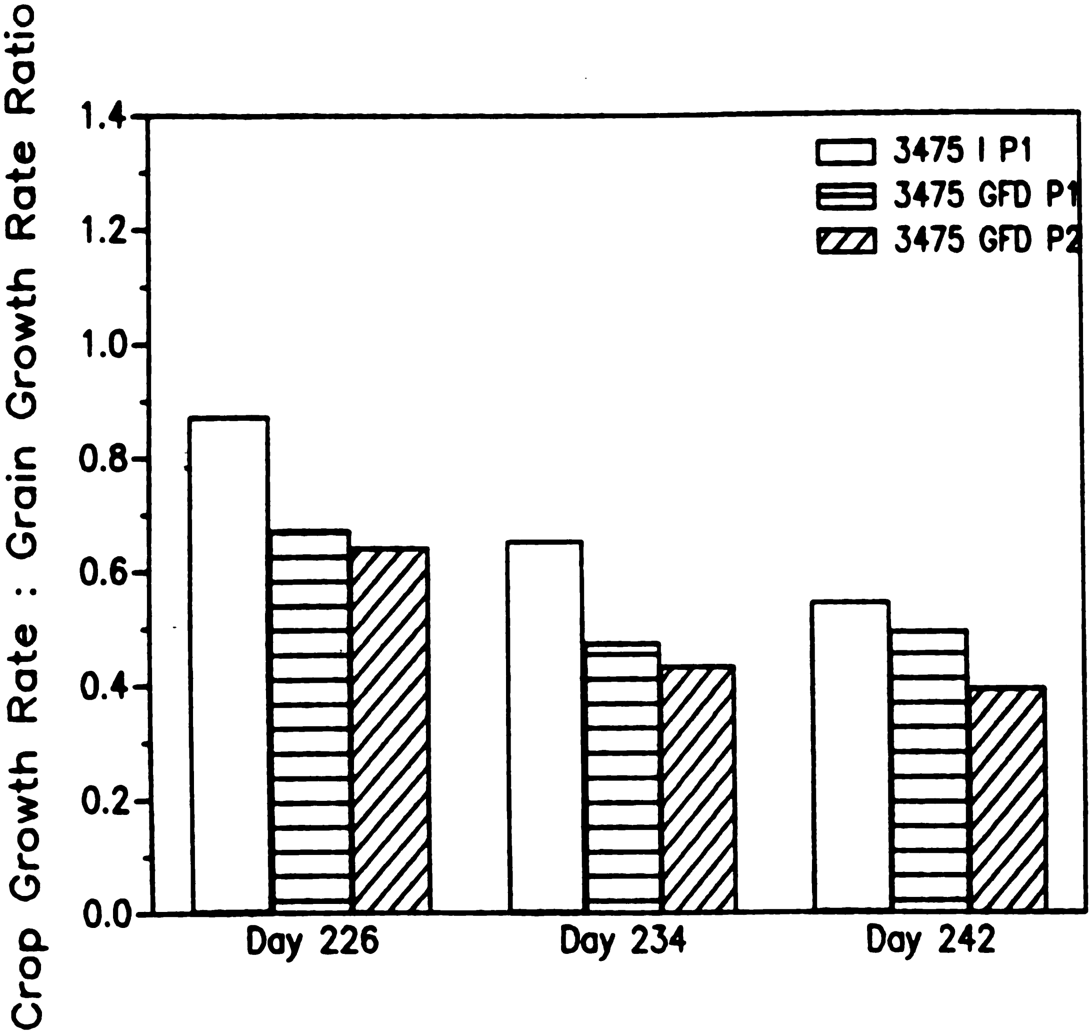

Figure 5.12b. Crop growth rate (CGR) to grain growth rate (GGR) ratios for treatments of hybrid 3475 during linear grain filling.

The grain growth results presented thus far have been for the entire plant. While these data are useful in some analyses, it is difficult to determine effects on rate and duration of grain filling from them. Figures 5.13a and 5.13b represent weight of individual kernels for the various treatments, and Figures 5.14a and 5.14b depict the rate of filling. For simplification, a linear extrapolation to zero grain filling was made. While this did not give the exact date of beginning grain fill because of the absence of the lag period, it did permit estimates of duration differences between treatments.

Water deficits did not affect the rate of linear grain filling of hybrid 3540, but it did decrease the duration by 7 to 8 days. As for hybrid 3475, rate was decreased by 14 % and 24 % for GFD P1 and GFD P2, respectively, and duration was decreased by 4 days and 2 days, respectively. These differences were apparently genetically related, as attempts to correlate rate or duration with developmental patterns (e.g. day of silking) were not successful. Also, there was no correlation with LAI or CGR. Mixed results of stress due to defoliation on grain filling rate and duration have been found. Tollenaar and Daynard (1978c) reported rate and duration were both affected, but there were little hybrid differences. Frey (1981) observed no influence on rate of filling for kernels in the middle position of the ear, and

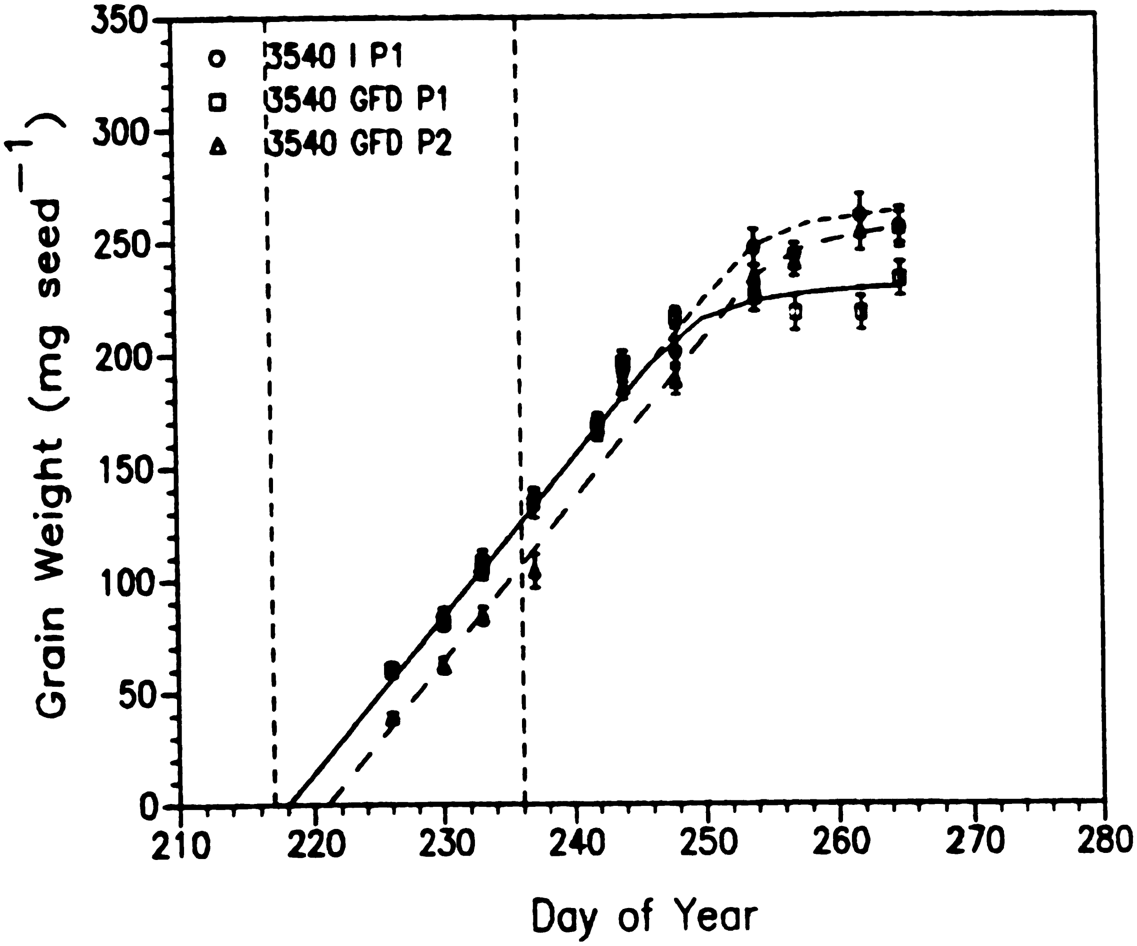

Figure 5.13a. Single kernel weights for treatments of hybrid 3540. Samples were from the middle of the ear. The region between the vertical dashed lines represents the water deficit period.

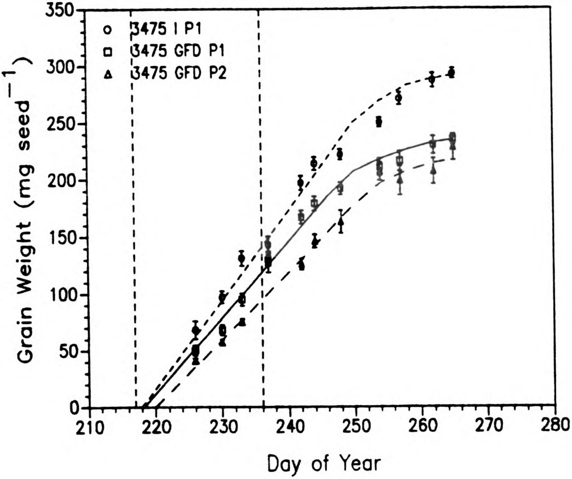

Figure 5.13b. Single kernel weights for treatments of hybrid 3475. Samples were from the middle of the ear. The region between the vertical dashed lines represents the water deficit period.

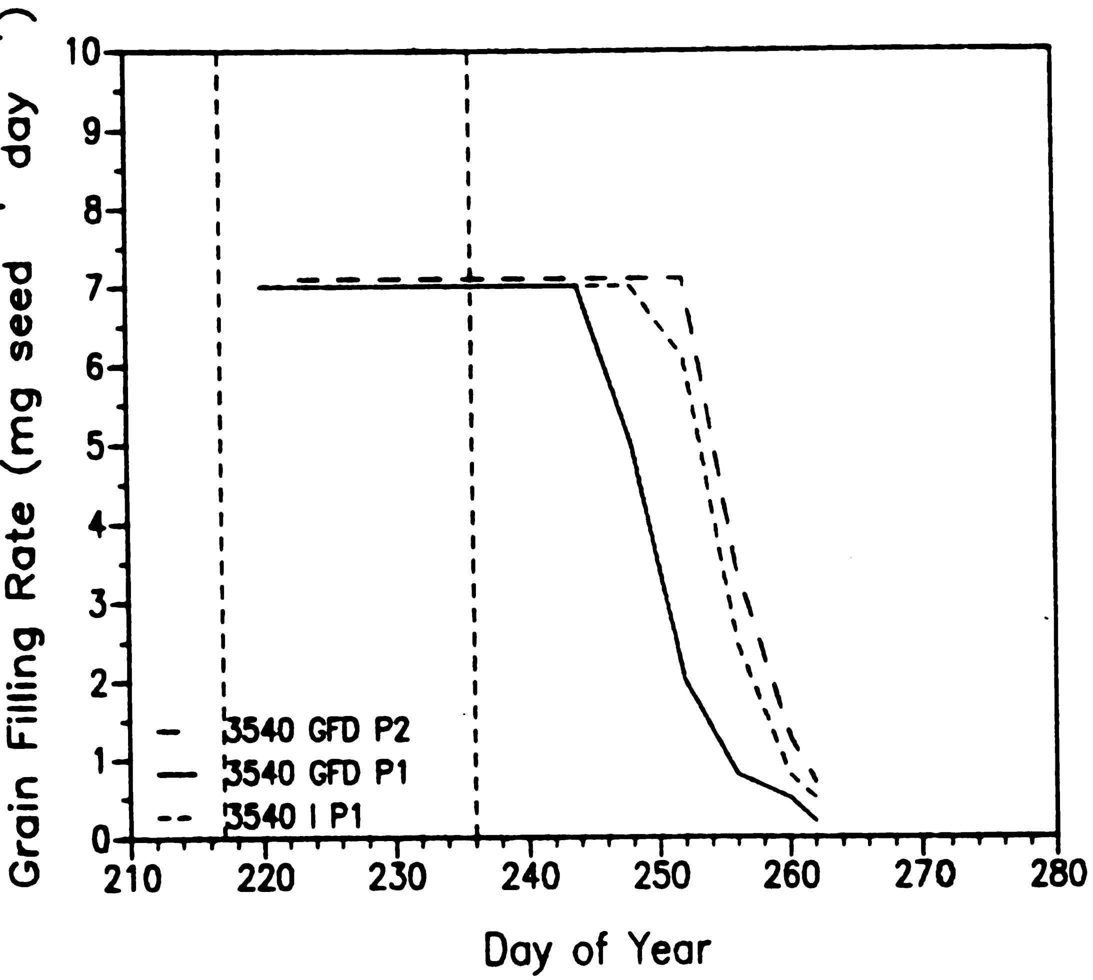

Figure 5.14a. Grain filling rate of single kernels for treatments of hybrid 3540. Samples were from the middle of the ear. The region between the vertical dashed lines represents the water deficit period.

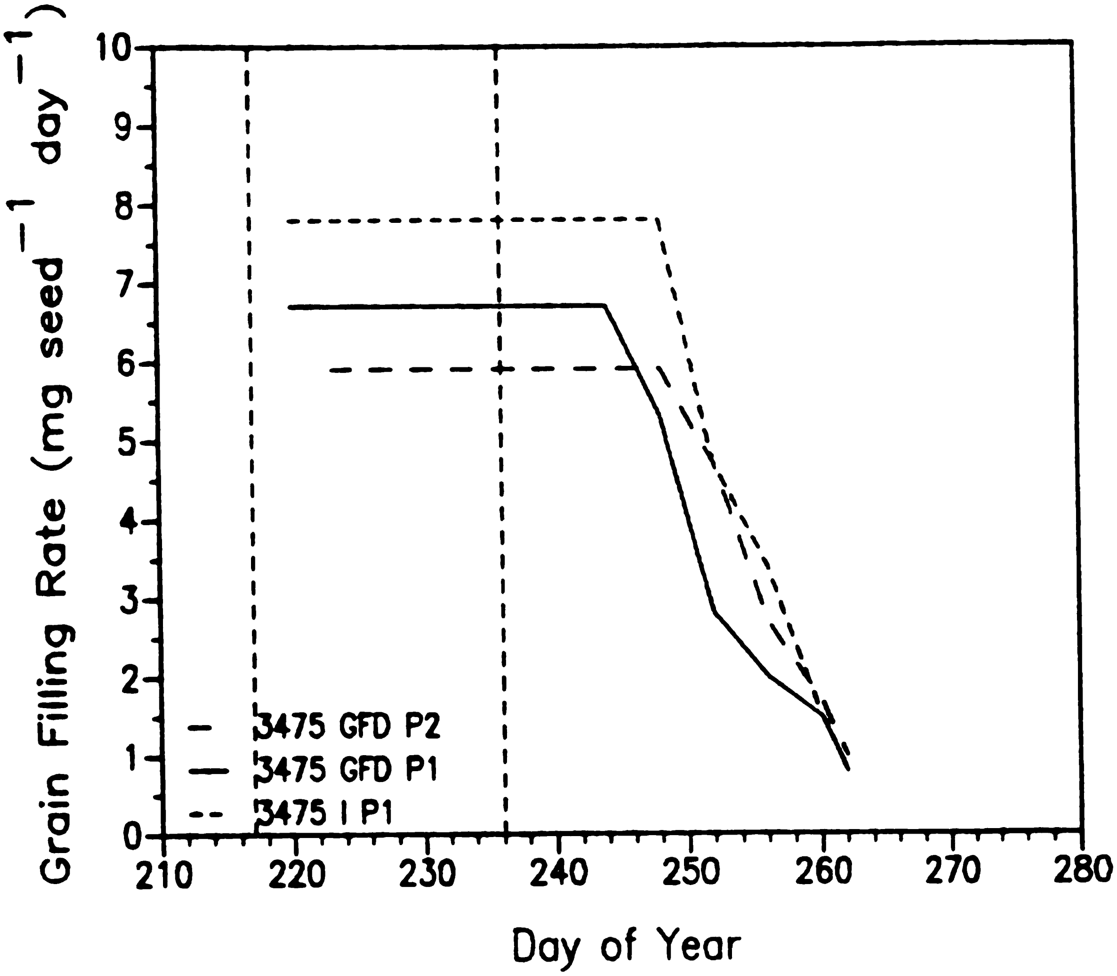

Figure 5.14b. Grain filling rate of single kernels for treatments of hybrid 3475. Samples were from the middle of the ear. The region between the vertical dashed lines represents the water deficit period.

Jones and Simmons (1983) denoted rate reductions ranging from 20 % to 60 %.

Final grain yield and yield components for treatments are depicted in Figures 5.15a and 5.15b. There was little difference between yields of the hybrids in response to the water deficits. Yield reductions for GFD P1 and GFD P2 plants were 21 % to 23 % and 35 % to 40 %, respectively. These results compared favorably to those reported for the field and container grown experiments discussed earlier in this manuscript. The yield component most reduced for GFD plants overall was grain weight. Results of grain number were variable, but generally P1 plants were less affected than P2 plants. This was due to P2 plants being nearer the critical time for grain number determination when water was withheld. Results from several experiments have indicated that stress drastically reduced grain numbers up until beginning linear grain fill, and after this, grain weight was the more affected component (Claassen and Shaw, 1970; Egharevba et al., 1976; Frey, 1981; Grant et al., 1989; Jones and Simmons, 1983; Kiniry and Ritchie, 1985).

Generally, final grain size is determined by weighing a large sample of seeds and then dividing by the count. This does not expose effects on grain variability within a treatment. Figures 5.16a through 5.16f depict grain size distribution for all the treatments. Compared to irrigated plants deficit plants in general had a larger number of seeds

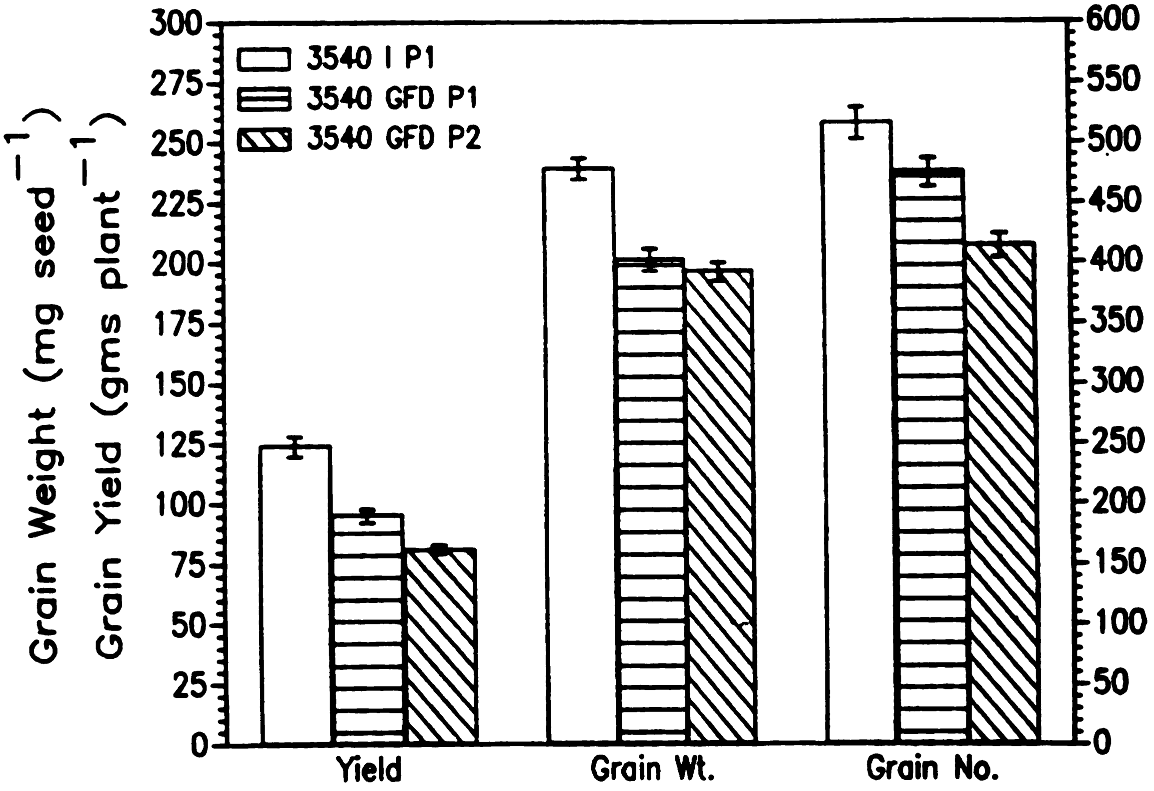

Figure 5.15a. Grain yields, final grain weight, and final grain number per ear for treatments of hybrid 3540.

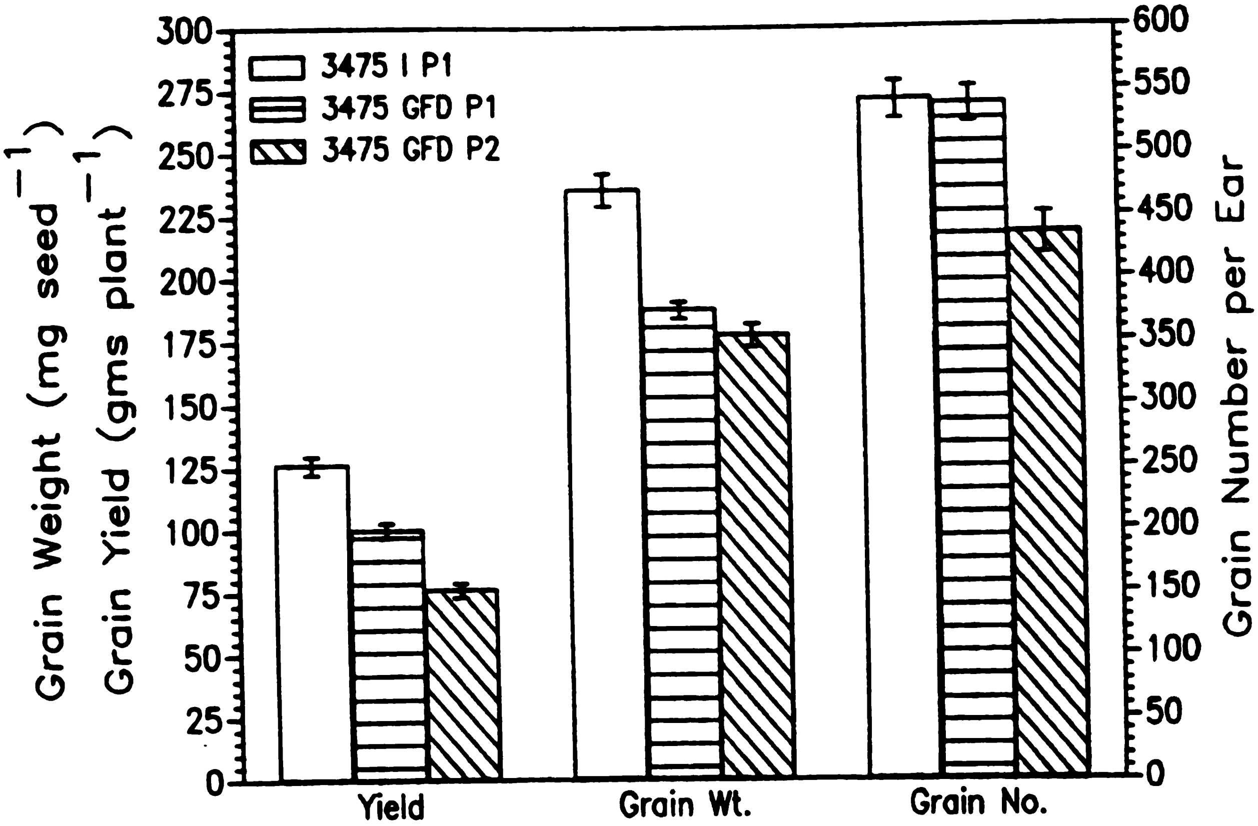

Figure 5.15b. Grain yields, final grain weight, and final grain number per ear for treatments of hybrid 3475.

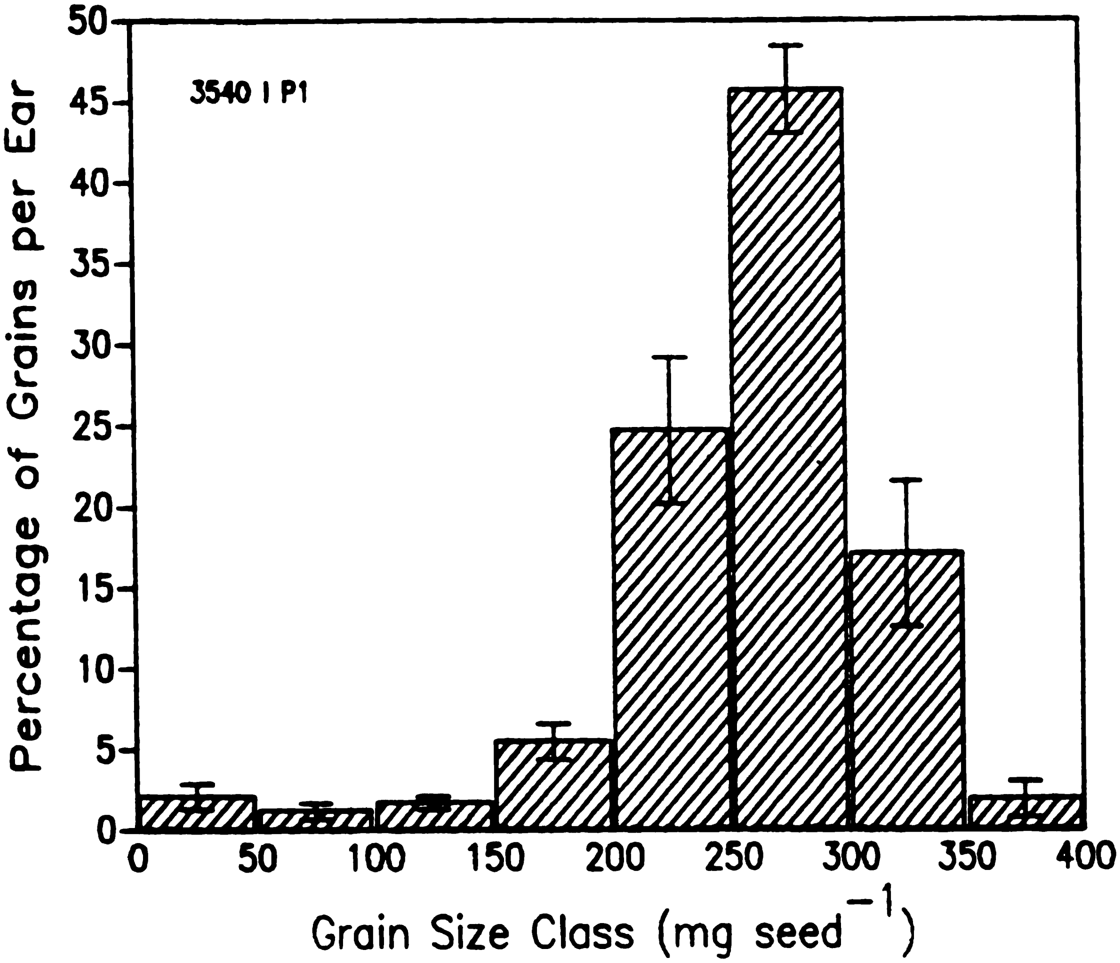

Figure 5.16a. Grain size distribution on single ears at harvest for the hybrid 3540 I P1 treatment.

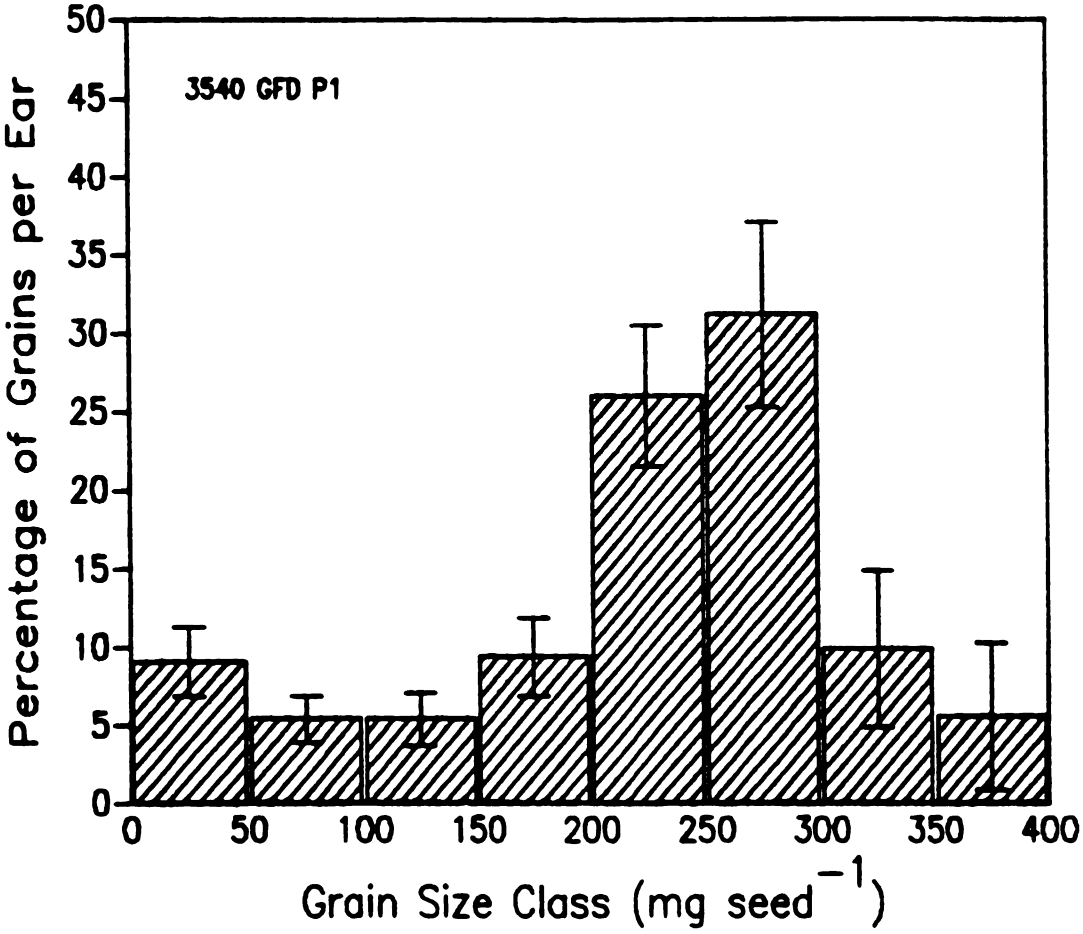

Figure 5.16b. Grain size distribution on single ears at harvest for the hybrid 3540 GFD P1 treatment.

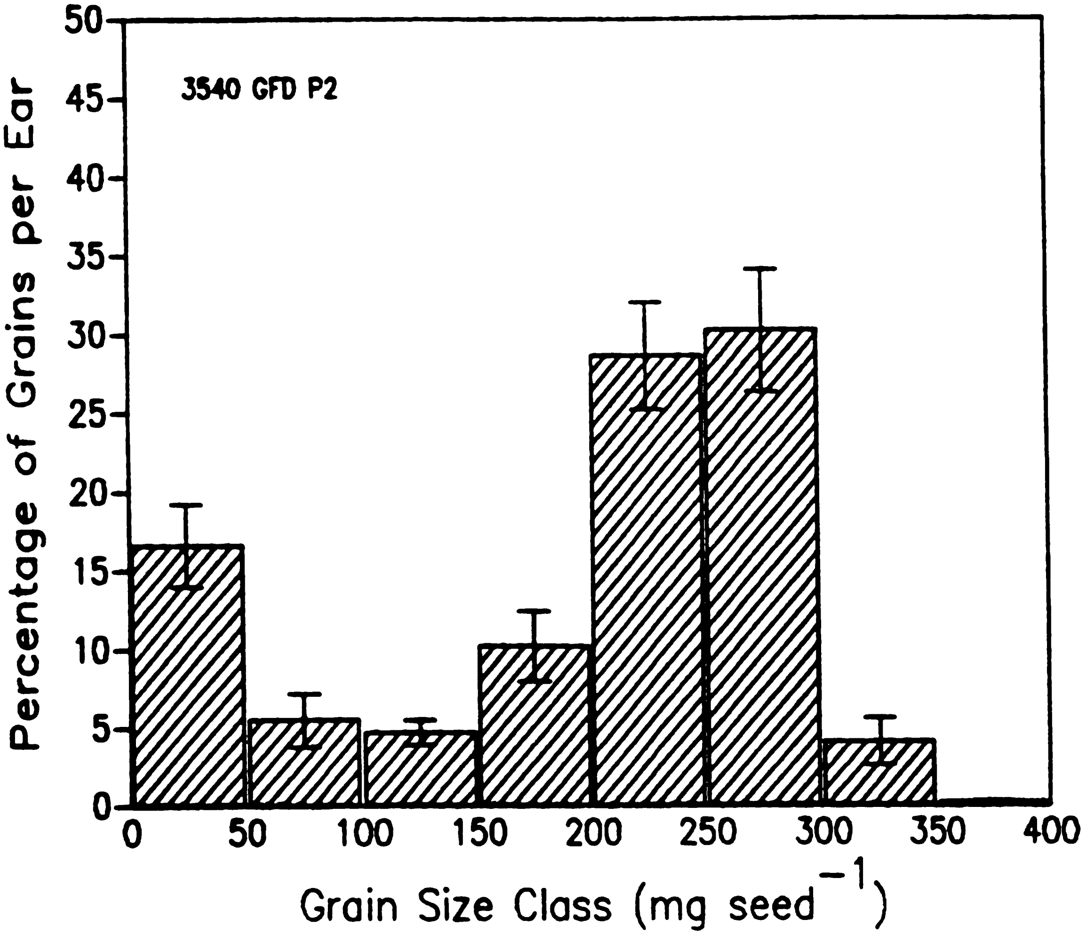

Figure 5.16c. Grain size distribution on single ears at harvest for the hybrid 3540 GFD P2 treatment.

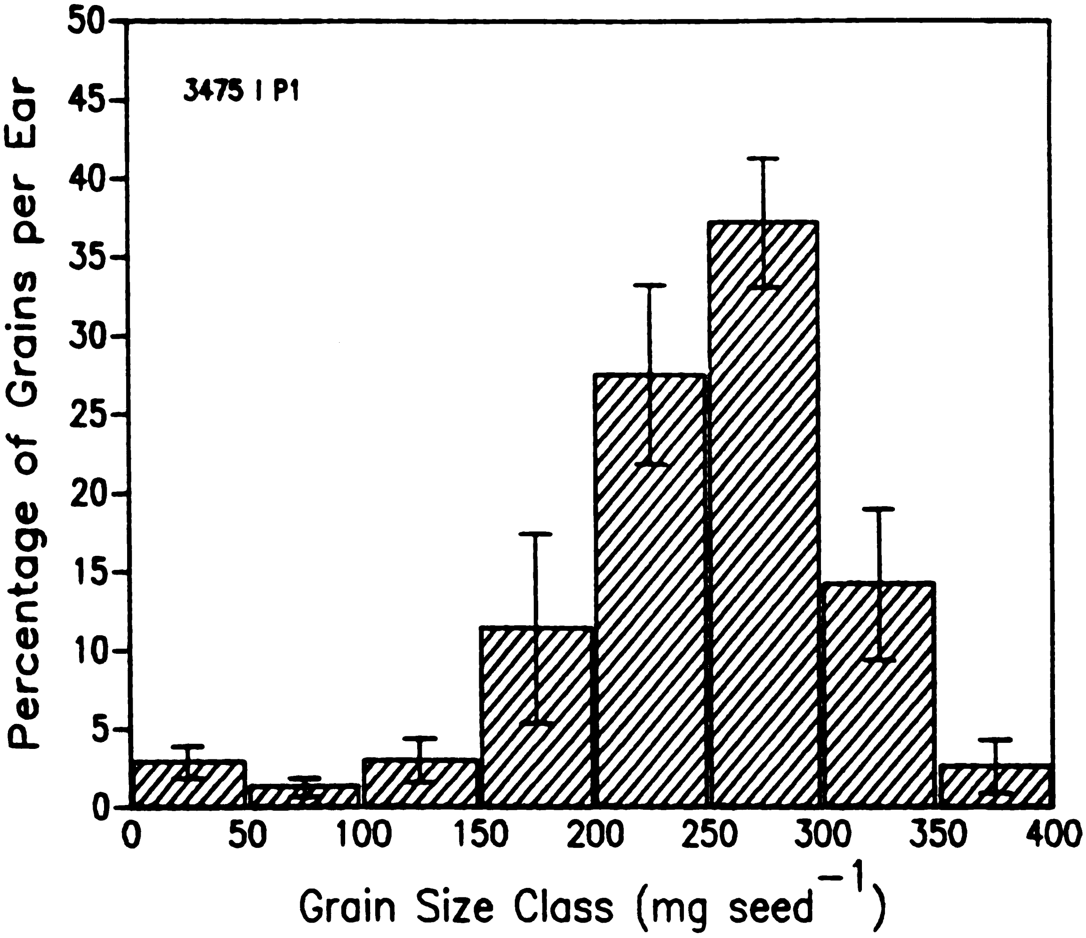

Figure 5.16d. Grain size distribution on single ears at harvest for the hybrid 3475 I P1 treatment.

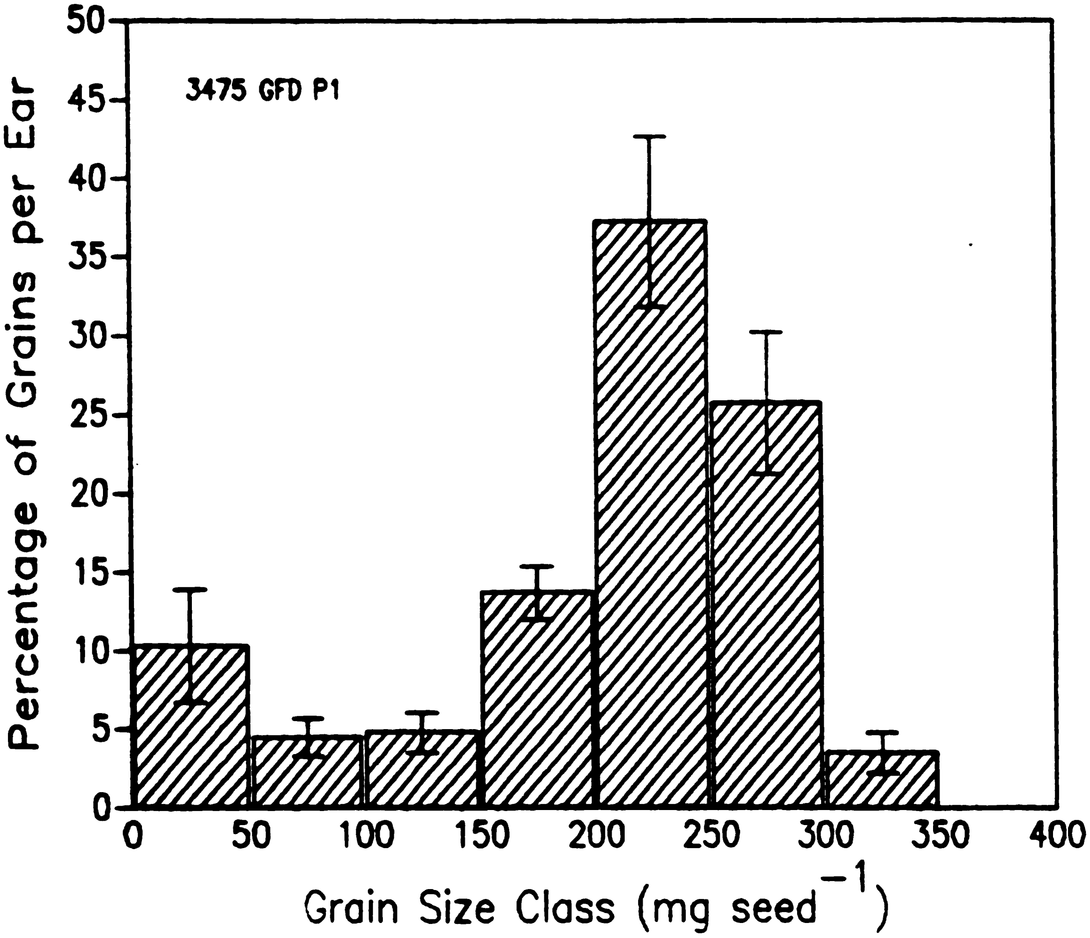

Figure 5.16e. Grain size distribution on single ears at harvest for the hybrid 3475 GFD P1 treatment.

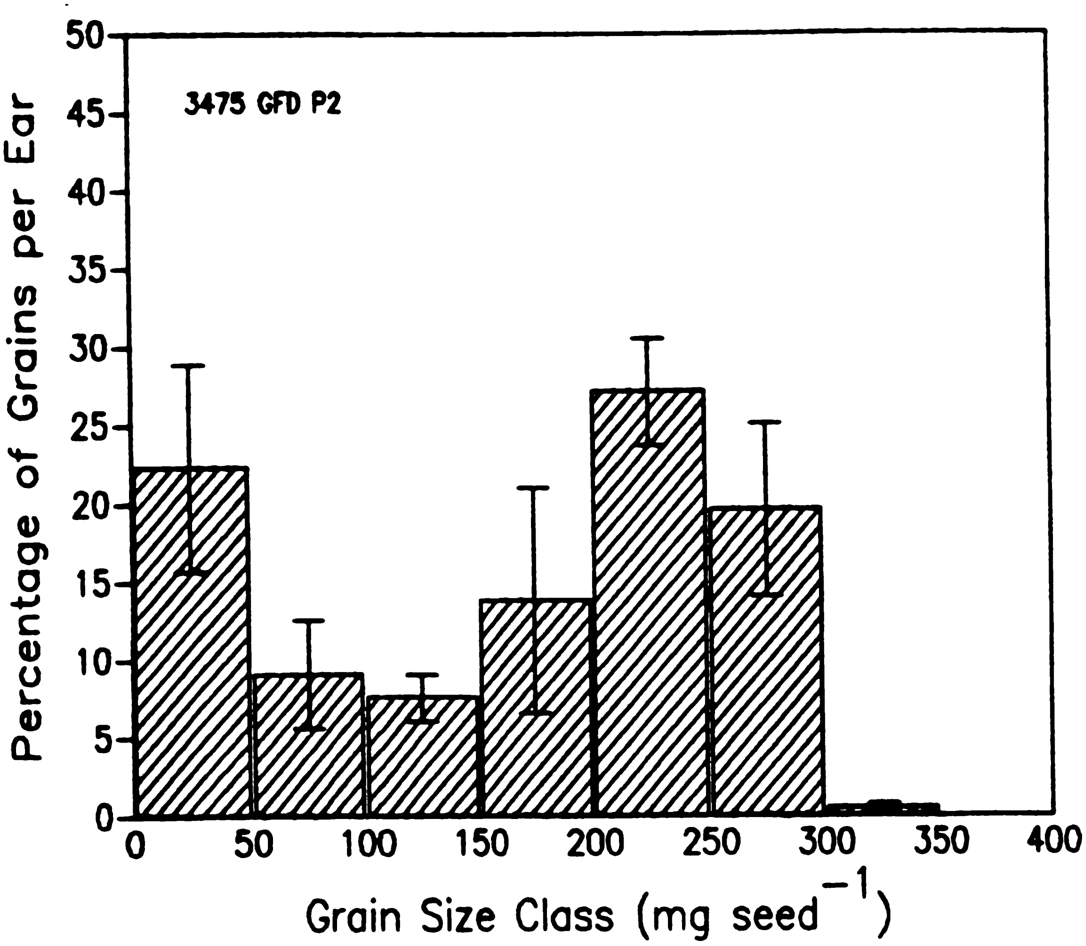

Figure 5.16f. Grain size distribution on single ears at harvest for the hybrid 3475 GFD P2 treatment.

weighing less than 100 mg and a smaller number in the range weighing greater than 200 mg. Effects on GFD P2 plants were more pronounced than on GFD P1 plants. The seeds less than 100 mg were smaller and less developed, and usually they were near the tip of the ear and were not really mechanically harvestable. If these were not considered, final grain weights would not have been as greatly different among treatments, however, grain number would have been more so. Claassen and Shaw (1970) also indicated grain size calculation varied considerably depending on whether all grains or only those more developed were regarded. The knowledge of which grains are used in size determination is helpful in comparing experiments and would be beneficial in using research work for crop model validation.

In summary, results have shown that soil water deficits during grain filling reduced green leaf area and crop and grain growth substantially for two corn hybrids. The effect on yield and yield components was dependent on how early in the grain filling process the deficit occurred. The nearer it was to the beginning of grain filling, the greater the reductions in grain number and yield were. Later deficits reduced primarily grain weight. Grain weight reductions were generally caused by a shortened linear grain filling period, although, one hybrid demonstrated a marked influence on rate of filling as well. Grain number reductions were magnified when less developed seeds (those less than 100 mg) were accounted for through grain size distributions. These results suggest it is critical in managing crop water supply through irrigation to avoid water deficits from flowering until linear grain filling so that maximum kernel number can be achieved.

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SUMMARY AND CONCLUSIONS

Results from these experiments have shown that potential reductions in the use of water on irrigated corn are dependent on the growth stage of the crop. Periods of 18 to 21 days without water on a sandy soil caused yield losses of 15 % to 25 % when the deficit occurred during pre-anthesis, as great as 90 % when the deficit occurred during anthesis, and 25 % to 40 % when the deficit occurred during the grain filling period. These yield reductions indicate that pre-anthesis is the stage when modifications in the use of water are the most feasible, however, water deficit periods of duration similar to that in these experiments are not recommended as yield loss was too great at any growth stage.

Water deficits during pre-anthesis growth reduced plant extension growth substantially, resulting in reduced plant size including leaf area. A correlation between extension growth and water absorption from the upper 0.25 m of soil was observed. Further investigations would be helpful in identifying reasons for this correlation. Some evidence indicated nitrogen uptake hinderance under deficit conditions could be linked to the extension growth reductions, yet the data were limited and inconclusive. Research is needed in the area of nutrient uptake under field water deficit conditions. Also, literature suggests that hormonal signals derived from the root system in response to soil drying exist which regulate above ground plant growth. The current experiments did not prove or disprove such signals, however, the correlation with surface soil drying, where roots are highly concentrated, and reductions in plant extension growth lend support to the concept.

The time period from just before anthesis until linear grain filling was identified as being the most crucial to obtaining maximum kernel number. Achieving a substantial number of kernels to be filled was necessary in securing high yields as compensation in grain weight was minimal for water deficit plants which had reduced grain numbers. Timely emergence of tassels and silks appeared to be necessary in obtaining adequate pollination. Additionally, ear extension growth was identified to occur over a finite period of time, and interruption of this process was detrimental to yields.

The linear grain filling period was shortened under water deficit conditions, and rate of grain filling was reduced for one of the hybrids studied. These alterations in grain filling caused yield losses through lower final grain weights. Examination of crop growth rate and grain growth rate in response to water deficits during the grain filling period showed the former was decreased more than the latter.

Apparently, translocation of assimilates was less affected by water shortages than was production of assimilates. One hybrid maintained a higher crop growth rate to grain growth rate ratio longer than the other, however, this did not lead to superior yields. No evaluation of root growth and respiration was made for the grain filling water deficit experiment, and this would be an area for focus of future research in order to determine continuous whole plant carbon balance during this growth stage.

Above ground biomass accumulation was highly dependent on the production and maintenance of green leaf area. Differences in crop growth rate under deficit conditions could be attributed largely to less production or increased loss of plant leaf area. Limited information on leaf rolling and light interception demonstrated that these were important in the observed alterations in crop growth rate of water deficit plants. It was concluded that an assessment of the "effective" leaf area under stress conditions is necessary in interpreting biomass accumulation results. Research is needed in this area, especially in order to decipher how to better model the plant carbon balance under diverse environments. Additionally, root growth data revealed increased partitioning of carbon to roots of stressed plants, as rapid proliferation at deeper depths occurred in response to a paucity of water.

Large, consistent differences in response to water deficits between the hybrids used in this investigation did not occur, especially in final yield. Most differences were related to slightly different development of the cultivars. Differences of 3 to 4 days in silking and beginning grain filling are significant when plants are under deficit conditions. It is important when comparing cultivar responses to environmental conditions to insure that developmental stages are not different. The use of staggered planting dates to acquire similarly developing plants of different hybrids appears to be useful in determining which observed plant responses are genetic and which are developmentally derived.

Careful management of crops at specific growth stages may offer the possibility of reducing applications of water in more humid regions with acceptable yield losses. Periods of water deficit less than 10 days may have little affect on crop yields during certain growth stages, especially prior to anthesis. Irrigation strategies which allow short periods of water deficits, or that apply smaller quantities of water at each application, appear to be those that will be successful in reducing water use and maintaining production. These strategies need to be optimized through computer analysis to determine the risks involved so that management decisions can be made.

APPENDICES

Appendix 1. Weather data for the 1987 growing season at the Kellogg Biological Station.

Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
133	May	13	24.5	1.3	14.1	29.6
134	May	14	28.1	13.8	19.6	14.1
135	May	15	21.9	6.2	14.4	29.5
136	May	16	25.6	5.7	15.8	28.5
137	May	17	29.3	12.1	21.3	28.4
138	May	18	22.6	10.9	16.6	5.3
139	May	19	18.3	10.8	14.1	10.0
140	May	20	27.6	14.7	19.3	16.8
141	May	21	30.9	18.5	23.3	24.0
142	May	22	25.2	12.8	19.5	23.9
143	May	23	14.5	6.2	11.6	11.8
144	May	24	17.8	4.6	11.2	11.6
145	May	25	22.9	8.4	14.9	16.1
146	May	26	29.5	15.2	21.7	24.4
147	May	27	31.2	18.1	24.6	26.2
148	May	28	31.4	19.7	25.4	28.0
149	May	29	31.7	19.5	25.8	28.1
150	May	30	31.2	18.3	24.0	20.0
151	May	31	29.6	18.3	23.3	26.1
152	June	1	26.9	16.5	21.3	18.9
153	June	2	28.1	18.7	21.8	15.7
154	June	3	25.5	16.5	20.8	30.3
155	June	4	22.0	9.4	15.9	31.1
156	June	5	27.0	7.7	18.2	29.9
157	June	6	28.3	11.4	19.4	16.4
158	June	7	30.8	17.3	24.2	25.5
159	June	8	26.9	17.0	23.2	17.0
160	June	9	22.6	10.0	16.6	31.1
161	June	10	25.6	5.9	15.9	26.8
162	June	11	28.7	12.5	19.4	18.5
163	June	12	30.7	19.2	23.7	21.8
164	June	13	31.9	16.0	24.0	28.9
165	June	14	35.5	16.6	26.3	29.7
166	June	15	33.7	18.4	25.4	30.7
167	June	16	34.5	12.5	24.2	30.6
168	June	17	34.8	16.5	25.6	28.8
169	June	18	36.7	15.6	25.9	28.9

Appendix 1 (cont.)

Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
170	June	19	37.1	15.7	26.0	23.3
171	June	20	29.0	20.7	22.1	5.3
172	June	21	27.3	20.5	22.3	13.1
173	June	22	23.1	17.5	20.3	8.9
174	June	23	30.9	16.3	23.1	27.6
175	June	24	31.3	16.8	23.4	24.8
176	June	25	30.1	17.9	22.1	18.9
177	June	26	23.8	15.0	19.5	27.1
178	June	27	21.0	13.8	17.0	22.2
179	June	28	26.6	12.1	19.5	25.4
180	June	29	27.3	16.1	21.3	15.1
181	June	30	23.9	18.1	20.3	13.2
182	July	1	23.5	14.6	18.4	9.5
183	July	2	29.1	15.0	21.0	24.5
184	July	3	28.4	17.2	22.5	26.5
185	July	4	28.5	12.0	20.0	26.1
186	July	5	25.0	14.1	18.7	10.0
187	July	6	28.0	18.0	22.0	12.7
188	July	7	30.8	18.6	24.1	24.2
189	July	8	31.4	20.5	25.3	21.6
190	July	9	31.9	19.0	24.8	18.8
191	July	10	31.3	20.6	25.0	18.3
192	July	11	31.3	19.9	25.8	22.6
193	July	12	32.4	22.0	26.0	23.8
194	July	13	28.3	17.4	21.7	14.3
195	July	14	22.5	10.3	16.5	25.0
196	July	15	15.3	8.2	11.7	4.9
197	July	16	27.1	11.3	18.4	27.2
198	July	17	28.8	12.5	21.3	26.0
199	July	18	31.3	17.9	24.7	25.8
200	July	19	31.7	19.9	26.0	22.3
201	July	20	34.0	19.1	27.0	23.7
202	July	21	30.9	18.9	24.3	26.5
203	July	22	32.5	19.1	25.5	23.7
204	July	23	32.2	20.0	25.7	20.0
205	July	24	32.0	21.7	26.4	20.9
206	July	25	32.2	21.4	26.0	24.8
207	July	26	29.1	18.4	23.6	20.9
208	July	27	30.6	13.5	21.0	22.2
209	July	28	27.2	12.1	20.0	16.4
210	July	29	30.8	13.4	20.6	19.0
211	July	30	32.3	16.5	23.7	22.5
212	July	31	33.1	18.5	25.0	23.8
213	Aug.	1	32.3	21.2	25.0	15.9
214	Aug.	2	32.4	22.9	26.8	21.6

Appendix 1 (cont.)

Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
215	Aug.	3	34.1	18.3	26.1	26.0
216	Aug.	4	29.8	18.3	23.9	20.1
217	Aug.	5	28.0	13.9	20.0	19.8
218	Aug.	6	28.8	12.9	20.6	25.1
219	Aug.	7	30.6	15.2	22.7	24.0
220	Aug.	8	21.4	18.0	19.5	4.7
221	Aug.	9	28.2	18.5	22.0	15.1
222	Aug.	10	27.8	16.8	20.7	17.1
223	Aug.	11	30.0	13.5	21.1	24.4
224	Aug.	12	30.6	13.9	21.7	21.2
225	Aug.	13	31.2	15.0	23.2	21.3
226	Aug.	14	27.2	21.0	23.6	6.7
227	Aug.	15	31.9	22.8	26.5	20.3
228	Aug.	16	30.5	18.9	24.3	13.0
229	Aug.	17	28.6	17.7	24.2	24.1
230	Aug.	18	25.8	13.5	18.2	14.0
231	Aug.	19	24.8	13.1	19.0	24.2
232	Aug.	20	28.0	11.5	19.1	23.0
233	Aug.	21	28.8	17.3	22.4	18.9
234	Aug.	22	24.1	12.6	20.9	17.9
235	Aug.	23	20.9	10.1	15.3	20.4
236	Aug.	24	21.9	8.3	14.4	23.6
237	Aug.	25	20.1	8.2	13.7	12.3
238	Aug.	26	15.2	12.3	13.6	1.5
239	Aug.	27	15.6	13.6	14.6	2.6
240	Aug.	28	17.9	13.4	15.1	5.7
241	Aug.	29	23.2	9.3	16.5	22.4
242	Aug.	30	26.5	12.9	19.2	19.1
243	Aug.	31	20.7	8.5	15.6	20.7
244	Sept.	1	21.1	8.5	15.0	21.3
245	Sept.	2	21.5	11.1	15.4	20.2
246	Sept.	3	23.9	6.2	14.6	21.6
247	Sept.	4	27.0	7.3	16.7	22.1
248	Sept.	5	29.4	10.0	19.4	18.5
249	Sept.	6	28.3	14.9	21.3	18.9
250	Sept.	7	29.4	15.6	21.9	16.4
251	Sept.	8	22.7	15.7	18.6	6.0
252	Sept.	9	25.3	13.6	18.6	19.7
253	Sept.	10	27.9	11.6	18.9	18.2
254	Sept.	11	26.4	15.9	19.8	17.2
255	Sept.	12	25.8	13.9	18.7	18.5
256	Sept.	13	21.4	9.9	15.4	15.0
257	Sept.	14	24.9	6.3	14.7	21.0
258	Sept.	15	24.6	11.2	16.7	11.2
259	Sept.	16	21.6	16.0	18.3	4.8
260	Sept.	17	24.7	17.1	18.8	8.2

Appendix 1 (cont.)

Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
261	Sept.	18	17.6	15.1	16.4	3.3
262	Sept.	19	21.6	12.4	16.7	18.2
263	Sept.	20	17.3	9.5	12.4	7.4
264	Sept.	21	15.4	10.4	12.0	6.9
265	Sept.	22	19.4	9.4	12.8	9.7
266	Sept.	23	21.1	8.9	14.9	16.4
267	Sept.	24	20.4	9.5	14.9	17.4
268	Sept.	25	18.6	2.6	10.4	18.8
269	Sept.	26	24.4	7.7	15.0	17.6
270	Sept.	27	27.2	11.5	18.7	14.0
271	Sept.	28	26.6	12.7	18.8	13.4
272	Sept.	29	21.2	12.5	16.4	10.6
273	Sept.	30	17.0	6.8	11.8	12.2
274	Oct.	1	17.7	1.0	9.9	14.7
275	Oct.	2	14.7	4.2	9.1	7.0
276	Oct.	3	10.3	1.5	5.0	13.8
277	Oct.	4	17.1	-0.2	8.4	16.1
278	Oct.	5	16.8	6.9	11.0	9.5
279	Oct.	6	10.5	4.0	8.8	4.6
280	Oct.	7	7.6	2.6	5.1	5.2
281	Oct.	8	11.6	0.3	4.7	9.1
282	Oct.	9	14.8	4.3	9.2	11.7
283	Oct.	10	9.6	2.9	5.7	5.8
284	Oct.	11	9.4	-0.9	4.4	7.4
285	Oct.	12	12.5	-3.1	3.6	10.8
286	Oct.	13	15.6	-3.8	5.3	14.4
287	Oct.	14	18.4	3.1	9.7	11.0
288	Oct.	15	21.3	7.4	13.0	12.4
289	Oct.	16	21.2	3.6	12.3	10.9
290	Oct.	17	15.1	8.4	10.2	3.1
291	Oct.	18	18.0	5.8	10.8	13.4
292	Oct.	19	13.1	4.5	7.8	4.7
293	Oct.	20	9.5	2.4	5.4	6.8
294	Oct.	21	4.8	0.3	2.5	3.2
295	Oct.	22	5.5	0.2	2.6	1.5
296	Oct.	23	11.0	-0.3	5.4	11.8
297	Oct.	24	5.4	-1.7	2.2	2.1
298	Oct.	25	12.6	-4.2	3.0	13.1
299	Oct.	26	11.9	-2.6	4.3	9.1
300	Oct.	27	11.0	1.6	6.5	10.6

Appendix 2. Weather data for the 1988 growing season at the Kellogg Biological Station.

Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
112	April	21	9.78	-3.92	2.93	21.27
113	April	22	15.71	0.33	7.30	22.95
114	April	23	14.97	1.84	5.60	6.97
115	April	24	10.98	1.58	5.18	20.57
116	April	25	16.63	-3.41	7.93	23.79
117	April	26	16.95	5.34	10.90	16.47
118	April	27	10.25	2.50	4.53	4.56
119	April	28	13.60	2.22	6.91	22.50
120	April	29	17.28	1.13	8.48	25.33
121	April	30	20.44	2.46	11.35	27.28
122	May	1	22.40	1.05	12.61	27.81
123	May	2	23.38	4.02	14.58	28.15
124	May	3	18.99	4.31	11.63	20.44
125	May	4	19.39	1.75	10.70	23.08
126	May	5	22.01	4.35	13.17	21.77
127	May	6	26.31	5.43	16.47	28.21
128	May	7	25.64	6.58	16.55	23.26
129	May	8	27.50	13.13	18.94	19.68
130	May	9	18.14	11.43	13.67	13.38
131	May	10	15.04	7.98	12.31	9.16
132	May	11	20.78	1.47	11.58	28.87
133	May	12	24.02	8.49	16.23	20.68
134	May	13	19.43	8.61	15.45	28.46
135	May	14	23.87	4.16	14.04	28.51
136	May	15	26.82	11.57	16.97	12.89
137	May	16	18.88	9.92	14.11	26.37
138	May	17	21.49	8.33	13.37	25.18
139	May	18	24.84	5.96	15.27	28.88
140	May	19	24.81	7.43	16.16	21.59
141	May	20	26.16	13.20	18.47	20.75
142	May	21	27.68	13.85	19.77	18.43
143	May	22	31.64	11.99	22.31	25.61
144	May	23	20.75	16.15	17.56	5.26
145	May	24	21.18	5.96	14.83	28.00
146	May	25	18.81	1.41	9.53	30.21
147	May	26	24.11	2.36	14.52	29.82
148	May	27	27.50	11.51	19.74	29.09

Appendix 2 (cont.)

Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
149	May	28	29.83	10.77	20.63	22.92
150	May	29	31.06	14.59	22.74	28.17
151	May	30	31.58	12.31	22.56	27.83
152	May	31	34.03	12.50	22.77	28.83
153	June	1	32.45	14.55	23.69	27.96
154	June	2	20.42	9.38	13.25	11.31
155	June	3	22.26	5.77	13.73	28.89
156	June	4	24.42	4.44	15.22	30.32
157	June	5	29.28	10.80	20.35	28.94
158	June	6	31.70	16.33	23.51	28.89
159	June	7	31.77	16.07	23.87	29.53
160	June	8	24.58	7.74	16.29	26.63
161	June	9	20.65	4.00	12.11	30.21
162	June	10	22.73	4.35	14.22	30.52
163	June	11	26.68	4.54	17.00	29.17
164	June	12	30.33	11.08	21.81	30.15
165	June	13	33.45	15.02	24.25	29.27
166	June	14	34.12	19.18	26.48	27.69
167	June	15	32.41	20.28	25.56	26.72
168	June	16	29.46	14.55	21.18	26.55
169	June	17	30.33	11.62	20.66	25.42
170	June	18	32.93	11.10	22.27	30.30
171	June	19	32.65	17.76	25.13	25.96
172	June	20	32.85	19.57	25.75	24.73
173	June	21	35.85	16.06	26.22	27.23
174	June	22	33.67	21.18	26.64	15.19
175	June	23	29.28	13.21	21.42	30.77
176	June	24	29.16	13.70	21.63	24.97
177	June	25	35.82	22.04	28.29	27.62
178	June	26	25.89	13.18	18.65	24.30
179	June	27	29.06	10.08	19.15	29.85
180	June	28	24.13	12.49	16.82	8.47
181	June	29	25.27	11.06	18.02	31.46
182	June	30	25.37	7.38	17.06	28.69
183	July	1	25.63	6.82	17.12	26.93
184	July	2	28.99	7.57	18.69	29.28
185	July	3	31.82	7.82	20.78	28.75
186	July	4	34.62	10.71	23.71	28.36
187	July	5	37.74	14.43	26.37	26.23
188	July	6	38.58	15.89	27.27	25.73
189	July	7	37.89	17.65	27.46	21.88
190	July	8	35.65	18.75	27.04	25.09
191	July	9	35.09	17.21	26.53	24.07
192	July	10	29.01	20.08	22.71	12.54
193	July	11	29.73	17.12	22.93	26.57
194	July	12	30.43	11.67	21.47	26.91

Appendix 2 (cont.)

Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
195	July	13	32.16	11.85	23.15	25.55
196	July	14	33.30	20.48	27.22	28.39
197	July	15	37.13	14.98	23.33	17.37
198	July	16	34.98	20.65	26.64	17.61
199	July	17	32.66	20.04	24.77	25.29
200	July	18	24.61	18.72	21.48	4.46
201	July	19	31.07	18.43	23.71	21.97
202	July	20	24.57	16.48	20.09	8.91
203	July	21	28.14	15.79	21.14	20.74
204	July	22	29.84	15.90	19.67	16.12
205	July	23	30.09	14.04	19.62	20.70
206	July	24	28.88	13.45	21.05	26.87
207	July	25	27.91	17.26	21.42	17.53
208	July	26	28.40	14.44	20.81	24.61
209	July	27	29.64	13.40	21.60	23.94
210	July	28	33.07	19.59	25.85	26.92
211	July	29	32.24	19.90	26.08	25.72
212	July	30	30.27	20.67	24.91	17.59
213	July	31	31.21	15.27	23.27	23.97
214	Aug.	1	36.76	20.63	28.07	25.94
215	Aug.	2	35.51	23.16	29.18	24.53
216	Aug.	3	35.94	22.17	27.55	19.66
217	Aug.	4	34.40	21.67	27.86	20.76
218	Aug.	5	31.77	21.26	24.53	10.39
219	Aug.	6	29.21	18.30	23.67	26.34
220	Aug.	7	32.56	15.58	23.92	26.74
221	Aug.	8	31.93	18.10	25.01	21.74
222	Aug.	9	28.84	21.62	24.34	11.17
223	Aug.	10	29.98	19.75	23.67	11.84
224	Aug.	11	30.81	19.57	24.71	19.39
225	Aug.	12	32.82	20.87	26.65	20.61
226	Aug.	13	31.90	22.35	26.66	20.50
227	Aug.	14	32.32	18.47	27.60	21.23
228	Aug.	15	31.43	18.78	24.79	24.46
229	Aug.	16	32.85	15.68	24.33	21.54
230	Aug.	17	34.03	22.83	28.69	23.76
231	Aug.	18	22.79	15.44	20.29	5.48
232	Aug.	19	23.05	14.73	17.98	7.51
233	Aug.	20	27.26	13.83	20.19	24.39
234	Aug.	21	27.51	12.16	19.18	23.71
235	Aug.	22	24.58	11.05	17.65	18.01
236	Aug.	23	25.02	14.31	18.44	13.20
237	Aug.	24	24.24	15.73	19.17	19.76
238	Aug.	25	23.53	15.00	18.81	22.98
239	Aug.	26	23.35	10.83	17.25	22.30
240	Aug.	27	20.96	9.14	14.32	6.09

Appendix 2 (cont.)

Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
241	Aug.	28	21.85	10.67	16.82	19.74
242	Aug.	29	21.77	6.08	14.16	22.57
243	Aug.	30	23.92	8.21	15.73	21.78
244	Aug.	31	26.58	11.35	18.44	21.86
245	Sept.	1	27.42	10.33	19.01	21.22
246	Sept.	2	27.92	12.64	20.66	14.76
247	Sept.	3	25.04	15.86	19.44	11.94
248	Sept.	4	22.77	13.72	16.71	11.97
249	Sept.	5	16.52	7.85	11.89	17.46
250	Sept.	6	18.30	3.51	10.48	18.02
251	Sept.	7	21.70	3.03	12.38	22.09
252	Sept.	8	23.39	8.78	15.89	19.48
253	Sept.	9	25.21	9.38	18.62	21.46
254	Sept.	10	26.36	7.33	16.39	17.90
255	Sept.	11	27.46	10.48	18.08	17.50
256	Sept.	12	26.03	17.16	20.47	10.00
257	Sept.	13	20.94	10.11	16.64	18.71
258	Sept.	14	23.94	8.69	15.35	20.63
259	Sept.	15	22.97	5.89	14.20	19.81
260	Sept.	16	24.30	7.44	15.58	13.50
261	Sept.	17	28.61	18.18	22.04	11.77
262	Sept.	18	25.73	17.48	19.74	6.08
263	Sept.	19	21.12	13.74	18.07	3.29
264	Sept.	20	14.32	11.77	12.96	2.43
265	Sept.	21	14.43	10.75	12.43	5.41
266	Sept.	22	19.49	10.58	14.59	4.84
267	Sept.	23	19.59	8.51	15.79	17.91
268	Sept.	24	21.70	4.85	12.16	17.24
269	Sept.	25	21.93	4.63	12.89	18.15
270	Sept.	26	23.33	6.83	14.49	16.45
271	Sept.	27	25.64	12.93	18.03	13.50
272	Sept.	28	15.96	10.10	12.63	6.70
273	Sept.	29	23.93	8.14	14.85	13.37
274	Sept.	30	24.79	11.36	17.44	8.72
275	Oct.	1	22.67	16.13	18.54	5.51
276	Oct.	2	17.20	7.59	12.49	7.42
277	Oct.	3	15.63	4.51	8.82	16.97
278	Oct.	4	10.47	3.97	6.73	10.05
279	Oct.	5	12.40	1.74	6.01	13.75
280	Oct.	6	13.15	-1.76	5.08	10.85
281	Oct.	7	13.98	-0.32	6.46	13.84
282	Oct.	8	16.81	5.91	9.91	10.92
283	Oct.	9	16.69	6.64	10.13	11.63
284	Oct.	10	16.65	6.16	10.92	10.44
285	Oct.	11	7.91	2.08	4.49	7.24

Appendix 3. Weather data for the 1989 growing season at the Kellogg Biological Station.

Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
91	April	1	6.9	-3.0	2.1	17.2
92	April	2	11.1	5.1	6.8	6.7
93	April	3	10.3	5.4	7.5	5.4
94	April	4	16.8	4.3	9.5	19.0
95	April	5	5.1	0.8	3.7	4.6
96	April	6	9.5	-0.2	3.9	16.0
97	April	7	8.5	-2.4	2.5	15.7
98	April	8	9.4	-2.2	1.8	11.4
99	April	9	-0.7	-6.5	-3.4	11.0
100	April	10	0.8	-9.5	-3.9	13.8
101	April	11	7.8	-6.8	0.7	19.4
102	April	12	6.6	-1.0	2.4	9.2
103	April	13	9.9	-3.1	2.8	24.7
104	April	14	13.2	1.0	7.3	7.9
105	April	15	17.1	0.7	8.6	22.0
106	April	16	20.2	-1.0	10.2	23.4
107	April	17	16.4	3.2	10.8	8.8
108	April	18	8.0	-0.5	3.0	9.8
109	April	19	13.5	-0.9	5.5	25.3
110	April	20	19.4	0.7	9.9	20.9
111	April	21	18.3	6.0	10.3	16.6
112	April	22	16.4	5.4	9.7	16.2
113	April	23	16.7	-0.9	7.6	25.9
114	April	24	20.9	0.0	10.6	24.3
115	April	25	27.4	9.2	16.9	21.3
116	April	26	24.0	11.6	17.1	24.1
117	April	27	22.7	9.7	14.6	18.3
118	April	28	11.1	6.7	9.1	4.4
119	April	29	17.6	6.4	10.0	10.8
120	April	30	14.5	5.2	9.4	24.5
121	May	1	16.6	2.1	9.2	23.0
122	May	2	8.4	2.7	5.9	7.6
123	May	3	16.9	1.9	8.9	27.0
124	May	4	19.5	6.1	12.0	21.8
125	May	5	16.3	5.3	11.4	20.8
126	May	6	6.8	-2.3	2.4	12.3
127	May	7	8.6	-4.1	2.4	25.1

Appendix 3 (cont.)

Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
128	May	8	16.5	-0.4	8.0	17.8
129	May	9	16.9	6.6	11.7	21.0
130	May	10	18.5	0.9	10.3	27.7
131	May	11	17.3	2.7	9.4	29.1
132	May	12	15.5	6.1	9.7	8.9
133	May	13	16.3	6.6	9.5	9.3
134	May	14	18.4	5.8	11.2	15.2
135	May	15	16.9	8.2	11.7	12.9
136	May	16	24.9	5.1	14.3	23.5
137	May	17	27.3	5.7	17.1	26.4
138	May	18	24.1	10.1	18.3	14.9
139	May	19	20.5	15.3	17.7	5.0
140	May	20	21.2	11.1	16.7	9.8
141	May	21	24.6	8.9	16.5	29.1
142	May	22	27.2	7.1	17.0	21.1
143	May	23	26.8	11.1	18.6	29.8
144	May	24	26.3	10.3	18.7	19.8
145	May	25	23.7	14.4	19.2	13.9
146	May	26	22.7	11.2	18.1	29.1
147	May	27	17.4	8.2	12.4	27.3
148	May	28	21.4	2.3	12.9	28.2
149	May	29	21.3	8.2	15.1	15.1
150	May	30	27.5	17.1	20.9	15.6
151	May	31	27.8	17.3	20.7	10.9
152	June	1	24.5	17.2	19.1	12.4
153	June	2	25.2	14.2	19.7	29.9
154	June	3	20.7	13.8	16.9	7.7
155	June	4	22.8	10.3	16.5	29.2
156	June	5	24.2	10.7	17.1	20.9
157	June	6	27.6	10.0	19.7	28.3
158	June	7	29.6	15.5	22.3	26.7
159	June	8	28.1	15.8	21.6	20.2
160	June	9	23.3	11.5	17.4	21.9
161	June	10	19.8	10.1	13.5	19.8
162	June	11	25.6	5.0	15.9	29.9
163	June	12	17.0	14.8	15.6	5.5
164	June	13	22.2	14.5	17.5	10.6
165	June	14	24.1	13.7	16.9	14.9
166	June	15	19.1	10.7	15.0	12.5
167	June	16	13.8	10.0	11.6	6.9
168	June	17	23.1	10.0	16.7	24.8
169	June	18	25.9	14.3	20.1	26.8
170	June	19	21.9	16.8	19.4	7.4
171	June	20	25.9	15.9	19.2	17.7
172	June	21	28.4	13.7	19.7	21.5
173	June	22	28.2	16.0	21.2	12.7

Appendix 3 (cont.)

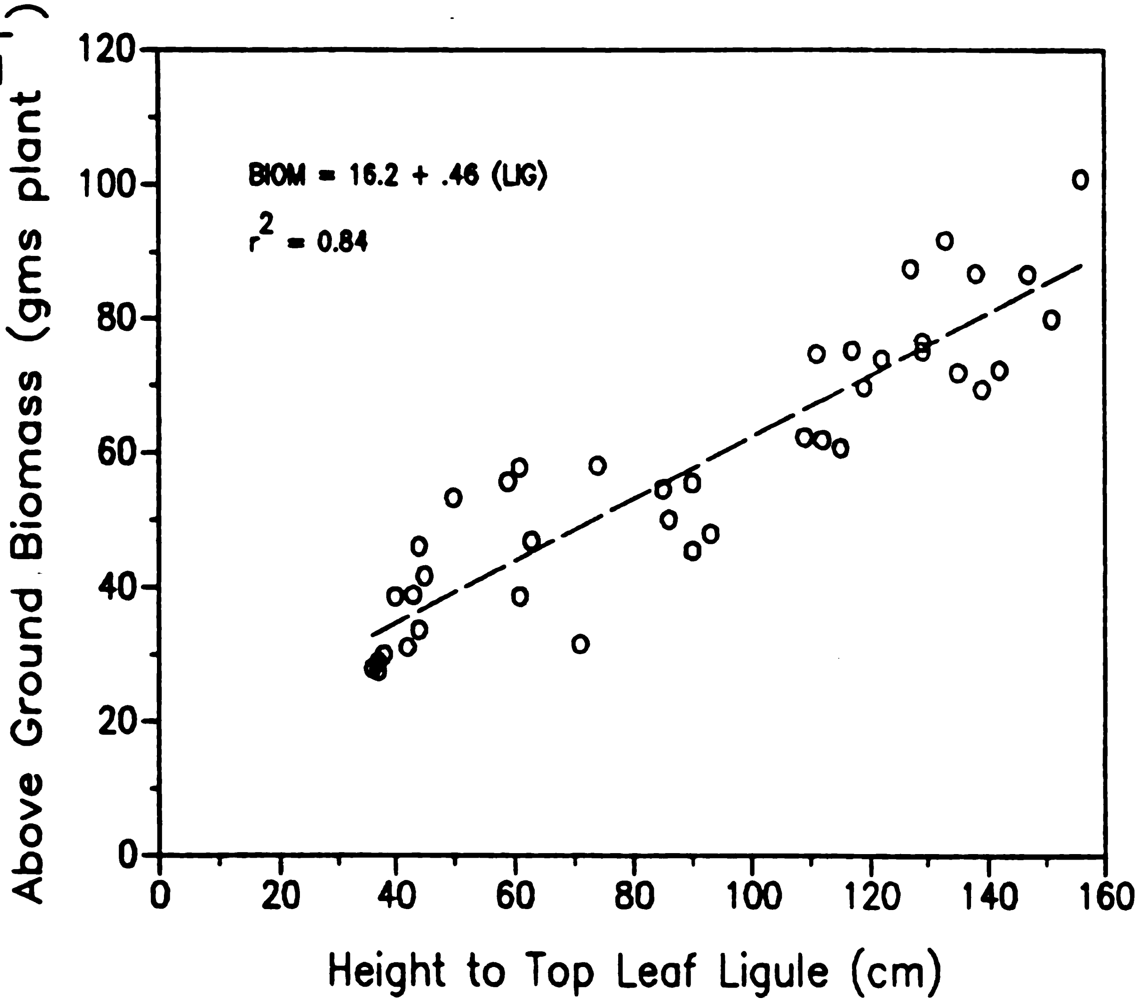
Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
174	June	23	32.2	18.1	23.3	21.1
175	June	24	30.8	18.2	24.0	27.0
176	June	25	33.9	17.5	24.4	26.7
177	June	26	32.0	19.0	23.7	19.8
178	June	27	24.2	18.2	20.7	8.3
179	June	28	24.5	15.0	19.9	29.1
180	June	29	24.5	7.8	16.4	30.4
181	June	30	27.4	8.5	18.1	30.0
182	July	1	29.8	10.9	20.7	28.9
183	July	2	30.9	15.4	22.1	22.1
184	July	3	28.5	17.8	22.7	23.8
185	July	4	31.7	17.0	23.9	24.0
186	July	5	30.4	17.5	23.8	25.7
187	July	6	32.5	18.1	25.0	26.7
188	July	7	29.9	17.9	24.1	27.0
189	July	8	28.7	14.3	22.1	22.0
190	July	9	31.0	19.6	25.1	22.5
191	July	10	31.5	24.3	27.7	25.2
192	July	11	31.1	18.5	23.5	18.4
193	July	12	24.5	15.5	19.8	12.1
194	July	13	26.1	15.1	19.3	14.7
195	July	14	26.6	11.8	18.7	28.1
196	July	15	27.2	11.5	18.7	21.8
197	July	16	28.2	11.4	19.9	21.9
198	July	17	28.5	12.4	20.7	26.6
199	July	18	28.9	13.1	21.0	20.0
200	July	19	22.7	17.2	19.0	7.6
201	July	20	19.9	15.9	17.7	5.1
202	July	21	25.4	16.3	19.8	11.2
203	July	22	30.5	16.7	22.9	22.5
204	July	23	31.4	17.1	24.0	25.9
205	July	24	32.5	18.9	25.1	18.0
206	July	25	30.7	20.2	24.0	14.9
207	July	26	31.0	20.0	25.1	22.8
208	July	27	29.1	18.8	24.0	17.0
209	July	28	26.0	14.4	20.2	19.8
210	July	29	25.8	9.1	17.7	21.5
211	July	30	19.6	15.4	17.6	5.8
212	July	31	28.7	13.2	20.5	22.8
213	Aug.	1	29.8	14.5	22.0	23.5
214	Aug.	2	28.6	15.3	22.0	24.7
215	Aug.	3	31.6	17.4	24.6	21.3
216	Aug.	4	29.4	21.7	25.1	16.6
217	Aug.	5	29.3	18.7	23.9	24.1
218	Aug.	6	24.0	10.0	18.2	15.6
219	Aug.	7	19.8	7.7	12.7	23.3

Appendix 3 (cont.)

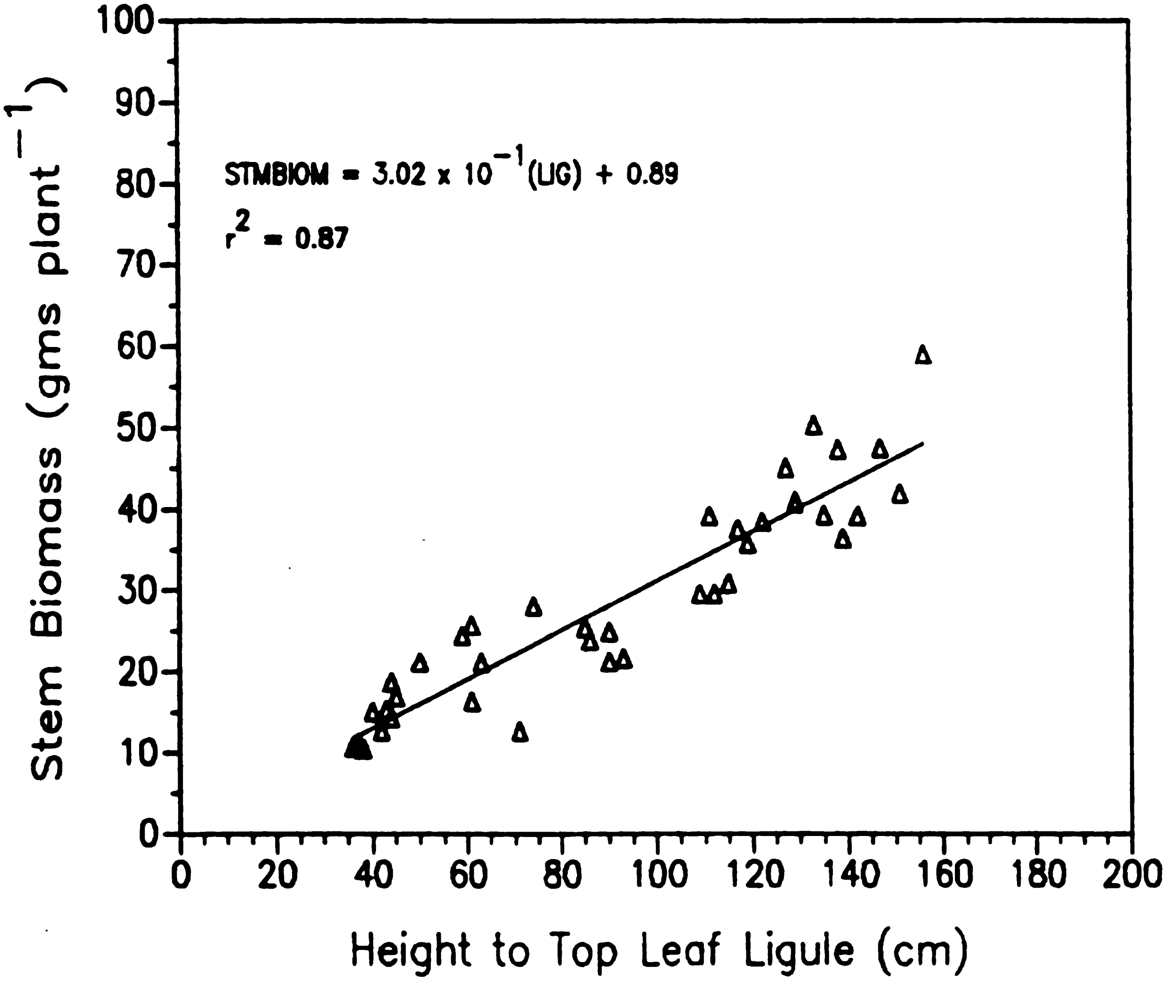
Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
220	Aug.	8	24.0	5.7	15.1	22.0
221	Aug.	9	26.0	11.0	18.5	20.8
222	Aug.	10	27.8	12.6	18.6	15.8
223	Aug.	11	29.4	12.4	19.9	18.2
224	Aug.	12	27.4	13.7	19.6	14.3
225	Aug.	13	27.6	13.4	20.3	22.0
226	Aug.	14	27.4	15.4	20.1	16.1
227	Aug.	15	25.6	15.9	19.9	15.4
228	Aug.	16	24.1	12.7	17.6	18.5
229	Aug.	17	27.2	10.6	18.6	24.3
230	Aug.	18	25.8	10.0	17.5	20.5
231	Aug.	19	27.5	10.2	18.4	21.5
232	Aug.	20	27.2	16.9	20.9	15.0
233	Aug.	21	28.0	17.1	22.0	24.0
234	Aug.	22	27.4	16.9	21.9	13.8
235	Aug.	23	22.7	17.3	20.5	9.7
236	Aug.	24	25.9	13.3	18.8	20.2
237	Aug.	25	27.0	9.2	17.7	21.9
238	Aug.	26	28.8	11.2	19.5	22.5
239	Aug.	27	29.8	16.4	21.9	17.5
240	Aug.	28	25.2	16.4	20.7	6.0
241	Aug.	29	26.4	19.8	22.2	8.0
242	Aug.	30	25.2	15.1	19.5	23.0
243	Aug.	31	27.0	12.5	19.5	17.1
244	Sept.	1	25.2	17.3	20.4	13.7
245	Sept.	2	23.9	9.9	16.7	20.0
246	Sept.	3	25.7	8.9	16.4	20.7
247	Sept.	4	24.1	10.0	16.9	19.0
248	Sept.	5	27.6	15.4	20.4	15.4
249	Sept.	6	23.7	18.1	20.7	5.2
250	Sept.	7	28.8	18.3	22.1	13.2
251	Sept.	8	29.0	19.8	22.2	9.8
252	Sept.	9	27.0	17.7	21.3	10.7
253	Sept.	10	23.7	13.3	17.7	14.3
254	Sept.	11	24.2	10.7	16.7	11.6
255	Sept.	12	20.6	11.3	15.6	19.6
256	Sept.	13	11.2	8.9	10.1	1.9
257	Sept.	14	12.4	8.7	10.7	2.4
258	Sept.	15	21.7	4.8	12.6	20.8
259	Sept.	16	14.1	8.8	11.7	3.7
260	Sept.	17	23.9	6.1	14.7	18.9
261	Sept.	18	25.1	6.4	15.1	19.0
262	Sept.	19	25.5	6.9	15.6	18.3
263	Sept.	20	26.1	7.5	15.8	17.3
264	Sept.	21	26.2	8.1	16.7	15.0
265	Sept.	22	23.6	9.3	18.3	8.7

Appendix 3 (cont.)

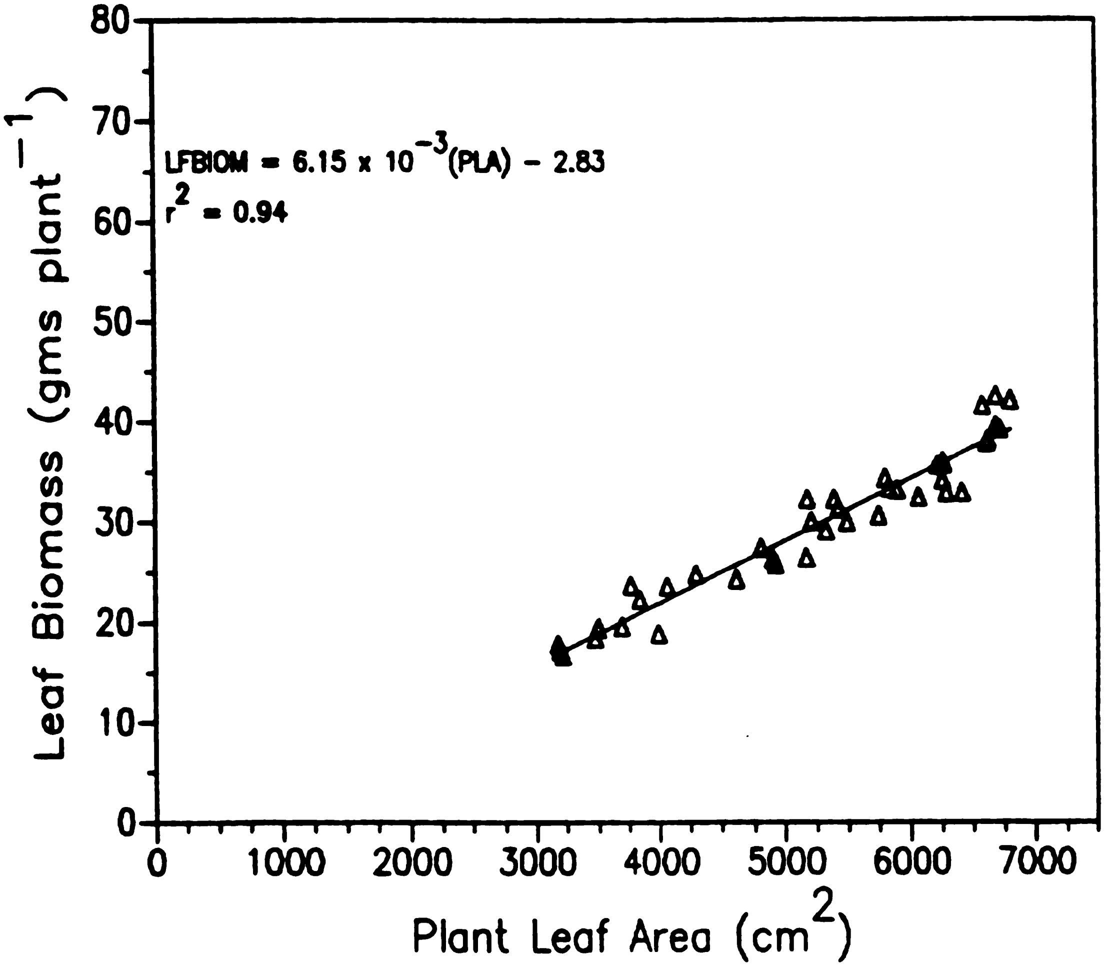
Day of Year	Mo.	Day	Air High Temp. (°C)	Air Low Temp. (°C)	Air Mean Temp. (°C)	Solar Radiation (MJ m^{-2})
266	Sept.	23	11.0	2.2	6.4	13.3
267	Sept.	24	16.9	-1.9	6.3	18.6
268	Sept.	25	18.9	-0.2	9.4	18.4
269	Sept.	26	14.9	3.5	9.4	17.0
270	Sept.	27	17.8	-1.5	7.3	18.2
271	Sept.	28	21.1	3.6	11.5	17.7
272	Sept.	29	22.9	9.8	15.8	17.0
273	Sept.	30	22.8	3.9	12.8	17.1
274	Oct.	1	26.1	7.1	15.3	15.3
275	Oct.	2	19.0	7.7	14.7	3.8
276	Oct.	3	11.7	0.0	6.9	15.3
277	Oct.	4	15.0	-3.1	5.3	16.6
278	Oct.	5	17.4	0.1	9.0	7.9
279	Oct.	6	15.1	7.8	11.5	10.2
280	Oct.	7	9.6	2.9	6.6	6.9
281	Oct.	8	11.2	-2.0	3.9	11.1
282	Oct.	9	11.5	-5.5	3.0	13.1
283	Oct.	10	11.5	5.7	8.5	4.0
284	Oct.	11	20.5	1.9	11.8	14.8
285	Oct.	12	24.4	4.4	15.7	15.3
286	Oct.	13	27.2	1.7	12.8	14.6
287	Oct.	14	28.8	9.0	17.3	12.6
288	Oct.	15	28.1	9.8	18.0	10.7
289	Oct.	16	21.8	7.3	14.6	6.3
290	Oct.	17	7.3	2.4	3.9	2.2
291	Oct.	18	6.3	-1.5	1.5	9.0
292	Oct.	19	0.8	-0.9	0.1	2.2
293	Oct.	20	3.2	-0.1	1.0	3.0
294	Oct.	21	20.4	-2.4	6.4	4.4



Appendix 4. Relationship between above ground biomass and height to the top leaf ligule from data taken during 1989.



Appendix 5. Relationship between stem biomass and height to the top leaf ligule from data taken during 1989.



Appendix 6. Relationship between leaf biomass and plant leaf area from data taken during 1989.