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EFFECT OF SOIL WATER DEFICITS ON THE GROWTH AND DEVELOPMENT OF DRY BEANS (*Phaseoulus vulgaris* L.) AT DIFFERENT STAGES OF GROWTH

By

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ABSTRACT

EFFECT OF SOIL WATER DEFICITS ON THE GROWTH AND DEVELOPMENT OF DRY BEANS (<u>Phaseoulus</u> <u>vulgaris</u> L.) AT DIFFERENT STAGES OF GROWTH

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Soil dehydration adversely affects crop productivity. An increased understanding of the whole plant response to water deficits is a prerequisite to increase production under water-limited environments. A rain shelter facility and two different-textured soils (sandy and loamy) were used to impose terminal drought on dry beans at various growth stages under field conditions. Results indicated that in the sandy soil water deficits hastened flowering and seed filling while delaying leaf appearance. In both soils, the deficits diminished leaf and pod expansion resulting in a small plant size. The duration of leaf growth and internode elongation was not affected as much as the growth rate of these organs. Changes in leaf area due to reduced leaf growth and accelerated leaf senescence appear to be one of the main mechanisms by which dry bean plants adapted to the declining soil water availability. Flowers and pod abscision were greater in the stress treatments decreasing final yield and harvest index. Photosynthetic rates were reduced to a lesser extent than stomatal conductances during progressive soil dehydration. Paraheliotropic leaf movement decreased light interception in a diurnal cycle. Above ground dry matter production was linearly related to the intercepted photosynthetic active radiation. However, the efficiency of energy conversion was slightly lower for the deficit treatments. Rapid root expansion was observed at the beginning of the water deficits followed by root death and compensatory root growth in deeper soil layers. Difference in rooting patterns changed the amount and timing of water extraction at various soil depths.

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INTRODUCTION

Environmental stresses may reduce crop yield to levels that are a third of the potential production in intensive agriculture, and to much lower values in less intensive systems such as those in developing countries (Vaadia, 1984). The extent of yield losses to disease is estimated to be about 12%, and the loss to insects can be as high or higher depending on the year, crop, and management practice (James, 1981). However, unfavorable physicochemical factors such as water shortages have one of the most detrimental effects on crop production. Boyer and McPherson (1975) estimated that low water availability may account for 50% of the decrease in yield observed in the main crops grown in the USA.

In semiarid zones, water deficits may depress yield by more than 80% as compared to irrigated conditions (Fisher and Turner, 1978). Countries like Mexico have a large proportion of its agricultural land (75%) under poor rainfed conditions (Acosta, 1988). Common bean, which originated in the Americas (Gentry, 1969), is an important crop in dryland farming that provides most of the protein consumed by low income families (Adams, et al., 1985).

Solving production constraints in this water-limited environment is a difficult task to achieve. For instance, genetic improvement programs have largely focused on the selection and breeding of genotypes solely based on grain yields. Temporal distribution of available water from year to year, however, influences the expression of different characters related to crop performance and yield. In addition, management practices that increase yield, often fail to account for the temporal and spatial variability of rain and crop water availability during the growing season. The strategies adopted by the plants in response to the changes in soil water content are also not well known.

In general, there are three basic strategies through which plants cope with limiting water regimes; escape, avoidance, and tolerance (Levitt, 1972). Plants may escape drought conditions by rapid growth and development, completing their life cycle before the water supply is exhausted. The avoidance strategy is related to plants more sensitive to dehydration. The plants avoid water deficits whenever they occur. Plants may also have tissues that tolerate water deficiencies. However, it is recognized that plants generally may posses a wide range of responses that include the use of several strategies at the same time (Fisher and Ludlow, 1984). An increased understanding of a whole plant response to water deficits is needed to improve crop productivity. One of the most important factors to consider is the phenological stage of growth at the time of the deficit. Ludlow and Muchow (1989) stated that genotypic variation in growth duration is one of the most obvious means of matching seasonal transpiration with the supply of water in the soil profile. They outlined several alternatives to explore. For instance, early flowering tends to give higher yield and greater yield stability than later flowering if rain does not occur during the later half of the growing season. Developing short season varieties may provide benefits for higher crop production. However, the sensitivity of crops to stress conditions at any stage of growth varies with the degree, duration, and timing of the stress (Begg and Turner, 1976).

Early water deficits reduce the rate of leaf expansion and hence, leaf area accumulation. A reduction of leaf area in dry beans has been associated with smaller size of individual leaves rather than leaf number (Bonnano and Mack, 1983). Leaf senescence, on the other hand, is considered to be a drought avoidance mechanism that allows the plant to survive dry periods (Kramer, 1983). Rapid senescence rates, however, may be detrimental to final yield. Laing et al. (1983) found that leaf duration was correlated with the variation in seed yield.

Although temperature and photoperiod are the most important environmental stimuli for most of the phenological events, water deficits also play a role in affecting initiation of such events. Flowering is usually slightly hastened by water deficits (Turner and Begg, 1977). Water deficits during grain filling will usually hasten seed maturation and increase leaf senescence (Mott and McComb, 1975). Drought stress may also interfere with pollination and fertilization as well as with the abortion of young seeds and the abscission of young fruits (Fisher, 1973; Slatyer, 1973). This change in the number of reproductive structures may seem wasteful in terms of carbon efficiency because carbon is lost during organ abscission. This phenomenon, however, is likely the mechanism insuring adequate seed size and viable seeds at the end of the growing season. In dry beans, water deficits early in the season reduce the number of pods per plant. When the deficit occurs at flowering, pod number and number of seeds per pod is diminished. Seed weight decreased when the deficit began late in the season, during the pod filling stage (Robins and Domingo, 1956; Dubetz and Mahalle, 1969).

Stomatal conductance has been reported to have a significant effect on transpiration and photosynthetic rate under a limited supply water (O'Toole, et al., 1977). Some investigators, however, suggest that an increase in transpiration efficiency with stomatal closure rarely occurs under field conditions because of the resulting rise in leaf temperature which increases the air-leaf vapor pressure difference, lowering transpiration efficiency (Ludlow and Muchow, 1989). In some instances, stomatal conductance has a small impact on photosynthesis. Farquar and Sharkey (1982) concluded that, apart from some transient hormonal effect on rapid stomatal closure, stomatal conductance is rarely the main cause of the decrease in assimilation rate that occurs with a declining plant water supply. There is a growing consensus among crop physiologists that the decrease in plant stomatal conductance under deficit condition is related to the avoidance of desiccation (Blum, et al., 1981; Ludlow, et al., 1983).

Much of our understanding of the relationship between water deficit and plant processes has evolved from container experiments. Ritchie (1981) pointed out that differing sensitivity of various plant processes to water deficits and the unrealistic rooting volume are the primary reasons for the difference between container-grown plants and field-grown plants. He emphasized that in the field, water deficits occur gradually, allowing the plant to acclimate to the drought. Container plants lose the water supply so rapidly that they do not have this opportunity to acclimate. One of the mechanisms in drought tolerance is osmoregulation. Osmotic adjustments result from the accumulation of solutes within the cell allowing turgor driven processes, such as expansion growth and stomatal opening, to continue at reduced rates at progressively lower soil water contents (Turner and Jones, 1980; Morgan, 1984).

Under increasing soil dehydration, differences in rooting patterns may change the amount and timing of water availability to crops (Ludlow and Muchow, 1989). Deeper root systems are advantageous when water is available lower in the soil profile. When water is not replenished in lower depths by rainfall, deep rooting patterns will not be useful to improve water supply. Sometimes, investment of carbon in roots under water deficit conditions may occur at the expense of shoot growth (Hoogenboom et al., 1987).

In the context of root-shoot relationships, there is an increasing amount of information showing that root signals control leaf and stem elongation (Passioura, 1988) as well as changes in stomatal conductance (Blackman and Davies, 1985). Root signals resulting from soil water deficits may occur without significant changes in bulk leaf water status. The nature of root signals generated by a drying soil has recently been the subject of considerable speculation. A reduced supply of cytokinins, which are known to be produced in the roots, was thought to be responsible for stomatal closure in fully turgid leaves (Blackman and Davies, 1985). Other investigators have shown that abscisic acid is produced in roots in response to soil and root dehydration. When the abscisic acid moves to the leaves, it reduces extension growth and stomatal conductance (Hubick and Reid, 1988; Lachno and Backer, 1986). Root signals are important mainly because of their influence on leaf growth, light interception and hence dry matter production and economic yield.

The complexity of the different processes occurring between roots and shoots as well as their interaction with the atmospheric demand for water needs more detailed investigation at a whole plant level, especially under field conditions. This information should improve our capability to predict management strategies that optimize water use and selection of genetic material that will cope with the seasonal availability of water. This wholistic approach will improve the decision making process to increase economic yield under limited water conditions.

The objective of this investigation was to study dry bean response to water deficits imposed during different stages of growth under field conditions.

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CHAPTER 1

EFFECT OF SOIL WATER DEFICITS ON DRY BEANS (P. *vulgaris* L.). I. EXTENSION GROWTH OF LEAVES, STEMS, AND PODS.

ABSTRACT

Soil dehydration adversely affects the growth of different organs in the plant and hence, crop productivity. This study was conducted to examine the effect of water deficits on the elongation of leaves, stems, and pods under field conditions in a Spinks soil (Psammentic Hapludalfs) and a Kalamazoo soil (Typic Hapludalfs). The research was conducted in Michigan utilizing a rain shelter to control the water regimes. In 1988, an early (ES) and mid season (MS) water deficit treatment began 15 and 29 days after planting (DAP). The mid season treatment in 1989 started 27 DAP. Leaf appearance was slightly decreased by the water deficit conditions in the Spinks soil. Leaf, pods, and internode elongation were sensitive to a decrease in water content in both soils. Leaf expansion decreased when plant available water (PAW) declined by about 30%. Elongation of stem internodes lagged behind the control after about 40% of the PAW was depleted. The growth of individual pods was observed

to be less sensitive than that of leaves and internodes. However, total pod elongation was much greater in the control than in ES and MS because of an increase on pod abortion under advancing drying conditions. Total pod elongation decreased when more than 40% and 60% of PAW was depleted in the Spinks and Kalamazoo soils, respectively. In the Spinks soil, dry matter production of stems and leaves decreased by about 38%, 34% and 15% in ES, MS and LS, respectively. In the Kalmazoo soil, leaf and stem dry matter decreased by about 23% and 11% for MS and LS, respectively. Number of leaves was less affected by the deficits than the pod number. Additional information on reproductive growth is reported in Chapter 2.

INTRODUCTION

Organ expansion is one of the earliest discernible effects of soil water deficits on crop growth when compared to other plant processes (Hsiao, 1973). Processes such as stomatal conductances and photosynthesis become progressively more affected as the deficits become greater in the soil. The magnitude of the water deficit required to reduce growth varies with the timing of the deficit and the conditions under which plants are grown. Leaf extension of plants grown in pots has been found to decline at leaf water potentials below -0.2 MPa and to cease at potentials of -0.7 to -0.9 MPa (Acevedo et al., 1971; Boyer, 1970). On the other hand, field experiments have shown that a decline in leaf water potential to -1.2 MPa had little effect on the rate of leaf expansion in soybean (Bunce, 1977). For maize, Watts (1974) found that water potentials of -0.8 MPa did not decrease leaf elongation. These attempts to find a general trend relating plant water status to organ expansion have not been successful. Ludlow (1987) suggested that the lack of a unique relationship between leaf water potential and critical physiological processes has led to a greater use of measurements of soil water status to understand shoot performance. Recent investigations have indicated that plants growing in a drying soil may reduce leaf and stem elongation independently of the shoot turgidity (Passioura, 1988; Blackman and Davies, 1985). However, changes in soil water content, as well as plant water availability, are largely influenced by the physical and chemical soil conditions (Larson, et al., 1983). Russell and associates (ICRISAT, 1978) showed that a coarse-textured alfisol had less PAW and produced less dry matter than a fine-textured vertisol when compared under the same climatic conditions. More information is still needed on the water availability in the field for different soils and its effect on shoot and root growth processes during advancing drought conditions. The objective of this investigation was to study the effects of decreasing plant water availability in two contrasting soils on elongation and expansion of leaves, internodes and pods in dry bean plants.

MATERIALS AND METHODS

A field study was conducted at the Kellogg Biological Station near Kalamazoo, MI, during the summers of 1988 and 1989. Weather data for both years is reported in Appendices 2 and 3. Dry bean plants (Phaseolus vulgaris L., cv. Seafarer) were grown in a rainout shelter facility (Martin, et al., 1988). The experimental unit consisted of a plot of 6 rows, 6m long with an inter-row spacing of 0.71m. Each plot had an independent control system for irrigation. Soils types included were a Spinks sand (Psammentic Hapludalfs) with an average plant water availability of 104 mm in the upper 1.5 m profile and a Kalamazoo loamy soil (Typic Hapludalfs) with an average of about 118 mm. Plant available water (PAW) is defined as the difference between the highest volumetric water content in the field after drainage and the lowest measured water content when plants are very dry and leaves are dead or dormant (Ritchie, 1981). Some physical and chemical characteristics for both soils are described in Appendix 1. A dry bean variety (cv. Seafarer), was planted on July 8, 1988 and June 12, 1989. The variety belongs to a navy bean class, also referred to as the pea bean. Seafarer is an early bush type plant with white flowers and chalky white roundish seeds. It is resistant to both common bean mosaic and anthracnose and is widely accepted by Michigan growers because of its high yield and earliness (Adams, 1982). The two planting dates provided different thermal regimes during the seasons for beans to grow.

In the experiment, seeds were planted in excess and thinned out after emergence to a density of 16 plants/m^2. Fertilizer was applied in doses of 120 Kg/ha N, 100 Kg/ha P, and 100 Kg/ha K. Nitrogen supply was split in two applications, at planting and 20 DAP. The irrigation system (NeSmith, et al., 1990) was operated 2-3 times a week to keep the soil water content close to the drained upper limit (DUL)(Figures 1.1A and 1.1B). In 1988, soil water deficits began at 15 DAP and 29 DAP, resulting in an early season (ES) and a mid season (MS) water deficit commencing during the vegetative and flowering stages, respectively. In 1989 the mid season deficit began 27 DAP. Water content at five different soil depths (25, 50, 75, 100, 125 and 150 cm) was monitored at 7-day intervals using the neutron scattering technique. These readings provided estimates of the DUL and lower limit (LL) of plant water availability.

Leaf initiation on the main stem was recorded as soon as each small trifoliate leaf began to unfold (about 1 cm length). Three small initial leaves were selected in each treatment to determine leaf extension. Leaves were tagged at node 6 and 7 on the main stem and at node 2 of the first lateral branch, the branch emerging from the first node. Measurements were taken daily on the length (L) and width (W) of individual leaflets. Leaf area (LA) was estimated utilizing a regression equation determined for this variety using L and W:

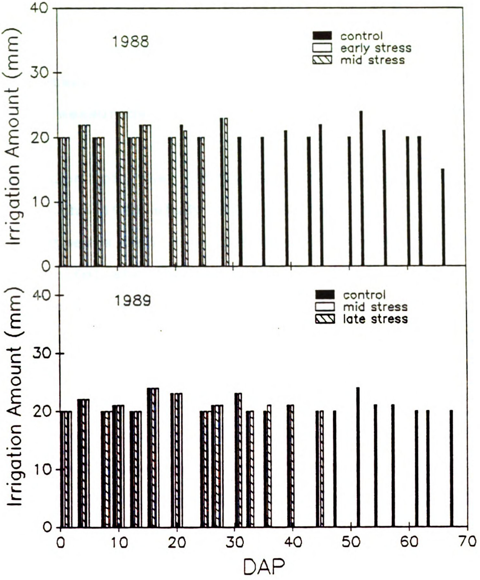

Figure 1.1. Irrigation amounts applied to different treatments during 1988 and 1989.

$$LA = 0.603 + 0.581\ (L*W), \quad (R^2 = 0.98).$$

To determine the equation, the length and width of 40 individual leaves of different sizes were correlated with the leaf area obtained in a leaf area meter (Licor, model 1500, Lincoln NB). Leaves were randomly selected from irrigated and stress treatments. This equation facilitated the non-destructive measurements of leaf area during the growing season.

Elongation of the internodes on the main stem was measured in the 1989 study only on three plants of MS and control treatments on 7-day intervals after the appearance of the third trifoliate leaf. Individual pod elongation was determined in both soils in 1989 on a daily basis for both the MS and control treatments, taking into account the position of the pod within the plant. Three different pods were selected for measurement between nodes 8 and 9 of the main stem. Total pod length was estimated at 5-day intervals using the total number of pods per plant and the average pod length. Relative extension was determined by dividing the rate of elongation of the stressed treatments by those of the control.

Dry matter production of various plant parts was measured at the end of the season. Leaves, stems, and pods from 6 plants in each treatment were separated into paper bags and dried in a forced air oven at 70 °C for 72 hours before weighing. Weather information of maximum and minimum temperature and radiation was collected near the rainout shelter using a Licor model 1200S data acquisition system.

RESULTS AND DISCUSSION

Different climatic conditions were obtained in both years by planting late in 1988 and early in 1989. In 1988, maximum and minimum temperatures as well as solar radiation tended to decrease from 42 DAP to the end of the season, reaching lower values than the ones observed in 1989 (Figures 1.2A and 1.2B). However at the beginning of the season, the same climatic factors were slightly higher in 1988 (Figures 1.3A and 1.3B).

Irrigation ceased 15 and 29 DAP in 1988, and 27 and 45 DAP in 1989, initiating a terminal water deficit at different stages of phenological development. In the first year, the soil water content for ES (Spinks soil) rapidly decreased in the upper 50 cm followed by water uptake from deeper layers 43 DAP (Figure 1.4A). Toward the end of the season, soil water content began to reach the lower limits of PAW. For the MS treatment, the pattern of water extraction was different. The decrease of soil water content in the first 15 days after the onset of the drought period was greater than those observed in ES (Figure 1.4B). However, the total water depletion in the upper 75 cm was greater for the ES than for the MS treatment. For soil depths below 75 cm, the water content in MS reached lower values than that in ES. This suggested greater root activity of ES in the upper soil layers decreasing with depth as the water deficit progressed during the season. The opposite action seemed to occur with the MS treatment (see

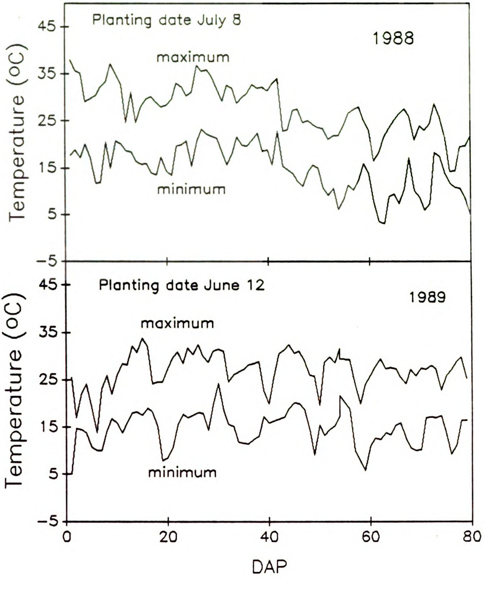

Figure 1.2. Seasonal patterns of minimum and maximum temperatures during 1988 and 1989.

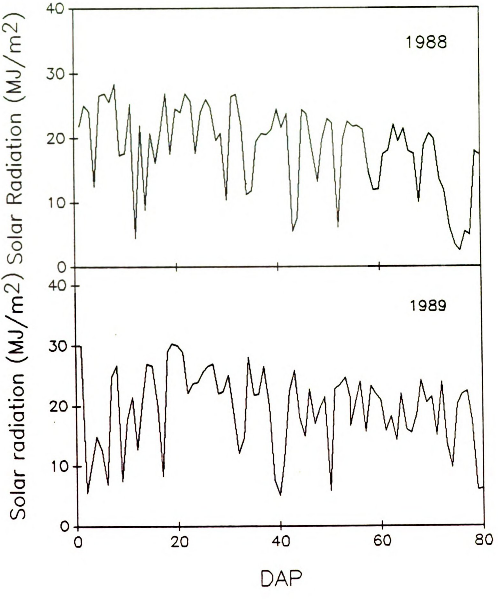

Figure 1.3. Seasonal patterns of solar radiation during 1988 and 1989.

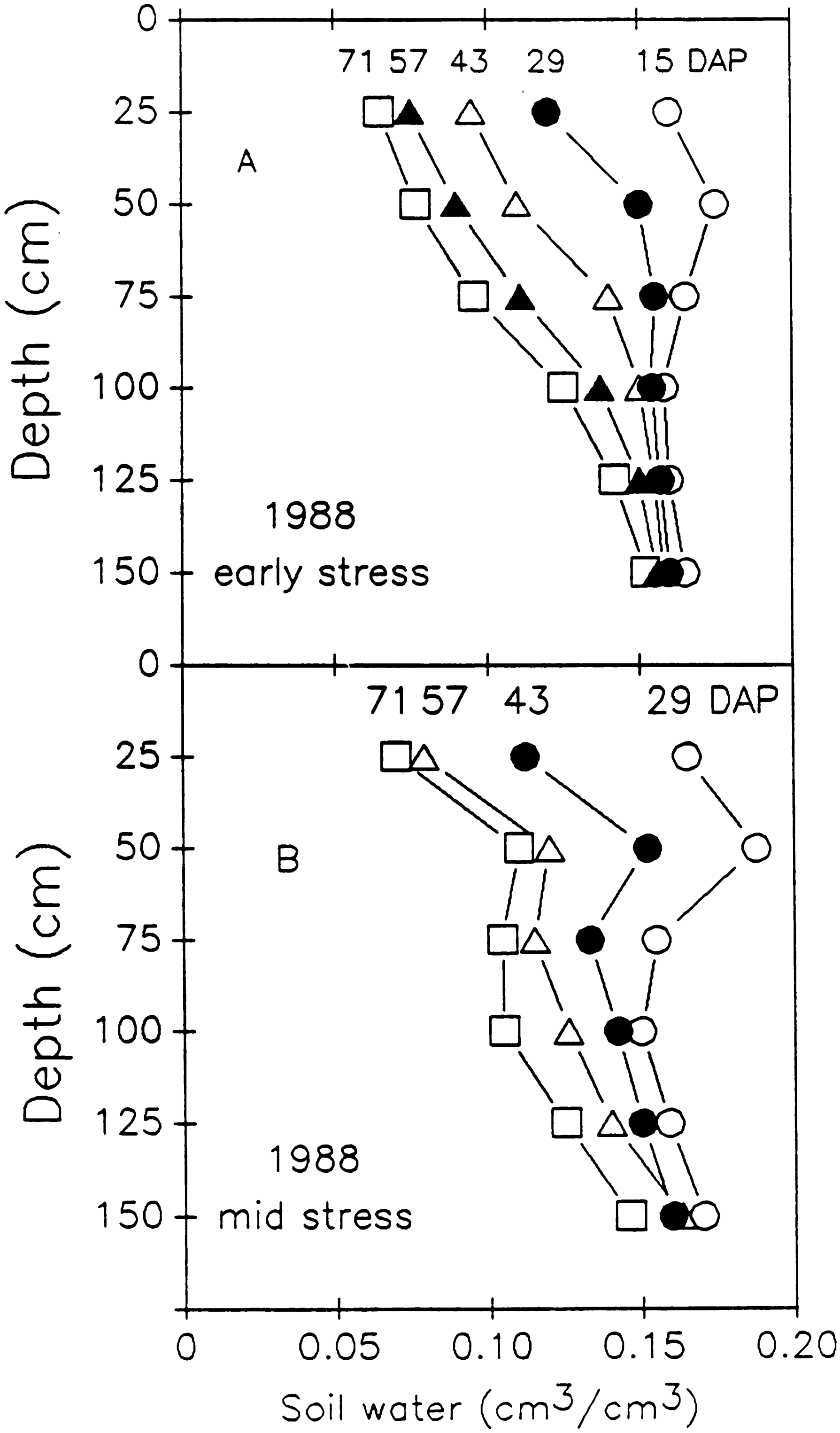

Figure 1.4. Soil water content with depth at several dates for early and mid stress treatments for Spinks soil during 1988.

Chapter 4).

In 1989, the MS treatment of the Spinks soil resembled the patterns of water extraction of those in the MS of the previous year. Rapid water depletion was observed in the top 75 cm at the beginning of the water deficit followed by increased water uptake from deeper layers as the upper soil dried out (Figure 1.5A). In the LS treatment, a greater decrease in soil water content was observed in the upper 75-100 cm 2 weeks after the last day of irrigation. By the end of the season, most of the water available to the plant was found in the region of the soil below 75 cm depth (Figure 1.5B).

In the Kalamazoo soil, both the initial soil water content after the last irrigation and the patterns of water extraction were different to those same treatments in the Spinks soil. The DUL reached average values of 0.27 cm^3/cm^3 in the top 50-75 cm. A decrease in soil water content was observed after the onset of the water deficit in both treatments (Figures 1.6A and 1.6B). By 50 DAP, soil water began to be depleted below 75 cm in the MS treatment. In contrast, changes in the water content of LS were very small below 75 cm depth.

The soil water deficits imposed in the 1988 season slightly changed leaf appearance and final number of leaves in the main stem. Leaf number in the ES treatment began to lag one leaf behind the control after the unfolding of leaf number 6. In the MS treatment, leaf number lagged behind the

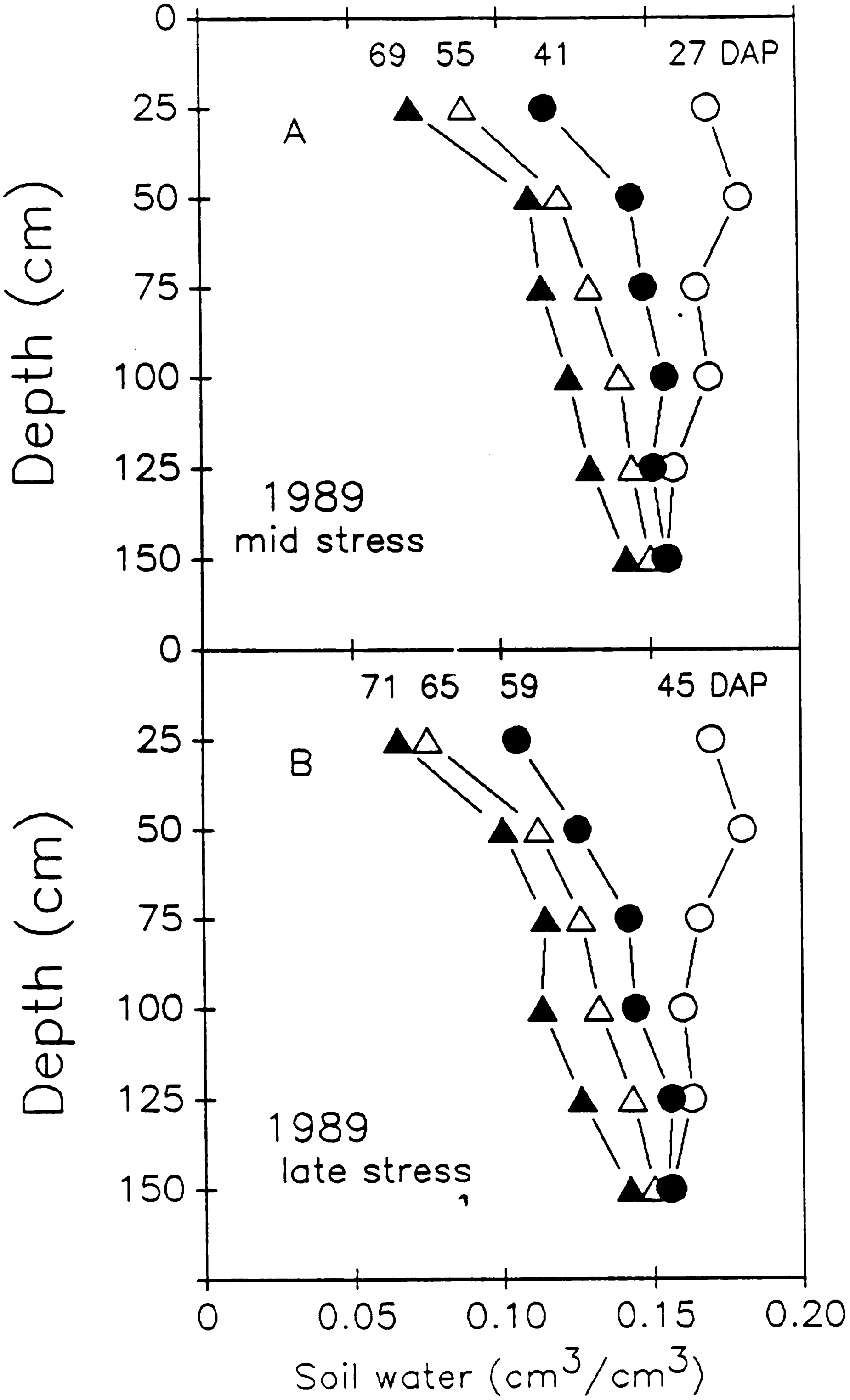

Figure 1.5. Soil water content with depth at several dates for mid and late stress treatments for Spinks soil during 1989.

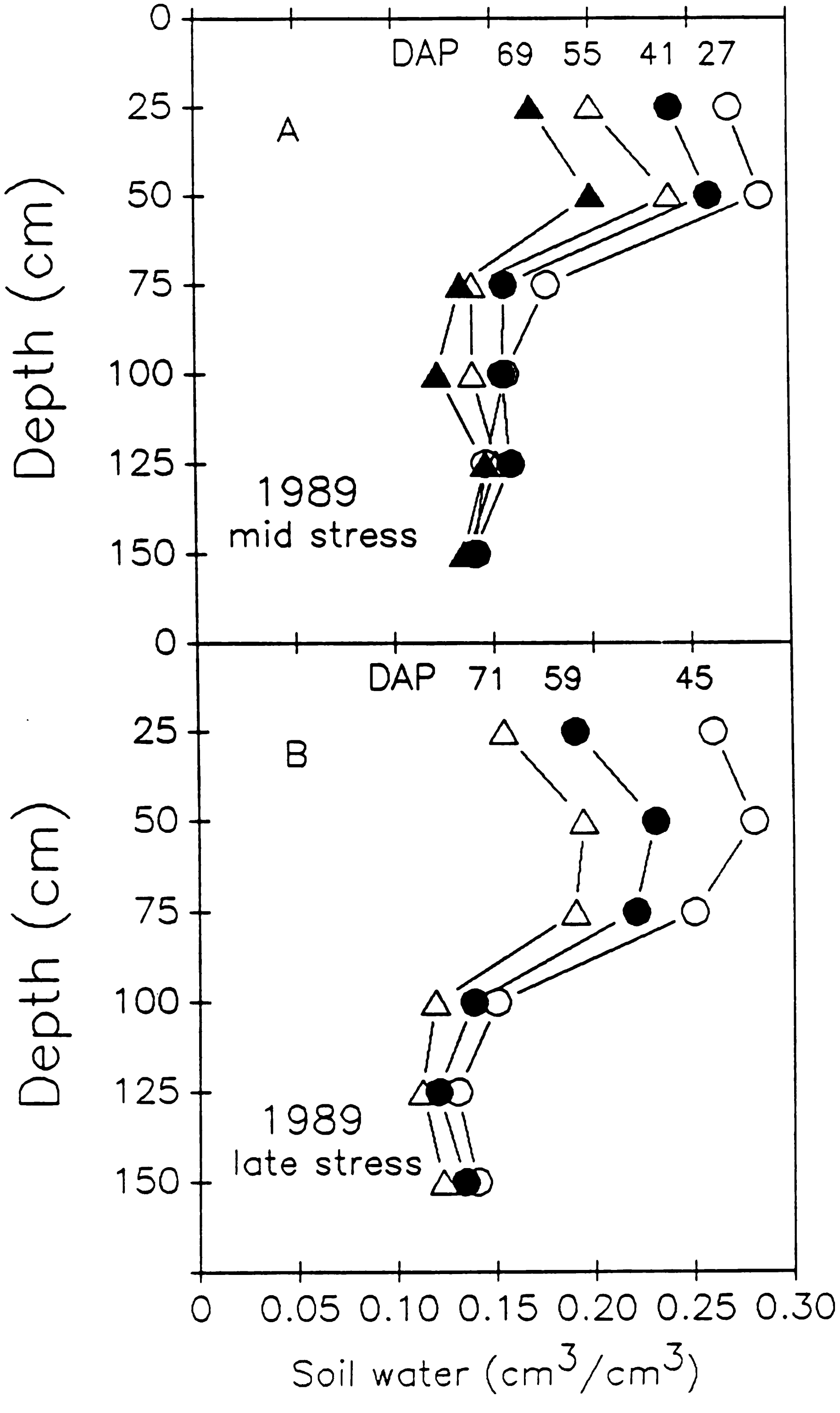

Figure 1.6. Soil water content with depth at several dates for mid and late stress treatments for Kalamazoo soil during 1989.

control by one leaf after leaf number 9 (Figure 1.7). The near-linear response observed in leaf appearance, as well as the small effect of water deficits on this process, has been shown for other legumes (Sinclair, 1984; Huck et al., 1983). Leaf appearance and other developmental events are much more influenced by temperature than by limited water conditions (Hesketh et al., 1973).

Leaf expansion was greatly affected by all water deficit treatments in both years. In 1988, leaf area in MS (leaf 6, main stem) began to differ from the control 5 days after the initiation of the soil water deficits (Figure 1.8). Leaf 6 for the ES treatment began to grow when the plants had been under stress conditions for 14 days. The rate of leaf expansion for this treatment was 5.0 cm^2/day as compared to 16.7 and 27.8 cm^2/day in the MS and control treatments, respectively. In 1989, expansion of leaves in the main stem differed from that observed in the leaves of branches (Figure 1.9). Under irrigated conditions, leaves from branches became a competitive sink for assimilates with those growing on the main stem. Leaf expansion in branches was more affected than in the main stem as soil water deficit progressed in the season, indicating a priority for the main stem. Leaf number 7 on the main stem was 70% smaller in the MS treatment than in the control and leaf area of number 2-branch decreased by about 75% when subjected to drought stress.

Under the same water deficit treatment, plants in the Kalamazoo soil had a greater rate of leaf expansion than the

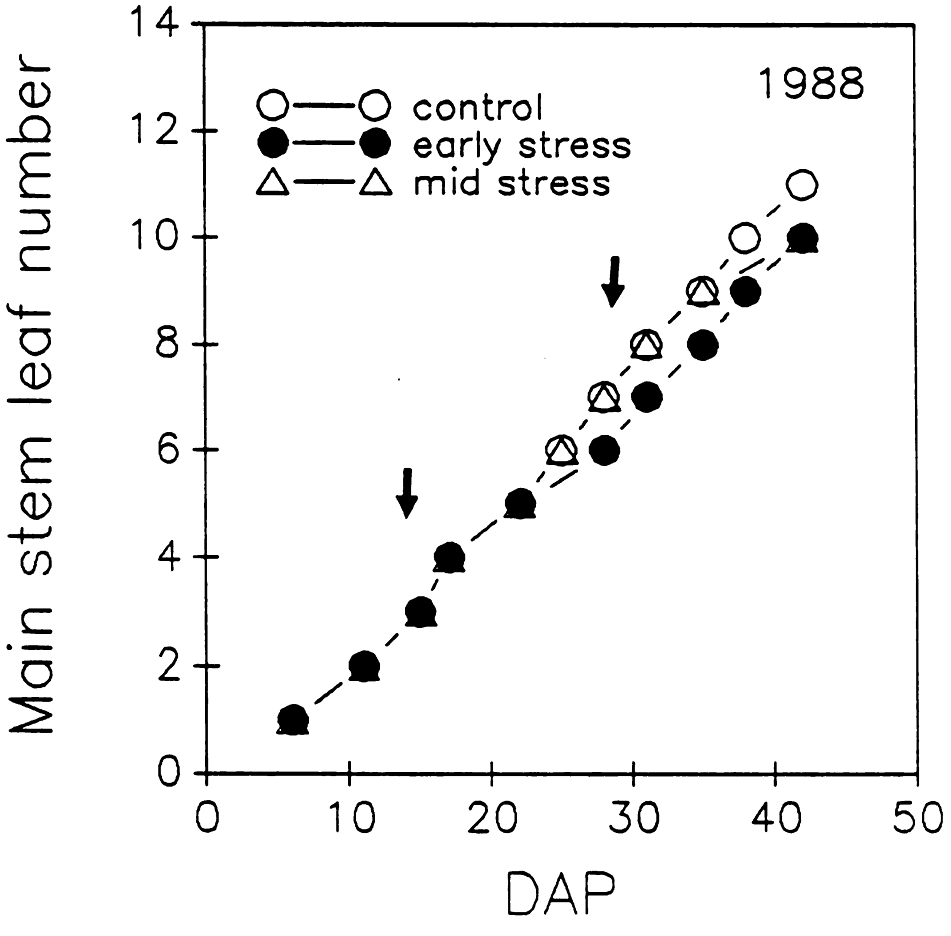

Figure 1.7. Seasonal changes in leaf appearance on the main stem for different water deficit treatments for Spinks soil during 1988. Arrows represent initiation of water deficit.

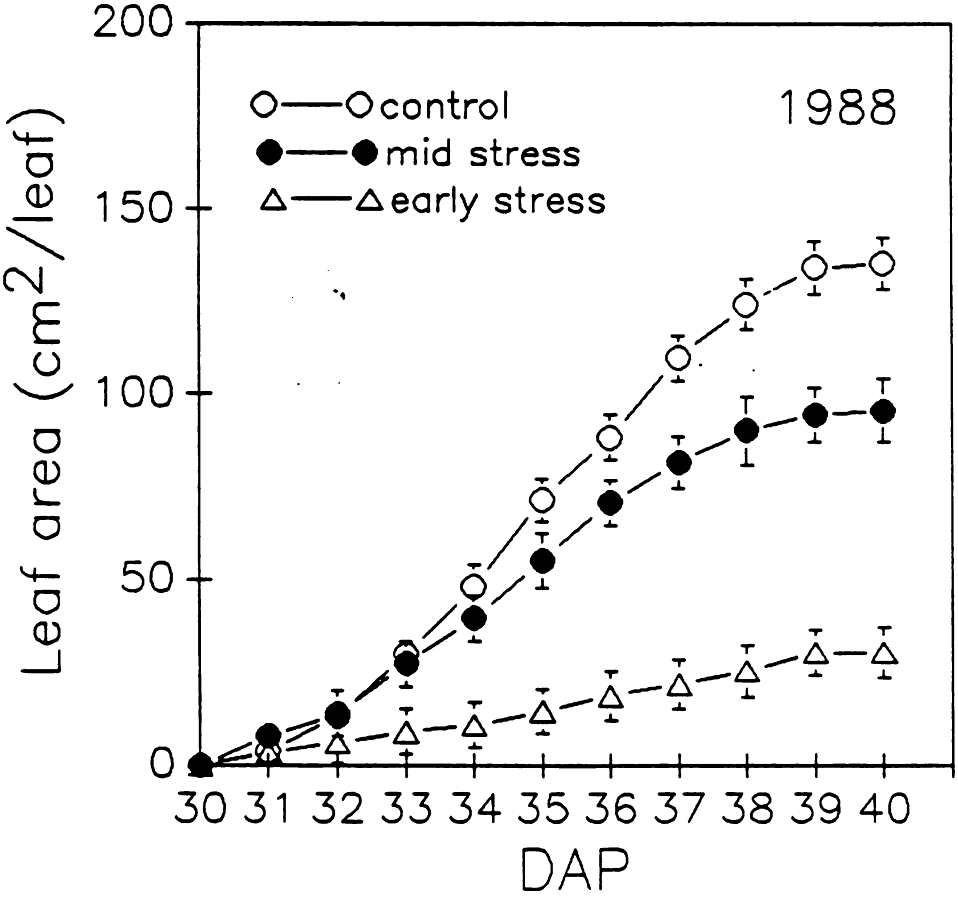

Figure 1.8. Seasonal changes in area of leaf 6 on main stem in different water deficit treatments for Spinks soil during 1988. Deficit treatments started 15 DAP for ES, and 29 DAP for MS.

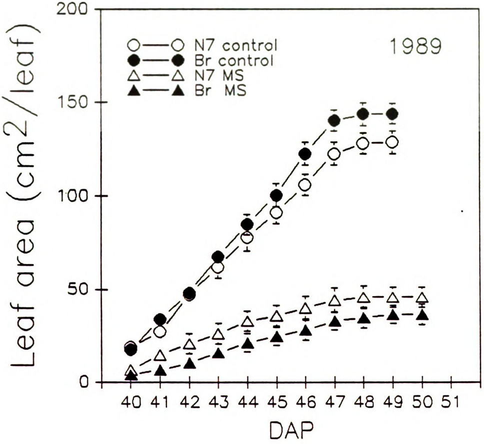

Figure 1.9. Seasonal changes in area of leaf 7 (n7) on main stem and leaf 2 (Br) on the first branch for Spinks soil during 1989. Deficit treatment started 27 DAP

comparative one in the Spinks soil (Figure 1.10). Leaf number 7 in the main stem was growing at a rate of 9.4 cm^2/day as compared to 4.7 cm^2/day observed in the one from the Spinks soil. The sensitivity of leaf expansion to soil water deficits is the result of two growth components, cell division and cell expansion (Hsiao et al., 1976). Boyer (1970) showed differing sensitivity to water deficits for the major metabolic processes in maize, soybean, and sunflower, with expansion growth being the most sensitive. Under field conditions, NeSmith (1990) found that maize growing under water deficit in a sandy soil had a measurable decrease in leaf extension within five days after withholding water. Hoogenboom et al. (1987), showed that leaf extension in soybean declined as soon as soil water potential began to fall below 0.03 MPa in the upper 40 cm of the soil.

The greater effect of soil water deficit on the extension of branch leaves resulted in different profiles of leaf area along the main stem (Figure 1.11). In general, total leaf area measured 45 DAP was greater in the first nodes decreasing toward node 10-11. The main effect of the water deficit occurred in the first nodes where most of the branches are located. In node number one, leaf area diminished by 45% and 67% for MS and ES treatments, respectively. These differences in leaf area greatly affected ground cover and light interception (Chapter 3).

The effect of soil water deficit on leaf area index (LAI) was observed in plants grown in the Spinks soil a few days

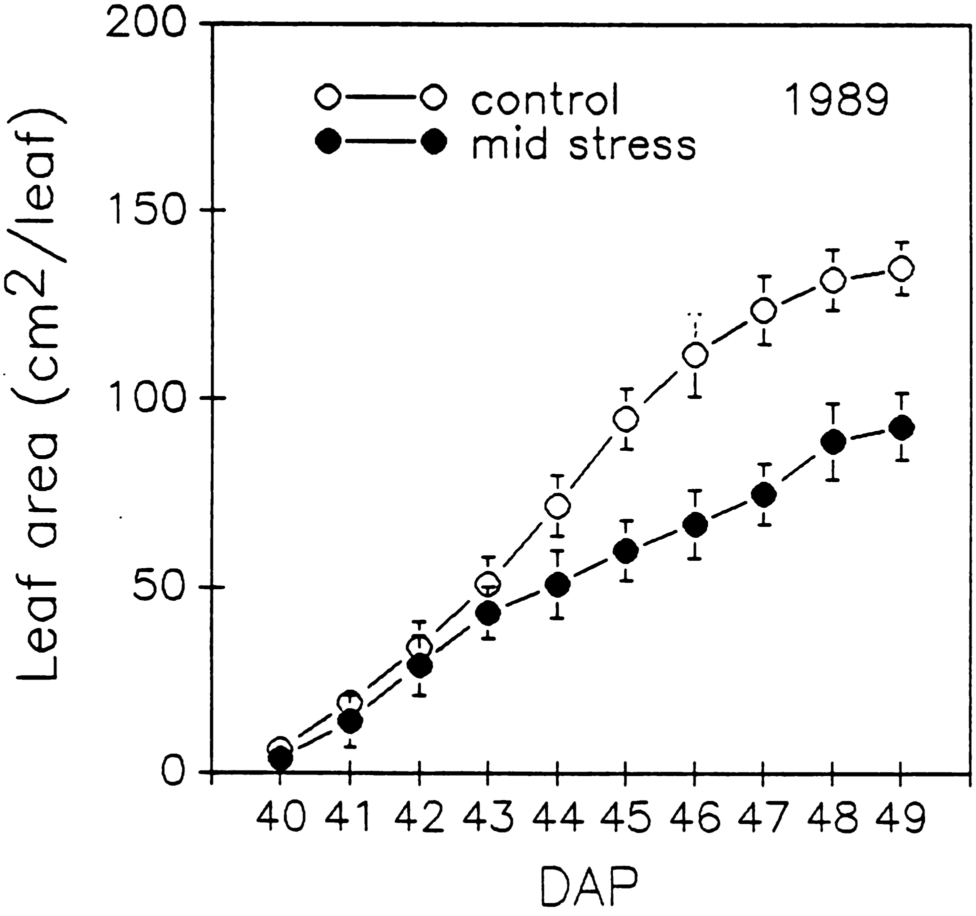

Figure 1.10 Seasonal changes in area of leaf 7 on main stem, for Kalamazoo soil during 1989. Deficit treatment started 27 DAP.

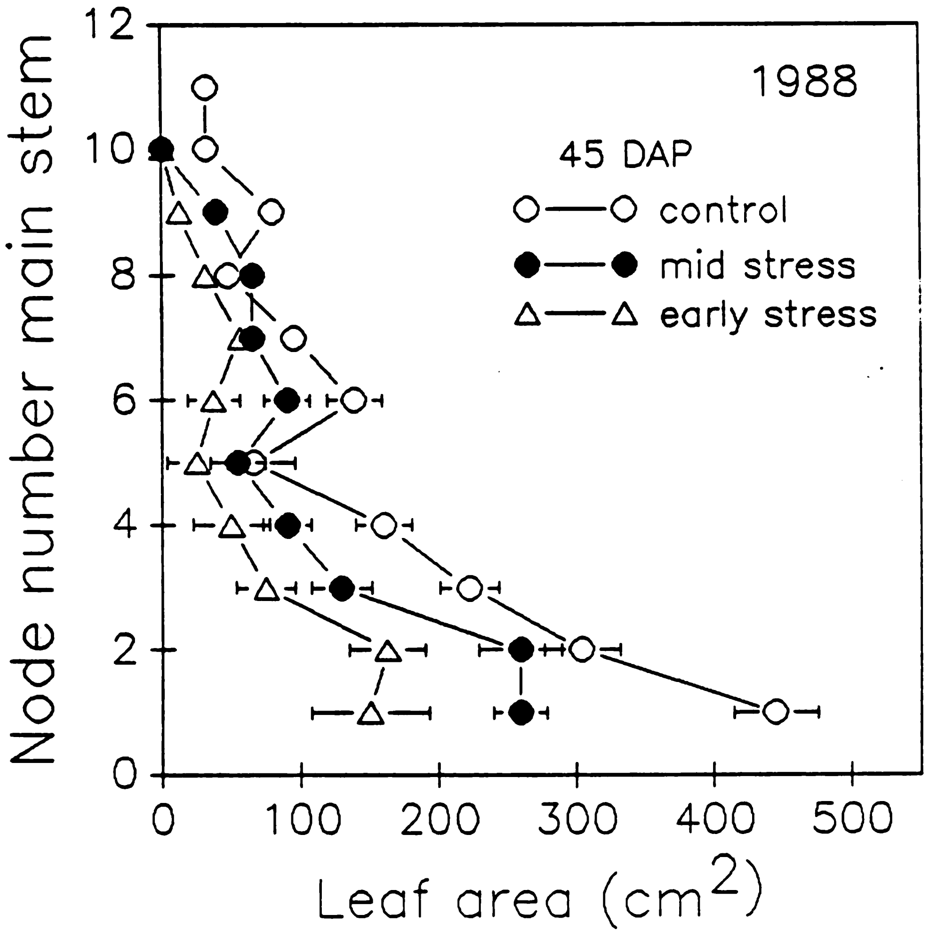

Figure 1.11 Seasonal changes in leaf area distribution along nodes of the main stem on 45 DAP for different water deficit treatments for Spinks soil during 1988.

after the onset of the drought treatments (Figure 1.12A and 1.12B). A rapid senescence rate was observed as the drought progressed in the MS treatments in both years causing low LAI values compared to the control. Rapid senescence rate was also observed in LS after the onset of the deficit. The MS and LS deficits had less effect on the LAI of plants growing in the Kalamazoo soil, both in the rate of increment until 50 DAP and in the rate of leaf area decrease from 50 DAP until the end of the season. On the other hand, the effect of the ES treatment resulted in an apparent preconditioning of the plants by the early season soil water regime, resulting in less senescence beyond 50 DAP (Figure 1.12A). Morgan (1984) showed that wheat undergoing water deficits at an early stage of growth will increase solute accumulation which leads to the maintenance of turgor and hence continued plant growth. Rapid senescence rate is also a plant adaptation mechanism to decreasing soil water content (Turner, 1979). However, rapid loss of leaves in short season dry bean varieties may be detrimental to yield (Laing, et al., 1983).

Although internode length on the main stem of dry beans is influenced by genetic factors (Acosta, 1988), soil water deficits also affected the growth rate (Figure 1.13) as well as the final size of each internode (Figure 1.14). Internode 7 was the longest internode on the main stem for both treatments, with a growth rate of 0.62 and 0.39 cm/day for the control and MS treatment, respectively. Elongation rate for internode 9 was 0.38 and 0.21 cm/day under irrigated and MS

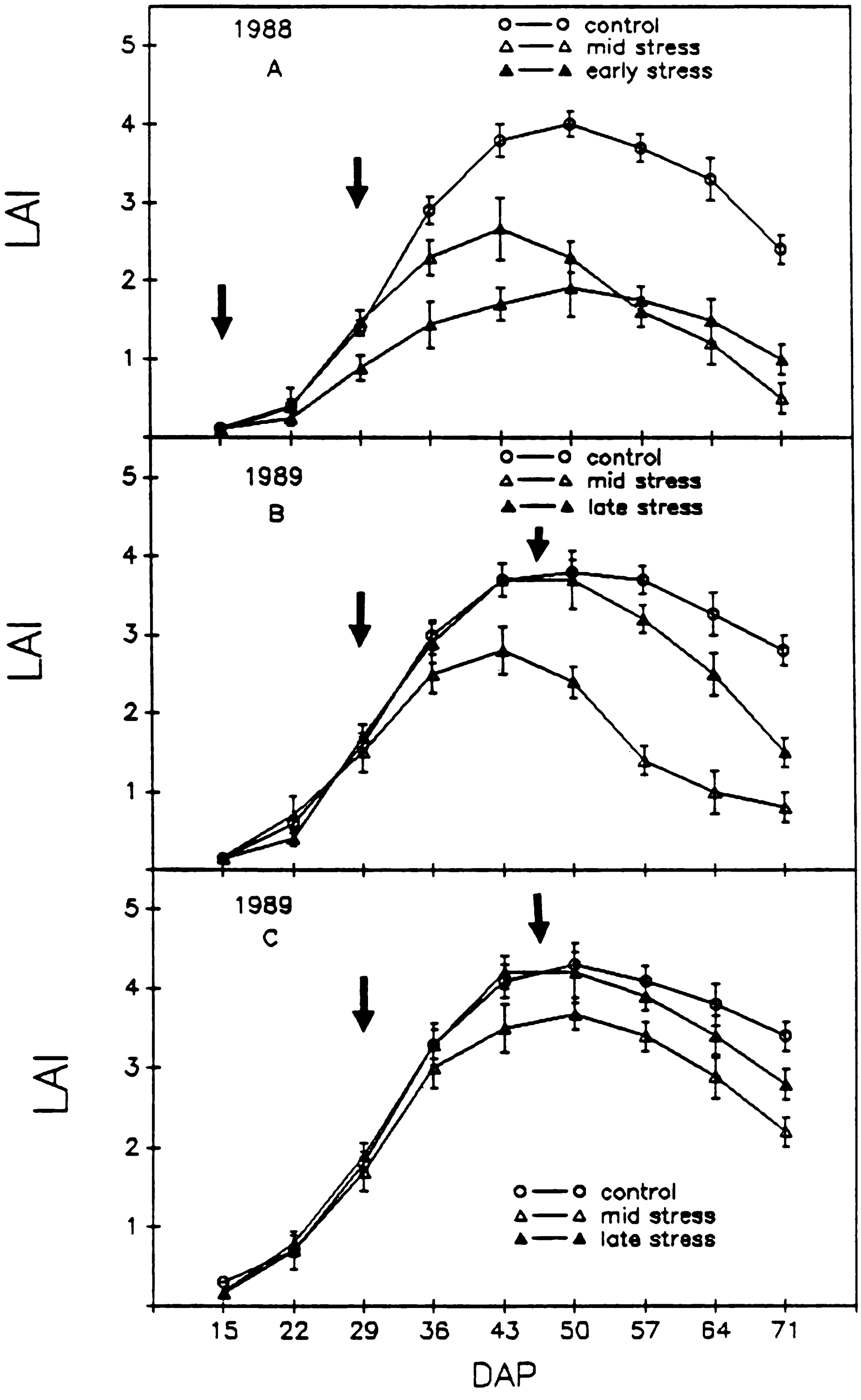

Figure 1.12 Seasonal changes in leaf area index for different water deficits treatments for Spinks (A,B) and Kalamazoo soil (C). Arrows represent initiation of water deficits.

conditions, respectively. In general, soil water deficits reduced internode length an average of 41% in comparison to the control. This reduction was mainly observed above internode number 4 (Figure 1.14). These results agree with those of Hoogenboon et al. (1987) who showed that internodes of soybeans elongated significantly slower during drought periods.

Elongation of individual pods in the plants of the Spinks soil was less affected than the elongation of internodes and the expansion of leaves. Individual pods in the control reached an average length of 8.4 cm, with a growth rate of about 0.93 cm/day (Figure 1.15A). Under the stress conditions of the MS treatment, the rate of pod elongation was 0.78 cm/day, reaching a final pod length of 7.1 cm. This difference is rather small considering that more than 50% of PAW was already depleted from the upper 50 cm of soil.

The number of pods per plant is an important factor explaining the lower sensitivity of individual pods to soil water deficits. Drought stress during flowering and pod filling increased the rate of flower and pod abortion (Chapter 2). In this experiment the control in the Spinks soil had 14.5 pods per plant versus 6.5 in the MS treatment (1988-1989). The reduction in pod number also decreased the competition for plant resources resulting in a greater rate of elongation on main stem pods as compared to that observed in leaves and internodes. In the Kalamazoo soil, individual pod elongation in MS was not significantly different when compared

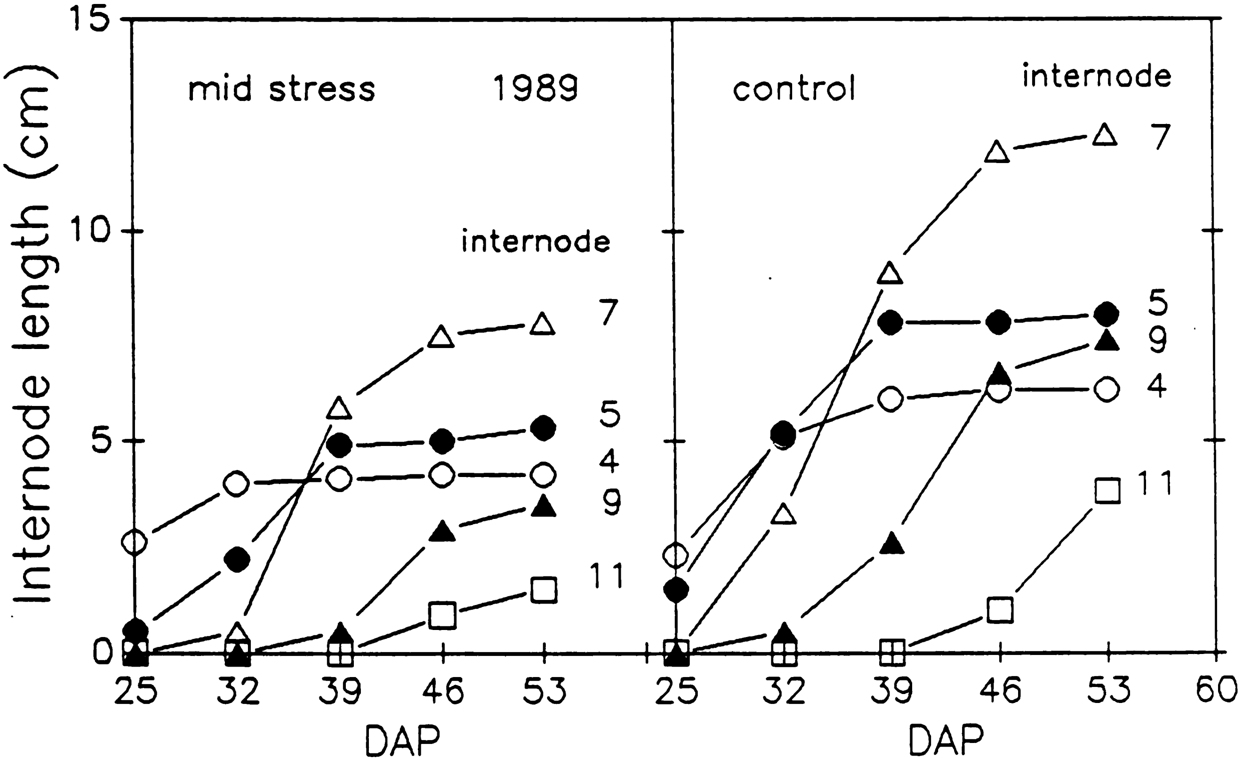

Figure 1.13 Seasonal changes in internode elongation for MS and control treatments for Spinks soil during 1989.

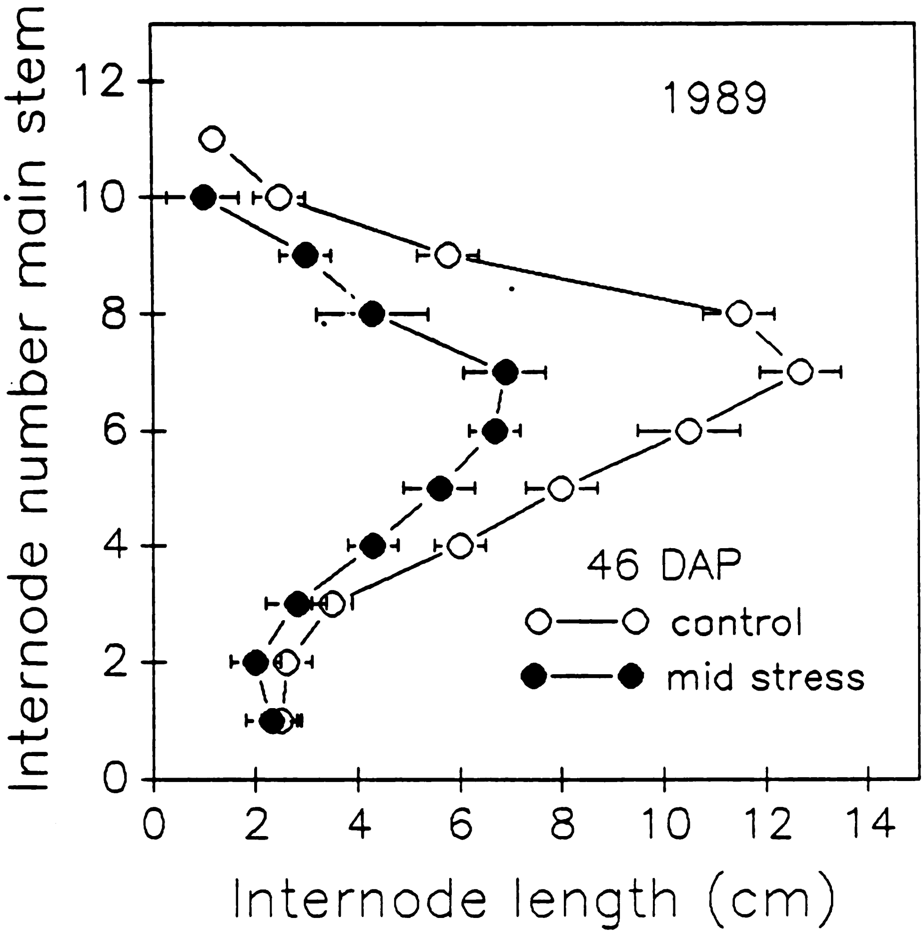

Figure 1.14 Length of different internodes on the main stem at 46 DAP for MS and control treatments for Spinks soil during 1989.

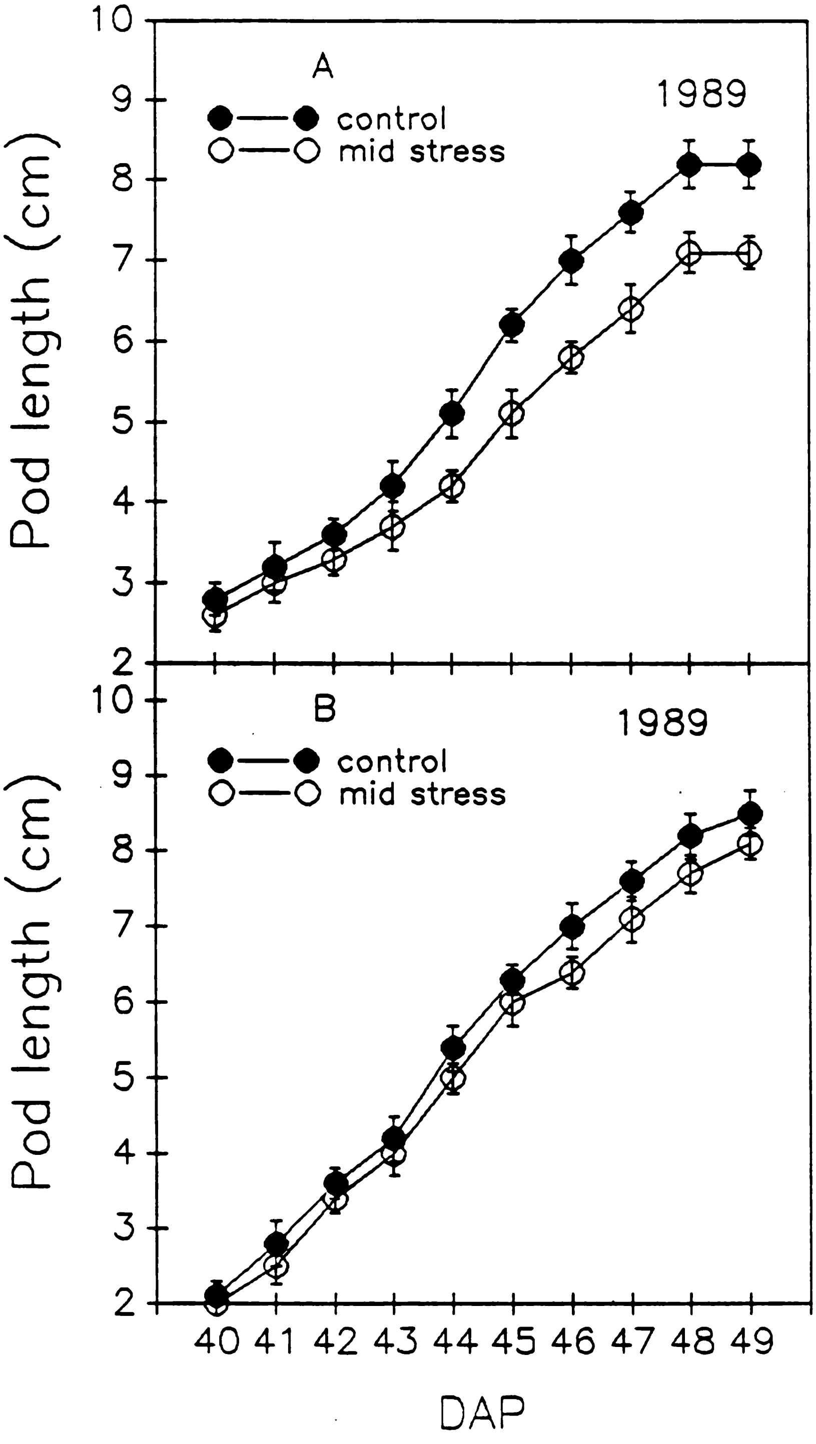

Figure 1.15 Seasonal changes in individual pod length for MS and control treatments for Spinks (A) and Kalamazoo (B) soils during 1989.

to control plants (Figure 1.15B), however total pod elongation for MS was significantly lower than that of the control for both soils. Total pods in the Kalamazoo soil had an elongation rate of 3 cm/day compared to 1 cm/day observed in the corresponding treatment in the Spinks soil (Figures 1.16A and 1.16B).

Plant available water in the soil profile influenced organ elongation in dry beans in both soils (Figures 1.17 and 1.18). In the Spinks soil, relative leaf expansion in terms of LAI, fell when PAW decreased to 68%, but reached a lower value of 0.34 when PAW decreased to 42%. Relative total pod elongation decreased at 62% of PAW. Stem elongation began decreasing at 60% of PAW. In the Kalamazoo soil, relative leaf expansion began declining at 70% of PAW, however, the relative elongation of total pods decreased at PAW values of 45%.

Different patterns of organ expansion affected the final accumulation of dry matter (Table 1). In 1988, dry matter of stems and total leaves in the Spinks soil was greater for the control than for ES and MS, where branches were most affected. The number of pods on the control plants was greater compared to the ones in the deficit treatments. However, leaf number was less affected by the drought condition. In 1989, dry matter production as well as leaf number and pods were consistently greater for the Kalamazoo soil as compared to the Spinks soil. For the MS treatment in Spinks soil, the number of pods was 54% less than those in the MS of the Kalamazoo soil. For the same treatment, dry matter

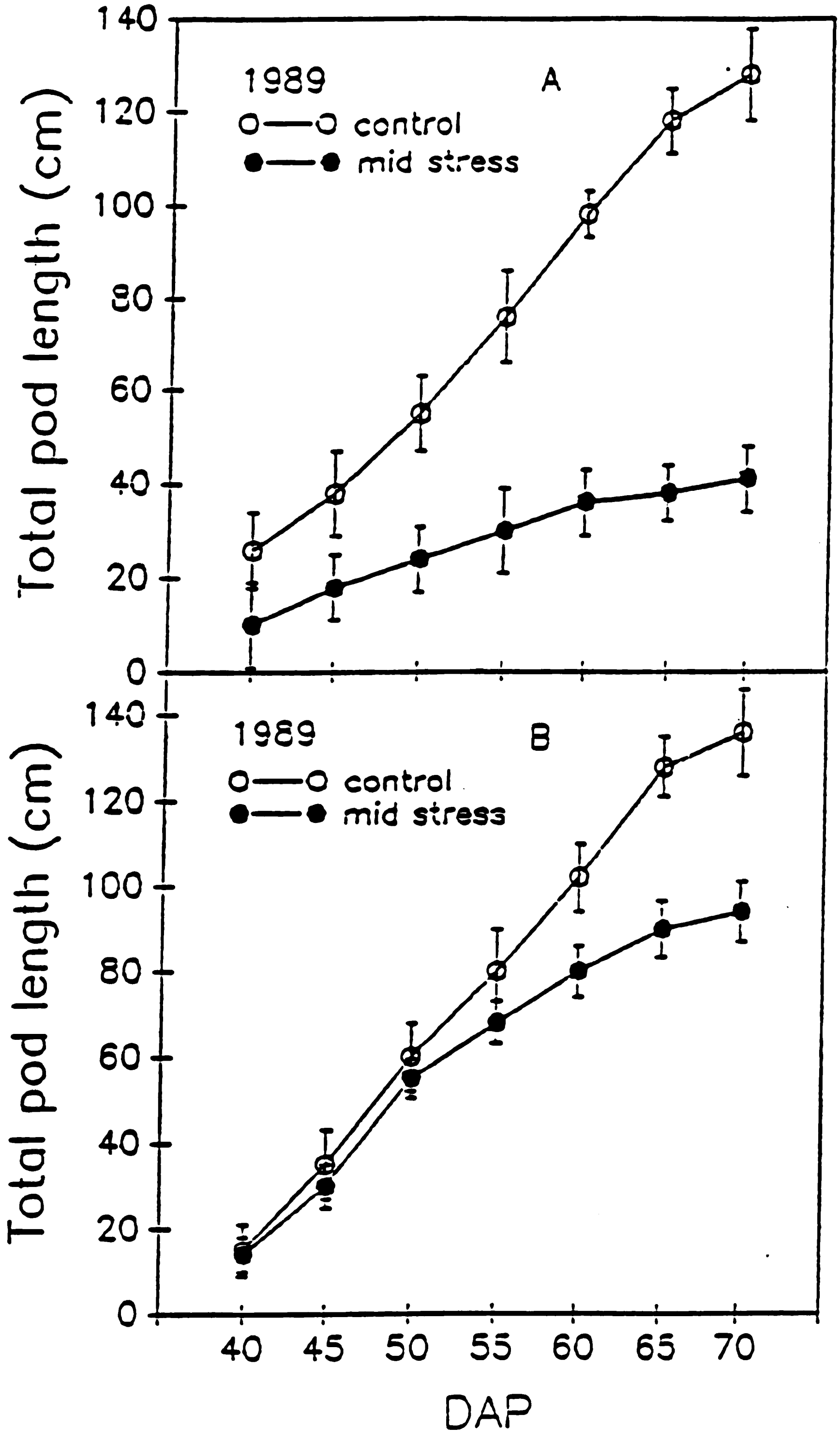

Figure 1.16 Seasonal changes in total pod length for MS and control treatments for Spinks (A) and Kalamazoo (B) soils during 1989.

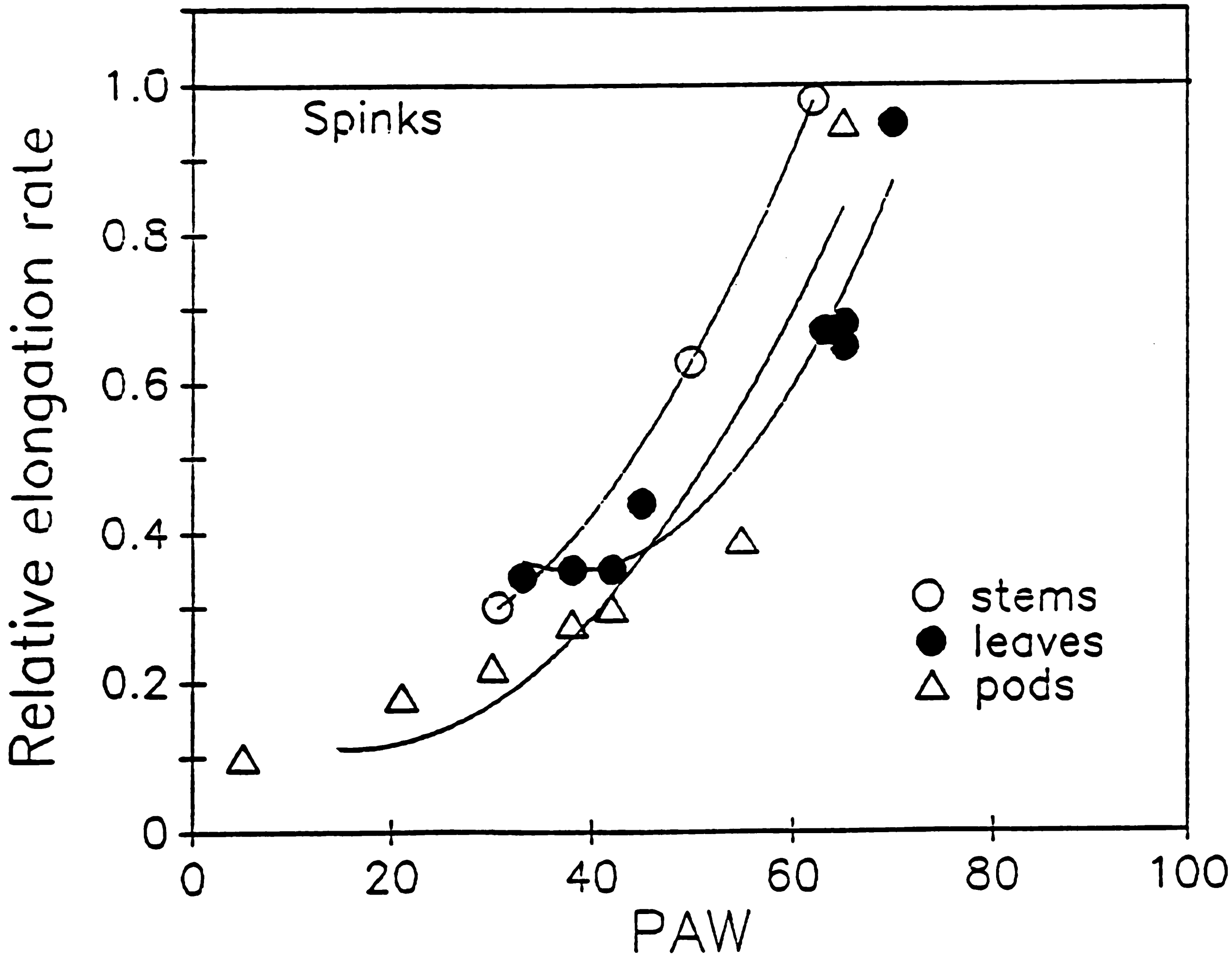

Figure 1.17 Relative elongation rates of different plants organs as influenced by the percentage of plant extractable water (PAW) in the root zone for Spinks soil during 1989.

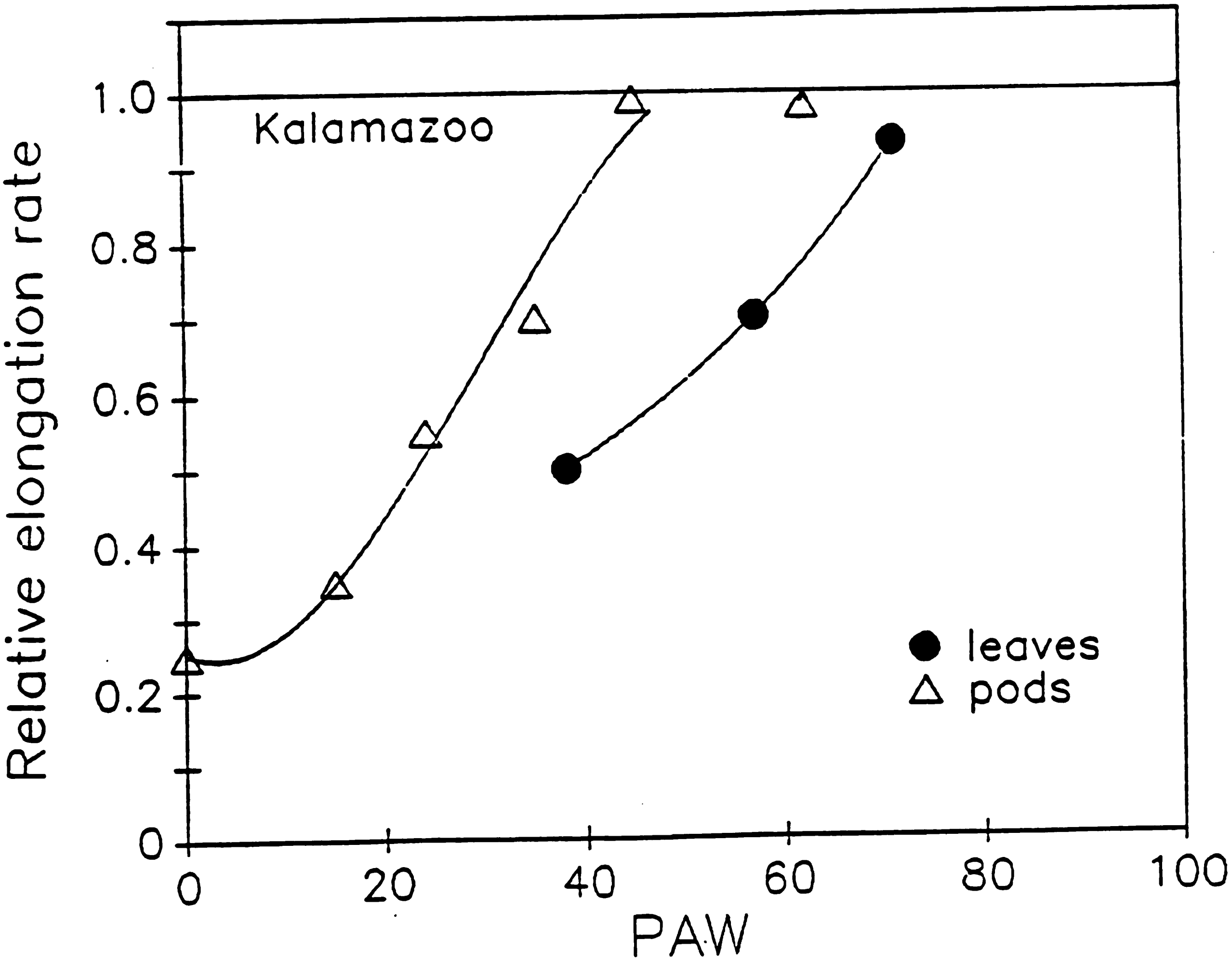

Figure 1.18 Relative elongation rates of different plants organs as influenced by the percentage of plant extractable water (PAW) for Kalamazoo soil during 1989.

Table 1.1. Number of leaves, pods, and dry matter production of different plant parts at maturity for various soil water deficit conditions.

Treat.	Dry Weight (g/plant)			Number/plant	
	Main Stem	Branches	Leaves	Leaves	Final pods
1988 Spinks Soil					
Control	1.99±0.17	3.84±0.14	6.20±0.35	42.7±1.9	15.2±2.0
Mid stress	1.65±0.09	2.15±0.07	4.39±0.43	39.2±1.6	6.4±1.8
Early stress	1.59±0.13	1.85±0.09	4.03±0.51	34.8±2.8	9.1±0.9
1989 Spinks Soil					
Control	1.90±0.10	3.21±0.19	5.28±0.29	40.6±1.3	16.1±1.1
Late stress	1.83±0.07	2.61±0.15	4.49±0.31	39.1±1.7	9.9±0.9
Mid stress	1.48±0.22	1.83±0.08	3.36±0.38	36.2±2.1	5.9±1.4
1989 Kalam. Soil					
Control	2.10±0.21	3.57±0.24	6.30±0.19	43.2±1.5	17.5±1.6
Late stress	1.79±0.15	2.98±0.13	5.88±0.29	41.4±0.9	15.4±1.2
Mid stress	1.52±0.18	2.59±0.20	5.07±0.27	40.3±1.7	12.7±1.1

accumulation in branches was 43% lower in the Spinks soil.

In summary, deficit water conditions in both soils adversely affected the growth and expansion of different organs in dry beans. Leaf appearance for plants grown in the Spinks soil was slightly delayed in ES and MS. Significant reductions in leaf, stem and pod elongation were observed with relatively small decreases in soil water content. Leaves were the most susceptible organs, followed by pods and stems. Along the plant main axis, the greatest reduction in leaf area and stem dry weight was observed in the branches of the first four nodes. Dry beans became more susceptible to periods of drought as canopy size increased. Mid season water deficits caused a rapid senescence rate. However, plants experiencing early stress showed better adaptation to the deficit conditions.

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CHAPTER 2

EFFECT OF SOIL WATER DEFICITS ON DRY BEANS (P. vulgaris L.) II. REPRODUCTIVE ORGANS AND YIELD.

ABSTRACT

Little is known about the effect of soil water deficits on the setting and distribution of pods and flowers along the different axes of the dry bean plant. The objective of this study was to investigate the effect of water deficit treatments, during different growth stages, on the number and distribution of pods and flowers on the main stem and branches as well as the dry matter production and yield under field conditions. A rainout shelter facility was used to control the water regimes of early (ES), mid (MS), and late (LS) season treatments. A Spinks soil (Psammentic Hapludalfs) and a Kalamazoo soil (Typic Hapludalfs) were utilized in the experiment.

Soil water deficits in the Spinks soil decreased total flower formation by about 32%. Branches on the first four nodes were most severely affected. Flower formation at those nodes declined by more than 40% and pod abortion reached nearly 100% in the MS treatment. For LS, a decrease in soil water content, 10 days after the onset of the deficit, induced

substantial (48%) pod abortion. In the Kalamazoo soil, the number of flower and pods, as well as seed dry matter production, were diminished in the water deficit treatments.

Results indicated that the rapid water deficits observed in the Spinks soil reduced the number of flowers and pods growing on branches, suggesting that under drought stress the main stem had priority for the plant resources. In the Kalamazoo soil, water deficits effect on the number of flowers and pods was small when compared to those observed in the Spinks soil.

INTRODUCTION

Soil water deficits occurring during the reproductive stages of growth are considered to have the most adverse effect on crop production (Begg and Turner, 1976; Herrero and Johnson, 1981). Bean plants are sensitive to drought stress during flowering and pod filling. Robins and Domingo (1956) found that water deficits imposed during flowering reduced both pod number and the number of seeds per pod and that water stress imposed prior to harvest was observed to decrease seed weight. Dubetz and Mahalle (1969) also reported that severe stress at flowering resulted in inhibition of subsequent flower formation, but water stress imposed during pod filling resulted in a higher percentage of empty seeds. Harvest time and pod length were not affected.

The rate of seed growth decreases under limiting soil water conditions (Spaeth and Sinclair, 1983; Snyder et al., 1982). Rate and duration of seed growth are important components in determining whole plant yield from the contribution of individual pods and seeds. To improve yield predictions, however, additional information is needed to understand the effect and severity of soil water deficits on the setting, production, and distribution of individual pods along the different plant axes, such as the main stem and branches. The objective of this investigation was to determine the effect of different soil water deficits on flower and pod production and the distribution between the main stem and branches in dry beans.

MATERIALS AND METHODS

During the summers of 1988 and 1989, dry bean plants (*Phaseolus vulgaris* L. cv. Seafarer) were grown in a Spinks soil in a rain shelter at the Kellogg Biological Station near Kalamazoo, MI. A Kalamazoo soil was included in the second year. In 1988, a control and a mid season water deficit treatment (MS) were established in the Spinks soil. The water deficit treatment started 29 DAP at the time of flower initiation. In the second year (1989), a Spinks and Kalamazoo soil were utilized. The mid season deficit began 27 DAP and an additional water deficit treatment (LS) was imposed late in the season (45 DAP) at the beginning of pod filling. The control was well irrigated throughout the growing season in both years. Soil water content for this treatment was maintained close to the drained upper limit of approximately 0.16 cm^3/cm^3 for the Spinks soil and 0.27 cm^3/cm^3 for the Kalamazoo soil (upper 75 cm). Irrigation schedule, soil water contents, and the experiment establishment are described in Chapter 1.

During flower initiation, three plants per treatment were tagged and measured for changes in the total number of flowers. Flowers were counted every other day on the main stem and branches. At 40-42 DAP, when flowering reached a maximum in Spinks soil, flower number was determined for each node on the main stem, and the branches of the first 4 nodes. This approach provided a profile of flower and pod distribution along the main axis of the bean plant at different dates during the growing seasons (40 DAP, 1988; 42, 50, 65 DAP, 1989). Three more plants per treatment were randomly selected in both soils in 1989 to measure the effect of water deficits on pod setting through maturity. The number of pods per plant was counted at 5-day intervals.

Dry matter production of individual pods was measured in both soils (1989) during the reproductive period of the bean plants. Thirty pods, about the same age, were tagged in each treatment at the beginning of the pod filling stage. A sample of five pods was harvested at 5-day intervals. Pods were then placed in an oven to dry at 70 °C for 72 hours. After drying, seeds from each pod were removed from the shell and weighed separately. At the end of the season, six plants were sampled in each treatment to calculate an average number of pods per plant. A sub-sample of ten pods was used to determine the number of seeds per pod as well as the weight of individual seeds. The frequency distribution for individual seed weight was estimated for both soils in MS and control treatments. This was accomplished by weighing 100 individual seeds categorized in 0.02 g increments. For final dry matter production, an area of 4 m^2 per plot was harvested.

RESULTS

Soil water deficits imposed at flowering time (MS) had an adverse effect on leaf extension and cumulative leaf area (Chapter 1). In the Spinks soil, the early and mid season deficit treatment slightly hastened flower initiation and decreased the total number of flowers per plant observed in both years (Figures 2.1A and 2.1B). Flowering was hastened from 1 to 4 days. Flower number in MS reached a maximum of 26 and 32 (42 DAP) in 1988 and 1989, respectively. In contrast, there were 39 and 44 flowers for the control at 42 and 44 DAP, respectively. The rate of flowering increase was 2.1 and 2.3 for MS and 3.3 and 3.8 flowers/plant/day for the control during the period from flower initiation to pod set in 1988 and 1989, respectively. In the Kalamazoo soil, flower initiation was not affected by the deficit, however total number of flowers in MS was significantly lower than that of the control. In MS, the rate of growth was about 3.5

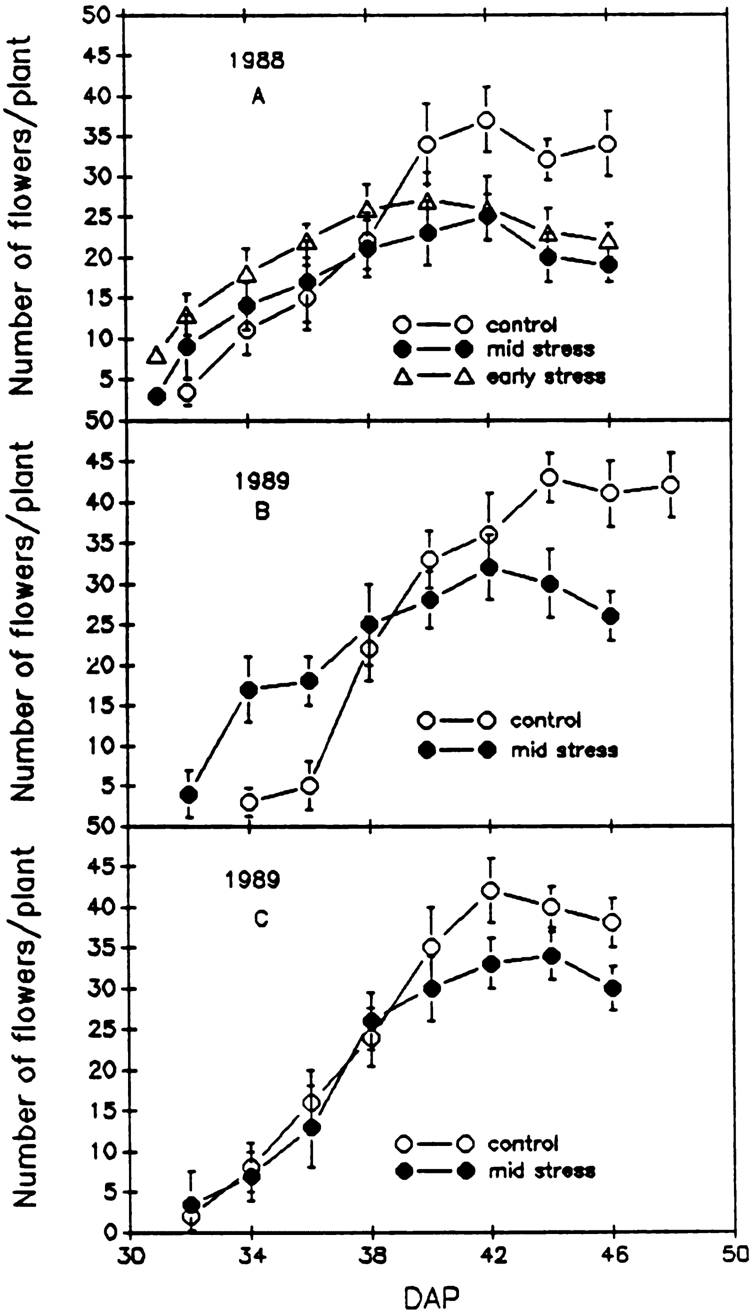

Figure 2.1. Seasonal changes in number of flowers for different water deficits treatments for Spinks (A,B) and Kalamazoo (C) soils.

flowers/plant/day as compared to 4.1 flowers/plant/day in the control (Figure 2.1C). For MS treatments in the Spinks soil, the number of flowers was described along the main stem in day 40 and 42 for 1988 and 1989, respectively. This corresponds to the time of maximum flowering. All flowers counted on the first 4 nodes of the main stem were located in branches and these flowers were the most severely affected by the water deficit. In node number 1, the number of flowers decreased by 43% and 50% when compared to the control (Figures 2.2A and 2.2B). In nodes 2 and 3, flowers decreased by an average of 45%. Above node number 5, all flowers for the MS treatment were found on the main axis and the differences between the two treatments were small.

The total number of pods in both soils decreased with time for all treatments, including the control (Figures 2.3A and 2.3B). From a maximum of 23 initial pods in the Spinks soil, the irrigated treatment decreased to 16 pods by the end of the season, a decrease of 36% due to pod abortion. Soil water conditions in the late stress treatment caused a rapid decline in the number of pods. Pod number decreased 39% between 50 DAP and 55 DAP. For the MS treatment, a total of 12 pods were counted during pod initiation. Between 55 DAP and 70 DAP, a decrease of about 1 pod/day was observed in this treatment reaching a final number of 6 pods/plant (Figure 2.3A). In the Kalamazoo soil, pod number decreased from 25 to 18 and from 20 to about 13 in the control and MS treatment, respectively (Figures 2.3A and 2.3B).

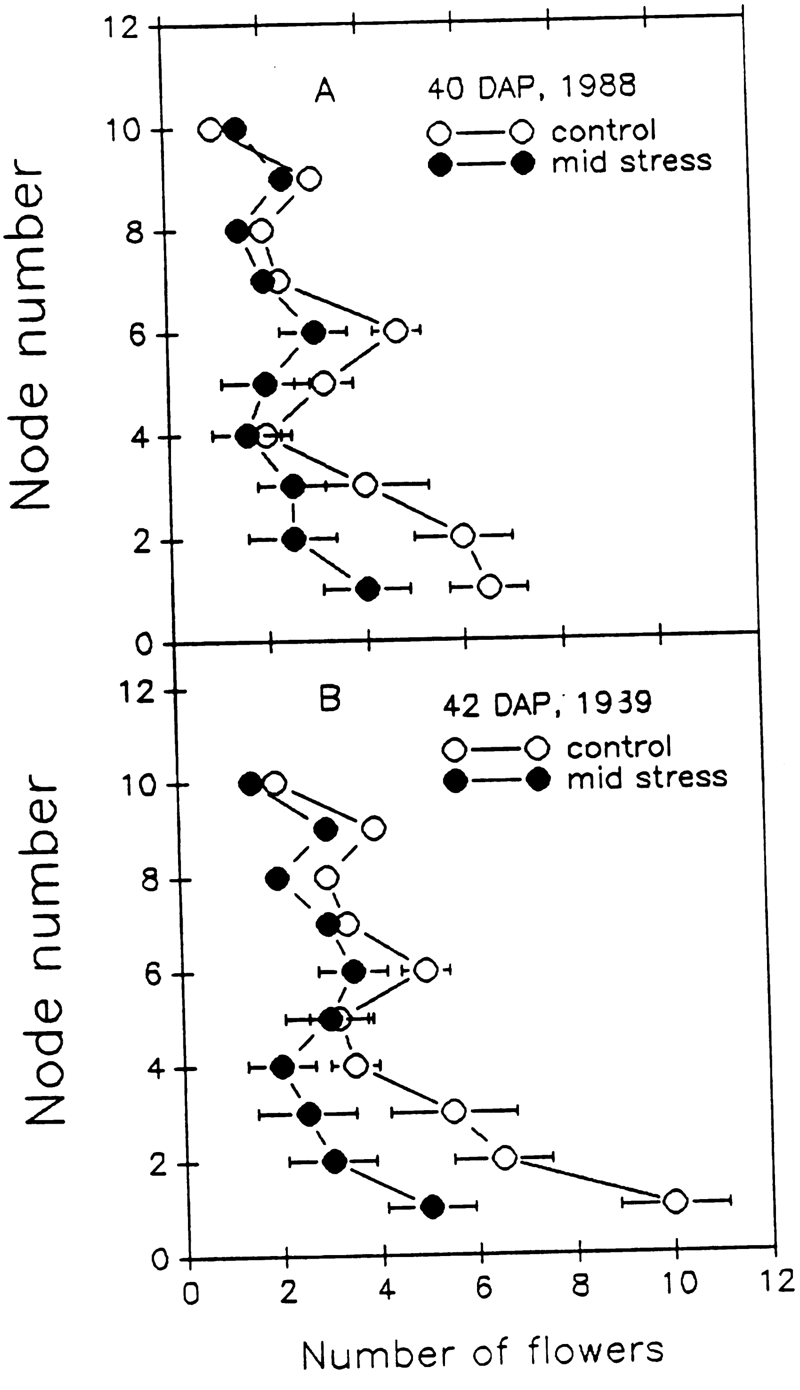

Figure 2.2. Distribution of flowers along the main stem in MS and control treatments, on the day when maximum flowers number occurred.

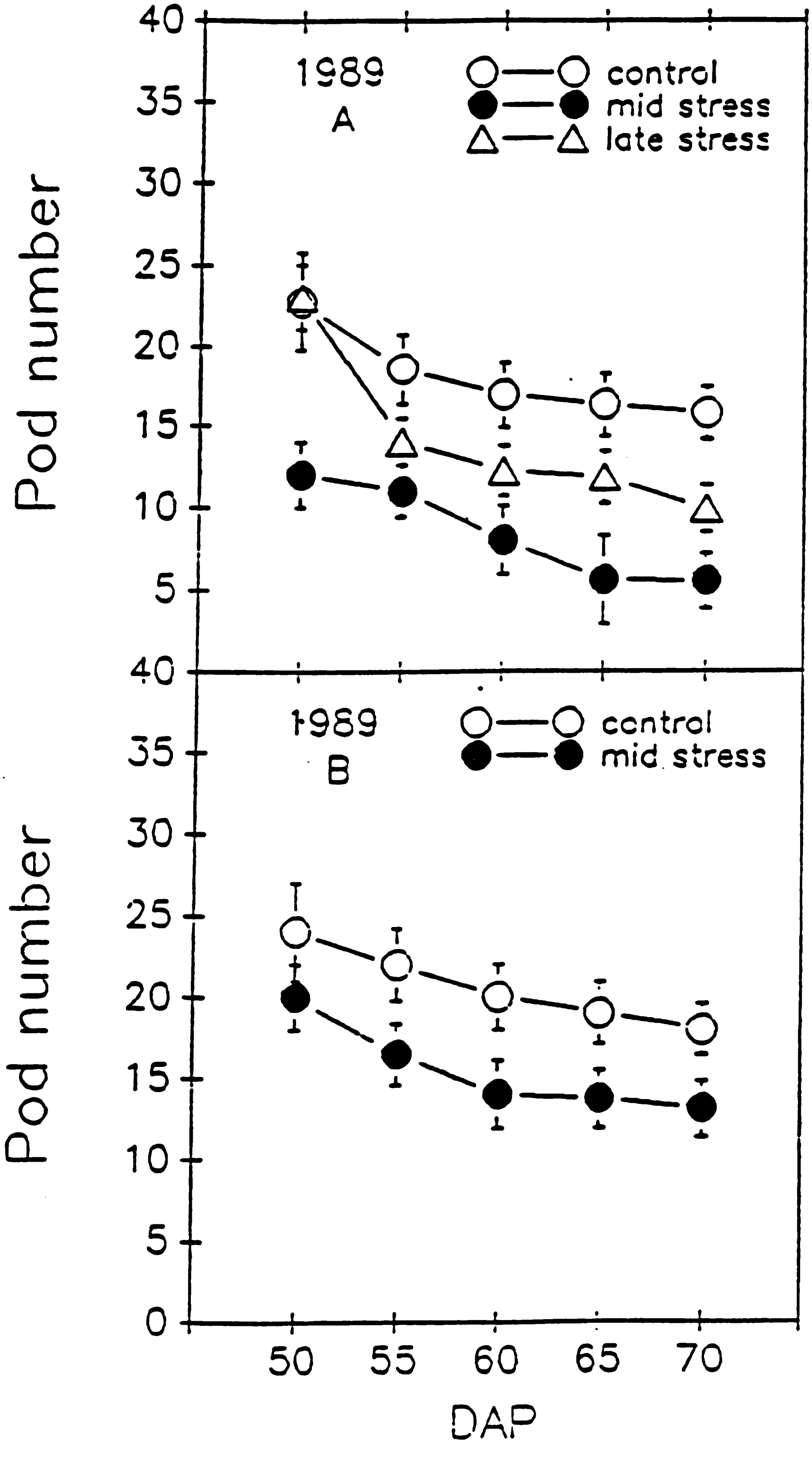

Figure 2.3. Seasonal changes in pod number as affected by different water deficit treatments for Spinks (A) and a Kalamazoo (B) soils during 1989.

Pod abortion occurred mainly in the branches of the first 4 nodes (Figures 2.4A and 2.4B). For the MS treatment of the Spinks soil, almost 100% of the pods were aborted from node 1 to node 4 between 50 DAP and 65 DAP. From node 5 to node 10, the abortion rate in the same period of time was only 15%, largely pods growing on the main stem. For the control, the decrease in pod number in the first branches was 32%.

Duration and rate of seed growth were different for MS as compared to late stress (LS) and control treatments in the Spinks soil (Figure 2.5A). The MS treatment seemed to hasten the initiation of seed growth. Seeds began to grow 3 to 4 days earlier for MS than for LS and the control. Seed growth in MS had an estimated duration of about 12 days with a growing rate of 0.045 g/pod/day. The duration of growth in the control was about 14 days with a growth rate of 0.06 g/pod/day, about 20% greater than the one observed in the MS treatment. Differences in seed dry matter accumulation were not significant between control and LS treatments. During pod elongation, there was significant growth in pod walls. For the MS treatment, the dry matter of pod walls increased at a rate of 0.028 g/pod/day from 50 DAP to 55 DAP and decreased significantly between 55 DAP to 60 DAP (Figure 2.5B).

In the Kalamazoo soil, the MS treatment did not hasten the initiation of seed growth when compared to the control, but significantly decreased seed weight per pod at the end of the season (Figure 2.6A). Seed growth rate was 0.05 and 0.06 g/pod/day for MS and control, respectively. The dry weight of

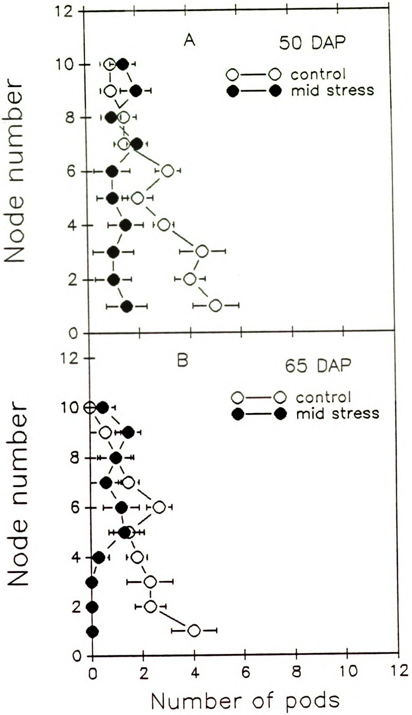

Figure 2.4. Pod distribution along nodes of the main stem at 50 and 65 DAP for Spinks soil during 1989.

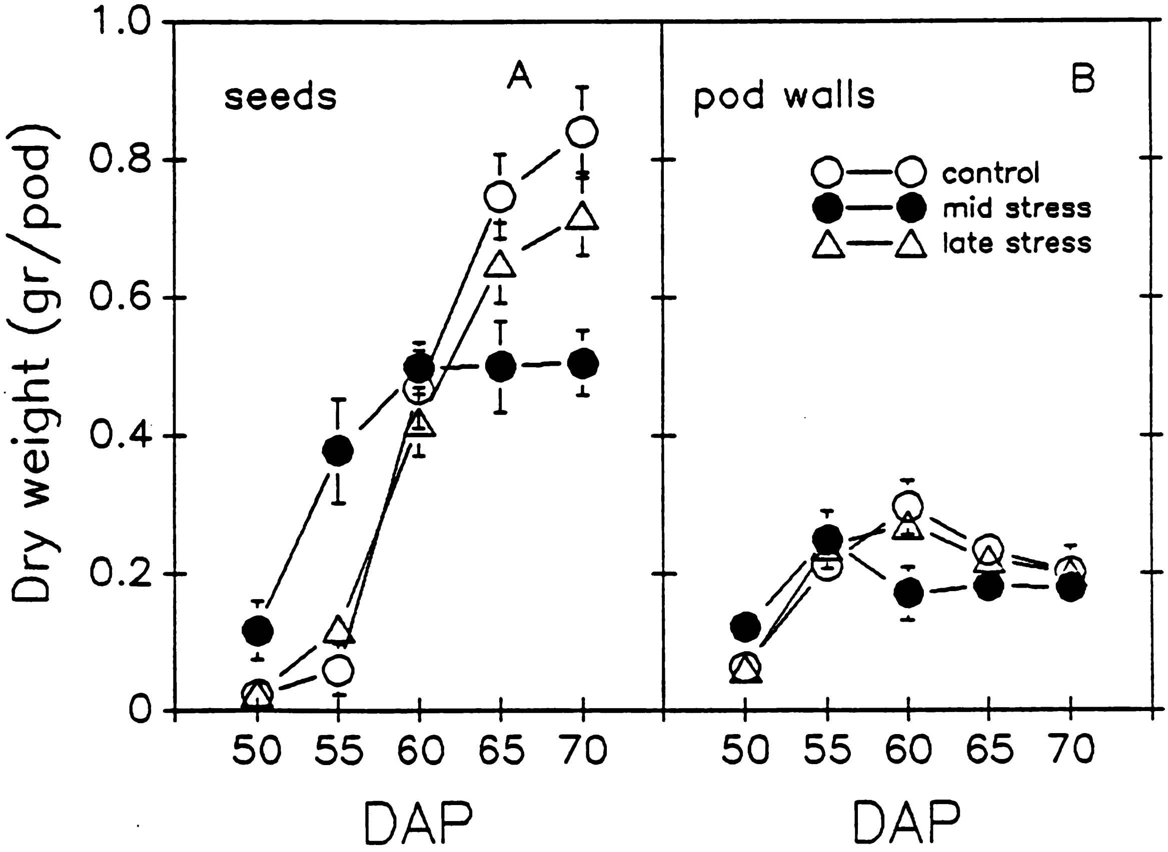

Figure 2.5. Seasonal changes in dry weight of seeds (A) and pods walls (B) for different water deficit treatments for Spinks soil during 1989.

the pod wall was lower but not significantly different in MS compared to the control (Figure 2.6B).

Seed weight distribution was more affected in the Spinks than in the Kalamazoo soil. The range of seed weight for the MS treatment in the Spinks soil was between 0.04 and 0.18 g/seed with a maximum frequency in the 0.12-0.14 class size. The control had a range between 0.16 and 0.24 g/seed with a maximum frequency in the class size between 0.18 and 0.20 (Figure 2.7). For the Kalamazoo soil, the range of seed weight in MS was between 0.8 and 0.22 g/seed as compared to the 0.14-0.24 range observed in the control treatment (Figure 2.8). Both treatments had the maximum frequency in the second class size, 0.16-0.18 and 0.18-0.20 g/seed in MS and control, respectively.

Pods per plant, seeds per pod, and seed weight were decreased by the soil water deficit treatments in both years (Table 2.1). In the Spinks soil, MS decreased total seed weight by an average of 77% in both years. This is the result of lower seed weight and less seeds/pod and pods/plant. For instance, pod number reached a maximum of 6 and 7 for 1988 and 1989, reflecting a reduction of 40% and 46% compared to their respective controls. The early stress treatment had more pods per plant than MS, reaching a higher total seed weight (1988). When compared to the control, the MS treatment had 33% and 38% less seeds per pod in the first and second year, respectively. Seed weight was 20% less in MS than in the control. The late stress treatment resulted in a lower number of pods/plant and

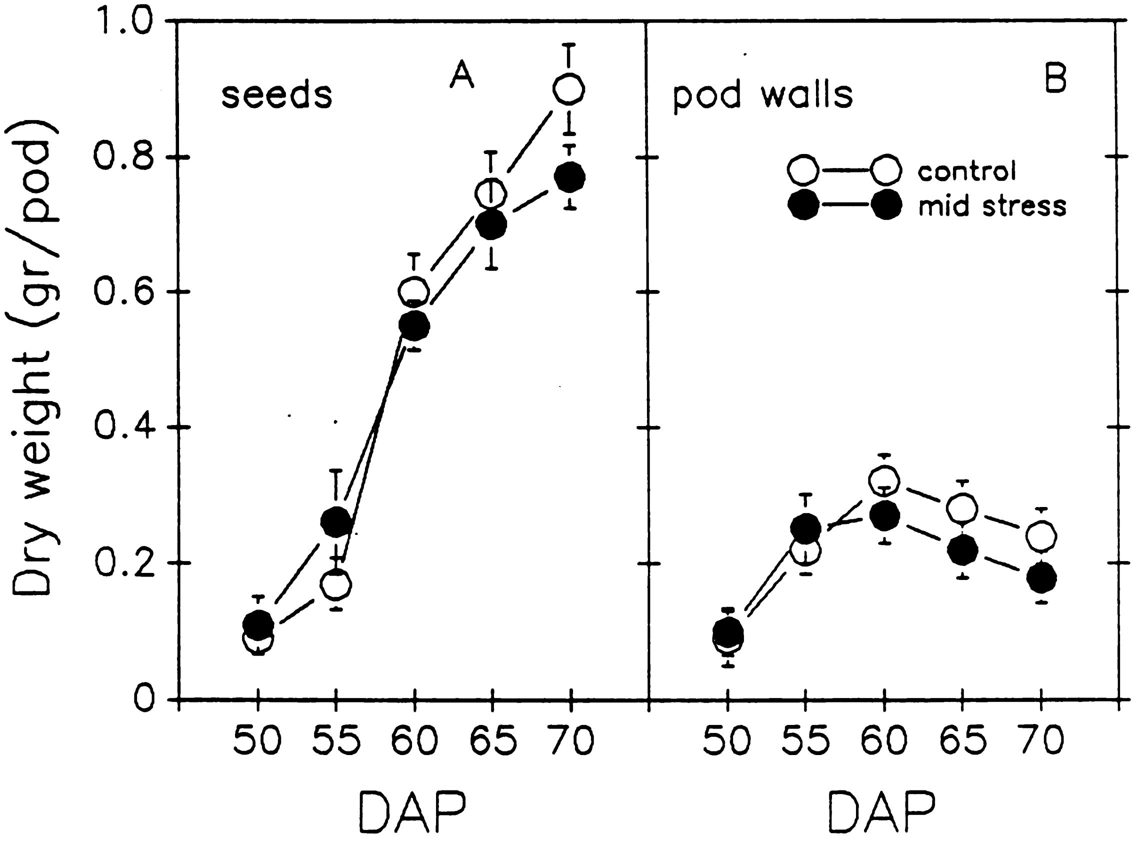

Figure 2.6. Seasonal changes in dry weight of seeds (A) and pod walls (B) for different water deficit treatments for Kalamazoo soil during 1989.

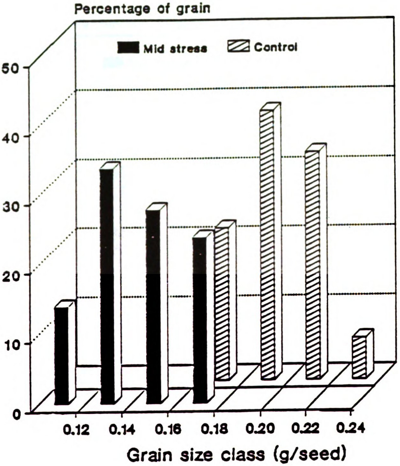

Figure 2.7. Seed weight distribution for different water deficit treatments for Spinks soil during 1989.

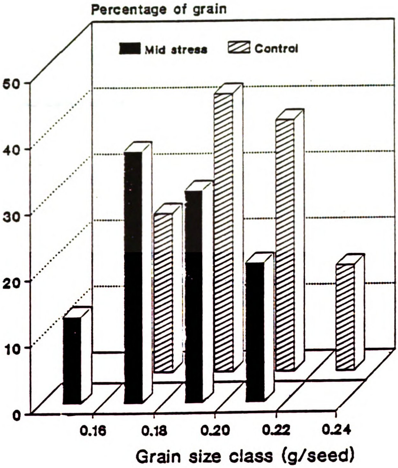

Figure 2.8. Seed weight distribution for different water deficit treatments for Kalamazoo soil during 1989.

Table 2.1. Yield components in dry beans for various soil water deficit conditions.

Treatment	Pods/Plant	Seeds/Pod	Seed wt (g)	Tot. seed wt (g/plant)
1988 Spinks Soil				
Control	15.2±2.00	4.6±0.40	0.185±0.012	12.93±1.50
Mid stress	6.4±1.60	3.1±0.32	0.148±0.008	2.93±0.90
Early stress	9.1±0.90	2.6±0.25	0.163±0.009	3.85±0.06
1989 Spinks Soil				
Control	16.1±1.10	4.5±0.23	0.180±0.009	13.04±1.90
Late stress	9.9±0.90	4.2±0.41	0.171±0.010	7.11±2.10
Mid stress	5.9±1.40	3.2±0.15	0.150±0.006	2.8±1.60
1989 Kalamazoo Soil				
Control	17.5±1.60	5.1±0.20	0.189±0.07	16.86±1.80
Late stress	15.4±1.20	4.7±0.36	0.178±0.08	12.88±2.60
Mid stress	12.7±1.10	4.5±0.17	0.172±0.09	9.82±1.20

seeds/pod as well as lesser weight per seed than the control. However, the only value significantly different was the number of pods/plant, with a decrease of 29%. In the Kalamazoo soil, the yield components were lower in LS but not significantly different to those in the control. However, the effect of MS significantly decreased seed weight, seed/pod and pods/plant as compared to the control. Pods/plant was the most affected component, with a reduction of 28% compared to a decrease of 12% and 9% in seeds/pod and seed weight, respectively.

The adverse effect of soil water deficits on total seed weight (and hence harvest index) was greater for MS in both soils. Harvest index decreased by 27% and 15% in the Spinks and Kalamazoo soil, respectively. This reduction was lower for ES and LS treatments (Table 2.2).

DISCUSSION

Results indicated that soil water influenced the dynamics of flower and pod production. Early and mid stress treatments hastened flowering in the Spinks soil. Robins and Domingo (1956) showed that plant development in dry beans was retarded by stress before blooming and hastened when deficits occurred during flowering and maturity. ES and MS deficits decreased the total number of flowers in the spinks soil. The MS treatment also decreased the number of flowers, though to a less extent, in the Kalamazoo soil. Dubetz and Mahalle (1969) found that water deficits at flowering resulted in inhibition

Table 2.2. Total dry matter, seed yield, and harvest index of dry beans for various soil water deficit conditions.

Year	Soil	Treatment	Total Dry Weight Kg/ha	Seed Weight Kg/ha	Harvest Index
1988	Spinks	Control	4868	1850	0.38
		Mid Stress	1467	411	0.28
		Early Stress	1906	572	0.30
1989	Spinks	Control	4884	1905	0.39
		Late Stress	2776	913	0.33
		Mid Stress	1372	398	0.29
1989	Kalamazoo	Control	5821	2387	0.41
		Late Stress	4862	1799	0.37
		Mid Stress	3428	1201	0.35

of subsequent flower formation. In this study, the inhibition of the formation of new flowers occurred mainly on the branches of the first 4 nodes in the main stem (Spinks soil).

Water deficits imposed at the beginning of flowering (MS) induced flower abortion and subsequent lower percentage of pod setting, reducing the total number of pods at the end of the season. Vittum et al. (1963) found that irrigation of snap beans and lima beans increased the percentage of flowers that set fruits. The adverse effect of water deficits in pod setting was mainly observed in the branches of the bean plant. Results of water deficit treatments imposed prior or during flowering were shown by Robins and Domingo (1956) and Stoker (1974). They found that the total number of pods per plant decreased significantly when deficits began 15 days prior to blooming, but that the greatest decrease was observed with the onset of water deficits at the time of flowering.

Soil water retention capacity had a significant effect on the dynamics of flowering and pod setting. For the deficit treatments in the Kalamazoo soil, total number of flowers and pods were less affected than in the Spinks soil. Dubetz and Mashalle (1969) found no changes in flower abscission of bush beans in a fine-textured soil when soil water potential reached values of about -0.8 MPa both before and during flowering.

A decrease in seed weight was found to be one of the main effects of late season water deficits (Classen and Shaw, 1970; Couto, 1978; Robins and Domingo, 1956). However, the timing of the deficit may change its effect on a given yield component. In this experiment, the drought stress of the LS treatment began at pod initiation, and although seed weight values were lower than those in the control, the main effect of the deficit was a rapid decrease in pod number.

Rate and duration of seed growth are important components in determining its final mass. Growth rate in the irrigated control was greater than that in the MS treatment in both soils, affecting final seed size and seed yield. Water deficits during seed formation have been reported to lower the rate of seed growth resulting in yield reductions (Sionit and Kramer, 1977; Constable and Hearn, 1978).

A longer duration of seed growth was also observed in the Spinks soil control as compared to MS. However, this measurement was extrapolated from the linear response of seed growth. Difficulties in estimating duration of seed growth have been discussed by Spaeth and Sinclair (1983).

Pod length was more restricted by the mid season stress treatment in the Spinks than in the Kalamazoo soil (Chapter 1). Pod length may have an effect on seed size. Corner (1951) and Duncan et al. (1978) suggested that pod size determines seed size in legumes and it has been shown that physically restricting fruit size significantly reduces seed size (Egli et al., 1987).

The effect of soil water deficits on seeds and pods caused a reduction in the harvest index. It has been shown that patterns of water supply have a large influence on the partitioning of assimilate between seeds and other organs. Bond et al. (1964) observed in sorghum that an adequate water supply until heading, followed by drought, gave a large biomass and small harvest index. The reverse sequence in the supply of water resulted in nearly as much grain with much less biomass. For crops that rely on stored water, the harvest index is highly correlated to the amount of water available after anthesis (Passioura, 1977).

CONCLUSIONS

Soil water deficits hastened flowering in the Spinks, but not in the Kalamazoo soil. Deficits decreased the formation of pods and flowers. This effect was mainly observed on the branches growing in the lower 4 nodes of the main stem. Branches, as growing sites for pods and flowers, were more susceptible than the main stem to the drought conditions. Pod number was the yield component most severely affected by the stress in both years, followed by seed weight and seed number. Rate of growth was more affected than duration of growth. Harvest index decreased considerably when the deficit began at the time of flowering.

More information is needed to understand the effect of water deficits on stem branching and yield production. This may increase the predictive capabilities of the bean model and enhance management practices and genetic programs seeking an improvement of grain yield under drought conditions.

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CHAPTER 3

EFFECT OF SOIL WATER DEFICITS ON DRY BEANS (P. *vulgaris* L.) III. STOMATAL CONDUCTANCE, PHOTOSYNTHESIS, LIGHT INTERCEPTION, AND DRY MATTER PRODUCTION.

ABSTRACT

Soil water deficits adversely affect light interception, and hence, assimilate production in plant canopies. However, the interaction of factors highly correlated with assimilate production such as leaf area, leaf movement, photosynthesis, etc. is not well understood. The objective of this study was to investigate the effect of soil dehydration on the changes in light interception, photosynthesis, and stomatal conductance as related to the production of dry matter. Research was carried on in the field utilizing a rain shelter facility. A mid season (MS) water deficit treatment began 27 DAP and 29 DAP in 1988 and 1989 respectively. An irrigated control was used for comparison. Stomatal conductance in both years rapidly declined after the onset of the water deficit, remaining significantly lower than the control for most of the dry period.

In 1989, midday partial stomatal closure was observed at 42 DAP and 52 DAP. Photosynthetic rates (Pn) were less affected by the water deficit than stomatal conductances. Pn rates were lower in MS than in the control at the end of the season and during stomatal closure. Light interception in the MS treatment was decreased during the drought period when compared to the control. Heliotropic leaf movement in MS contributed to the reduction in the diurnal amount of light intercepted, providing the plant with a mechanism to reduce energy load at the same LAI as an irrigated treatment. Dry matter production was closely related to the cumulative intercepted photosynthetic active radiation (IPAR), although, MS had slightly less biomass than the control at the same IPAR.

INTRODUCTION

Dry matter accumulation in plants is largely a function of net photosynthesis rates and light interception by the canopy. Monteith (1977) showed that with an adequate supply of water, the accumulated interception of light by a wide variety of crops, such as apples, barley, potatoes and sugar beet, was closely related to biomass production. Gallagher and Biscoe (1978) reported that dry matter accumulation in cereals was found to be linearly correlated to the seasonal cumulative light interception at different stages of growth.

Leaf expansion, and to some extent assimilation rates, are adversely affected by water deficit conditions. They limit both the amount of light that can be intercepted by the foliage (Monteith, 1965) and the total uptake of carbon dioxide through the stomata (Moldau, 1973; Hall and Schultz, 1980). Light interception in a plant canopy is largely a function of leaf area (size and distribution) and leaf movement (Blaine and Baker, 1972). Stomatal closure, on the other hand, has been reported to have a significant effect on photosynthesis during periods of drought stress (O'Toole et al., 1977; Througthon and Slatyer, 1969). However, there is a growing question about the real limitations of a reduction in stomatal conductance on plant dry matter production. After an extensive literature review, Farquhar and Sharkey (1982) concluded that apart from some transient hormonal effects on rapid stomatal closure such as that of abscisic acid, stomatal conductance is rarely the main cause of the decrease in assimilation rate that may occur with a declining soil water supply.

The objective of this experiment was to investigate the effect of soil water deficits on stomatal conductance and photosynthetic rates as well as light interception and dry matter production in dry beans.

MATERIALS AND METHODS

A two-year investigation (1988-1989) was carried on at Kellogg Biological Station, near Kalamazoo, MI. Dry bean plants (Phaseolus vulgaris L. cv. Seafarer) were grown in a rain shelter facility in a Spinks sandy soil (Psammentic

Hapludalfs). A mid season water deficit treatment was established in both years a few days before the beginning of flowering. Irrigation was halted 27 and 29 days after planting (DAP) in 1988 and 1989, respectively. An irrigated treatment was kept throughout the growing season for comparison. Irrigation schedule, soil water content, weather and other experimental details are described in the Chapter 1.

Stomatal conductance and photosynthesis were measured in the upper leaves of bean plants using an ADC portable open gas exchange system (Analytical Development Company, Haddesdon, UK). Four completely expanded leaves that were fully exposed to solar radiation, were randomly selected in each treatment. The instrument was clamped onto the leaf and exposed to the incoming solar radiation in a perpendicular orientation. Each reading took approximately 30 seconds before reaching a stable value. Measurements were taken between 10 and 12 am EDT for several days. Photosynthesis was calculated as described by Moon and Flore (1986).

Light interception was measured in 1989 at about solar noon by evaluation of shaded areas with a meter stick (Adams and Arkin, 1977). They found that measurements of light interception by this method were closely correlated with those measured by spatial traversing quantum sensors. This procedure was thought to work well because a sunny leaf absorbs about 95% of PAR.

Readings of shade accumulation were taken with the meter stick at 7-day intervals from late vegetative stage to maturity. At noon, the meter stick was placed on the soil surface perpendicular to the plant row. The shaded area on the meter stick was measured and summed to the nearest centimeter. Then the stick was moved for repeated measurement along the row covering 1.6 m length at space intervals of 20 cm. The same segment of row in each treatment was used for subsequent measurements. Intercepted photosynthetically active radiation was estimated by taking 48% of the solar radiation as measured near the experimental site (Monteith, 1977).

A daily pattern of leaf angle was determined on one day at the beginning of the stress period. A protractor with a small level (5 cm long) attached to it was used to measure the angle of 10 randomly selected upper leaves. Leaves with a parallel orientation to the soil surface were considered to have zero angle.

Leaves, stems, and pods of three plants were harvested at a 7-day interval throughout the drought period to determine dry matter production. They were separated into paper bags and placed in a forced air oven dryer at 70 °C for 72 hours before weighing.

RESULTS

Stomatal conductance and photosynthesis. Changes in volumetric soil water content for both years are described in Chapter 1. Stomatal conductances observed 36 DAP were lower in the mid stress treatment (MS) than in the control (Figure 3.1). This difference was also significant at 46 DAP, but not at 55 DAP. In 1989, the water deficit created a similar response to stomatal action. As soon as soil water content decreased in the upper layers, stomatal conductance in MS began to lag behind the control. In 1989 at 42 DAP and 52 DAP, very low stomatal conductances with values less than 0.06 cm/sec were observed in the water deficit treatment. Those two days were hot with a maximum air temperatures of 30 and 32 °C, respectively. The sharp decrease in stomatal conductance for 42 and 52 DAP had an adverse effect on carbon assimilation. Photosynthesis rates in MS were diminished 60-80% in comparison to the control. However, the difference lessened toward the end of the season. In 1988, the low values for stomatal conductance were not observed and the difference in photosynthetic rate between the control and MS treatment was significant only at 55 DAP (Figure 3.2).

The effect of stomatal conductance on Pn is best depicted in Figure 3.3. For the irrigated treatment, there is an increase of Pn between stomatal apertures of 0.6 and 1.8 cm/sec reaching a maximum of 25.5 mg $CO2/dm^2/hr$. Under drought stress, the maximum Pn observed was near 20 mg $CO2/dm^2/hr$. However, photosynthesis was not significantly different between treatments in the range of stomatal conductance from 0.6 to 1.4 cm/sec. The values for MS below 10 mg $CO2/dm^2/hr$ represent the amount of CO2 fixed at the time of near stomatal closure as shown in Figure 3.1.

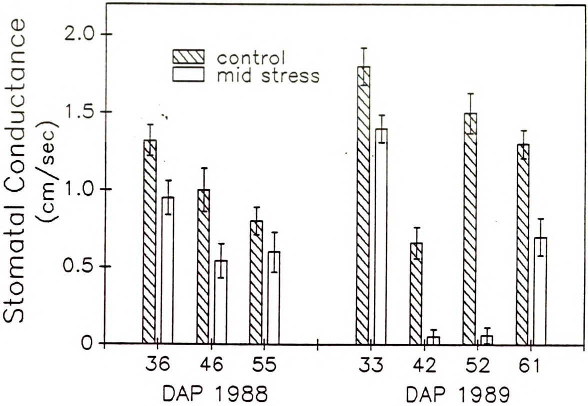

Figure 3.1. Stomatal conductances at different days during late stages of growth in MS and control treatments during 1988 and 1989.

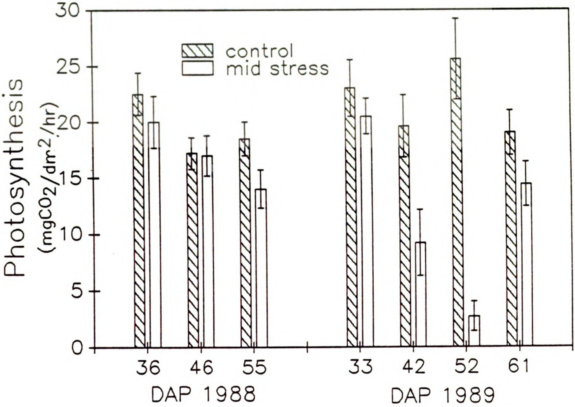

Figure 3.2. Photosynthesis rates at different days during late stages of growth in MS and control treatments during 1988 and 1989.

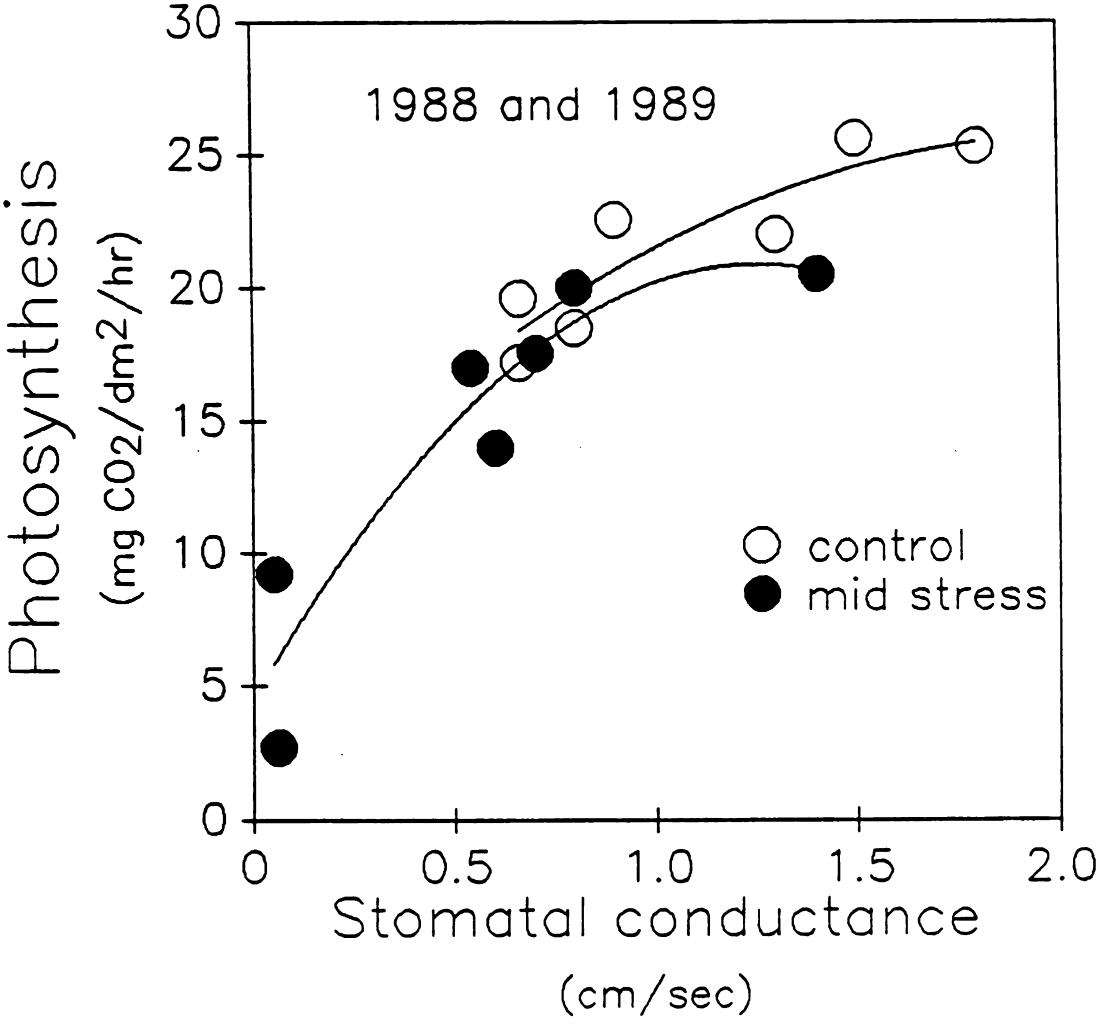

Figure 3.3. Relationship between stomatal conductance and photosynthesis rate in MS and control treatments during 1988 and 1989.

Light interception. The effect of soil water deficits on leaf extension is shown in Chapter 1. Leaf area growth rate decreased after the beginning of the drought stress affecting the total amount of light intercepted by the canopy. Light interception for MS lagged behind the control, reaching a maximum of 52% at 46 DAP (Figure 3.4). The maximum mid day light interception in the control was 92% achieved at 53 DAP. After 46 DAP, a rapid decrease in the percentage of light interception was observed in the MS treatment because of leaf senescence. Between 46 and 60 DAP, light interception decreased from 52% to 24%. By the end of the season, interception of light was less than 18% in MS as compared to 76% in the control.

Heliotropic leaf movements were also observed in this experiment for both treatments. Leaf angle in the upper leaves of MS increased from less than 10 degrees at 0700 hrs to nearly 62 degrees by noon (Figure 3.5). In the control, a maximum value of 30 degrees was observed at 1300 hrs, declining toward the end of the day. These differences in leaf orientation produced a daily pattern of light interception with lowest readings around midday (Figure 3.5A). The difference in heliotropic leaf movements had an effect on the percentage of light interception between MS and control at approximately the same LAI. At an LAI of 2.5 the MS treatment was intercepting about 50% of the light at mid day as compared to 60% in the control (Figure 3.6). Dry matter accumulation decreased after the onset of the water deficits (Figure 3.7).

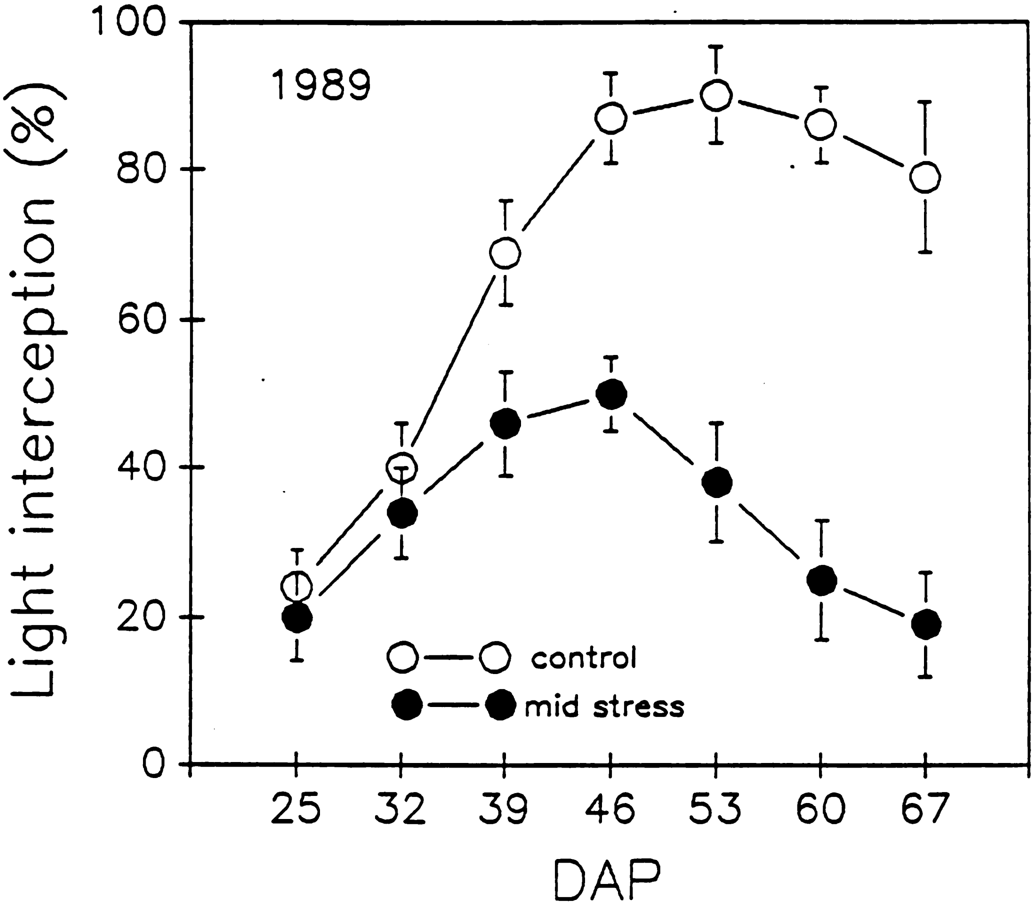

Figure 3.4. Seasonal changes in light interception at mid day for control and MS treatments during 1989.

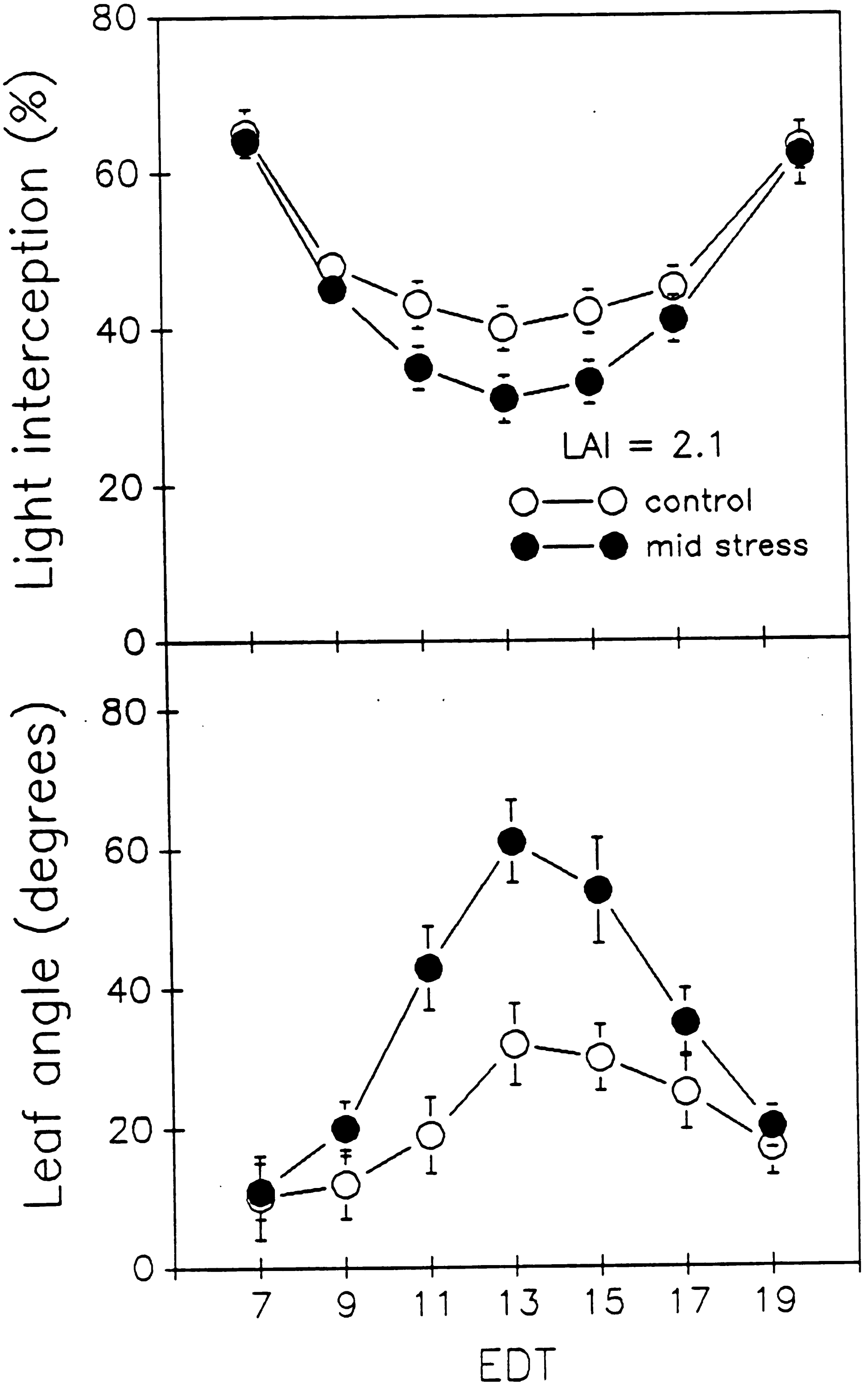

Figure 3.5. Diurnal changes of leaf angle and light interception for MS and control treatments at 36 DAP in 1989.

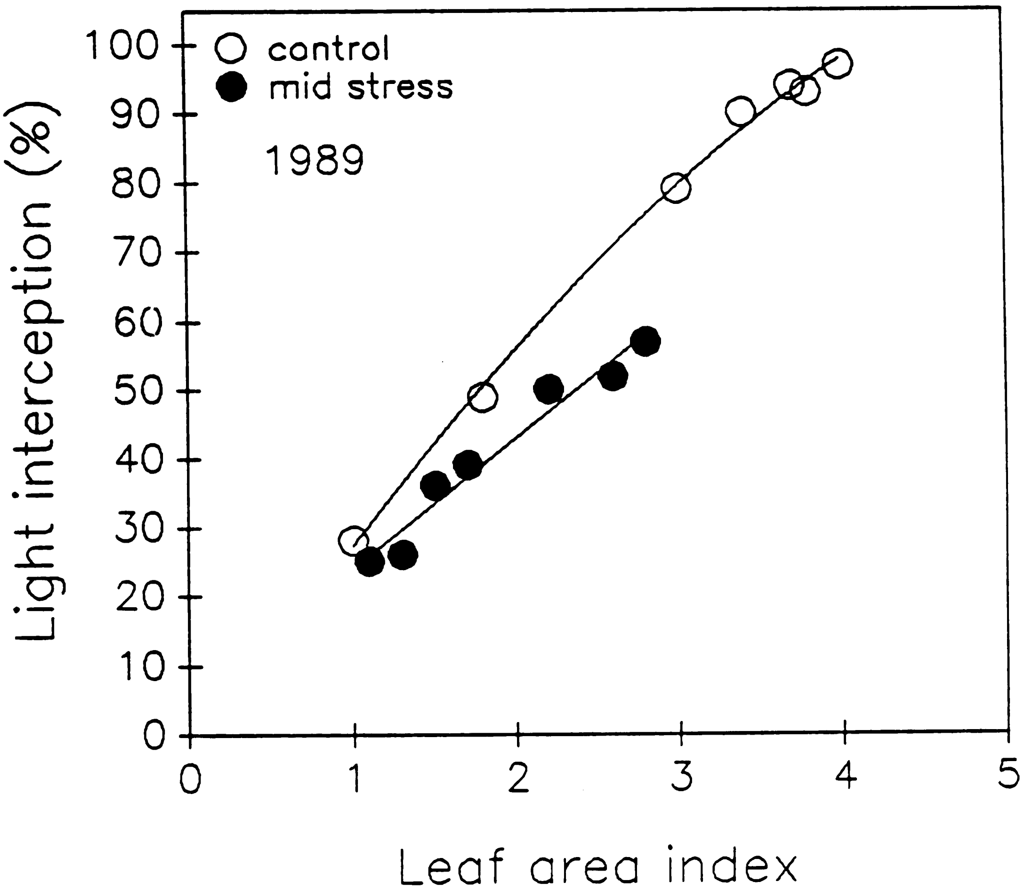

Figure 3.6. Relationship between leaf area index and light interception for the control and MS treatments.

In 1988, ES had an average growth rate (until maximum growth) of about 0.16 g/plant/day as compared to 0.022 g/plant/day of MS. However, the duration of growth was about a week longer before a decrease in dry matter (64 DAP). In 1989, MS increased at a growth rate 0.24 g/plant/day, compared to 0.33 and 0.40 g/plant/day for the LS and control treatment, respectively.

The relationship between cumulative IPAR and total biomass production is depicted in Figure 3.8. Dry matter production in MS began to lag behind the control after about 100 MJ/m^2 of cumulative PAR was intercepted. This is when the soil water deficit began to have effect on the MS treatment.

DISCUSSION

The results indicate that stomata respond to a decrease in soil water content as well as an increase in the evaporative conditions of the atmosphere. Lower stomatal conductances were measured in MS at the beginning of the dry period in both years and near stomatal closure was observed in 1989 during days with high air temperature. There is evidence that changing air temperature and humidity affect stomatal movement. Losch (1977) was able to induce stomatal closure in an isolated epidermis by increasing temperature and/or decreasing humidity. In the field, midday stomatal closure has been observed in several crops (Turner and Kramer, 1980).

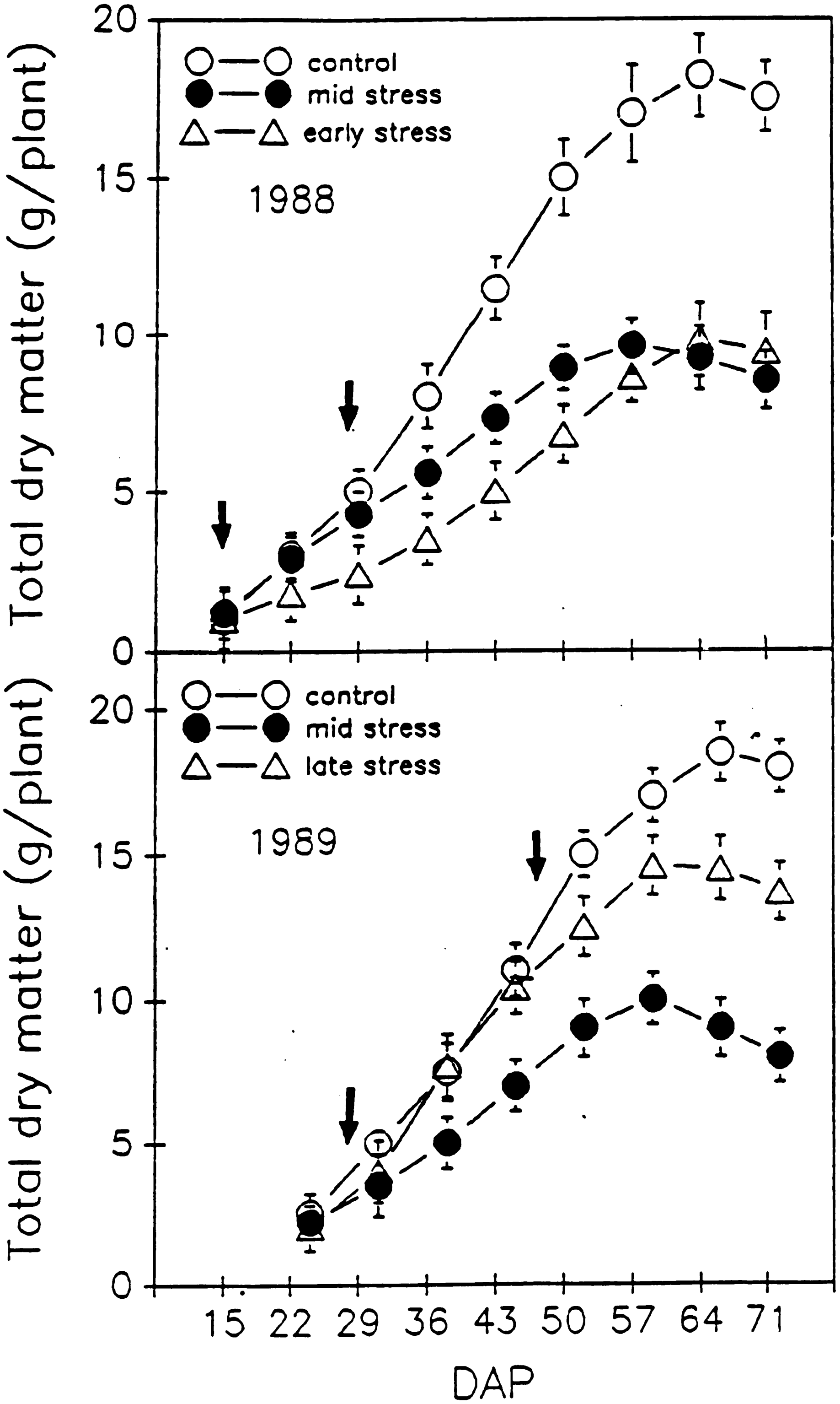

Figure 3.7. Seasonal changes in dry matter production for different soil water deficits treatments during 1988 and 1989.

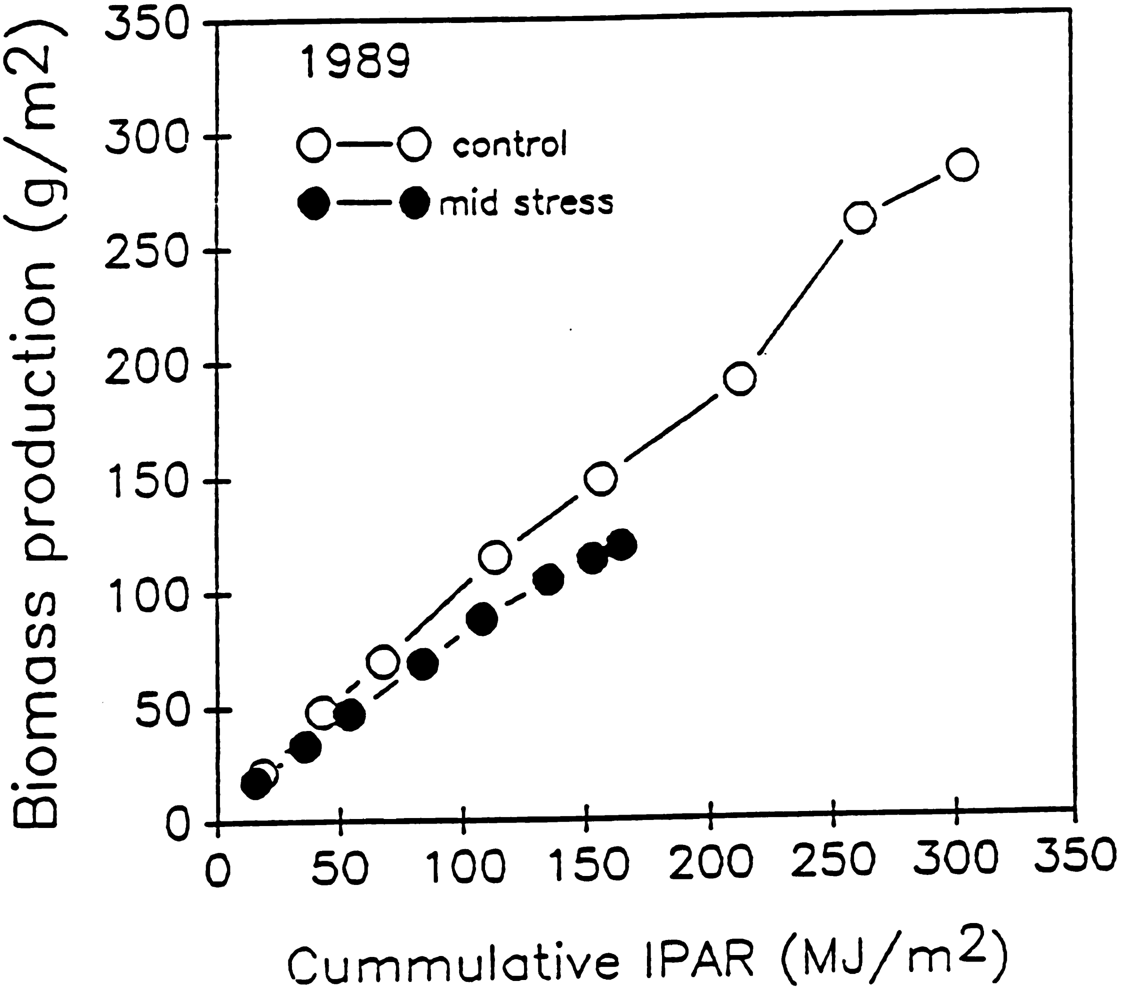

Figure 3.8. Relationship between biomass and cumulative intercepted photosynthetic active radiation (IPAR) measured in 1989.

In the current experiment, stomata response to atmospheric conditions seems to be occasional and related to days where air temperatures are high. However, the effect of decreasing soil water content seems to affect stomata for most of the days where measurements were made. There is evidence from field studies that stomata responses correlate with soil water supply but not with leaf water status (Bates and Hall, 1981). This independent control of leaf conductance by changes in soil water status was shown by Turner et al. (1985). Gollan et al. (1986) claimed that leaf water potential could be substantially changed without altering leaf conductance; however, stomata did temporary close when soil extractable water was depleted by 30%. Gollan et al., (1986) also found that stomata closed when full turgor was maintained in wheat and sunflower leaves while soil dried, suggesting a direct signal from the root to the stoma.

Photosynthesis was less affected than stomatal conductance. The largest difference between the control and the MS treatment was observed in 1989 with midday stomatal closure (42 and 52 DAP). For the other days of measurements, the difference between treatments was relatively small. Shultz and Hall (1982) found that with drying soil, stomates of C3 plants generally decreased their aperture prior to changes in their photosynthetic capacity. Wong (1979) found that stomatal conductance adjusted to changes in mesophyll resistance under stress so that variation in internal CO2, and hence photosynthesis, is minimized.

Interception of radiation was less than the control after the onset of the water deficit. Light interception was influenced by a rapid decrease in leaf expansion (Chapter 1) and by heliotropic movements observed with the upper leaves of the bean canopy. Solar radiation penetrated deeper in canopies with a leaf orientation toward the sun such as soybean and dry beans (Lemeur, 1973). Leaf movement also affects the daily pattern of light interception by increasing leaf angle with respect to the soil surface. The difference in light interception between treatments was greatest around noon. The midday depression of light interception has been shown for several crops (Shell and Lang, 1976; Blaine and Baker, 1972). This difference in leaf movement is a plant mechanism geared to reduce energy load and allows plants under soil water deficit conditions to intercept less solar radiation at the same LAI than well watered plants.

Biomass production was highly correlated to the interception of photosynthetic active radiation by the dry bean canopy (Figure 3.8). The same relationship has been shown for several crops such as apples, barley, potatoes, sugarbeet, and wheat (Monteith, 1977; Gallagher and Biscoe, 1978). However, when we compare MS and the control in this experiment, there is a small but increasing difference of above ground dry matter accumulation with time at the same percentage of PAR interception. The control produced slightly more dry matter than the MS treatment and this may be due to an increase in the translocation of a assimilates to the root system during periods of water deficits. This effect of water deficit on rapid root growth is shown in Chapter 4. Hoogenboom et al., (1987) found that during a declining water content, root growth increased at the expense of shoot growth.

CONCLUSIONS

Soil water deficits decreased stomatal conductance and to a lesser extent, photosynthesis rate. Light interception was adversely affected by drought conditions, mainly because of a decrease in leaf area expansion growth (Chapter 1), but also because heliotropic leaf movements. Leaf movement in MS decreased light interception at the same LAI than the control. Above ground dry matter production was highly correlated to the amount of PAR intercepted by the plant canopy in both treatments. However, at the same value of IPAR, the MS treatment had slightly lower shoot biomass production as compared to the control, suggesting a possible increase in the translocation of assimilates to the root system.

The prediction capabilities of the dry bean model may be improved if we take into account the differential amount of assimilates translocated to the root system during water deficit conditions.

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CHAPTER 4

EFFECT OF SOIL WATER DEFICITS ON DRY BEANS (*P. vulgaris* L.) IV. ROOT GROWTH AND WATER EXTRACTION.

ABSTRACT

Soil water deficits may influence the dynamic of root growth in dry beans. This investigation was performed to study the response of root growth to different terminal drought conditions. Research was conducted in the field using a rain shelter facility. Early (ES) and mid stress (MS) treatments were imposed in 1988. In 1989, the treatments were a MS and a late stress (LS). An irrigated control was used in both years. Root growth was monitored with a system of minirhizotron tubes. Total root length in ES and MS treatments rapidly increased at the onset of the water deficits reaching a peak length of 650 m and 700 m, respectively. The control reached a maximum root growth of about 780 m.

Rapid root growth in the upper soil layers occurred when soil water content fell below the drained upper limit. This rapid growth was followed by root death and compensatory root proliferation in deeper layers. Root death was observed when the soil water content approached the lower limit. The

fraction of water supplied by different soil layers changed with increasing total soil water use. After the initiation of the water deficits, most of the water absorbed (>70%) came from the upper 75 cm of soil, but toward the end of the season there was an increasing fraction of water depleted from lower depths. Total root growth in the control reached greater value than the one in the deficit treatments. However, plants grown under water deficits had more roots in lower depths by the end of the season.

INTRODUCTION

Roots play an important role in the growth and survival of plants during periods of drought stress (Stypa et al., 1987; Sheriff and Ludlow, 1984). Elongation of primary roots becomes an important factor influencing the framework of future root distribution within the soil profile (Passioura, 1982) as well as plant water uptake, particularly for seedlings growing in a drying soil (Sharp and Davies, 1979).

Under water deficit conditions, root growth in the surface soil layers is relatively slow while the growth of new roots in deeper, wetter layers is hastened (Garay and Wilhelm, 1983). Newman (1966) claimed that the total length of flax roots decreased markedly as total soil water potential declined from about -0.2 to -0.7 MPa. Taylor and Klepper (1971) observed a significant decrease of cotton roots in the top part of a drying soil followed by compensatory growth in deeper layers where water was more available. The rapid proliferation of roots observed during drought periods seems to occur at the expense of shoot growth (Hoogenboom et al., 1987). However, the fraction of assimilates partitioned to the root system is not a constant value, but varies with the stage of plant growth and the severity of the water deficit (Smucker, 1984).

Progressive soil dehydration influences the changes in rooting pattern growth, thus affecting the amount and timing of water availability (Ludlow and Muchow, 1989; Nunez-Barrios et al., 1991). However, the dynamic nature of root growth and the timing of the water deficit at different phenological stages is not well understood.

The objective of this investigation was to study the dynamics of root growth and water extraction in dry beans under terminal drought conditions including an early, mid, and late season soil water deficit.

MATERIALS AND METHODS

A field study was conducted at the Kellogg Biological Station, near Kalamazoo, MI. A rain shelter facility was utilized to control the water regimes for the different treatments. The soil was a Spinks sandy soil with an average drained upper limit (DUL) of about 0.16 cm3/cm3. A dry bean variety was planted on July 8, 1988 and June 12, 1989. Early season (ES) and mid season (MS) water deficit treatments were established in 1988, beginning at 15 and 29 days after planting (DAP), respectively. In 1989, the MS and LS treatments began 27 DAP and 45 DAP, respectively.

Soil water content was monitored for the control and the water deficit treatments using a neutron probe technique. Experimental establishment, irrigation schedule, and soil water contents are described in Chapter 1.

A system of non-destructive minirhizotron plastic tubes (5 cm ID) were set in place to determine root growth at multiple depths. Establishment was done by hand using an auger with a diameter similar to that of the minirhizotron tube. The hole was augured at a 45 degree angle with respect to the soil surface. After the soil cores were removed, the cavity was cleaned up with a steel brush and tubes were installed by pushing them into the soil. Three replications were used in each treatment. Observations of roots intercepting the minirhizotron tubes were recorded on video tape using a video camera. The camera was lowered into the tube until the deepest observable root appeared intercepting the minirihzotron tube and the camera was then pulled up at equal space intervals (1.2 cm) until reaching the soil surface.

Root growth was monitored by recording the number of roots intercepting the upper surface of the minirhizotron tube. The counts were independent of the length or the diameter of the root at the interface. Root counts were converted to root length densities using the equation described by Upchurch and Ritchie (1983):

$$RLD = Nd/Ad$$

where N is the number of intersecting roots, d the outside tube diameter, and A the area of the tube observed. The assumption was that growing roots intersect the tube at various angles with equal probability and the average length of root displaced by the tube if the roots could continue grow at the angle of the interception, was equal to the tube outside diameter. Each root interception then corresponds to a root length of d, therefore the total root length displaced is Nd. The volume associated with this length is Ad.

Root growth was recorded at 26, 42, and 58 DAP in 1988 and at 28, 42, and 59 DAP in 1989 in the Spinks soil.

RESULTS

During the summers of 1988 and 1989, dry bean plants were subjected to soil water deficits at different stages of phenological development. Irrigation ceased 15 and 29 DAP in 1988 and 27 and 45 DAP in 1989, initiating terminal drought for ES, MS, and LS treatments. Soil water content details are provided in Chapter 1.

Total root length at 26 DAP was greater for the ES treatment than for MS or the control (Figure 4.1A). From 26 to 42 DAP, MS had a greater growth than ES and the control.

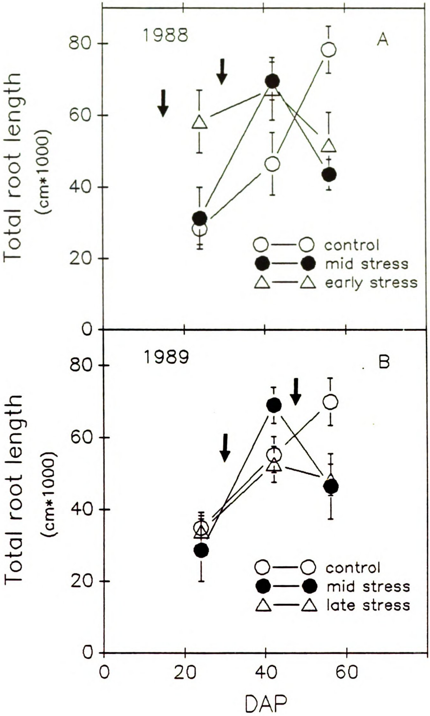

Figure 4.1. Total root length in the soil profile for different water deficit treatments. Arrows show the beginning of water deficits during 1988 and 1989.

Total root length in MS increased at a rate of 25 m/day as compared to 7 m/day and 10 m/day in ES and control, respectively. At 42 DAP, root death or turnover was observed in ES and MS. However, the roots in the irrigated treatment continued to grow at a rate of 23 m/day. In 1989, the results were similar for the MS treatment (Figure 4.1B). From 28 to 42 DAP, plants in MS experienced an increase in root growth of 27 m/day. From 42 to 59 DAP total root growth in MS had a significant decrease due to root death. The LS treatment also had decreased root length. Meanwhile the control continued to grow until the last day of readings (59 DAP). The rapid increase in total root growth in the ES and MS treatments was consistently observed after the onset of the soil water deficit.

Root distribution within the soil profile was affected by the water regimes. In 1988, maximum root growth in the control was observed at a depth of 20-40 cm (Figure 4.2A). In this treatment, roots continued to grow in most of the profile until 58 DAP. For MS, maximum growth in the upper 40 cm of soil was achieved 42 DAP (Figure 4.2B), 13 days after the initiation of the water deficit. At 50 DAP, there was rapid death in the upper region of the soil followed by compensatory root growth below the 60 cm depth. Similar changes in root growth were observed in ES (Figure 4.2C). Changes of root growth in the upper 70 cm between 26 and 42 DAP were not significant for ES. There was however, a significant decrease in root density at the same depth from 42 to 58 DAP.

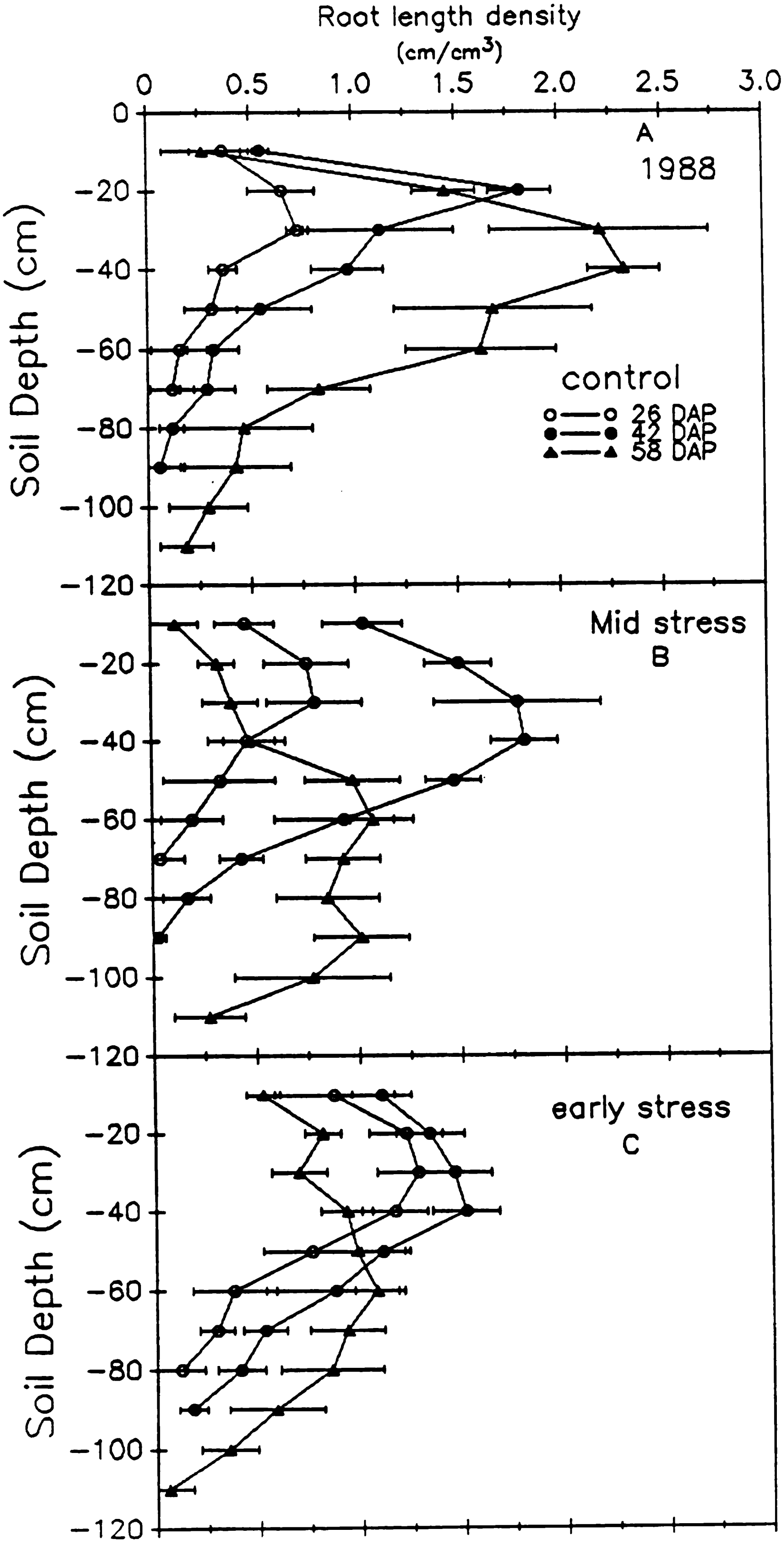

Figure 4.2. Root length density for three dates in the Spinks soil for different soil water regimes in 1988

In 1989, roots in the irrigated treatment continued to grow during the growing season in most of the soil profile until 59 DAP (Figure 4.3A). Roots in the MS and LS treatments began to die in the upper layers between 42 and 59 DAP, followed by compensatory root growth at lower depths (Figures 4.3B and 4.3C).

Changes in root length density are better depicted in Figures 4.4 and 4.5. Root death between 42 and 58 DAP was low in the control (Figure 4.4A). Root death in the control treatments was mainly observed in the upper 20 cm of soil. In MS, root death in the upper 50 cm was greater than the one observed in ES and control treatments. This rapid root death in the water deficit treatments occurred when water content in the top regions of the soil neared the lower limits of soil water availability. Root death in MS was also greater than the one observed in the LS treatment (Figures 4.5B and 4.5C).

Soil water content after the onset of the drought decreased rapidly in the top 20 cm, followed by a slower decline at 60 and 100 cm depths (Figures 4.6 and 4.7). In the ES treatment, soil water content began to decrease 15 DAP, with a resulting rapid response in root growth (Figure 4.6A). At a depth of 20 cm, root growth reached a value of 1.0 cm/cm3 at 26 DAP, followed by rapid root death when the soil water content was near 0.07 cm3/cm3. The rate of root growth decreased at 20 cm depth between 26-42 DAP, followed by a rapid increase observed at the 60 cm depth (Figure 4.6B). When root growth rate began to decrease at the 60 cm depth, a

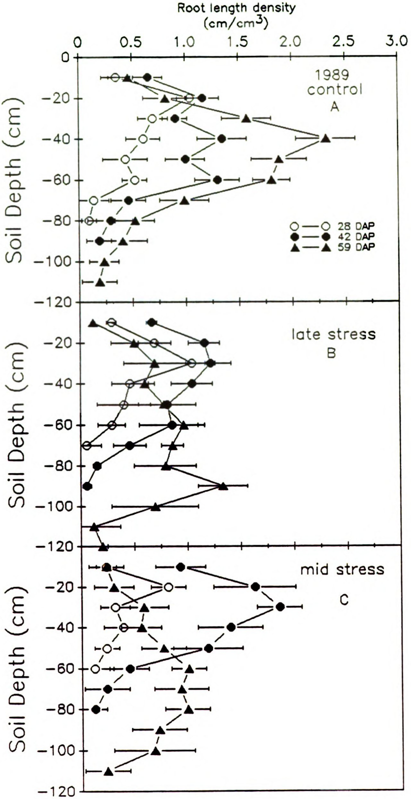

Figure 4.3. Root length density for three dates in the Spinks soil for different soil water regimes in 1989

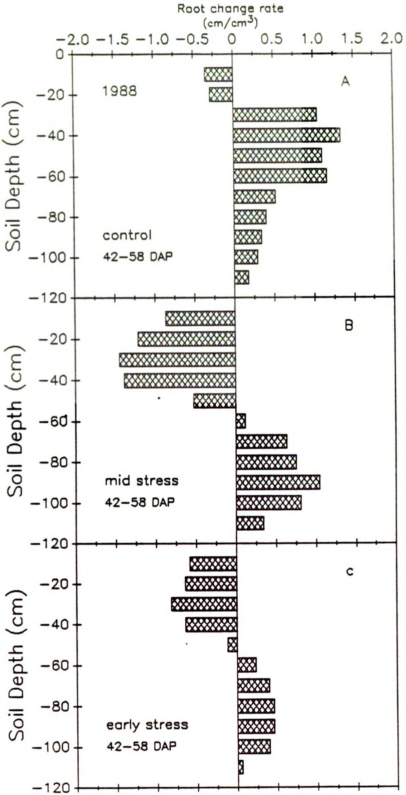

Figure 4.4. Changes in root growth between 42 and 58 DAP for different water deficit treatments and soil depths during 1988.

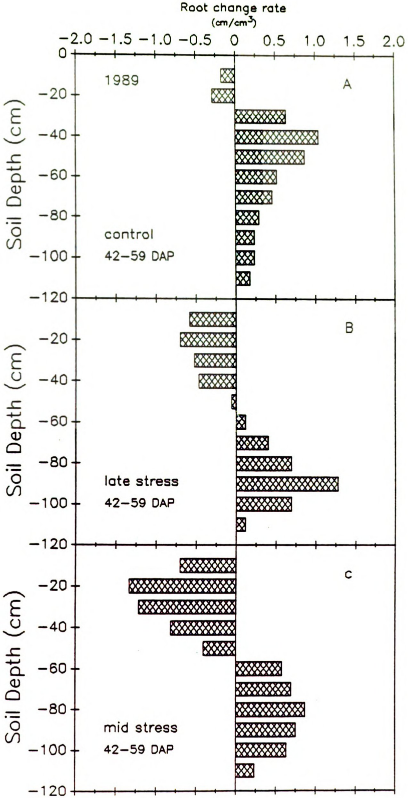

Figure 4.5. Changes in root growth between 42 and 59 DAP for different water deficit treatments and soil depths during 1989.

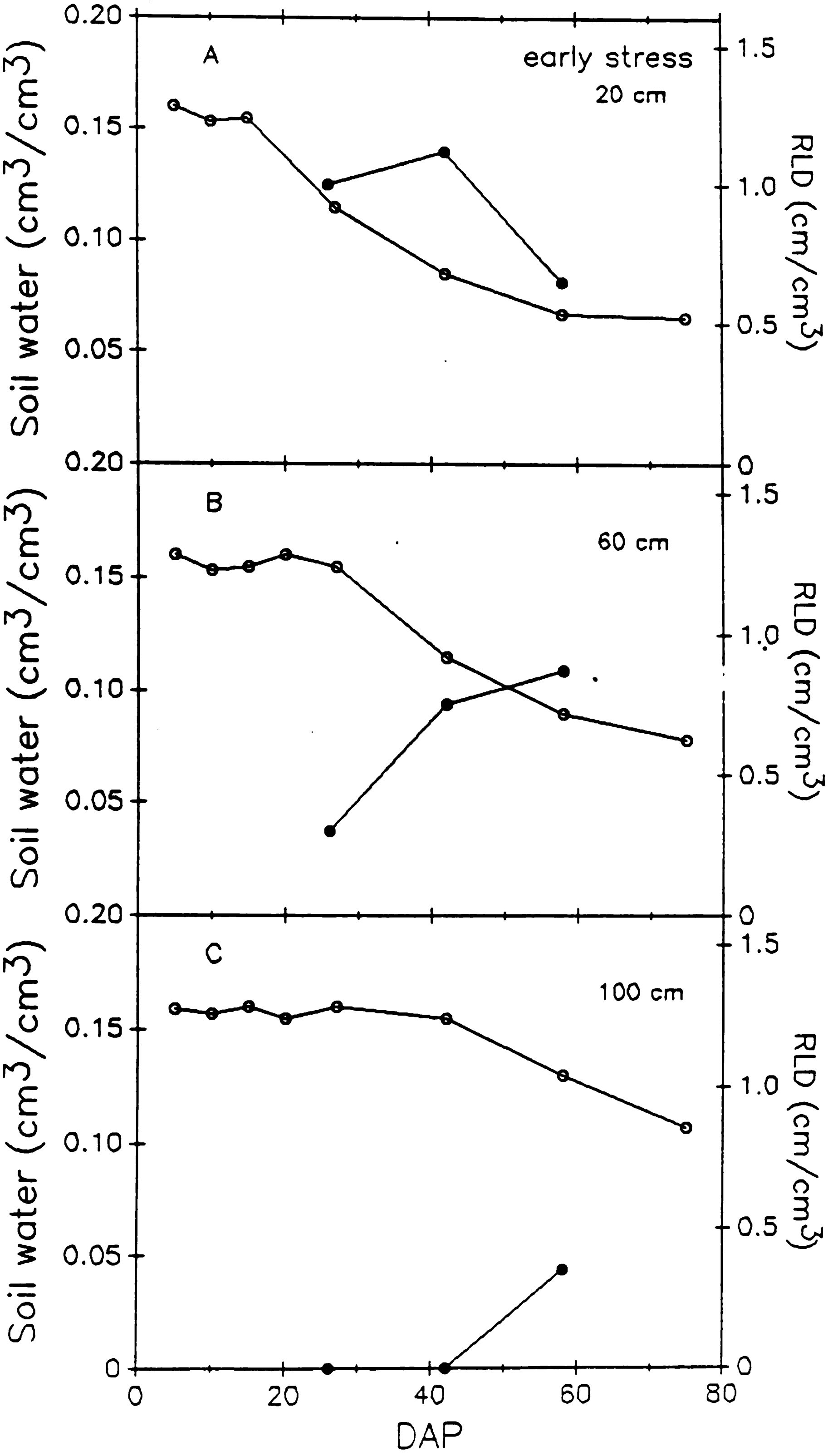

Figure 4.6. Dynamics of root density (RLD) and soil water content at 20, 60 and 100 cm depth in the ES treatment during 1988.

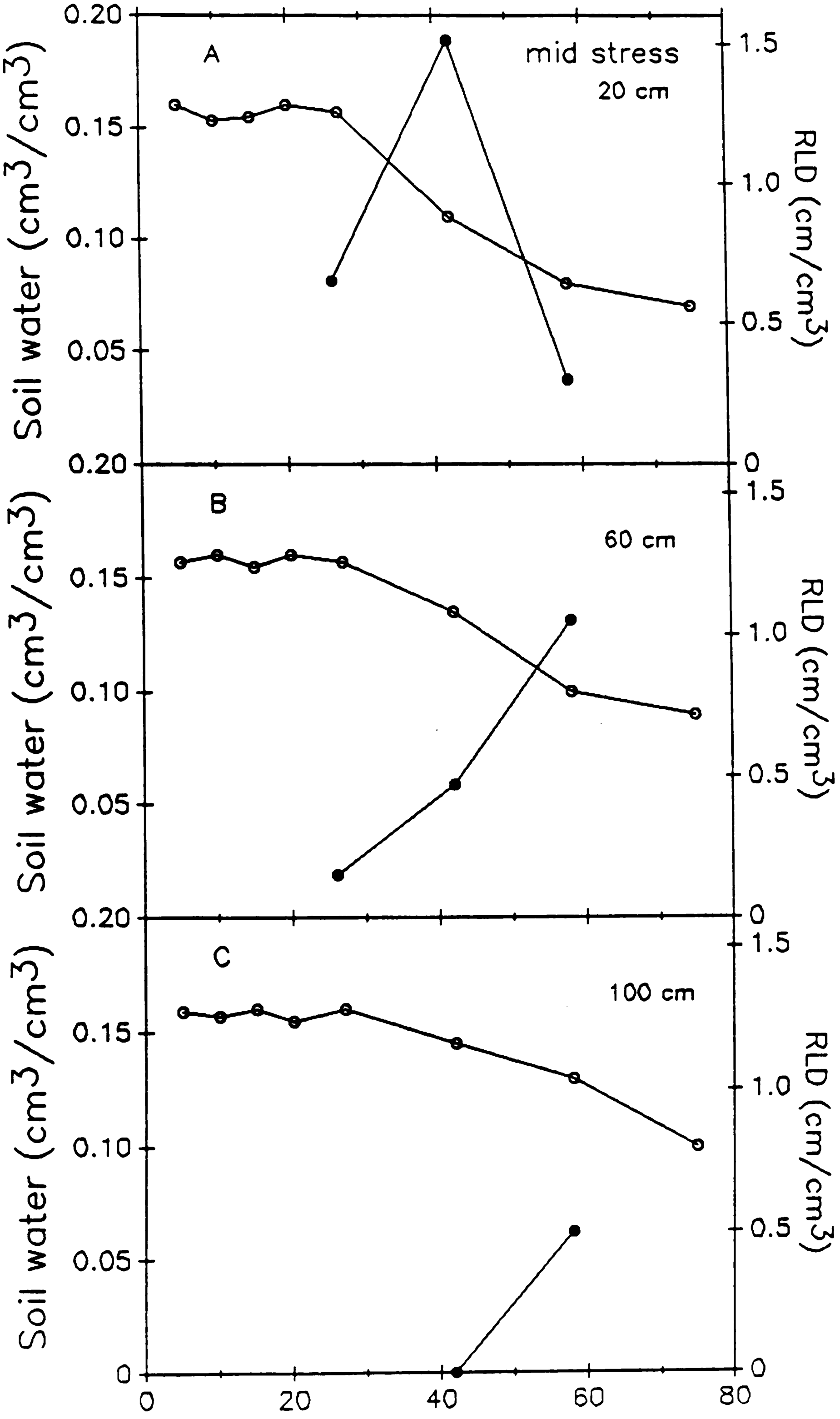

Figure 4.7. Dynamics of root density (RLD) and soil water content at 20, 60 and 100 cm depth, in the MS treatment during 1989.

rapid expansion of root growth was observed at 100 cm depth (Figure 4.6C).

For the MS treatment, the root response to declining soil water content in different layers was similar to that in ES. When water depletion began in the top 20 cm of soil, a rapid increase of root growth was observed (Figure 4.7A). Between 28 DAP and 42 DAP, root growth reached a density of 1.51 cm/cm3. When roots began to die at 20 cm, a surge of root growth (0.97 cm/cm3) was observed at 60 cm (Figure 4.7B). At 42 DAP, soil water content at 20 and 60 cm was approaching the lower limits of plant available water. At this time, roots at a depth of 100 cm started to grow reaching values of 0.7 cm/cm3 at 59 DAP.

The increase in root proliferation in deeper layers, as soil at upper layers dried out influenced the fraction of water absorbed in each layer. In the ES treatment (1988), more than 40% of the water uptake between 15 and 29 DAP came from the upper 25 cm (Figure 4.8A). From 29 to 43 DAP, the fraction of water absorption decreased in the top 25 cm and increased in the 50 cm layer. Toward the end of the season, increases in the fractions of water extracted were observed in depths below 100 cm, coinciding with a concomitant increase in root growth. Water extracted in depths of 125 and 150 cm began increasing 57 DAP. In the MS treatment, water was mostly absorbed from the upper 75 cm two weeks after the onset of the water deficit. Between 57 DAP and 71 DAP, more than 60% of the water absorbed came from depths below 100 cm

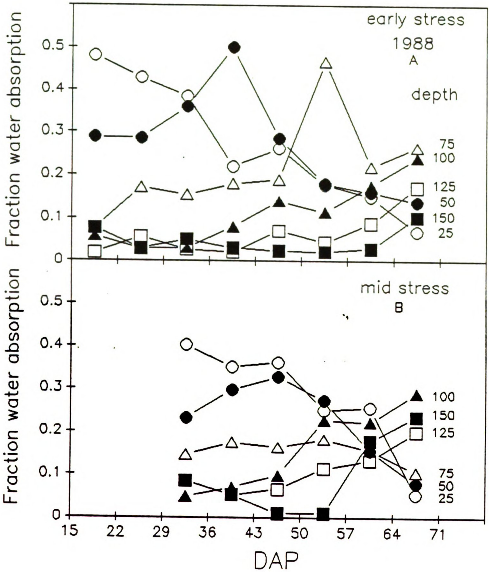

Figure 4.8. Fraction of the total water absorption for different soil layers in ES and MS in Spinks soil during 1988.

(Figure 4.8B). Similar patterns of water extraction per soil layer were observed in the deficit treatments of 1989 (Figures 4.9A and 4.9B). For the MS treatment, more than 70% of the water was absorbed from the upper 50 cm a week after the onset of the deficit. However, toward the end of the season these two depths contributed less than 20% to the total water extraction. Plants were absorbing water from layers below 100 cm depth.

DISCUSSION

Results indicated that soil water deficits influenced the dynamics and spatial distribution of roots in the soil profiles for both years of study. Rapid root growth was observed for the ES and MS treatments in the upper layers of the soil at the beginning of decreasing soil water contents. Sharp and Davies (1979) found that plants growing in a drying soil exhibited a greater net increase in root growth when compared to plants growing in soil regularly supplied with water. This phenomenon was shown in both dry weight and root length. Hoogenboom et al. (1987) found that a period of drought stress during vegetative development caused a marked increase in root growth rate of non-irrigated soybean plants.

After the first response of rapid root growth with declining soil water, roots began to die when plant available water in the upper soil reached values near the lower limit. Compensatory growth of new roots in deeper, wetter layers was

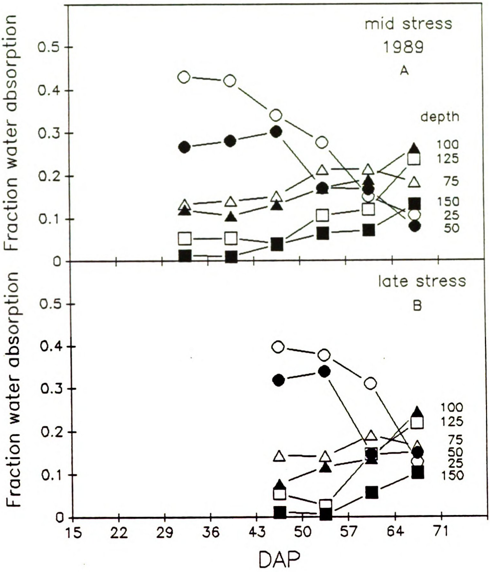

Figure 4.9. Fraction of the total water absorption for different soil layers in MS and LS in Spinks soil during 1989.

observed for all water deficit treatments, suggesting a significant effect of soil water in the reallocation of carbon in the soil profile. Lang and Thorpe (1986) found that under drought stress, portions of the plant with the lowest water potential attracted most of the assimilates.

At the end of the season in both years, more total roots were observed in the irrigated treatments. These observations coincided with the ones shown by Robertson et al. (1980). They found that total root length was greater for irrigated treatments, although non-irrigated plants produced more roots in the deeper part of the soil profile. Arya et al. (1975) reported that under field conditions, where rewatering occurred after a water deficit, most of the root mass was found in the upper soil layers for both irrigated and non-irrigated treatments.

Root death was greater for the MS treatment than for ES and LS. Plants in the MS treatment also experienced a rapid decline in leaf area (Chapter 1) caused by a rapid senescence rate. In dry beans, leaf senescence usually begins from the bottom to the top nodes in the plant. Waters et al. (1980), using radioactive $^{14}CO_2$, found that during flowering in dry beans more than 45% of the carbon fixed in the leaves of the first nodes was recovered in the root system. Upper leaves translocated more than 85% to the pods during the pod filling stage. However, the fraction of photosynthetically derived carbohydrates partitioned into the roots is not a constant value (Smucker, 1984) but varies with the timing and severity of the drought experienced by the plant.

Changes in root growth differentially affected the amount of water being extracted at different depths. In the ES treatment, water uptake from the bottom layers was postponed until the last part of the season, reflecting a conservation in water use allowing the plant to survive and produce some yield during the long dry spell. Plants in the MS treatment, because of their larger size, rapidly depleted the water available in the upper portions of the soil. They began water uptake from below a 1 m depth at least a week before those in ES. This rapid water absorption from lower depths in the soil indicated a lower adaptation process in the plants of the MS treatment as well as a possible slower downward root growth in the plants of ES. Ludlow and Muchow (1989) reported that changes in rooting patterns at different stages of growth affected the amount and timing of water availability in the soil profile.

The increase in root growth was closely coupled to the decrease in the rate of shoot growth. This type of plant adaptation to water deficits has been shown to help maintain absorption of sufficient water to meet the evaporative demand (Huck et al., 1983).

CONCLUSIONS

Soil water regime affected the dynamics of root growth and root distribution within the soil profile. Total root growth at the end of the season was greater in the control than in ES, MS, and LS, however, these deficit treatments produced more roots in deeper soil layers. Roots in the upper regions of the soil increased rapidly in response to a decrease in soil water content and died shortly thereafter. Rooting patterns affected the amount and timing of water extraction in different soil depths. For the ES treatment, the differential water extraction suggests a conservative approach to water use where the available water in the lower regions of the soil was only used at the end of the season during the seed filling stage. The MS treatments had the highest rate of root death which largely coincided with the rapid senescence rate observed in leaves. The description of shoot conditions, in terms of leaf area, is important in explaining the rooting patterns of plants undergoing water deficit conditions.

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SUMMARY AND CONCLUSIONS

The objective of this investigation was to study under field conditions the effect of water deficits on dry beans at different stages of growth.

The results obtained from these experiments indicate that soil dehydration hastened flowering and seed filling stages while delaying leaf appearance. This seems to be a plant mechanism related to earliness, which under drought conditions, is associated with a reduced vegetative phase.

Water deficits diminished leaf, internode, and pod expansion growth resulting in a small plant size. Reduced leaf growth and accelerated leaf senescence were a common response to the drought conditions and combined to decrease leaf area. Changes in leaf area appear to be one of the main means by which dry bean plants adapt to a declining soil water availability. This response enhances survival by conserving water as observed in ES and MS treatments. However, this mechanism was detrimental to yield because of the decrease in light interception when LAI was below 3. Organ expansion and LAI were more affected in sandy soil than in loamy soil.

Paraheliotropic leaf movement decreased the interception of solar radiation per unit leaf area between treatments. Under terminal stress conditions, these paraheliotropic movements may enhance yield by reducing the energy load on the plant and hence the rate of water loss. This allows the crop to have more water available during late stages of growth such as flowering and/or seed formation.

Excess production of flowers and pods was observed for all treatments, assuring that the plants had enough reproductive structures to cope with the uncertainties of the environment. Flower and pod abscision was greater in the MS and LS treatments. Organ shedding appears to be a wasteful process because of the loss of carbon. Under water deficits the plant priority seems to be focused on having fewer pods with more viable seeds at the end of the season. Flower and pod abscision occurred mainly in the plant branches indicating higher priority for the reproductive structures growing on the main stem.

Photosynthesis rate was reduced to a lesser extent than stomatal conductance in the MS treatment. Stomata remained partially open during progressive soil dehydration, with observable midday closures occurring mainly when the temperature and the atmospheric demand for water was high. The main response to reduced stomatal conductance in the field seems to be the avoidance of plant desiccation.

Above ground dry matter production was linearly related to the intercepted PAR. However, the efficiency of energy conversion was slightly lower for the deficit treatments as compared to the control. This suggests that there is an increase in the allocation of assimilates to the root system with a decreasing soil water content. Further investigation is needed to determine the dynamics of carbon allocation in the root/shoot system with advancing soil dehydration. This information is needed to better model dry bean production under deficit conditions.

A rapid response in root growth was observed shortly after the onset of the water deficit treatments. Root proliferation increased root density, allowing the plant to continue water absorption from the upper soil layers. As soon as the soil water content approached the lower limits of plant available water in the top regions of the soil profile, root death rapidly occurred followed by compensatory growth in deeper, wetter layers.

Differences in the rooting patterns changed the amount and timing of water extraction at different soil depths. For example, the plants in the ES treatment managed to have a conservative strategy for water absorption. They used most of the water in the upper soil profile at the beginning of the deficit, leaving the water available in deeper layers to be used later in the season to complete the seed filling stage.

Rapid expansion of root growth was observed during soil dehydration and coincided with a decrease in leaf elongation as well as with a partial decline in stomatal conductance. This suggests that root proliferation (more root branches and root tips) results in some type of communication between root and shoot. More research is needed to describe the effect of the root-to-shoot signals on the whole plant carbon balance under field conditions.

The main conclusions drawn from this investigation may be summarized in terms of the duration and rate of growth under soil water deficits.

Duration and development:

1. Water deficits hastened flowering and seed filling, reducing the vegetative phase. This phenomenon lowered water requirements allowing the plant to reach maturity with a limited supply of water.
2. Production of new leaves, internodes, flowers, and pods decreased with soil dehydration.
3. The duration of leaf growth and internode elongation was not affected as much as the growth rate of these organs.

Growth rate:

4. Leaf growth and flower and pod production were more affected on branches than on main stem during acclimation of the dry beans to water deficits, indicating a priority for the plant to allocate resources in the main stem.
5. Leaf size, leaf senescence, and leaf paraheliotropic movements greatly influenced light interception and water absorption.
6. In the water deficit treatments, stomata seemed to have little control on photosynthesis rates and on total crop evapotranspiration.
7. Plants under increasing soil dehydration may conserve soil water through two means: a) extracting water more slowly as

the soil water approached LL in the upper soil layers and b) changing the dynamics of root growth in the soil profile to use available water from deeper depths at late stages of growth.

8. Plants showed evidence of stress in the sandy soil as early as five days after the onset of the deficit when much of the available water was still in the soil. Roots expanded rapidly, apparently because the water could not move fast enough to the existing root system. The rapid expansion increased the total root surface bringing roots to a closer proximity with the water, especially when the rate of absorption was fast.
9. Roots death occurred when soil water content reached the LL, allowing plants to increase the growth of new roots in deeper layers where water was more available.
10. Dynamics of root growth patterns during soil dehydration implied a greater partitioning of assimilates to the root system at the expense of shoot growth and yield.
11. There is no simple solution to improve yield of dry beans under drought conditions. Defining the physical environment and matching phenology and plant growth to the patterns of water supply is one of the first steps to maximize water availability and yield.
12. The use of simulation models will provide a tool for integrating the information collected in the field under different drought scenarios. Models facilitate the

decision making process for the selection and improvement of varieties as well as for the use of management practices directed at optimizing the water availability during the growing season.

Recommendations:

Based on the experience acquired through the conduction of this investigation, a further understanding of the plant response to water deficits may be obtained by:

1. Quantifying the partitioning of assimilates to the root system using radioactive isotopes such as $^{14}CO_2$. This is an expensive and cumbersome goal to achieve under field conditions but it will provide a whole carbon balance needed to better understand the system.

2. Estimations of ET based on the neutron probe data seemed biased, primarily because the inaccurate readings near the soil surface. The use of more appropiate instruments such us TDR may help to improve ET estimations.

3. Although stomata did not have much effect on photosynthesis and ET in this investigation, more measurements describing the diurnal cycles of stomatal conductance may provide a better understanding of the role of stomatal action on plant productivity under drought conditions.

APPENDICES

Appendix 1. Description of the soil profile for Spinks and Kalamazoo soils.

Kalamazoo soil	Spinks soil
Ap. 0-11 inches; light brownish gray (day); weak medium granular structure; friable	Ap. 0-10 inches; dark brown loamy sand; weak fine granular structure; very friable; slightly acid.
B1. 11-16 inches; dark yellowish brown; weak medium subangular blocky structure; friable.	A21. 10-16 inches; dark yellowish brown; loamy sand; weak coarse subangular blocky structure, friable, slightly acid.
B21t. 16-20 inches; dark yellowish brown clay loam; moderate medium subangular blocky structure.	A22. 16-28 inches; yellowish brown loamy sand; very friable; 3% pebbles; neutral.
B22t. 20-30 inches; dark brown clay loam; same structure than B21t; 1% pebbles.	A&B. 20-86 inches; yellowish brown sand single grained; massive very friable; 1% pebbles; neutral
B23t. 30-38 inches; dark yellowish brown; sandy loam with clay films; medium acid.	
IIB31. 38-60 inches; dark yellowish brown; loamy coarse sand; massive friable; medium acid.	

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 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