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By

Reimar Carlesso

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ABSTRACT

INFLUENCE OF SOIL WATER DEFICITS ON MAIZE GROWTH AND LEAF AREA ADJUSTMENTS

By

Reimar Carlesso

Physiological aspects of leaf growth, leaf movements and morphological mechanisms have been studied extensively. However, there has been little effort to elucidate the adaptative importance of either of these types of leaf area adjustments during water deficit. The objective of this study was to: (i) identify morphological and physiological differences between two maize hybrids; (ii) Define the relation between LAI and radiation interception; (iii) Characterize the sensitivity and quantify the contribution of leaf rolling, leaf senescence and leaf expansion to the reduction of plant exposed leaf area and; (iv) Modify the CERES-Maize model to predict the daily fraction of radiation intercepted by maize plants. Pioneer varieties 3576 and 3615 were subjected to three irrigation managements: Well-irrigated, pre-anthesis water deficit and post-anthesis water deficit. Spinks loamy sand and Kalamazoo loam were the soils used. Post-anthesis soil water deficit was not imposed on the Kalamazoo loam soil. Results indicate that as the water deficit developed the maize tended to orientate its leaf blades in a more vertical position. The PAR interception declined for both maize varieties during the vegetative soil water deficit period due mainly to an increase in leaf rolling and a change in leaf

orientation and, to a decrease in leaf expansion. Leaf rolling and leaf expansion were influenced by periods of low VPD. Plant leaf rolling limited the activity of the leaf elongation mechanism. During post-anthesis soil water deficit plant leaf rolling was reduced due to length and width of the leaf blades (long leaf blades bend downwards). Thus, leaf rolling mainly occurred near the edges of the leaves, limiting further increases in leaf rolling and leaf orientation and, consequently, the reduction of exposed leaf area. The effectiveness of the leaf rolling mechanism, during post-anthesis water deficit, occurred mainly during the beginning of the water deficit period and leaf senescence was activated later when no further reduction in exposed plant leaf area was possible by increasing leaf rolling. Modifications in the CERES-Maize model enabled the model to predict intercepted PAR and the fraction of plant leaf area exposed to the incident solar radiation.

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CHAPTER 1

Effects of Pre-Anthesis Soil Water Deficit on Maize Growth.

I. Leaf Morphology, Leaf Rolling and Radiation Interception.

Abstract

Maize varieties differ in morphological responses to water deficit but morphological adaptations that confer water deficit resistance are not well understood. The objective of this study was to identify differences in interception of solar radiation, leaf rolling and leaf orientation between two maize varieties growing in water-limited conditions during the vegetative growth stage. Pioneer varieties 3576 and 3615 were subjected to two irrigation managements: well-irrigated and water deficit in the vegetative stage. As the water deficit developed the maize tended to orientate its leaf blades in a more vertical position. Expanding leaves were more sensitive to this movement. Light interception declined for both maize varieties during the water deficit period due mainly to an increase in leaf rolling and a change in leaf orientation, and to a decrease in plant leaf area. Pioneer variety 3576 was more sensitive in reducing the intercepted radiation to minimize water loss by transpiration.

Introduction

Responses among different maize varieties to water deficits have been reported, but quantification of morphological differences that confer drought resistance are not well explained. A better understanding of morphological and physiological differences among maize varieties that are responsible for the differential responses require additional investigation. While leaf development is one of the most important factors affecting crop productivity, it is also one of the components of growth that is the most sensitive to water deficit. Leaf growth is more sensitive to water deficit than stomatal conductance and carbon dioxide assimilation, because crop growth is reduced by water deficits that are too small to cause a reduction in stomatal aperture and photosynthesis (Acevedo *et al.*, 1971; Boyer, 1970; Fischer and Hagan, 1965; Hsiao and Acevedo, 1974; Claaseen and Shaw, 1970; Hsiao *et al.*, 1976).

Leaf response to water deficits include rolling, folding, and wilting as well as diaheliotropic and paraheliotropic movements (Rawson, 1979; Begg, 1980; Wilson *et al.*, 1980; Ludlow and Bjorkman, 1985). Leaf rolling reduces the effective leaf area (Begg, 1980; Duncan, 1980; Jordan, 1983), the energy load on the plant (Begg, 1980; O'Toole *et al.*, 1979; Duncan, 1980; and Jordan, 1983), leaf temperature (O'Toole *et al.*, 1979; Ludlow and Muchow, 1990) and water loss (Oppenheimer, 1960; O'Toole *et al.*, 1979; Austin and Jones, 1975; Jordan, 1983; Turner, 1979; Turner and Begg, 1973). Consequently, leaf movements reduce plant dehydration and, in intermittent water deficit situations or periods of high evaporative demand, they contribute to stability of the yield (Begg, 1980; Fisher and Ludlow, 1983; Ehleringer and Forseth, 1980; Forseth and Ehleringer, 1980). However, in terminal water deficit situations there is no benefit because leaf movements have little direct influence on the yield components and will reduce the water consumption rate, delaying the time the water deficit reaches a threshold level (Ludlow and Muchow, 1990).

In many monocotyledons plants, bulliform cells are found in the epidermis. These cells are single, translucent cells, or groups of colorless cells, constituting part of, or the entire epidermis (Ellis, 1976). These cells differ from other epidermal cells, being larger, thin-walled and highly vacuolated cells (Fahn, 1974; Esau, 1965). They occur most commonly, but not exclusively, at the base of adaxial furrows (Metcalfe, 1960; Fahn, 1974; Esau, 1965) and are low in solid contents, contain much water and are devoid, or nearly so, of chloroplast (Ellis, 1976; Fahn, 1974; Esau, 1965).

There are different opinions concerning the function of the bulliform cells. According to some researchers, they function in the opening of the rolled leaf as present in the bud. The conventional explanation is that bulliform cells regulate the rolling and unrolling of the blade. The sudden and rapid expansion of the bulliform cells during a certain stage of leaf development is assumed to bring about the unfolding of the blades from the bud (Esau, 1965). However, according to Ellis (1976), the unfolding involves general growth, particularly in the adaxial mesophyll, and does not result from the enlargement of the bulliform cells. These cells are thought to enlarge due to turgor changes.

Absorbed photosynthetically active radiation (APAR) is the appropriate way to express the quantity of energy absorbed by the crop canopy. However, intercepted photosynthetically active radiation (IPAR) by the crop canopy has been used in crop models (Arkin *et al.*, 1976; Stapper and Arkin, 1979; Steven, 1981). Comparisons of IPAR with APAR made by Gallo and Daughtry (1986) showed that the differences are less than 3.5%. In addition, measurements of light intercepted (IPAR) by the crop canopy requires the use of less equipment and time.

In the absence of other limiting factors, crop productivity is directly related to the APAR by a crop canopy (Blackman and Black, 1959; Loomis and Williams, 1963; Williams *et al.*, 1965; Monteith, 1977; Monteith, 1981; Tollenaar and Bruulsema, 1988; Ottman and Welch, 1989). Several studies have shown a linear relationship between APAR and the rate of crop dry matter production when no other limiting factor affects crop growth. However, Gosse *et al.*, (1986) demonstrated that the phase of the crop development affects the relationship.
Plant patterns influence the distribution of solar radiation in the canopy as well as the total radiation intercepted by a crop (Ottman and Welch, 1989). In dense populations, light interception occurs mainly in the top part of the canopy (Williams *et al.*, 1965). Total solar radiation available during the growing season is almost constant in each location and differs little from the average. Thus, light intercepted by the crop depends mainly on the leaf area index. Evans *et al.* (1975)

demonstrated that early in the growing season the quantity of light intercepted by the crop canopy is limited by the low LAI and as LAI increases to about 4 the light intercepted increases rapidly to about 95%.

The objective of this study was to identify differences in interception of solar radiation, leaf rolling and leaf orientation between two maize varieties under drought during the vegetative growth stage. Maize hybrids are normally selected for near optimal conditions of water availability, but frequently are grown in environments with less than ideal soil water conditions.

Methodology

This experiment was conducted in 1990 and 1991 at the Kellogg Biological Station, near Kalamazoo, Michigan. A rain shelter, described by Martin *et al.*, (1988), was used to prevent rainfall on the experiment.

Spinks loamy sand (mesic Psammentic Hapludalfs) was the soil at the site. Maize varieties, Pioneer 3615 and Pioneer 3576, were planted north-to-south at a high density on May 18 (DOY 138) in 1990 and on May 27 (DOY 147) in 1991. Emergence occurred on May 28 (DOY 148) in 1990 and on May 31 (DOY 151) in 1991. Plants were thinned in the seedling stage to a plant density of 7.2 plants/m^2. Weeds were controlled manually during both years. Plot size was 4.6 m x 6.2 m. Maize was planted in six rows, 0.71 m wide, giving two border rows and four main rows in each plot. The experimental layout was a split-plot design, with irrigation treatment as main plot and maize varieties as subplots.

Irrigation water was applied using an overhead Toro FS-LG series sprinkler system, mounted upside down on the trusses of the rain shelter operating with a constant pressure of 103.5 Kg.Pa^{-1}, at a rate of approximately 25 mm.hr^{-1} (NeSmith *et al.*, 1990). Two irrigation treatments were established: (a) well-irrigated (irrigation was applied to maintain the fraction of plant available water above 0.70); and (b) water deficit in the vegetative stage. The water deficit period (period between subsequent irrigations) occurred from day of year (DOY) 171 (sixth leaf ligule) to DOY 194 in 1990 and, from DOY 172 to DOY 200 in 1991. The irrigation amounts applied on each treatment in 1990 and 1991 are presented in Figure 1.1.

Before emergence, fertilizer was applied at rates of 60 Kg N ha^{-1} (45-0-0), 200 Kg P ha^{-1} (0-46-0), and 60 Kg K ha^{-1} (0-0-60). Nitrogen was applied at a rate of 100 Kg.ha^{-1} 19 days after emergence (DOY 166) and 17 days after emergence (DOY 168), in 1990 and 1991.

Soon after emergence, four plants per plot (two plant per variety) were randomly selected and marked for nondestructive measurements throughout the season. Measurements of leaf area were taken, approximately three times a week, once the leaves emerged from the whorl until the leaf ligule appeared. The area of each leaf was determined from measurements of leaf length and maximum leaf width multiplied by 0.75 (Stickler *et al.*, 1961).

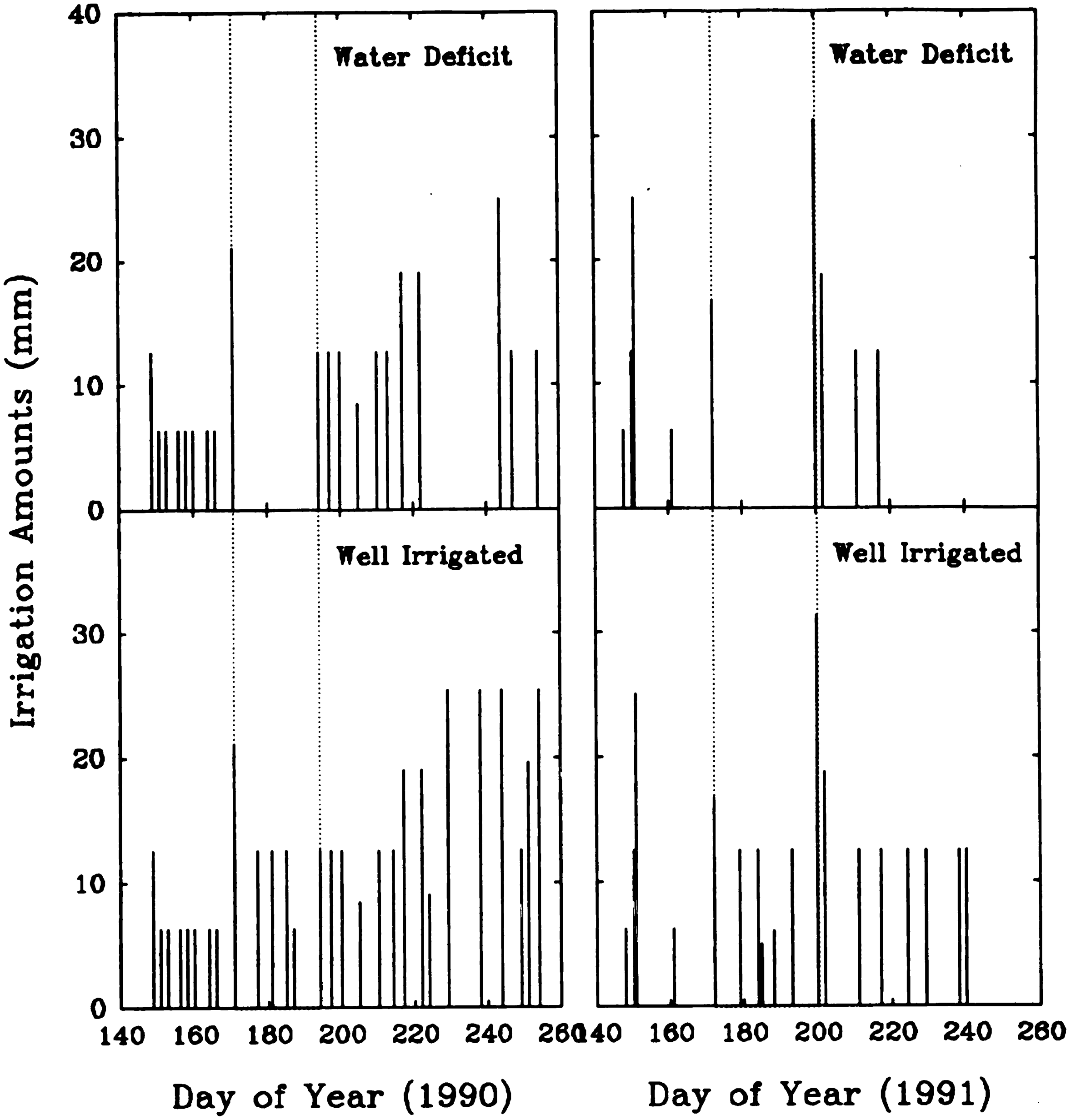

Figure 1.1. Irrigation amounts (mm) applied on each treatment in 1990 and 1991. The area limited by vertical dotted lines represents the period of vegetative soil water deficit.

Leaf rolling and leaf position were measured several times daily and weekly during the water deficit period in four selected plants per plot. Leaves 9 and 10, while they were growing, were selected to represent the plant leaf rolling and two positions were marked on each leaf (quarter-way and half-way from the tip). A family of individual leaf area curves measured on three different occasions for both varieties during the water deficit period in 1991 are presented in Figure 1.2. The leaf rolling index (LRI) was calculated from the fraction of the rolled leaf width (measured by a caliper) and fully open width. Leaf position was obtained by measuring the vertical and horizontal distances of four marked positions on each leaf (ligule, leaf tip, quarter-way and half-way from the tip). Plant stem and soil surface were the reference points for horizontal and vertical distances.

Photosynthetically active radiation (PAR) interception was measured several times daily in four marked sites in each plot, under clear sky conditions. At ground level, a minimum of three observations were made to compute an individual measurement in each side. A line quantum sensor (Model LI-191SB, Li-cor, Lincoln, NE) was leveled, placed perpendicular to the row direction and positioned so that no shadows from the handle influenced measurement. Canopy incident radiation was measured by placing the line quantum sensor above the crop.

A minimum data set recorder (Model LI-1200, Li-cor, Lincoln, NE) located outside of the rain shelter was used to record the solar radiation, minimum and maximum air temperature, and rainfall. Vapor pressure deficit of the air (VPD) was calculated as the difference between the saturation vapor pressure, e_s (minimum

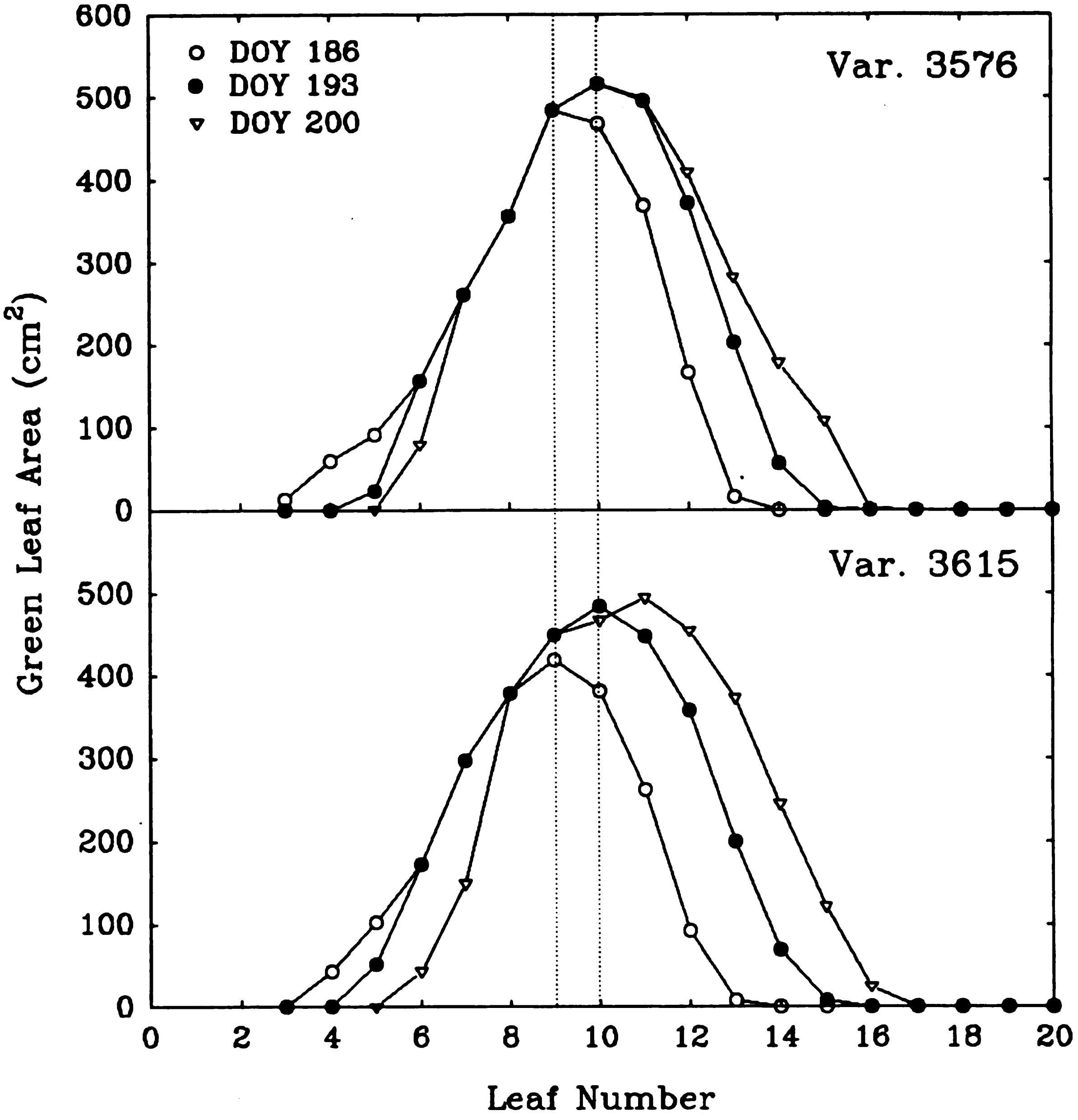

Figure 1.2. Leaf area of each leaf node number on three different occasions for both varieties in 1991. The two vertical dotted lines represent the leaves selected for leaf rolling and leaf orientation measurements.

temperature used as dew point temperature) and the actual vapor pressure, e_a (the drying power of the air was assumed to be the daily average temperature). Daily values of maximum and minimum temperature and solar radiation (MJ/m^2) and vapor pressure deficit of the air (kPa) for 1990 and 1991 growing seasons are shown in Figures 1.3 and 1.4.

Soil water content was measured by the neutron scattering technique (CPN, Model 503DR). Two access tubes (aluminum, 50 mm i.d.) were seated in the center row of each plot. Readings were made twice a week at 25 cm increments to a depth of 1.5 m. Field measurements of soil water content and neutron counts were used to calibrate neutron counts into volumetric water content. Regression equations, by depth, were determined using only two points: dry point (soil was allowed to dry out); and wet point (soil water content near saturation). Soil water content in the 0-12.5 cm and 12.5-25 cm layers were determined by the time domain reflectometry (TDR) technique. Steel rods were installed at each depth leaving 2 cm above the soil surface. Volumetric water content was estimated using the equations described by Topp *et al.*, (1982). Soil water availability in *mm* of equivalent depth was calculated for the top 1.5 m of profile as the difference between volumetric water content of the soil and water content at the lower limit of plant-extractable soil water in the rooting depth.

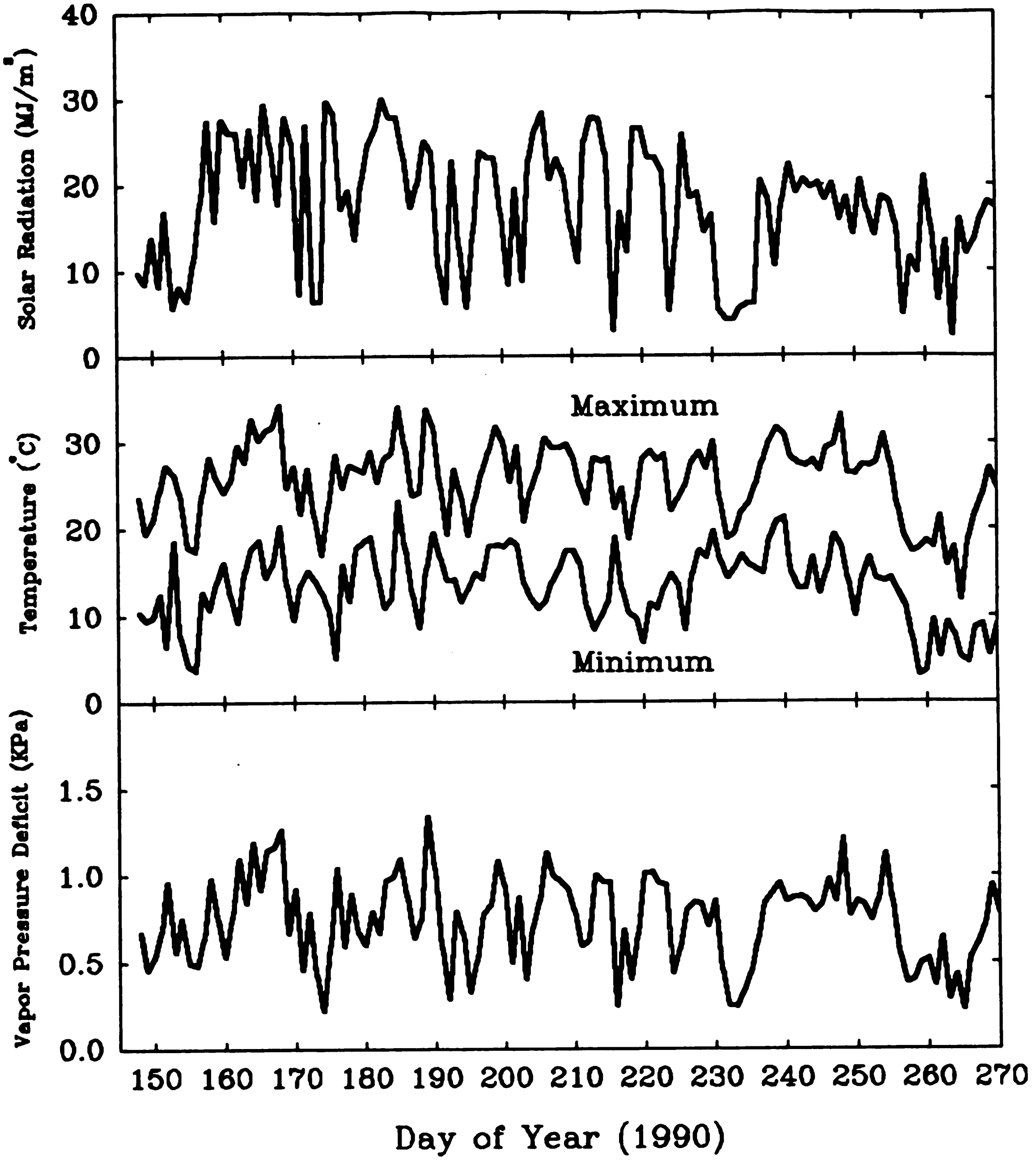

Figure 1.3. Daily incident solar radiation, daily maximum and minimum temperatures and daily vapor pressure deficit of the air during 1990.

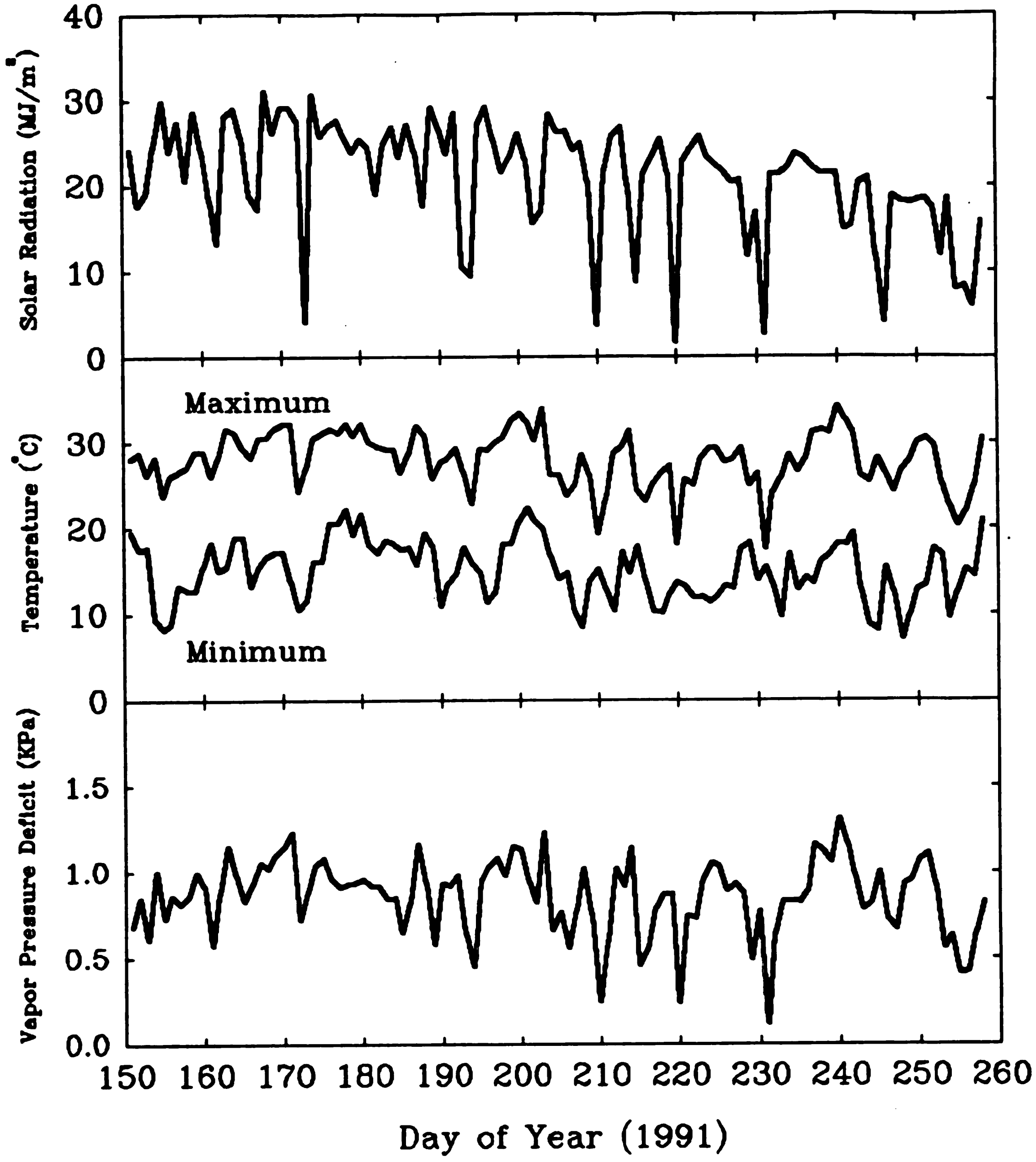

Figure 1.4. Daily incident solar radiation, daily maximum and minimum temperatures and daily vapor pressure deficit of the air during 1991.

Results and Discussions

Weather conditions observed during the experiment in 1990 and 1991 are presented in Figures 1.3 and 1.4. During the water deficit periods, from DOY 171 to 194 in 1990 and from DOY 172 to 200 in 1991, slightly different climatic conditions were observed. The mean daily incident solar radiation was 19.75 MJ/m^2 and 23.64 MJ/m^2, the mean daily minimum temperature was 14.4 °C and 16.8 °C and, the mean daily maximum temperature was 26.2 °C and 29.4 °C, for 1990 and 1991. In 1990 the rain shelter was frequently closed at night due to technical problems with the facility's automatic control system. This altered the internal microclimate somewhat. Consequently, plants experienced slightly warmer night temperatures, less dew formation, and lower wind velocities than plants growing outside the shelter.

Water Content and Extraction

Soil water content of the vegetative stage water deficit and well-irrigated treatments for 1991 are shown (Figures 1.5, 1.6) for the upper 75 cm of soil profile. During the water deficit period a similar pattern of profile drying was observed for the two varieties. The observed decline in soil water content for the well-irrigated treatment between the DOY 193 and DOY 200 was caused by a lack of irrigation due to mechanical problems with the irrigation system.

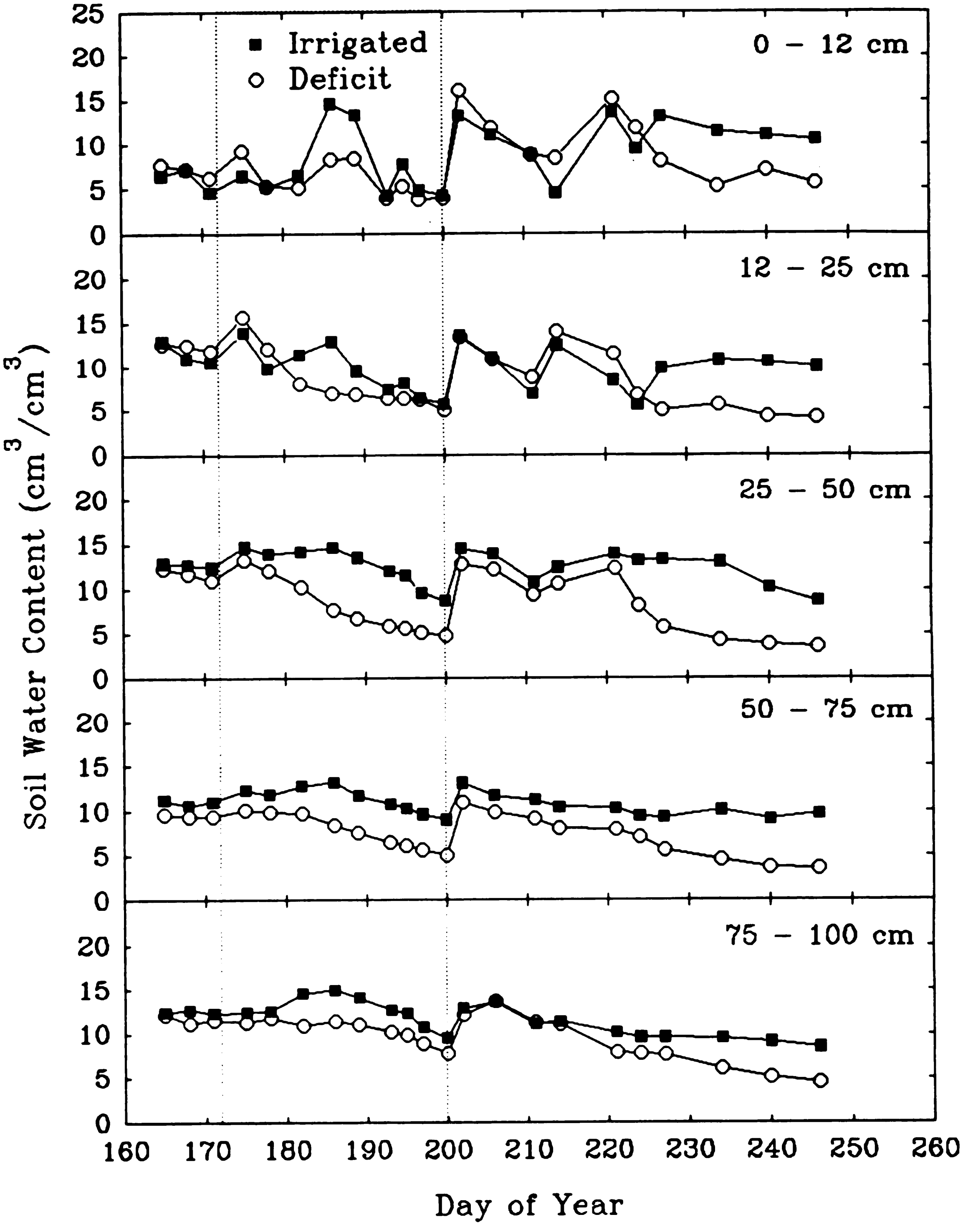

Figure 1.5. Soil water content with depth and time for the variety 3576 in 1991. The area limited by vertical dotted lines represents the period of soil water deficit.

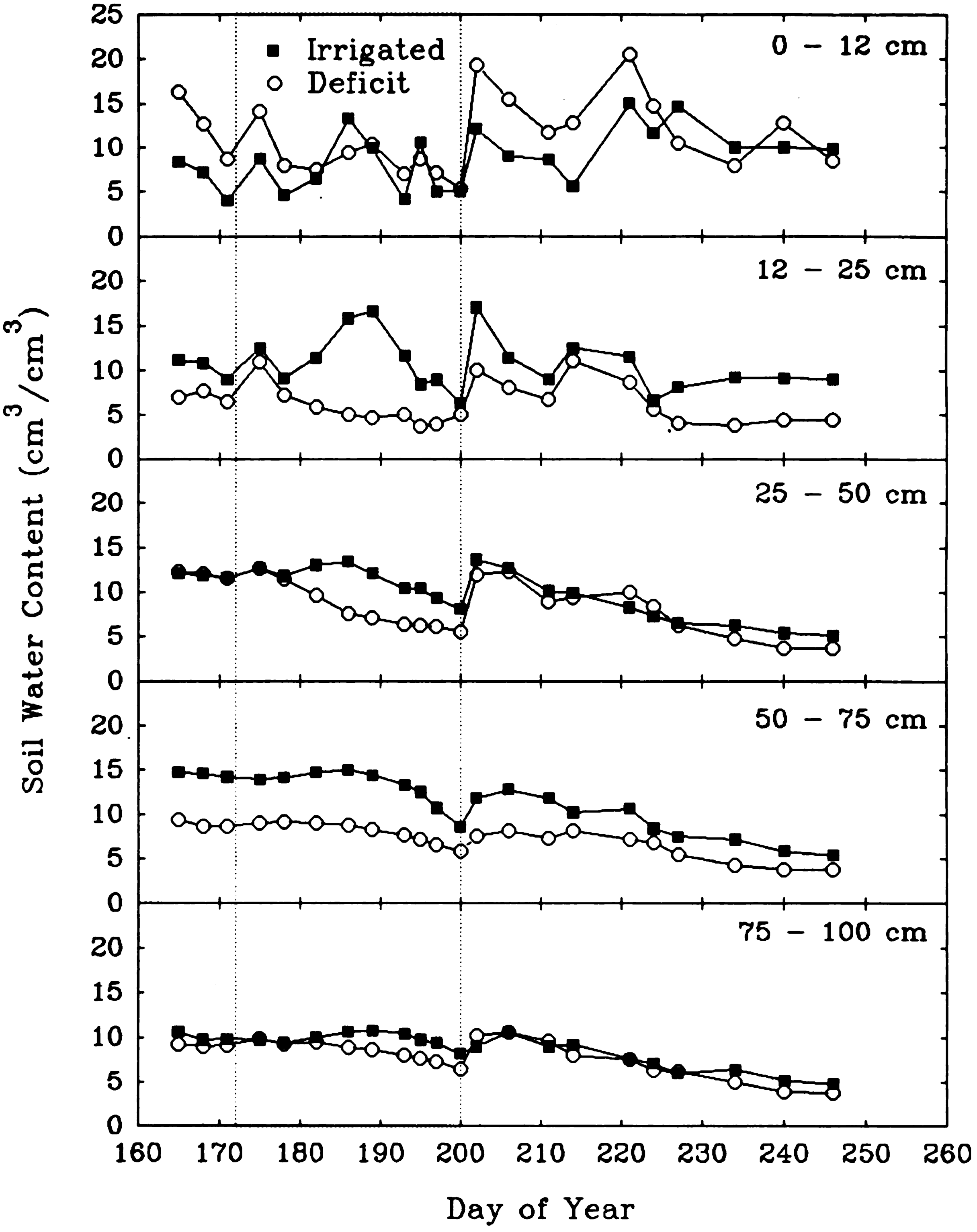

Figure 1.6. Soil water content with depth and time for the variety 3615 in 1991. The area limited by vertical dotted lines represents the period of soil water deficit.

The soil water depletion rate (mm/day) at different soil depths during the 1991 water deficit period is shown for both varieties in Figure 1.7. Soon after the water deficit began there was a rapid decline in the water depletion rate in the upper soil layer (0-25 cm). A marked increase of the water depletion rate was noted in the following soil layer (25 -50 cm) and almost steady extraction rates for the lower depths of the soil profile (50-75 cm and 75-100 cm). As the water deficit developed, little water extraction was observed near the soil surface and the water depletion rates for the 25-50 cm depth remained steady until about the end of the water deficit period. Maize was extracting water mainly from the lower depths at the end of the water deficit period. A marked increase in the soil water depletion rates at the 75-100 cm depth were only observed on DOY 197 (almost at the end of the water deficit period). During the water deficit period both varieties presented the same trend in terms of soil water depletion over time. However, the variety 3576 consistently presented higher extraction rates than the variety 3615.

A different pattern of water absorption rates during vegetative water deficit period was described by NeSmith (1990) working with maize in the same soil type. He found that a continuous decrease of water absorption rate was observed throughout the water deficit period in the upper soil layer (0-25 cm) and was nearly steady at the beginning of the water deficit period followed by a continuous decline in the water absorption rates in all layers between 25 and 100 cm. An agreement though was observed for the 75-100 cm depth where an increase of the soil water absorption rate was observed at the end of the water deficit period.

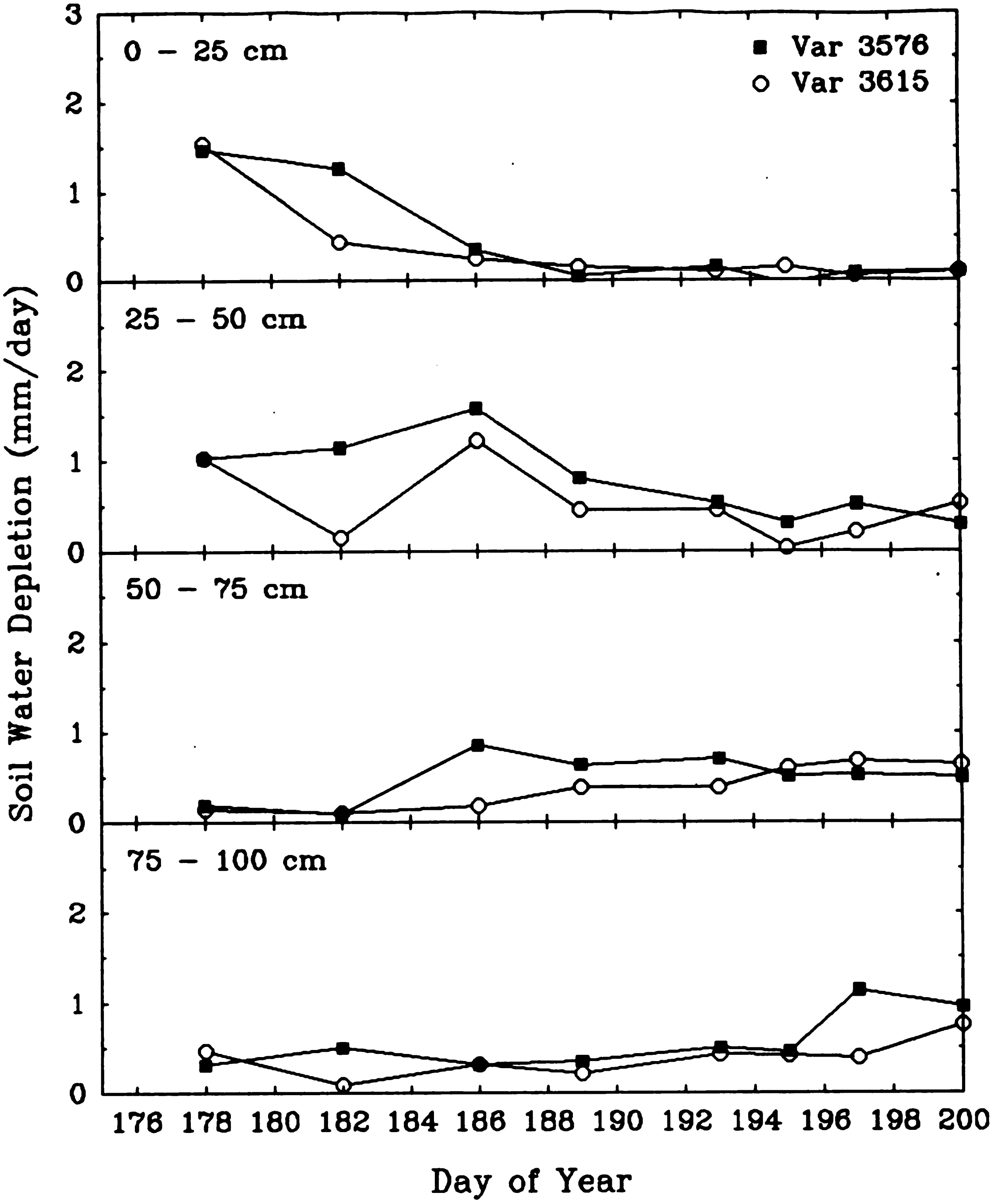

Figure 1.7. Soil water depletion rates with time for both varieties for the top 100 cm of the soil profile during the soil water deficit in 1991.

Although no measurements of the root system were made in this experiment, the observed pattern of soil water depletion rates could be explained by root distribution and root penetration into lower soil layers (extraction front of the root system). During the first half of the water deficit period the root system seemed to extract most of the water from the layer near the soil surface and, during the second half of the water deficit period, the root system moved into lower layers of the profile where more soil water was available. Taylor and Klepper (1973) noted an increased water extraction effectiveness of deeper roots of maize as the upper soil layers dried out and, a similar pattern has been documented for soybeans (Hoogenboom *et al.*, 1987) and sorghum (Blum and Ritchie, 1984). Results from Nakayama and van Bavel (1963) indicated that the root penetration rates ranged between 1.9 and 4.9 cm/day and Robertson (1991) working with sorghum found that the root extraction front descended linearly with time at a rate of 3.9 cm/day. The effectiveness of deeper roots to extract soil water combined with the root penetration rates explain the observed pattern of increased extraction rates of the adjacent lower layers (25 cm depth increment) in approximately every 4-6 days period as the upper soil layers dried out.

Soil water availability of the top 150 cm of the soil profile for both treatments and varieties are presented in Figure 1.8. A similar pattern of soil water availability was observed for both varieties in each treatment. At the end of the water deficit period the total soil water available in the profile was 20.8 mm and 11.4 mm for the varieties 3576 and 3615. The high amount of soil available water for the variety

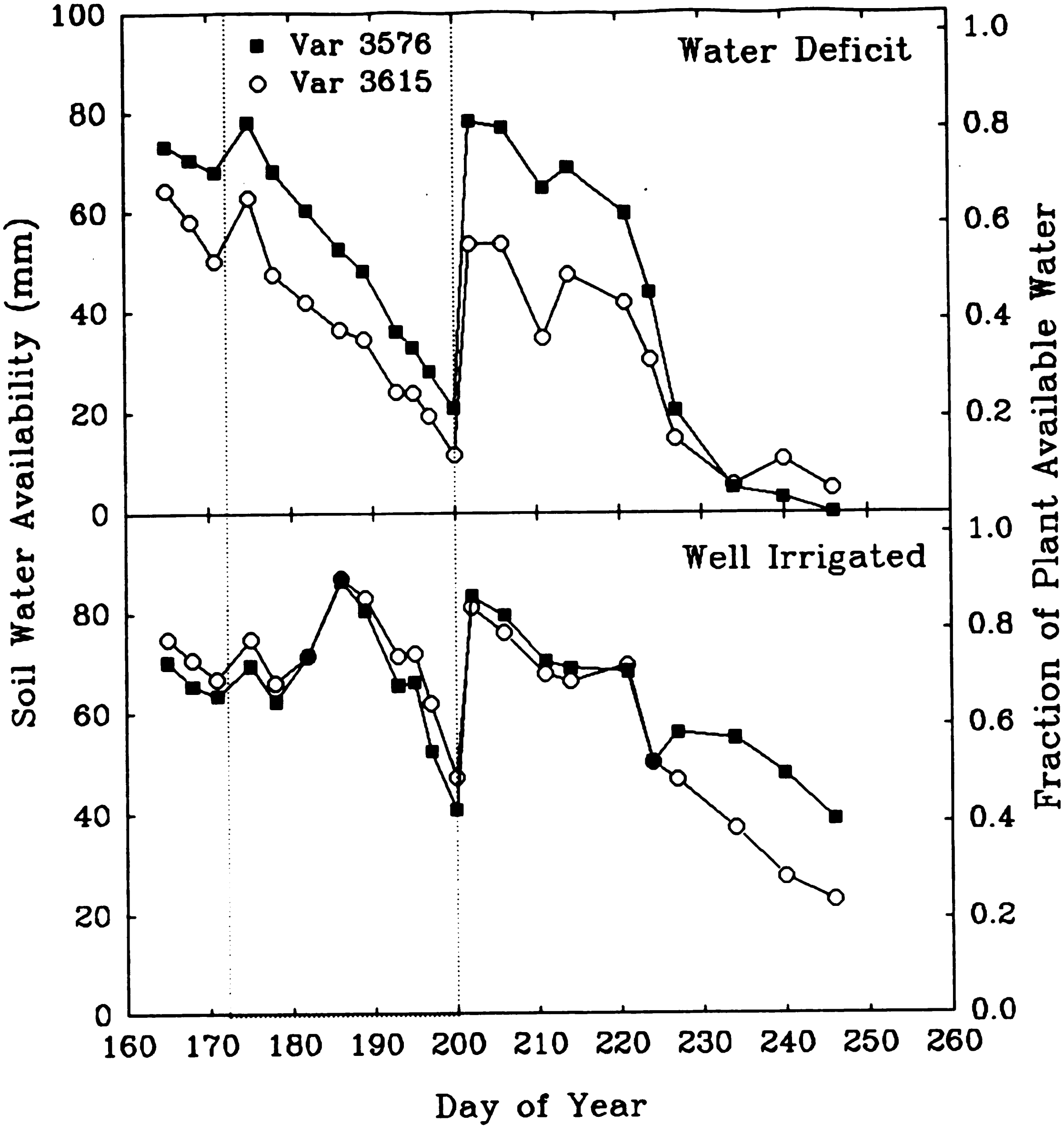

Figure 1.8. Total soil water availability with time for both varieties and treatments for the top 150 cm of the soil profile in 1991. The area limited by vertical dotted lines represents the period of soil water deficit.

3576 throughout the water deficit period as compared to the variety 3615 could be explained by its higher rate of water extraction during the water deficit period and its overall smaller soil water deficit.

Plant Leaf Area

Figures 1.9 and 1.10 present the green leaf area index (LAI) for both treatments and varieties in 1990 and 1991. In both years, the LAI of well-irrigated treatments, and vegetative stage water deficit treatments were similar for the two varieties at the beginning of the water deficit period. A larger difference between treatments was observed in 1991 due to a longer imposed water deficit period and to the warmer temperatures observed. Although a large difference in LAI was observed between treatments in both years, no difference in LAI was noted between varieties.

The level of water deficit that results in a reduction in plant growth varies with the conditions under which the plant is grown. For maize growth in the field, according to Ritchie (1981), Rosenthal *et al.*(1987) and Grant *et al.* (1989), a reduction in leaf expansion and plant transpiration occurs when the fraction of plant available water is between 0.70 and 0.30 and values below 0.30 enhance leaf senescence. During the water deficit period the fraction of plant available water, the soil maximum available water (96.1 mm) divided by soil water availability (Figure 1.8), was below 0.70 since after the beginning of the water deficit period. Values below 0.30 were observed on DOY 193 and 197 (with a corresponding

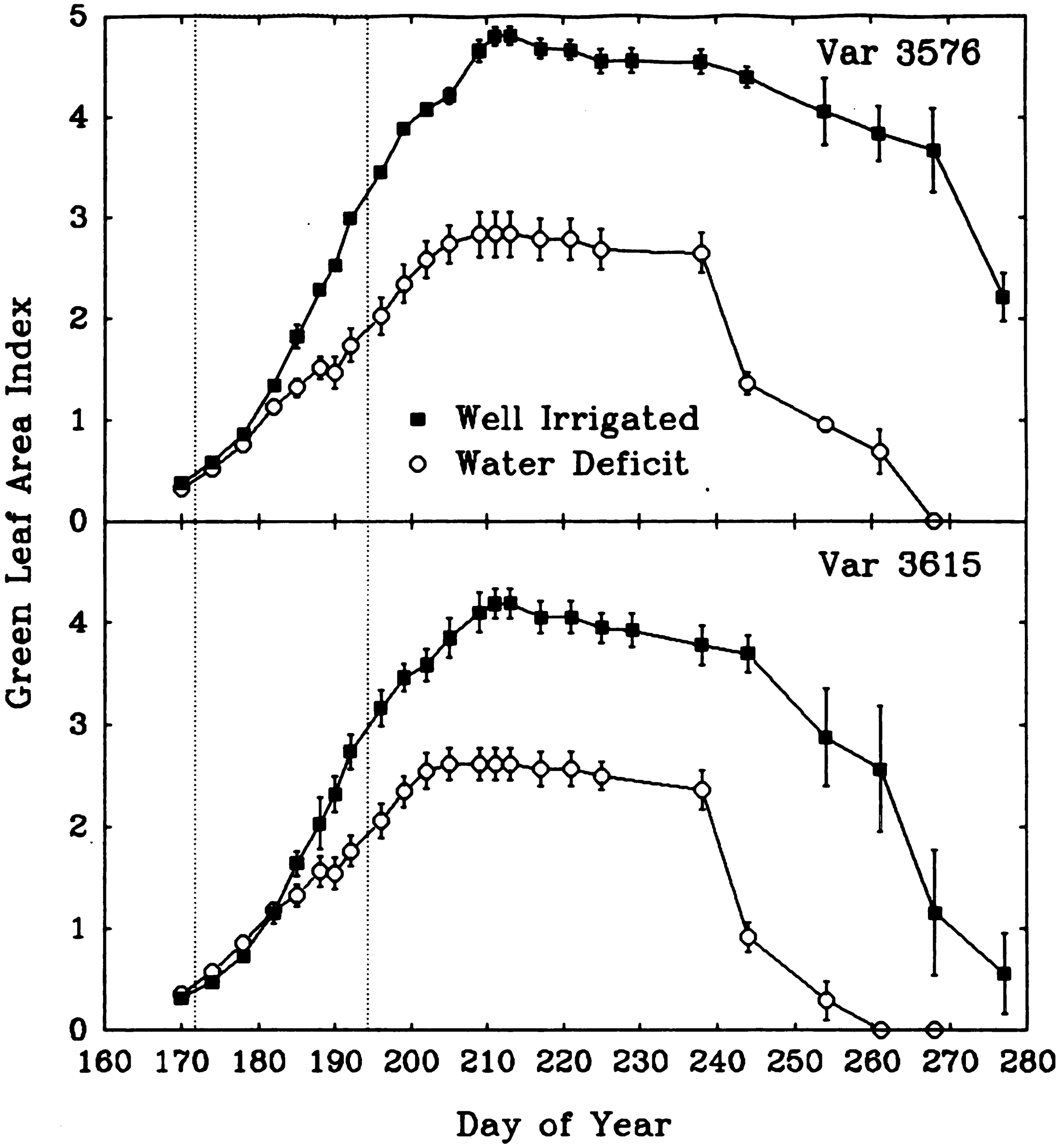

Figure 1.9. Green leaf area index for both treatments and varieties during 1990. The region between the vertical dotted lines indicates the water deficit period.

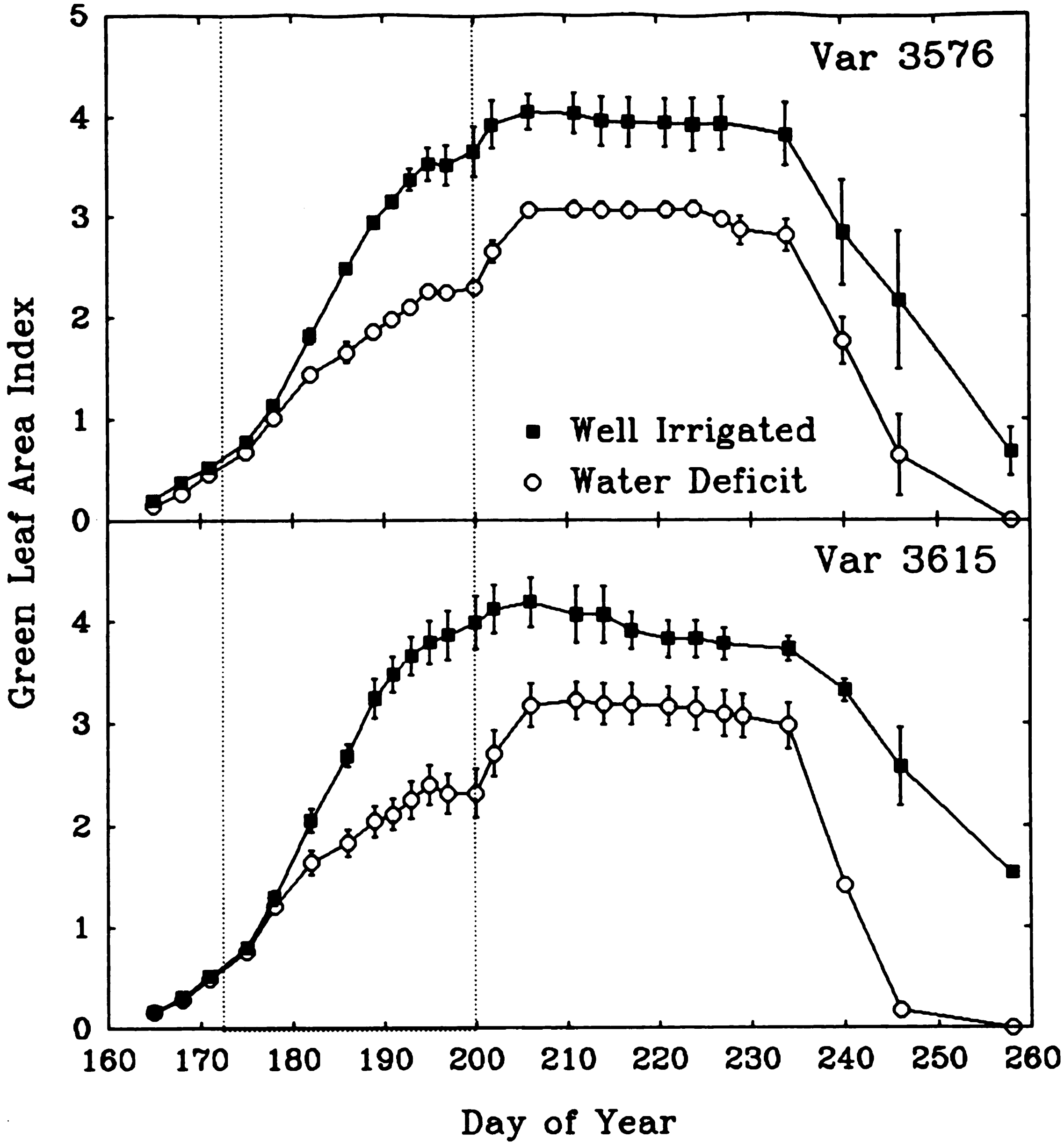

Figure 1.10. Green leaf area index for both treatments and varieties during 1991. The region between vertical dotted lines indicates the water deficit period.

observed increase in leaf senescence) for the variety 3615 and 3576. A companion paper includes results of leaf senescence of the current experiment.

The reduction in leaf expansion during water deficits causes a reduction in plant leaf area and less radiation is intercepted by the crop canopy and, as a consequence, the total plant photosynthesis is reduced. This, according to Begg (1980), provides a mechanism for the plant to reduce the amount of plant transpiration and provides one way to delay the onset of a more severe water deficit.

Radiation Interception

The daily variation of photosynthetically active radiation interception for the variety 3576 and 3615, on three selected days during the 1991 growing season, are presented in Figures 1.11 and 1.12. At the beginning of the water deficit periods, a slight difference in interception of radiation was observed between treatments on DOY 181. The low radiation interception was caused by the low LAI (incomplete canopy cover) observed for the varieties in both treatments (Figures 1.9 and 1.10). Although little difference in interception of radiation was observed between the two varieties, under water deficit conditions, the variety 3576 consistently presented a slightly lower radiation interception than the variety 3615.

In 1991, as the water deficit increased (DOY 195) radiation interception decreased near solar noon for the vegetative deficit treatment. However, the well-irrigated treatment intercepted more than 85% of solar radiation and little daily

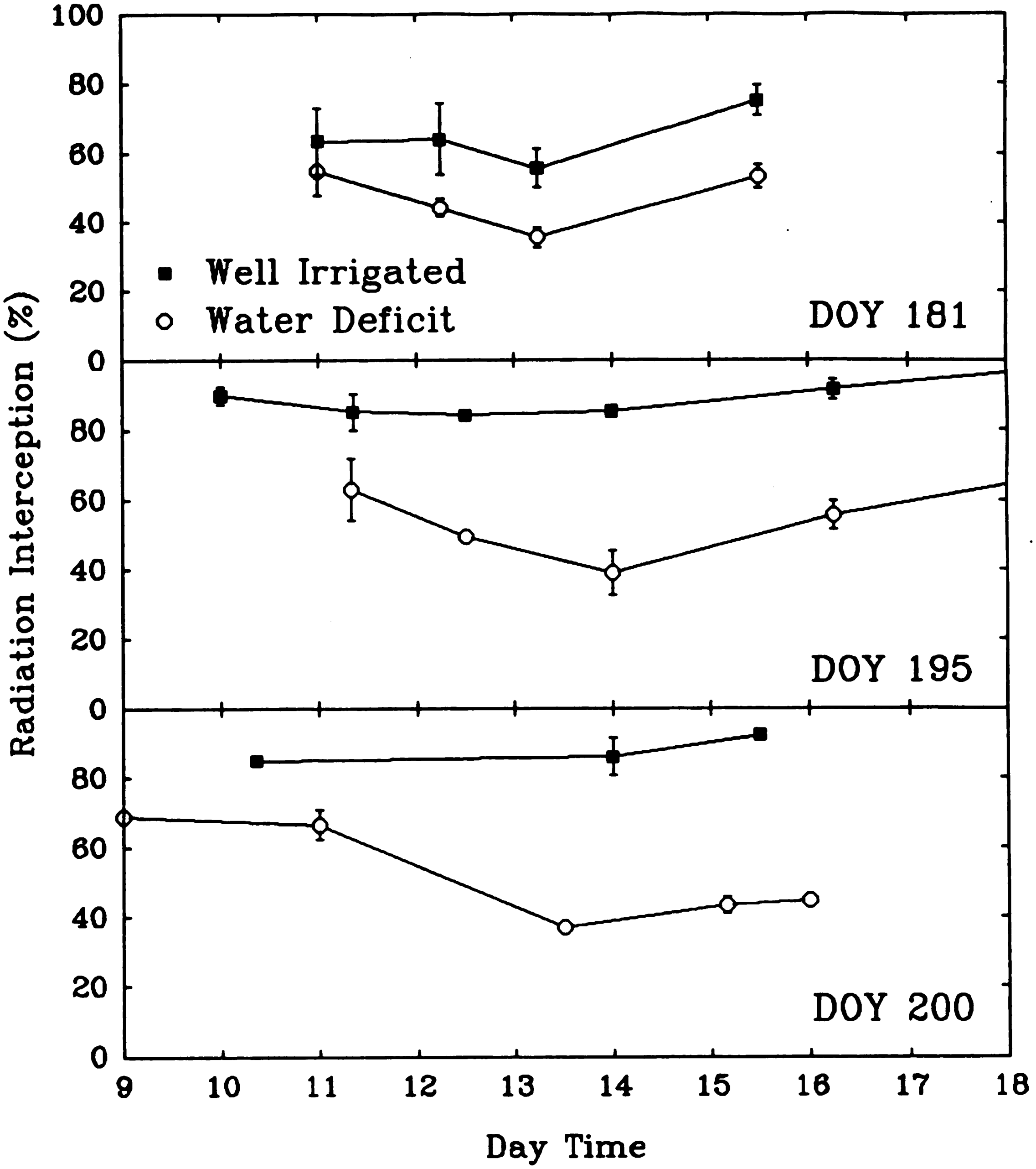

Figure 1.11. Daily variation of photosynthetically active radiation interception of the variety 3576 on three selected days (DOY 181, 195 and 200) in 1991.

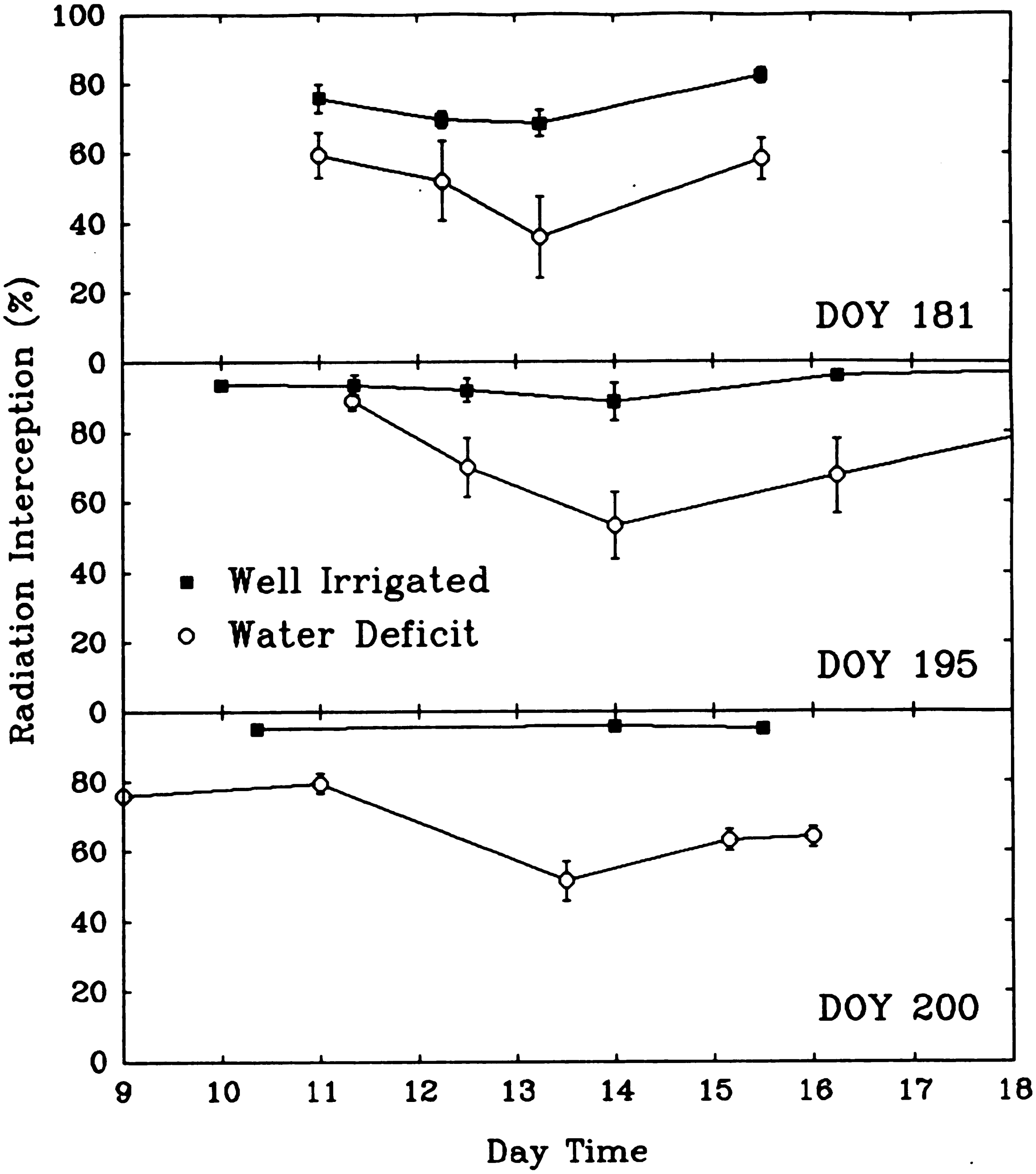

Figure 1.12. Daily variation of photosynthetically active radiation interception of the variety 3615 on three selected days (DOY 181, 195 and 200) in 1991.

variation in radiation interception was observed due to the large LAI of 3.5 and 3.8 for the varieties 3576 and 3615 (Figure 1.10). According to Evans *et al.* (1975), early in the growing season the radiation intercepted by a crop canopy is mainly limited by the LAI. The radiation interception increases rapidly to about 90% as LAI increases to about 4.0 for cereal crops.

Similar patterns of photosynthetically active radiation were observed for both varieties in 1990 (Figures 1.13 and 1.14). At the beginning of the deficit period (DOY 183), a low radiation interception was observed for both treatments and varieties, this was mainly caused by the low LAI (lower than 1.5). The variety 3576 also had a slightly lower radiation interception at the end of the deficit period compared to variety 3615. In both years, the radiation interception curves tended to raise (intercepting more radiation) early in the morning and late in the afternoon because the incident solar radiation had to pass through a more dense crop canopy than during the mid-day hours.

The seasonal variation of radiation interception measured near the solar noon hours in 1991 is presented in Figure 1.15. Although the LAI (Figure 1.10) steadily increased during the water deficit period, a remarkably small change of radiation interception by the variety 3576 was observed. At DOY 195 the variety 3576 and 3615, under water deficit treatment, intercepted 45% and 60% of the radiation intercepted by the well-irrigated treatment. This difference in radiation interception was not caused by a difference in plant leaf area index between the two varieties but rather was due to plant leaf area adjustment during the water

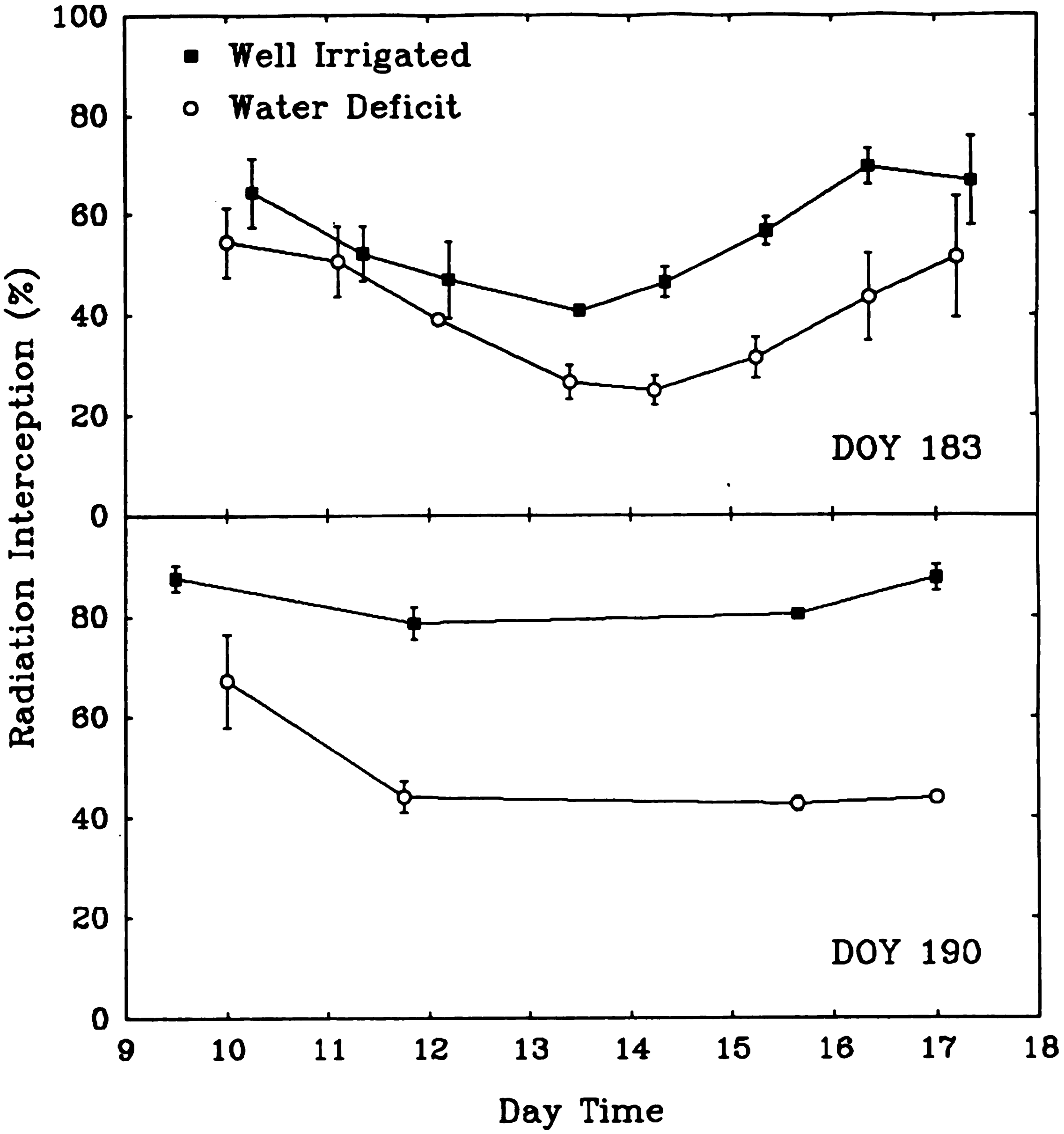

Figure 1.13. Daily variation of photosynthetically active radiation interception of the variety 3576 during the water deficit period in 1990 in two selected days (DOY 183 and 190).

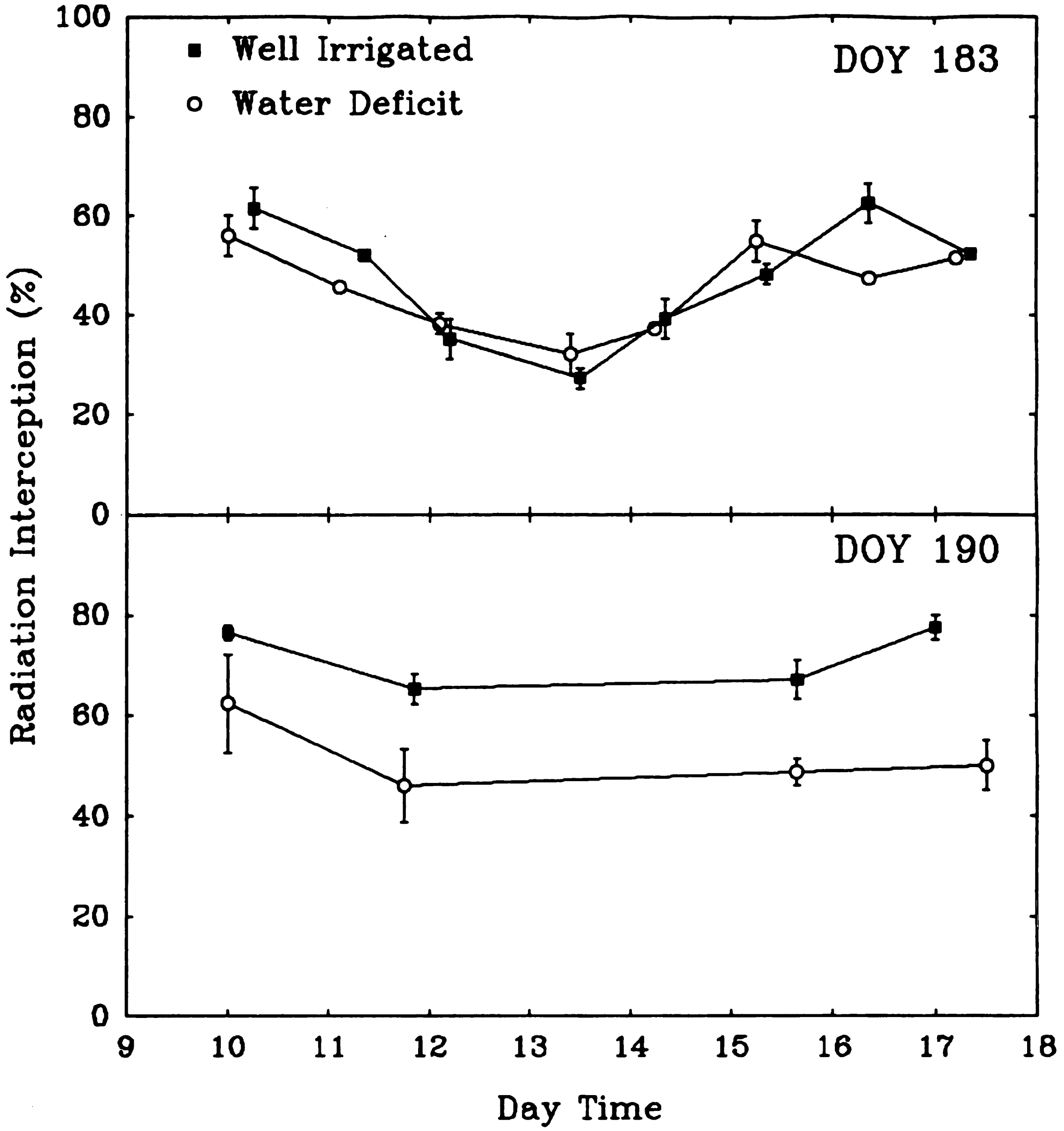

Figure 1.14. Daily variation of photosynthetically active radiation interception of the variety 3615 during the water deficit period in 1990 in two selected days (DOY 183 and 190).

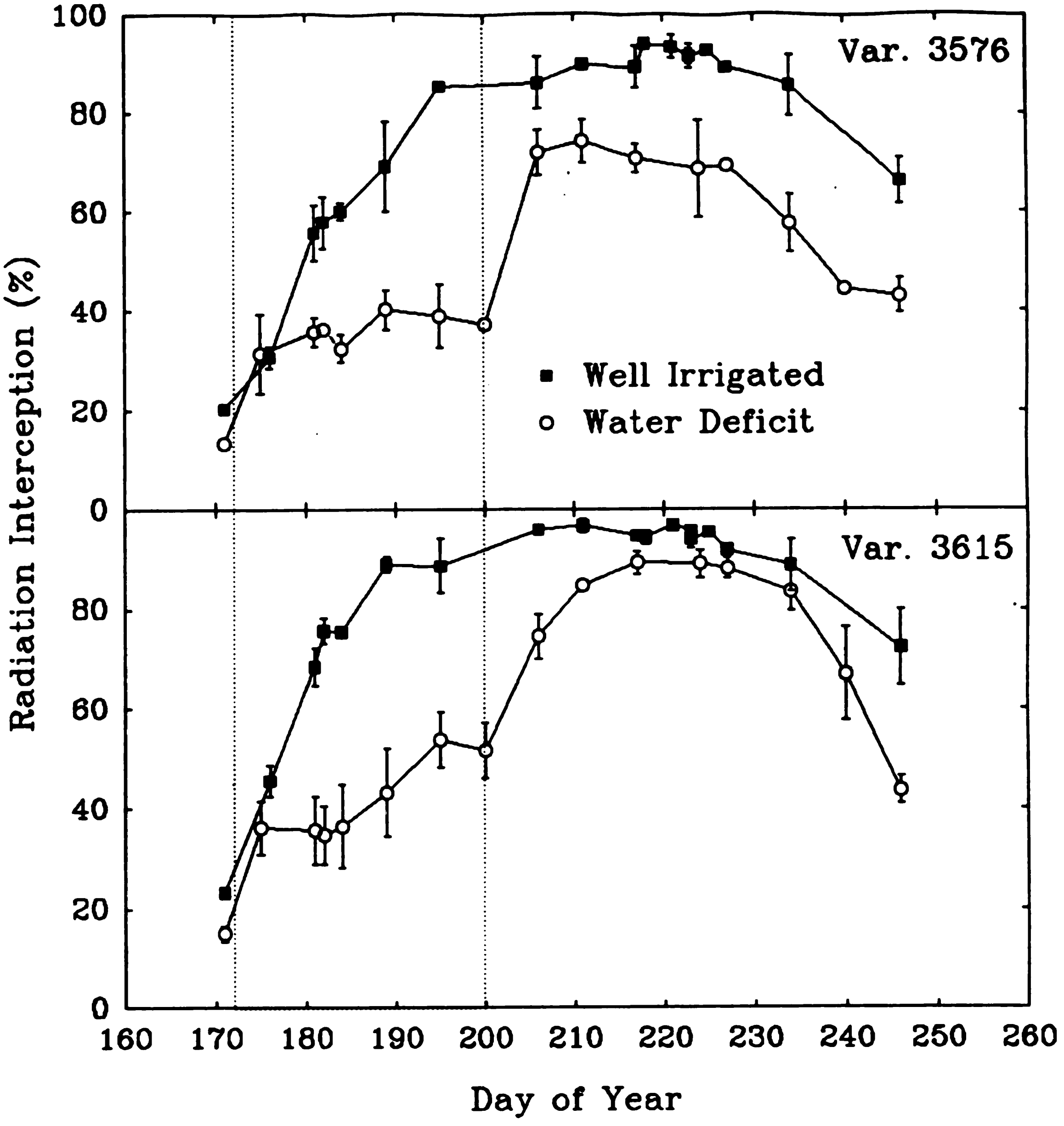

Figure 1.15. Seasonal variation of photosynthetically active radiation interception for both varieties in 1991 as measured near solar noon. The area limited by vertical dotted lines represents the period of soil water deficit.

deficit period. The lower radiation intercepted by the variety 3576 during the water deficit was because this variety was able to roll its leaves more effectively and can orientate its leaves more vertically.

Soon after irrigation was resumed (DOY 206) both varieties showed a marked increase in radiation interception. Variety 3576 increased its radiation interception by 95% (from 37% to 72%) and the variety 3615 increased its radiation interception by 42% (from 52% to 74%) although the measured LAI increased 33.6% (from 2.29 to 3.06) for the variety 3576 and 36.6% (from 2.32 to 3.17) for the variety 3615, during the same period. Approximately the same amount of radiation was intercepted for both varieties after the irrigation was resumed. This was due to the similar leaf area indexes (Figure 1.10) and the non-occurrence of leaf area adjustment.

Leaf Rolling

The daily variation of leaf rolling for both varieties during 1991 and 1990 are shown in Figures 1.16 and 1.17. In 1991, both varieties showed a similar behavior of daily variation of leaf rolling early in the deficit period. As the water deficit became more severe, less daily variation of leaf rolling was observed for both varieties and, at the end of the deficit period (DOY 200) almost no day time variation of leaf rolling. As the water deficit became more severe, variety 3576 consistently rolled its leaves more than variety 3615 . The daily average of exposed leaf blade area (leaf area) was 38% and 54% on DOY 195 and 22% and 40% on

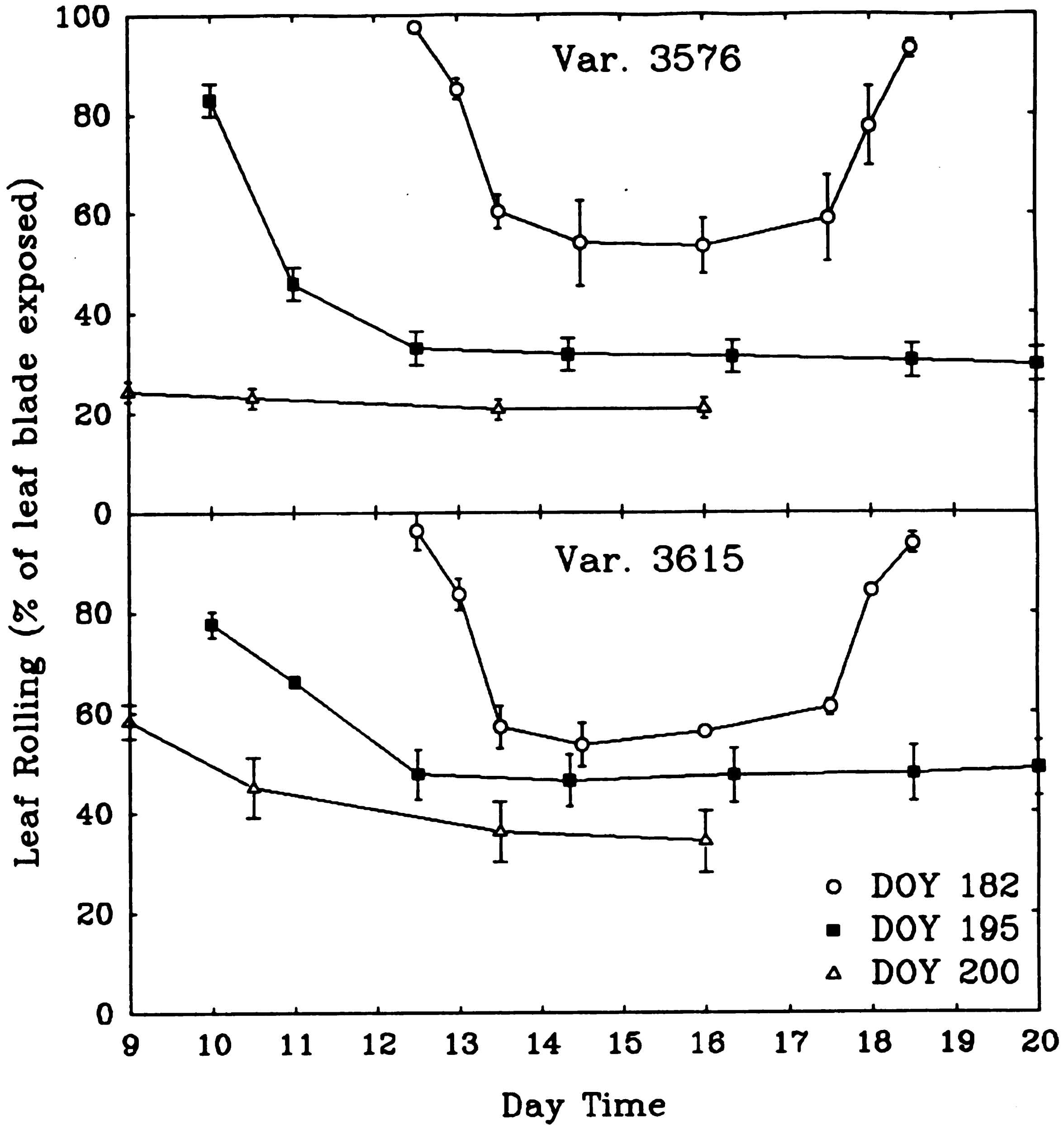

Figure 1.16. Daily variation of leaf rolling for both varieties on three selected days (DOY 182, 195 and 200) in 1991.

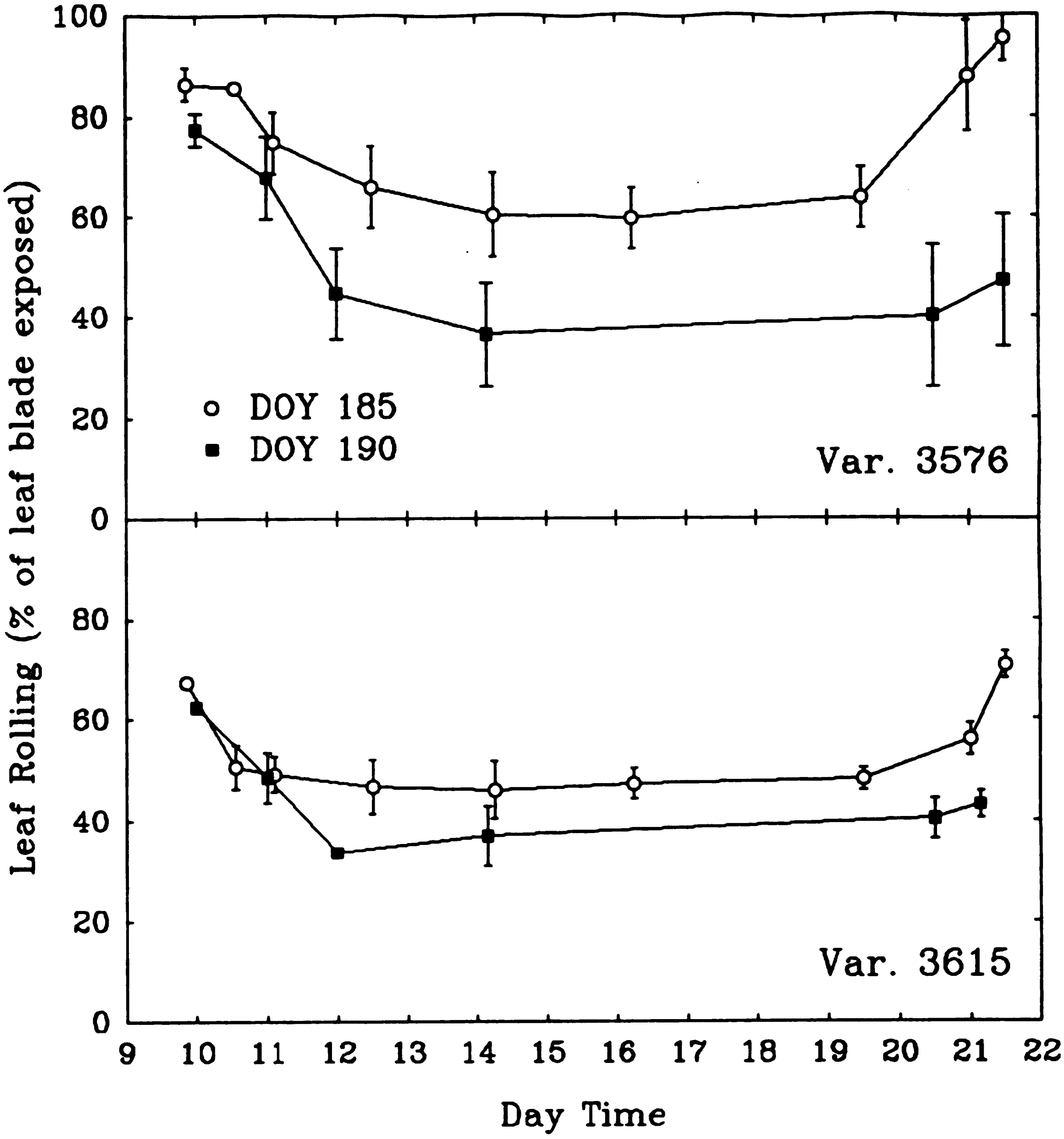

Figure 1.17. Daily variation of leaf rolling for both varieties in 1990 on two selected days (DOY 185 and 190).

DOY 200 for the variety 3576 and 3615.

A similar pattern of leaf rolling between the two varieties was observed during the water deficit imposed in 1990. Both varieties showed less leaf rolling in 1991. This was likely because of a shorter water deficit period and the colder temperatures observed. However, variety 3576 was more effective in reducing the exposed plant leaf area (lower values of leaf rolling).

Leaf rolling in response to water deficit provides a sensitive and rapid reversible conditions for controlling water loss (Austin and Jones, 1975). Based on stomatal conductance data, Begg (1980), working with maize, indicated that leaf rolling precedes the closure of abaxial stomata. Blum and Sullivan (1986), reported that leaf rolling did not occur until after stomatal closure in sorghum and millet grown in growth chambers.

Leaf Orientation

The daily changes in leaf orientation of leaf 9 and 10 of variety 3576 and 3615 during the 1991 deficit period are presented in Figures 1.18 and 1.19. During the water deficit period both varieties tended to orientate their leaves in a more vertical orientation (position). On DOY 184, as the leaf rolling increased (Figure 1.16) a steady increase in leaf orientation was observed for both varieties and a maximum vertical orientation of the leaf blades was reached near the solar noon hours. However, much less change in leaf blade orientation was observed near the end of the deficit period (DOY 195). Throughout the water deficit period the variety

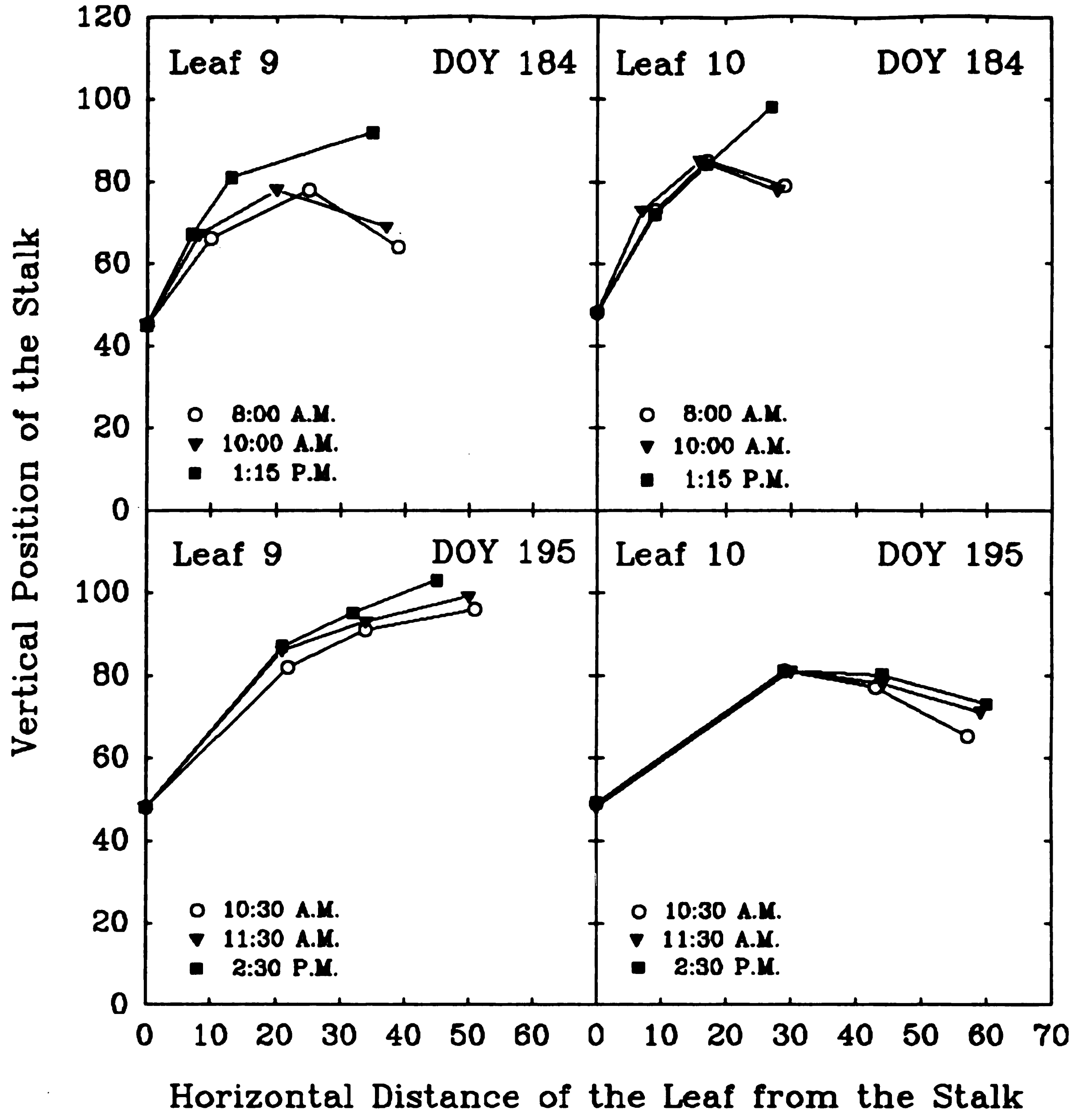

Figure 1.18. Daily variation of leaf orientation for the leaf 9th and 10th growing leaves for the variety 3576 in 1991 on two selected days (DOY 184 and 195).

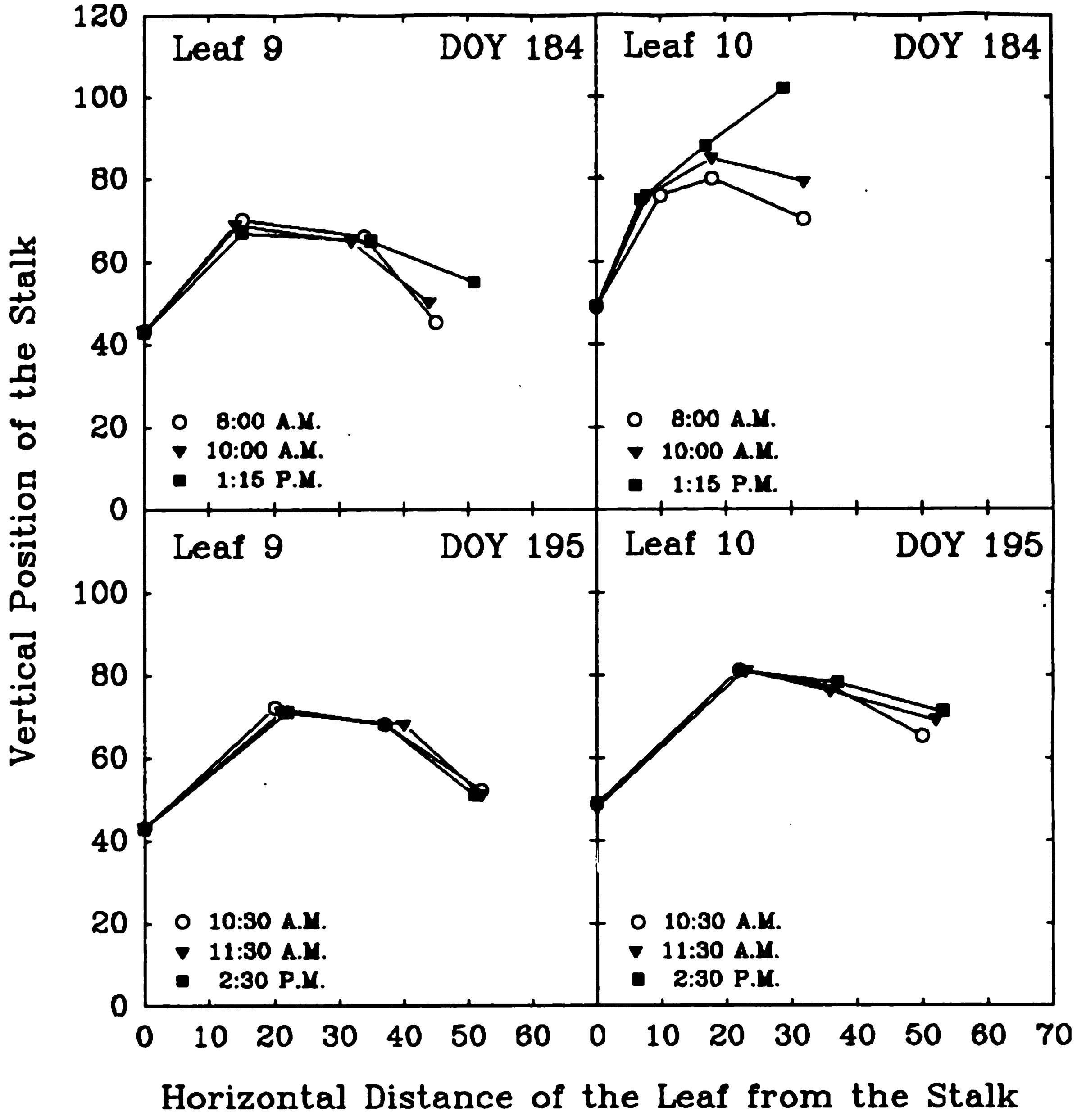

Figure 1.19. Daily variation of leaf orientation for the 9th and 10th growing leaves for the variety 3615 in 1991 on two selected days (DOY 184 and 195).

3576 displayed its leaves more vertically and a more marked change in leaf blade orientation was observed during the day as compared to the variety 3615.

Measurements made after solar noon hours were not included because no additional changes in leaf orientation occurred for either variety, nor was additional leaf rolling observed near the end of the water deficit period (Figure 1.16). On DOY 195, the 9th and 10th leaves were much longer (the 9th was fully expanded) and almost no change in leaf blade orientation was recorded. The length of the leaf blade and the intensity of leaf rolling are believed to be the main factor affecting the ability of the leaf to orientate its blade more vertically. Usually long leaf blades curve downward from about midway along their length, this imposes a physical restriction on the ability of the leaf to roll its blade and, as a consequence, to orientate the leaf blade more vertically. Younger leaves (expanding leaves) changed the leaf orientation during the water deficit periods to a lesser degree than older leaves (full expanded leaves) due to shorter leaf blades length.

The important feature of the mechanism responsible for changes in leaf rolling and leaf orientation is the reversibility and rapidity of recovery when water deficit is ended. The rolling and unrolling movement of mature leaves is presumed to be due to volume changes (loss or gain of water by changes in turgor) in the bulliform cells (Esau, 1965, 1977; Duncan, 1980; Bull and Glasziou, 1975; Ellis, 1976; Steponkus *et al.*, 1980; O'Toole and Cruz, 1980). However, numerous reports point to caution in assuming that the bulliform cells are the only driving mechanism for leaf rolling and unrolling. Evidence in opposition to this theory is that shrinkage is one contributing factor in the rolling phenomenon, for leaves without such cells likewise respond by rolling to prevent moisture loss (Esau, 1977). According to Brandis (1907), and Parry and Smithson (1964), the bulliform cells become filled with large masses of silica and their outer walls often become thick and cutinized.

Conclusions

The reduction in leaf expansion during water deficits causes a reduction in plant leaf area and less radiation is intercepted by the crop canopy and, as a consequence, the total plant assimilation is reduced. Results indicate that the smaller radiation interception of the variety 3576 during the vegetative stage water deficit is due to leaf rolling and leaf blade orientation rather than differences in leaf area index. The reduction in exposed plant leaf area by increasing leaf rolling reduced the amount of radiation intercepted by the crop canopy. This reversible modification of canopy interception area e.g. leaf rolling and leaf orientation conserves stored soil water and reduces water requirements late in the season. The reduction of maize canopy radiation interception due to vegetative stage soil water deficit is mainly due to slower leaf area expansion and the increase in leaf rolling. Expanding leaves (younger leaves) more easily change leaf orientation during water deficit periods than totally expanded leaves (shorter leaves) due to the shorter leaf blades length.

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CHAPTER 2

Effects of Pre-Anthesis Soil Water Deficit on Maize Growth.

II. Leaf Area Adjustments and Radiation Interception.

Abstract

Physiological aspects of leaf growth, leaf movements and morphological mechanisms have been studied extensively. However, there has been little effort to elucidate the adaptative importance of either of these types of leaf area adjustments during water deficit and environmental regimes in relation to radiation interception and biomass production. The objective of this study was to: (i) Identify morphological and physiological differences between two maize hybrids; (ii) Define the relation between LAI and radiation interception and; (iii) Characterize the sensitivity and quantify the contribution of leaf rolling, leaf senescence and leaf expansion to the reduction of plant exposed leaf area. Pioneer varieties 3576 and 3615 were subjected to two irrigation managements: Well-irrigated and water deficit in the vegetative stage. Results indicate that these two varieties have a different adaptative mechanism to water deficit conditions. During periods of low VPD the variety 3576 was able to activate the leaf expansion mechanism faster than the variety 3615. Leaf rolling was also influenced by periods of low VPD. The contribution of reduced leaf expansion and leaf rolling to diminish the exposed

plant leaf area was 30.5% and 26.7% for the variety 3576 and, 35.6% and 17% for the variety 3615. Plant leaf rolling reduced the exposed plant leaf area and, consequently, limited the activity of the leaf elongation mechanism.

Introduction

Physiological aspects of leaf growth, leaf movements and morphological mechanisms have been studied extensively. However, there has been little effort to elucidate the adaptative importance of either of these types of leaf area adjustments during water deficit and environmental regimes in relation to radiation interception and biomass production.

According to Taiz and Zeiger (1991), evaporative cooling lowers leaf temperature. Measurements of leaf temperature taken in Death Valley, California, were 8 °C below air temperature during the day on plants that had access to an ample supply of water. When water deficit limits plant transpiration, the leaf heats up unless other processes offset the heat buildup. Leaf temperature can be influenced by seasonal differences in leaf orientation and by diurnal solar tracking movements (Ehleringer and Forseth, 1980; Ludlow and Bjorkman, 1984). The heliotropic mechanism, according to Koller (1986) involves changes in hydrostatic pressure induced by the absorption of blue light by photoreceptor in the leaf veins, perhaps via steps similar to those for stomatal opening, leading to changes in leaf orientation. According to Ludlow and Bjorkmam (1984), the heliotropic leaf movements, however, usually coincide with stomatal closure during soil water deficits. In grasses, leaf rolling is a common response to water deficit and results in a marked reduction in effective leaf area and, consequently, the radiation load on the leaf (Begg, 1980). Many arid plants have very small leaves, which minimize the resistance of the boundary layer to transfer heat from the leaf to the air (Taiz and Zieger, 1991). However, other mechanisms that reduce photosynthesis and growth may also be beneficial during drought if they increase water use efficiency and enable sufficient water conservation to provide. an economic yield. Thus, mechanisms of stomatal control, leaf rolling, leaf orientation, leaf senescence, energy reflection, and increasing liquid flow resistance may all enable plants to survive or adjust to periods of water deficits and to conserve water for the stages of growth most sensitive to water deficits.

The term osmotic adjustment is widely used to describe osmoregulation in response to water deficit in higher plants. It is also used to describe changes in solute content after recovery from water deficit (Hsiao *et al.*, 1976; Steponkus *et al.*, 1980; Turner and Jones, 1980). Stomata provide control of water loss and consequently, regulate plant stress and the plants' ability to adapt to changing conditions. Stomatal behavior may enhance drought resistance by: (i) water conservation; (ii) prevention of potential damaging plant water deficit; and (iii) maximization of water use efficiency (Jones, 1979). However, Farquhar and Sharkey (1982) concluded that stomatal conductance has a small impact on photosynthesis because stomatal conductance is rarely the main cause of decrease in assimilation rate that occurs with a declining plant water supply.

In leaves of grasses, osmotic adjustment has been reported to maintain leaf turgor diurnally (Acevedo *et al.*, 1979), but at water potentials low enough to inhibit growth, turgor declined (Acevedo *et al.*, 1979; Boyer, 1970; Fereres *et al.*, 1978; Munns *et al.*, 1979; Sharp and Davies, 1979). Cell elongation is a turgor-dependent process and is extremely sensitive to water deficit. The decrease in cell volume results in lower turgor pressure and, as water loss progresses, the cells contract further and the solutes in the cells become more concentrated (Taiz and Zeiger, 1991). In intact leaves, water deficit not only decreases turgor pressure, but also decreases cell extensibility (Turner and Jones, 1980) and the pressure threshold, the pressure below which the cell wall resists plastic, or non-reversible deformation, (Taiz and Zeiger, 1991). However, the rate of loss of turgor pressure resulting from a reduction in water potential is less when cell walls are more elastic, and in instances where turgor maintenance is small, the effect of elasticity should be accounted for in estimating the contribution of osmoregulation (Morgan, 1984). Therefore, even after turgor pressure is lost, a leaf with higher osmoregulation has a higher water content at a low water potential level (Morgan, 1980). This, according to Jarvis and Jarvis (1963), appears to enable survival when lower levels of water potential are present. Several studies provide evidence though of an association of the turgor of the expanded leaf with the growth of the expanding leaf (Cutler *et al.*, 1980; Michelena and Boyer, 1982; Takami *et al.*, 1982). The difference in turgor between the expanded and expanding parts are reversed during the water deficit. This feature allows turgor maintenance within the cells at the base of the leaf even though stress prevented any further leaf elongation (Barlow, 1986).

Water deficit reduces leaf area by accelerating the rate of senescence of older leaves (Fischer and Hagan, 1965; Fischer and Kohn, 1966; Fischer, 1973; Slatyer, 1973; Ludlow, 1975). Rapid development of water deficit may accelerate senescence of lower leaves. However, according to Jordan (1983), the gradual development of water deficit in field conditions allows slow and continual adjustments in the plant's physiological processes. The adjustments are eventually manifested as alterations in growth and development, and the senescence of individual leaves is not seriously altered. According to Ludlow and Muchow (1990), under increasing soil dehydration, differences in rooting pattern may change the amount and timing of water availability to crops.

The objective of this study was to: (i) identify morphological and physiological differences between two maize varieties when water deficit was imposed during vegetative growth; (ii) define the relation between leaf area index and radiation interception; (iii) quantify the contribution of leaf rolling, leaf senescence and leaf expansion to the reduction of plant exposed leaf area and; (iv) characterize the sensitivity of the leaf rolling mechanism and leaf expansion in relation to plant available water and evaporative demand (VPD).

Methodology

This experiment was conducted in 1990 and 1991 at the Kellogg Biological Station, near Kalamazoo, Michigan, under a rain shelter, described by Martin *et al.* (1988), to prevent rainfall on the experiment.

The soil for the plots was Spinks loamy sand (mesic Psammentic Hapludalfs). Maize varieties, Pioneer 3615 and Pioneer 3576, were planted north-to-south at a high density on May 18 (DOY 138) in 1990 and on May 27 (DOY 147) in 1991. Emergence occurred on May 28 (DOY 148) in 1990 and on May 31 (DOY 151) in 1991. Plants were thinned in the seedling stage to a plant density of 7.2 plants/m^2. Weeds were controlled manually during both years. Plot size was 4.6 m x 6.2 m. Maize was planted in six rows, 0.71 m wide, giving two border rows and four main rows in each plot. The experimental layout was a split-plot design, with irrigation treatment as main plot and maize varieties as subplots. Before emergence, fertilizer was applied at rates of 60 Kg N ha^{-1} (45-0-0), 200 Kg P ha^{-1} (0-46-0), and 60 Kg K ha^{-1} (0-0-60). Nitrogen was applied at a rate of 100 Kg ha^{-1} 19 days after emergence (DOY 166) and 17 days after emergence (DOY 168), in 1990 and 1991.

Irrigation water was applied using an overhead Toro FS-LG series sprinkler system, mounted upside down on the trusses of the rain shelter operating with a constant pressure of 103.5 Kg Pa^{-1}, at a rate of approximately 25 mm hr^{-1} (NeSmith *et al.*, 1990). Two irrigation treatments were established: (i) well-irrigated;

and (ii) water deficit in the vegetative stage. The water deficit period (period between subsequent irrigations) occurred from DOY 171 (sixth leaf ligule) to DOY 194 in 1990 and, from DOY 172 to DOY 200 in 1991. Irrigation was resumed for the water deficit treatments in both years when no significant increase in leaf elongation was observed between two consecutive measurements.

Soon after emergence, four plants per plot were randomly selected and marked for nondestructive measurements throughout the season. Leaf elongation was determined from leaves that were still expanding by measuring the length of the visible blades from the leaf tip to the point at which the opposite edges of the leaf blade meet at the sheath, on four plants per plot. Relative plant expansion was calculated by the ratio of leaf elongation during the water deficit treatment and during the well-irrigated treatment, through two consecutive measurements. Leaf senescence was estimated for each leaf by measuring the percentage of leaf that was yellow or necrotic. Measurements of leaf area were taken, approximately three times a week, once the leaves emerged from the whorl until the leaf ligule appeared. The area of each leaf was determined from measurements of leaf length and maximum leaf width multiplied by 0.75 (Stickler *et al.*, 1961). Aboveground crop biomass was estimated by harvesting four plants in each plot several times during the growing season.

Leaf rolling was measured several times daily and weekly during the water deficit period in four selected plants per plot. The 9th and 10th growing leaves were selected to represent the average plant leaf rolling and two positions were marked on each leaf (quarter-way and half-way from the tip). The percentage of leaf rolling (percent of exposed leaf blade) was calculated from the fraction of the rolled leaf width (measured by a caliper) and fully open width. Daily average leaf rolling was calculated by the integration of leaf rolling measurements taken between 0800 hours and 1900 hours. Exposed leaf area index was calculated by incorporating the daily average leaf rolling measurements into plant leaf area index.

Photosynthetically active radiation (PAR) interception was measured in four marked sites per plot, several times daily for several weeks, under clear sky conditions. At ground level, a minimum of three observations were made to compute an individual measurement in each side. The line quantum sensor (Model LI-191SB, Li-cor, Lincoln, NE) was leveled, placed perpendicular to the row direction and positioned so that no shadows from the handle influenced measurement. Canopy incident radiation was measured by placing the line quantum sensor above the crop. The daily average PAR interception was calculated by integration of radiation interception measurements taken between 0900 hours and 1700 hours. Cumulative intercepted PAR was calculated by linear interception of fractional radiation interception between two consecutive measurements multiplied by the daily solar radiation (MJ/m^2). Radiation use efficiency (RUE) for the growing season was calculated as the slope of the linear regression between aboveground biomass and cumulative intercepted radiation with the equation forced through the origin.

Plant available water was calculated for the top 1.5 m of the profile as the difference between volumetric water content of the soil and water content at the lower limit of plant-extractable soil water in the rooting depth. Fraction of plant available water was calculated by the ratio between the plant available water and the maximum available water within the rooting depth. The drained upper limit and the lower limit soil water contents were assumed to correspond approximately to a soil matrix potential of 0.01 MPa and 1.5 MPa.

Results and Discussions

Weather conditions during the experiment in 1990 and 1991 are presented in Figures 2.1 and 2.2. During the water deficit periods, from DOY 171 to 194 in 1990 and from DOY 172 to 200 in 1991, slightly different climatic conditions were observed. The averages of weather conditions during the water deficit periods and the entire growing seasons for both years are presented in Table 2.1. A companion chapter (Chapter 1) presents daily incident solar radiation, daily maximum and minimum temperatures and daily vapor pressure deficit of the air.

Plant Expansion

The influence of the water deficit period on the growth of individual maize leaves is presented in Figures 2.1 and 2.2 for 1990, and in Figures 2.3 and 2.4 for 1991, for varieties 3576 and 3615. Leaf elongation was greatly affected by water

Table 2.1. Average of daily meteorological variables during the water deficit period and the entire growing season for 1990 and 1991.

	Deficit Period		Growing Season	
Meteorological Variables	**1990**	**1991**	**1990**	**1991**
Solar Radiation (MJ/m^2)	19.75	23.64	17.25	21.05
Minimum Temperature (°C)	14.40	16.80	13.27	15.02
Maximum Temperature (°C)	26.20	29.40	25.40	28.03
Vapor Pressure Deficit (Kpa)	0.74	0.91	0.74	0.86

deficit treatment in both years. In 1990, leaf elongation began to differ from the well-irrigated treatment 11 days and seven days after the initiation of the soil water deficit (Figures 2.3 and 2.4). However, in 1991, leaf elongation began to differ six days after the initiation of the water deficit (Figures 2.1 and 2.2). This difference in leaf growth was mainly caused by the higher temperatures and incident solar radiation observed during the beginning of the water deficit period in 1991 (a companion chapter presented the weather data). NeSmith (1990) found that maize grown in the same soil type had a measurable decrease in leaf elongation within five days after withholding water.

In both years, a marked reduction in the final leaf length was observed for both varieties during the water deficit period. In 1991, leaves that were expanding when the water deficit was imposed showed a delay of four to five days to achieve

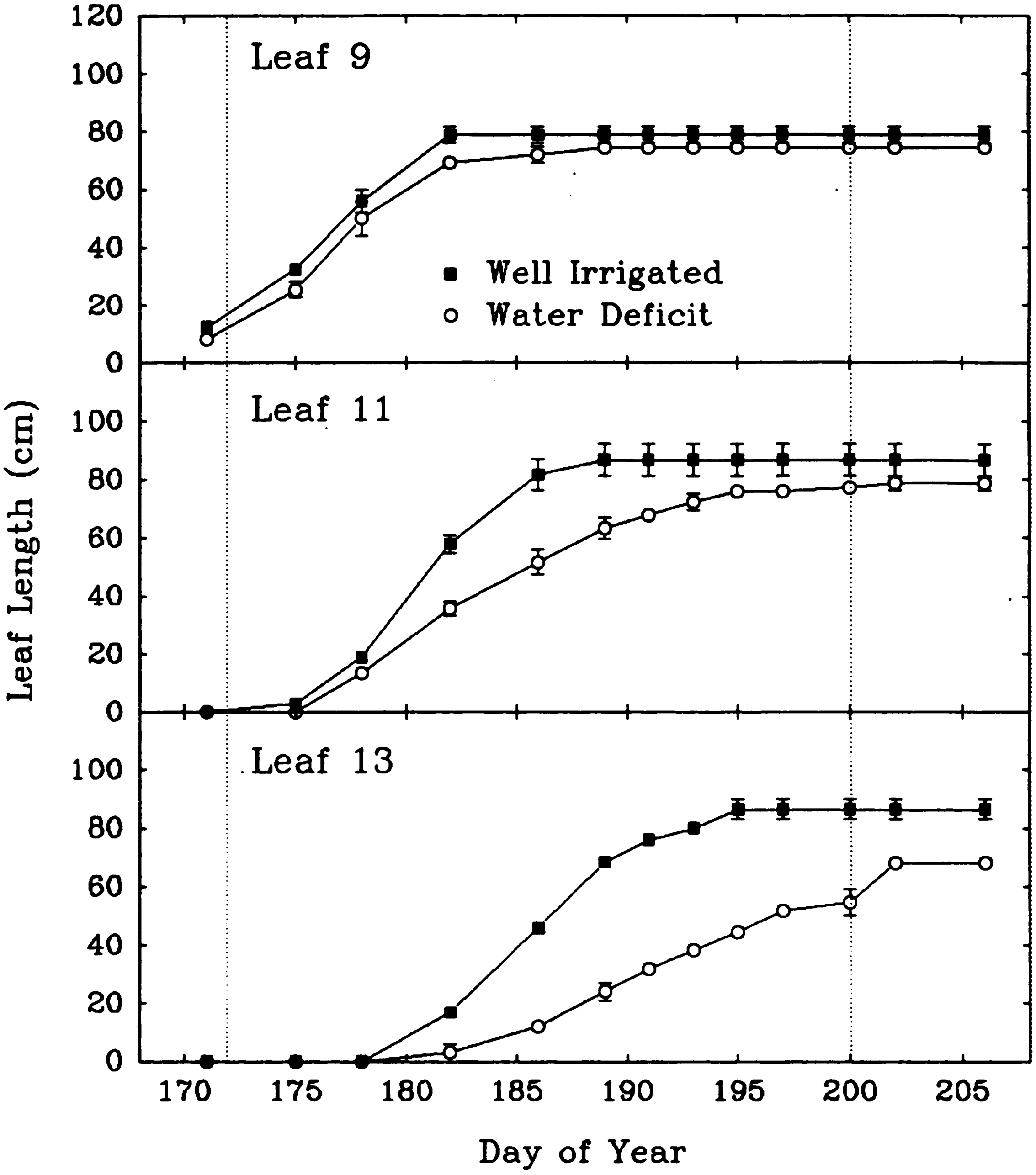

Figure 2.1. Expansion of individual leaf blades (9th, 11th and 13th leaf) for both treatments of variety 3576 during 1991.

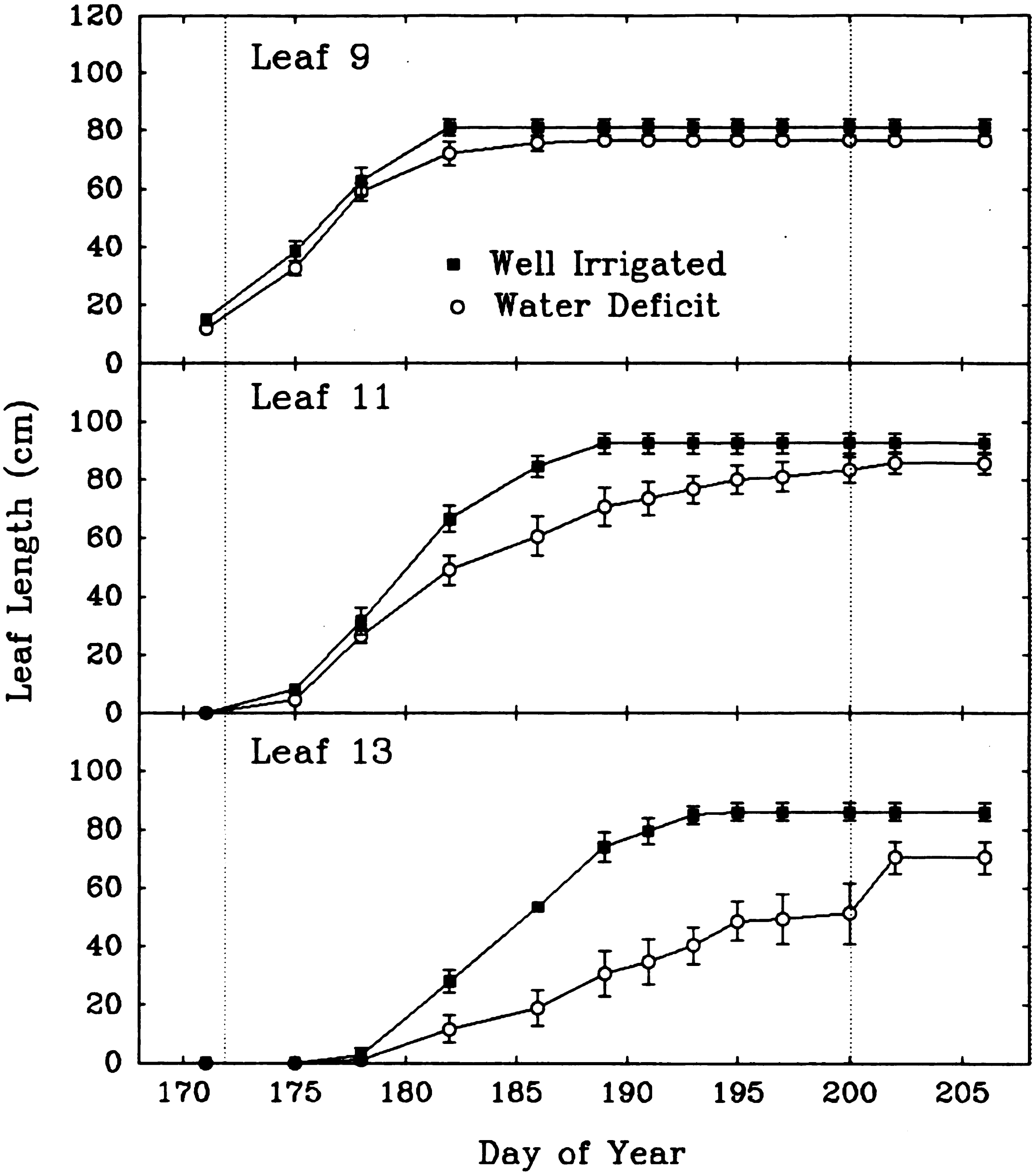

Figure 2.2. Expansion of individual leaf blades (9th, 11th and 13th leaf) for both treatments of variety 3615 during 1991.

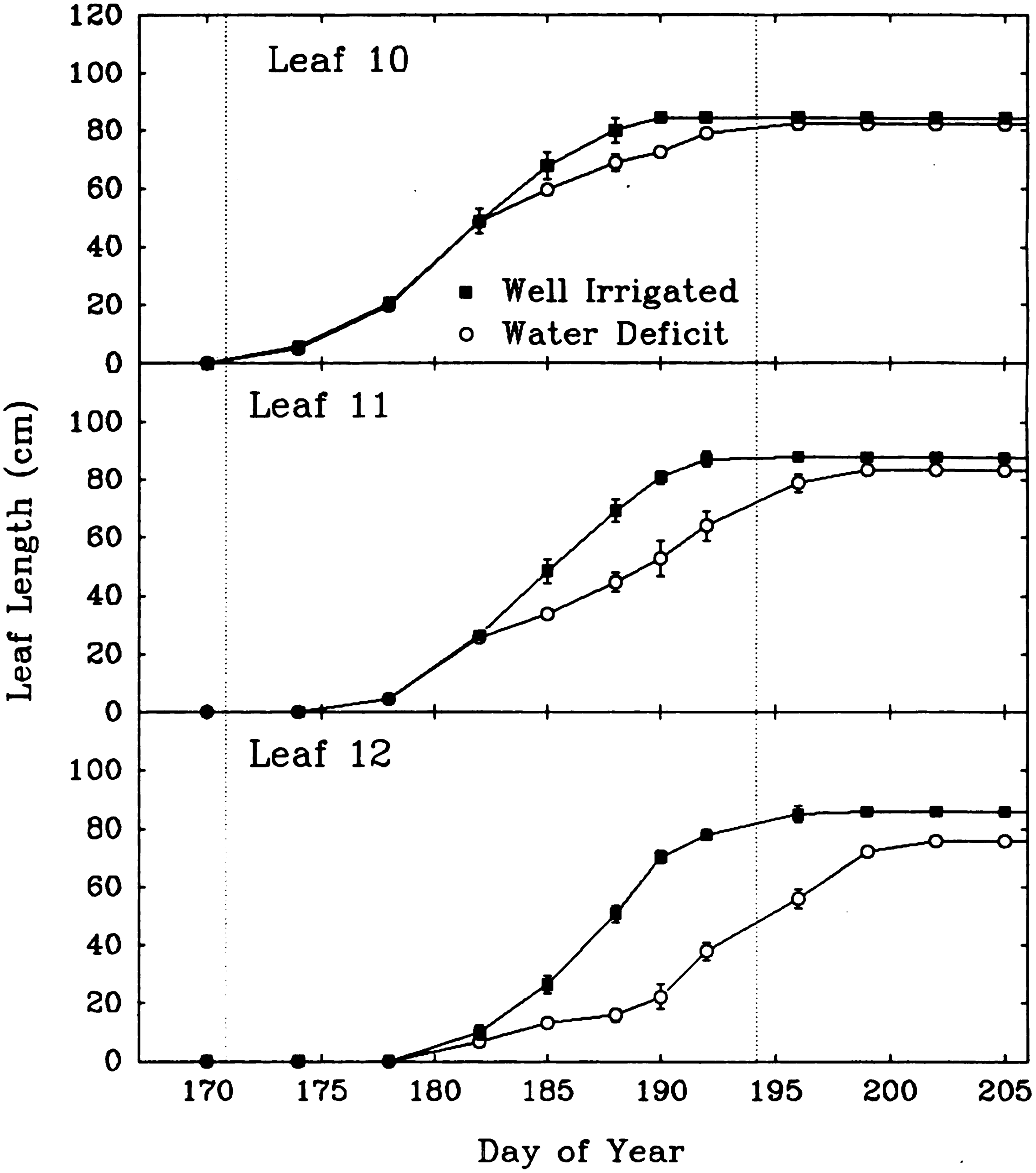

Figure 2.3. Expansion of individual leaf blades (10th, 11th and 12th leaf) for both treatments of variety 3576 during 1990.

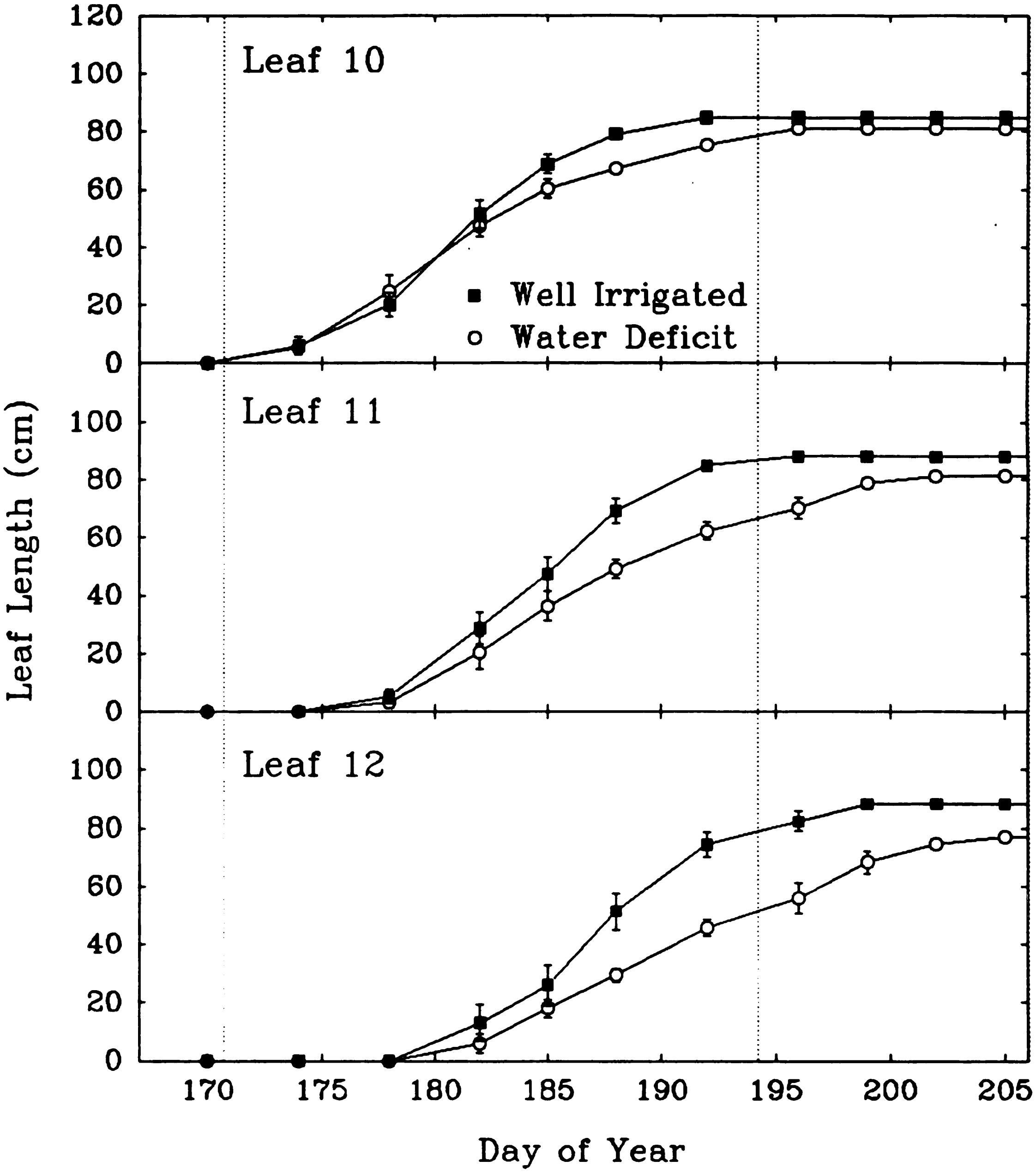

Figure 2.4. Expansion of individual leaf blades (10th, 11th and 12th leaf) for both treatments of variety 3615 during 1990.

their maximum length compared to the well-irrigated plants. Leaves that emerged during the water deficit period, however, were greatly affected by the water deficit and a delay of 11 days was observed.

Cumulative plant leaf length for both varieties during the 1990 and 1991 water deficit periods is shown in Figures 2.5 and 2.6. A similar pattern of the cumulative leaf elongation was observed in both years. The water deficit period affected the overall plant leaf expansion pattern and the final plant leaf length. At the end of the water deficit period, the plant leaf length of variety 3615 was reduced 31.8% and 29.8% compared to the well-irrigated treatment in 1990 and 1991. The overall reduction in plant leaf length, at the end of the vegetative growth (total plant leaf length), was 13.6% and 13.1% in 1990 and 1991.

These results indicate that these two varieties have a different adaptative mechanism to water deficit conditions. Rapid water deficit development (1990) reduced leaf expansion of variety 3576. However, slow development of water deficit (1991) allowed this variety to improve its response to the soil water deficit. Although the weather conditions (Table 2.1) were different in the two years, the variety 3615 showed a similar performance of leaf expansion. Monteith (1977) stated that the water deficit in plants can be induced in two ways: by a shortage of water supply to the root system (determined by the state of the soil); or by an excessive water demand from leaves (determined by the state of the atmosphere).

Relative plant expansion for the two varieties, in both years, is presented in Figure 2.7. A similar pattern of relative plant expansion was observed between the

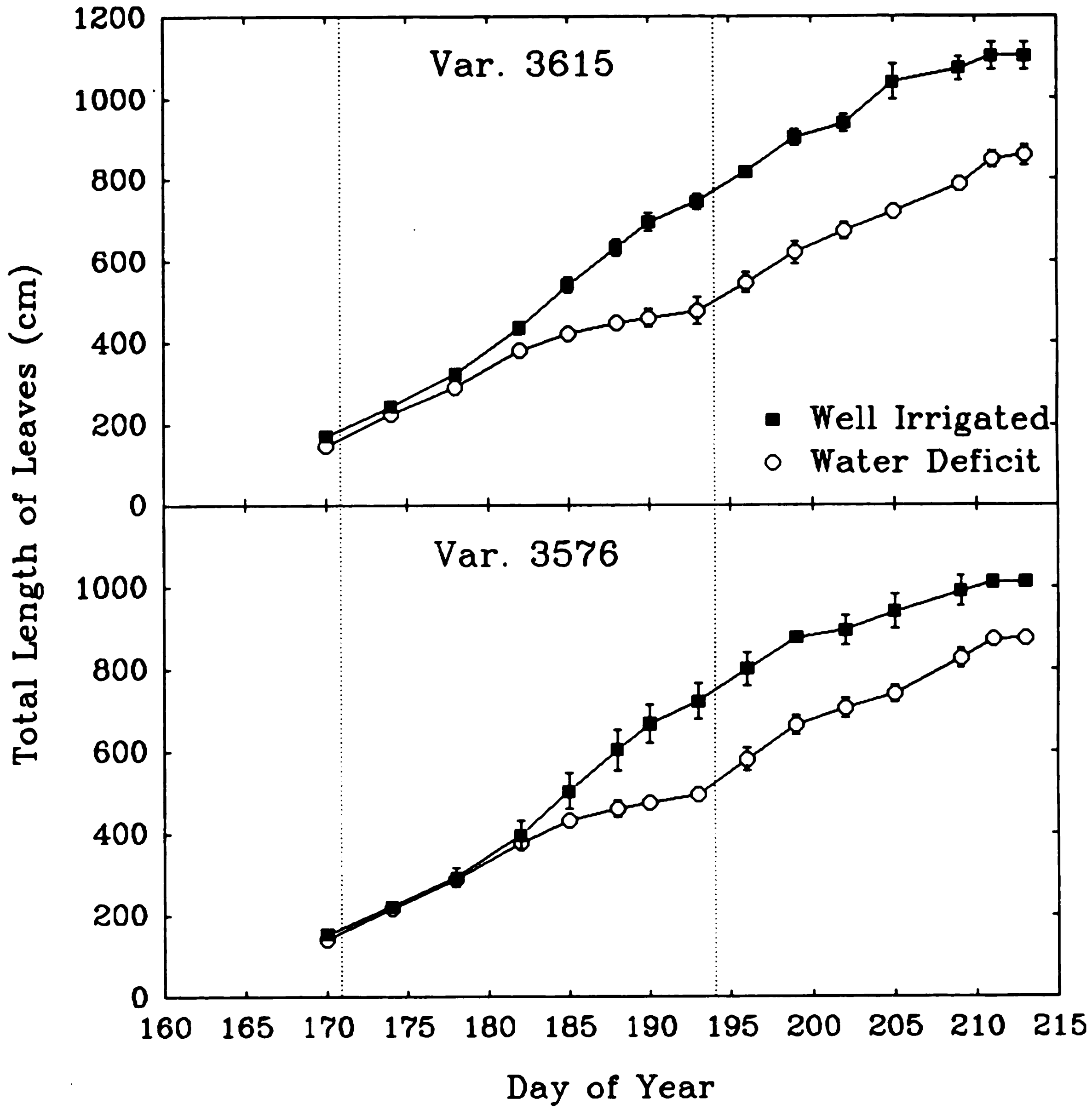

Figure 2.5. Cumulative plant leaf length for both treatments and varieties during vegetative growth in 1990. The area limited by vertical dotted lines represents the period of vegetative soil water deficit.

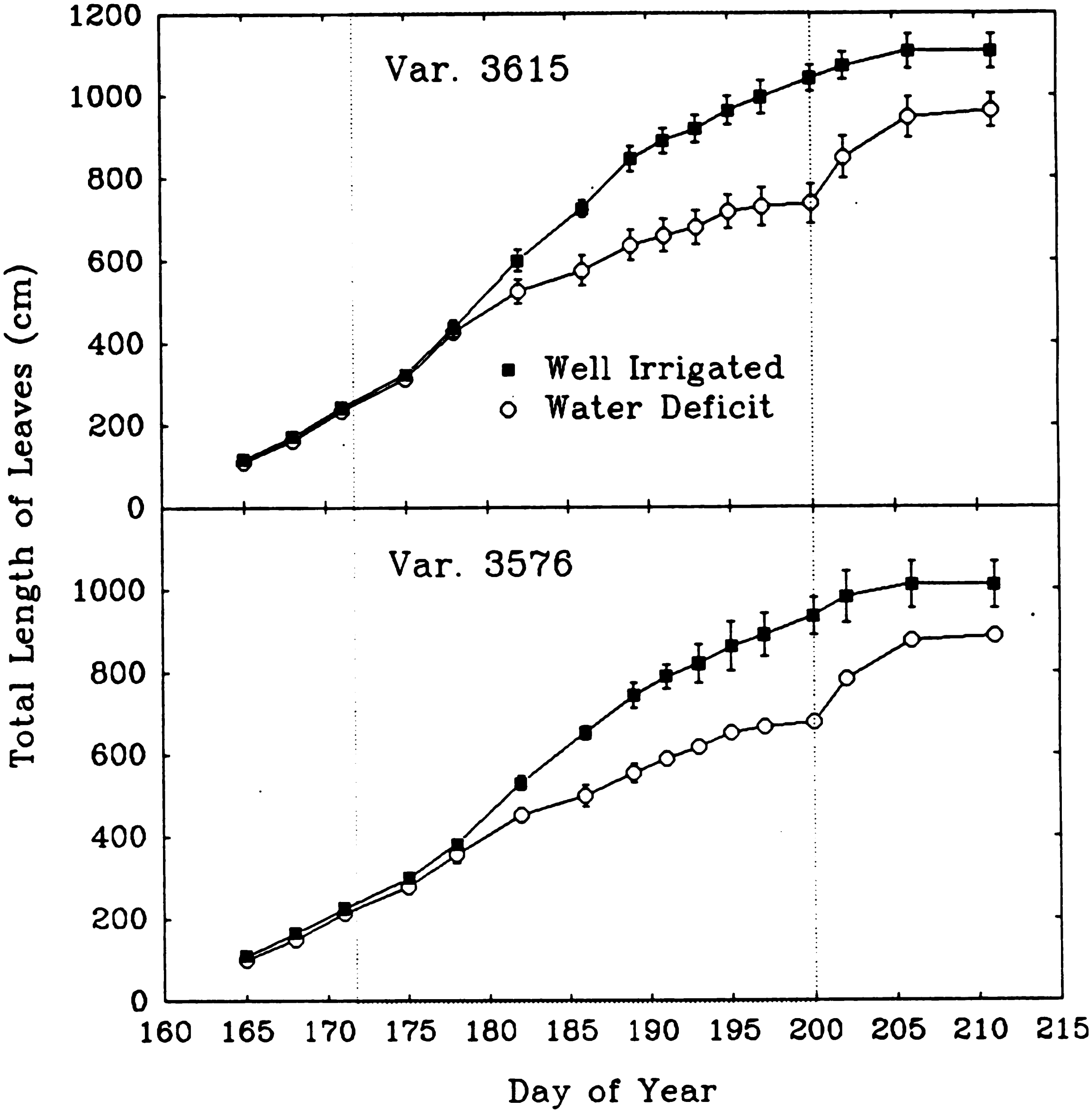

Figure 2.6. Cumulative plant leaf length for both treatments and varieties during vegetative growth in 1991. The area limited by vertical dotted lines represents the period of vegetative soil water deficit.

two varieties in both years. At the beginning of the two water deficit periods, the variety 3576 reduced leaf elongation rates more rapidly than the variety 3615. In 1991, a similar decrease in relative plant expansion was observed for both varieties until DOY 186. After this, a rapid recovery of plant expansion was observed due to the low VPD observed during DOY 186 and 193. The variety 3576, however, responded more quickly to the period of low VPD and increased the relative plant expansion rate. This result suggests that during periods of low VPD or periods of favorable soil plant water relations, the variety 3576 was able to activate the leaf expansion mechanism (by increasing the internal turgor pressure) faster than the variety 3615. Wright *et al.* (1983) in a series of experiments with grain sorghum, found genetic variation in sorghum in the ability of leaves to maintain turgor in response to changes in leaf water potential, through a lowering of osmotic potential. There is evidence that plants previously exposed to water deficit show an improved capacity to tolerate subsequent periods of water deficits through increase in solute levels (Morgan, 1984).

Leaf Rolling

The daily average values of leaf rolling (percent of leaf blade exposed) for both varieties during 1990 and 1991 is presented in Figure 2.8. In 1991, at the beginning of the water deficit period, leaf rolling (Percent of leaf blade exposed) decreased steadily and showed a similar trend for both varieties. The occurrence of a period of low VPD, between DOY 186 and 193, caused a change in the

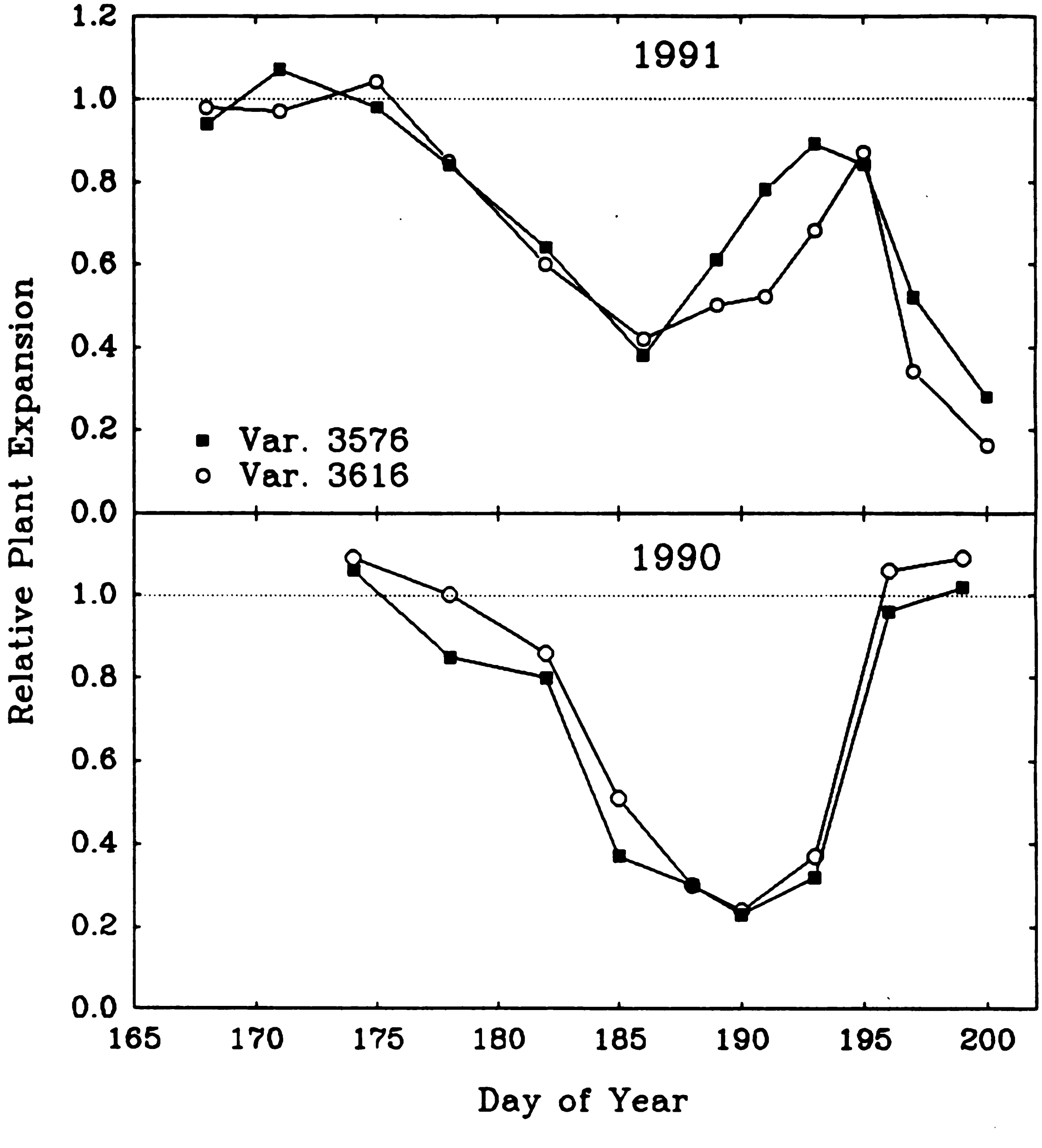

Figure 2.7. Relative plant expansion of the two maize varieties during the vegetative water deficit period in 1990 and 1991.

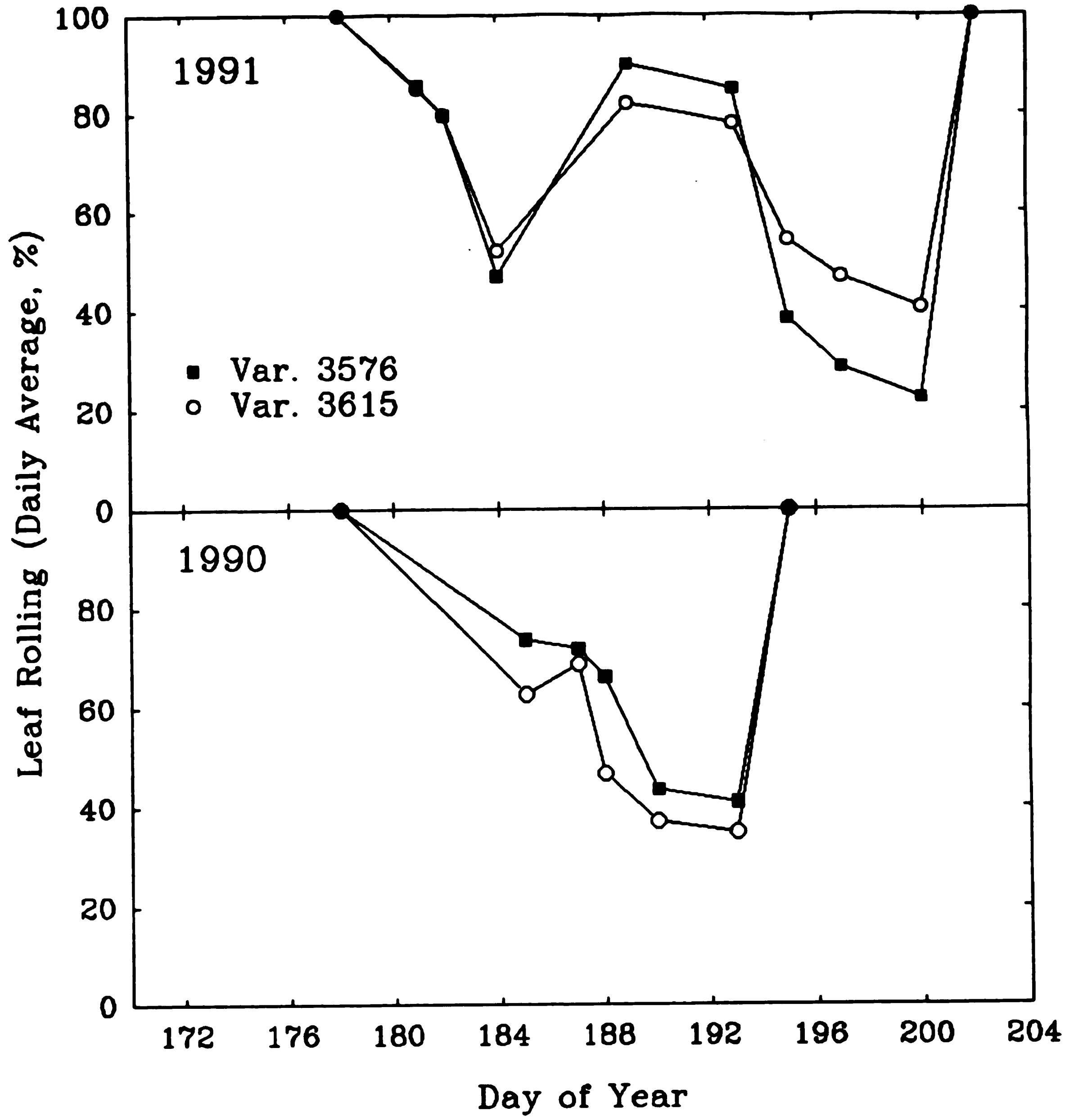

Figure 2.8. Daily average of leaf rolling (percentage of leaf blade exposed) for both treatments during 1990 and 1991 vegetative soil water deficit periods.

percentage of leaf rolling between the two varieties. Leaf rolling was slightly less for the variety 3576 when the VPD was low. However, under the onset of more severe soil water deficit conditions, variety 3576 was able to roll its leaves more effectively to reduce the radiation load than variety 3615. A sharper reduction in the percentage of leaf blade exposed was observed at the end of the water deficit period (DOY 200) for variety 3576.

In 1990, because weather conditions were relatively constant during the water deficit period, as the water deficit increased, the percentage of leaf blade exposed decreased almost linearly for both varieties. The variety 3615, however, showed a slightly lower percentage of leaf blade exposed, and at the end of the water deficit period the percentage of leaf rolling was 41% and 35% for the varieties 3615 and 3576. A rapid recovery of leaf rolling was observed for the two varieties in both years soon after irrigation was resumed. According to Duncan (1980), the rolling of maize leaves under moisture deficit reduced moisture loss by covering some stomata, reduced the exposed leaf area, and hence, the radiant energy intercepted. Leaf rolling is believed to cause a reduction in exposed LAI and, as a consequence, to reduce plant transpiration between 50% and 70% (Oppenheimer,1960) and increase water use efficiency (Johns, 1978).

These results clearly indicated that not only leaf rolling was influenced by periods of low VPD during water deficit periods but also plant expansion. These two adaptative mechanisms contributed to the reduction of exposed plant leaf area. The reduction in plant expansion caused an irreversible reduction in plant leaf area that was not recovered once the onset of better soil plant water relations began. The leaf rolling mechanism, however, allowed a rapid increase in exposed plant leaf area, increased the photosynthetic surface and conferred a faster recovery of plant growth.

Radiation Interception

The seasonal variation of radiation interception (daily average) during 1991 is presented in Figure 2.9. Although the LAI of variety 3576 increased from 1.44 to 2.24 between DOY 182 to 200, little change in radiation interception was observed. At the end of the water deficit period (DOY 200), the radiation interception of the water deficit treatment was 60.1% and 74.2% of the radiation intercepted by the well-irrigated treatment for the variety 3576 and 3615. The lower radiation interception of the variety 3576 is explained by its lower leaf rolling (Figure 2.8) and a more vertical leaf orientation.

Another confirmation of the effectiveness of the leaf movements to reduce the radiation interception was obtained for both varieties after the cessation of the water deficit. A rapid increase in radiation interception was observed for both varieties soon after irrigation was resumed. The daily average radiation interception of variety 3576 increased 54% (from DOY 200 to 206) while the LAI increased only 33%. This rapid increase of exposed LAI and resumption of crop growth is of major importance for the plants to recover from water deficit periods (Bull and Glasziou, 1980). Similar increases of LAI (33%) and radiation interception (30%)

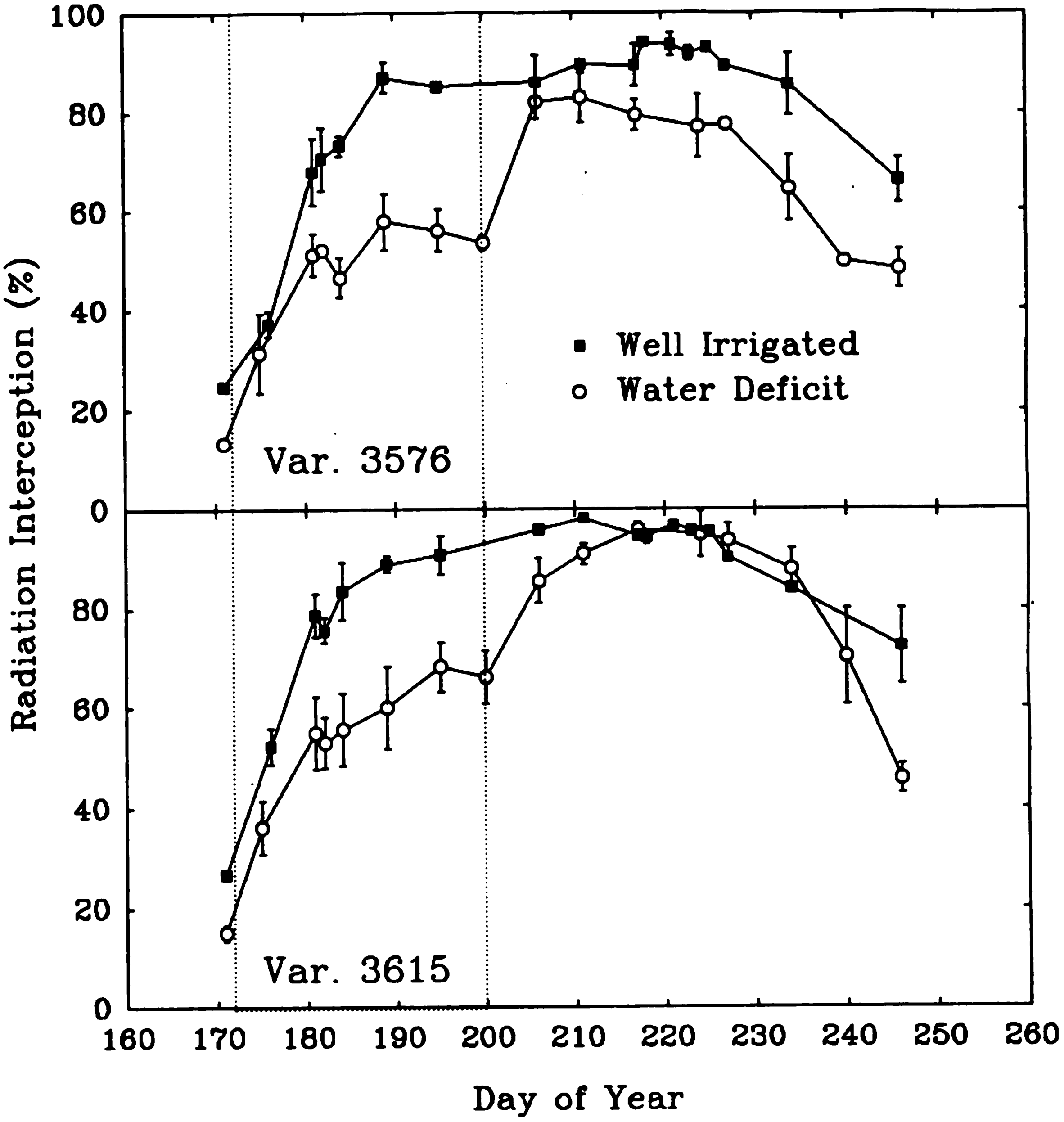

Figure 2.9. Daily average of radiation interception for both treatments and varieties during 1991. The area limited by vertical dotted lines represents the period of vegetative soil water deficit.

was observed for the variety 3615 during the same period. According to Duncan (1980), plant canopies intercept light with varying degrees of efficiency associated chiefly with their LAI, and the contribution of leaf rolling is to reduce the exposed leaf area, and hence, the energy radiant intercepted.

Plant Biomass Accumulation

Aboveground biomass accumulation began to decline for both varieties shortly after the water deficit was imposed (Figure 2.10). A similar pattern of biomass accumulation was observed for both varieties during the water deficit period. At the end of the water deficit period (DOY 200), the aboveground biomass production of the water deficit treatment was 46.9% and 46.6% of the well-irrigated treatment for the variety 3576 and 3615. Linear aboveground biomass accumulation started for the water deficit treatment after the water deficit was relieved. Despite the large difference in total aboveground biomass production between the two varieties observed during the water deficit period, at harvest the water deficit treatment produced 68.3% and 66.7% of the aboveground biomass of the well-irrigated treatment, for variety 3576 and 3615.

The relationship between aboveground biomass and cumulative intercepted radiation is presented in Figure 2.11. The radiation intercepted by the variety 3576 and 3615 during the entire growing season was 77.3% and 82.6% of the radiation intercepted by the well-irrigated treatment. Radiation use efficiency (RUE) was higher for both varieties grown under well-irrigated conditions (Table 2.2). The

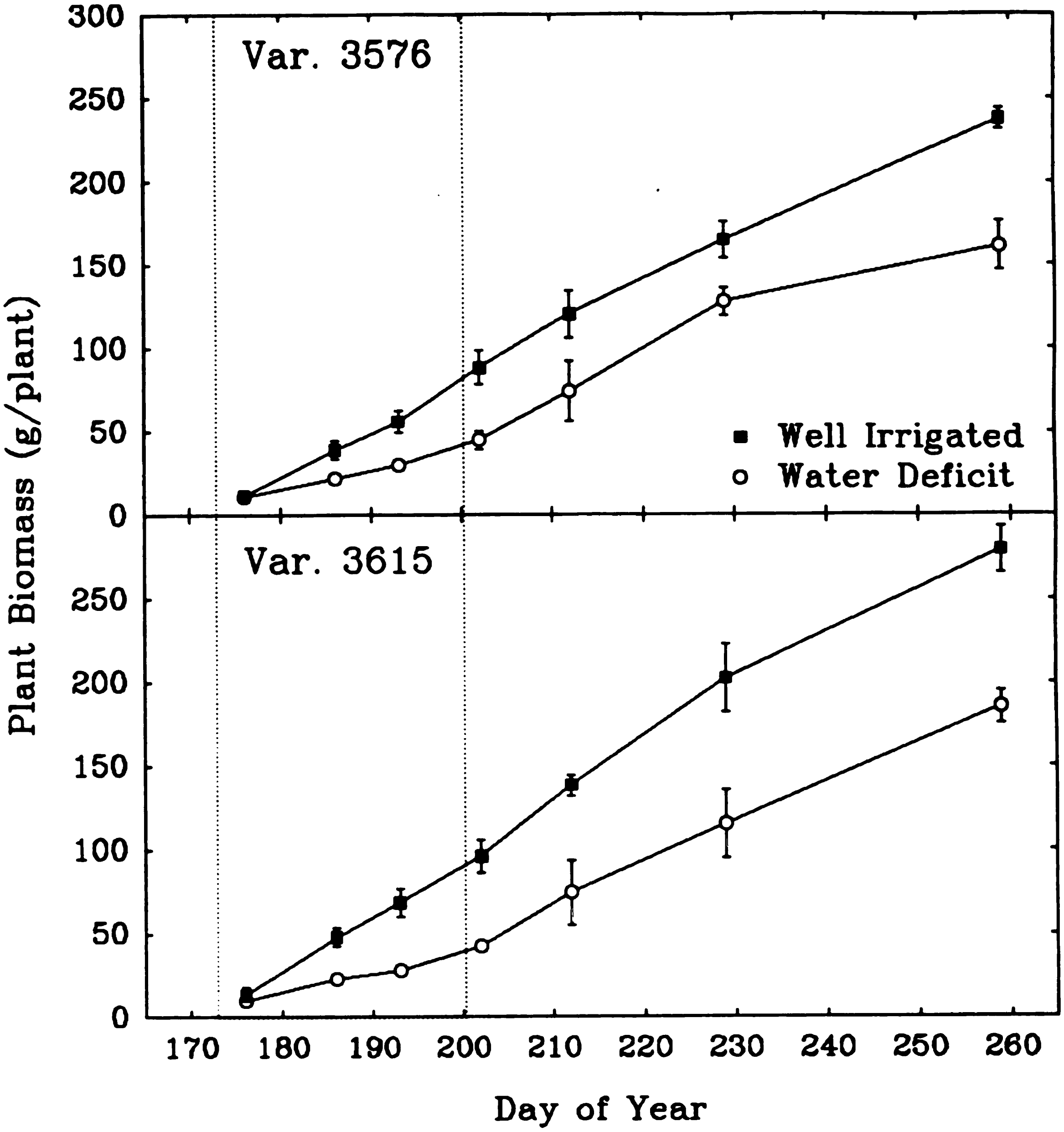

Figure 2.10. Aboveground biomass for both treatments and varieties in 1991. The area limited by vertical dotted lines represents the period of soil water deficit.

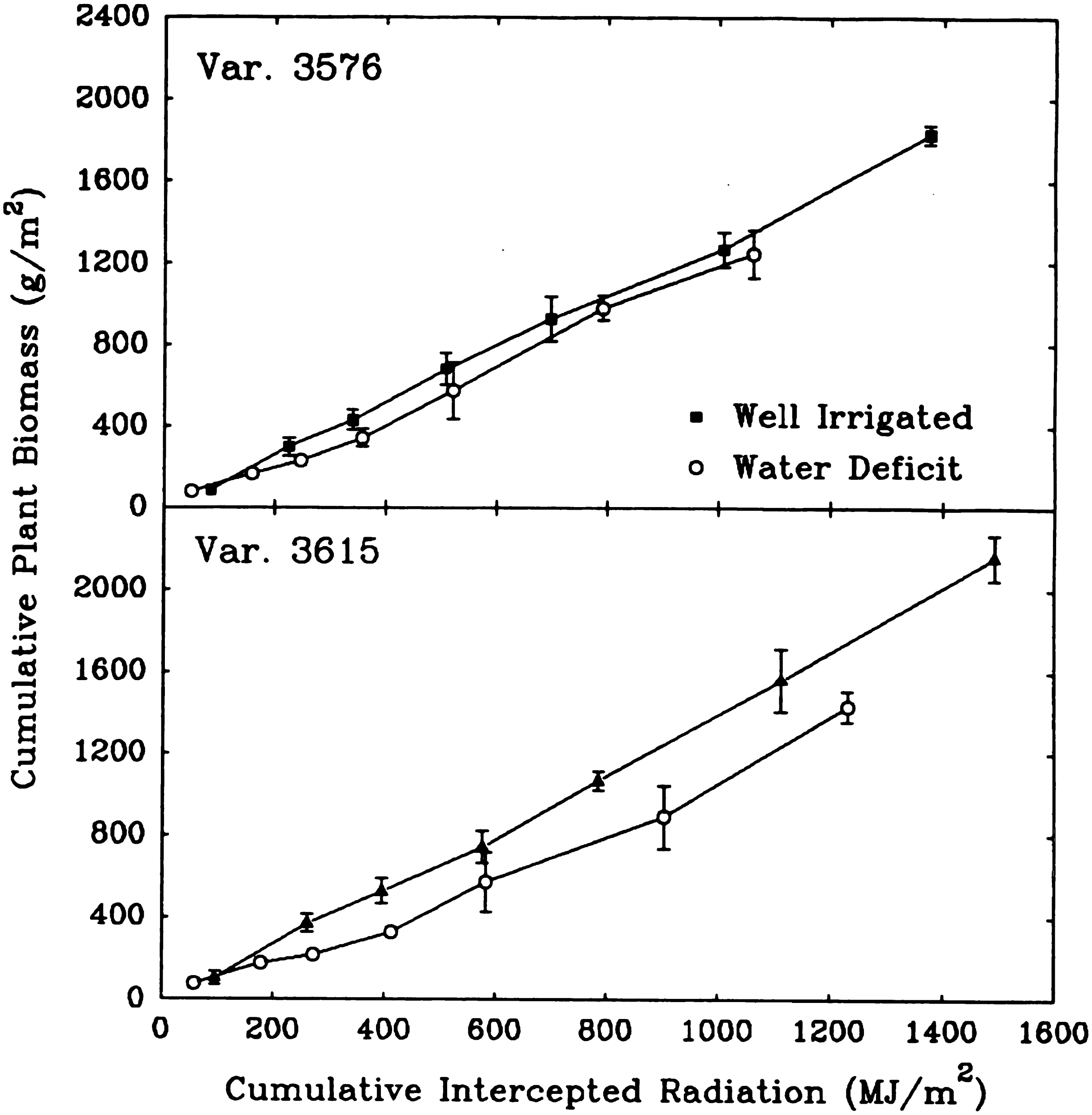

Figure 2.11. Relationship between aboveground biomass and cumulative intercepted radiation in 1991.

water deficit imposed during the vegetative growth caused differences in RUE between the two varieties. Although the variety 3615 had a larger LAI and a consequent higher daily average radiation interception (Figure 2.9) during the growing season, the variety 3576 was more efficient in converting the intercepted radiation into aboveground biomass. The linear relationship observed between biomass accumulation and intercepted radiation corresponds with results obtained by Monteith (1981); Gallagher and Biscoe (1978); and Sibma (1977).

Table 2.2. Total intercepted radiation, radiation use efficiency (RUE) and above ground biomass for both treatments and varieties in 1991. Values in brackets are percentages of the well irrigated treatment.

Treatment	Variety	Intercepted Radiation	Biomass Production	RUE	R^2
Water Deficit	3576	1063.0 (77.3)	1250.0 (68.3)	1.16 (88.5)	0.987
	3615	1231.6 (82.6)	1434.1 (66.7)	1.05 (77.9)	0.962
Well Irrigated	3576	1376.7	1830.0	1.31	0.998
	3615	1491.9	2151.0	1.40	0.996

This discrepancy in radiation use efficiency between the variety 3576 (1.16 g/MJ) and the variety 3615 (1.05 g/MJ) during the entire growing season is explained by the lower values of RUE observed for the variety 3615 during the water deficit period (Figure 2.12). As the water deficit developed, the reduction in RUE was almost linear. At the end of the water deficit period, the RUE of the variety 3615 was 0.43 g/MJ versus 0.70 g/MJ of variety 3576. A similar pattern of RUE was observed for both varieties under well-irrigated conditions. Monteith (1977) found that the production of aboveground biomass by barley, potatoes, sugar beet, and apples is strongly correlated with intercepted radiation and the RUE was approximately 1.4 g/MJ for all crops. A typical value of RUE for grain sorghum under non-stressed conditions before grain filling is 1.25 g/MJ (Muchow, 1985). The relative contribution of reduced radiation interception and reduced RUE to a reduced biomass production under water deficit conditions was different for both varieties. The variety 3576 responded better during the gradual development of water deficit. The reduction in its biomass was mainly due to a reduction in intercepted radiation rather than a reduced RUE. This result is in agreement with Legg *et al.* (1979) with barley, Garrity *et al.* (1984) with sorghum and, Muchow (1985) with tropical grain legumes.

These data indicate that during the water deficit period the assimilation rate was more affected for the variety 3615. Steven *et al.* (1983) stated that the biomass production is a function of the total incident solar radiation, the fraction of radiation interception, and the efficiency of conversion of solar energy to phytomass. Leaf movements (leaf rolling and orientation) seemed to contribute to the reduction of radiation interception of the variety 3576 and, consequently, to

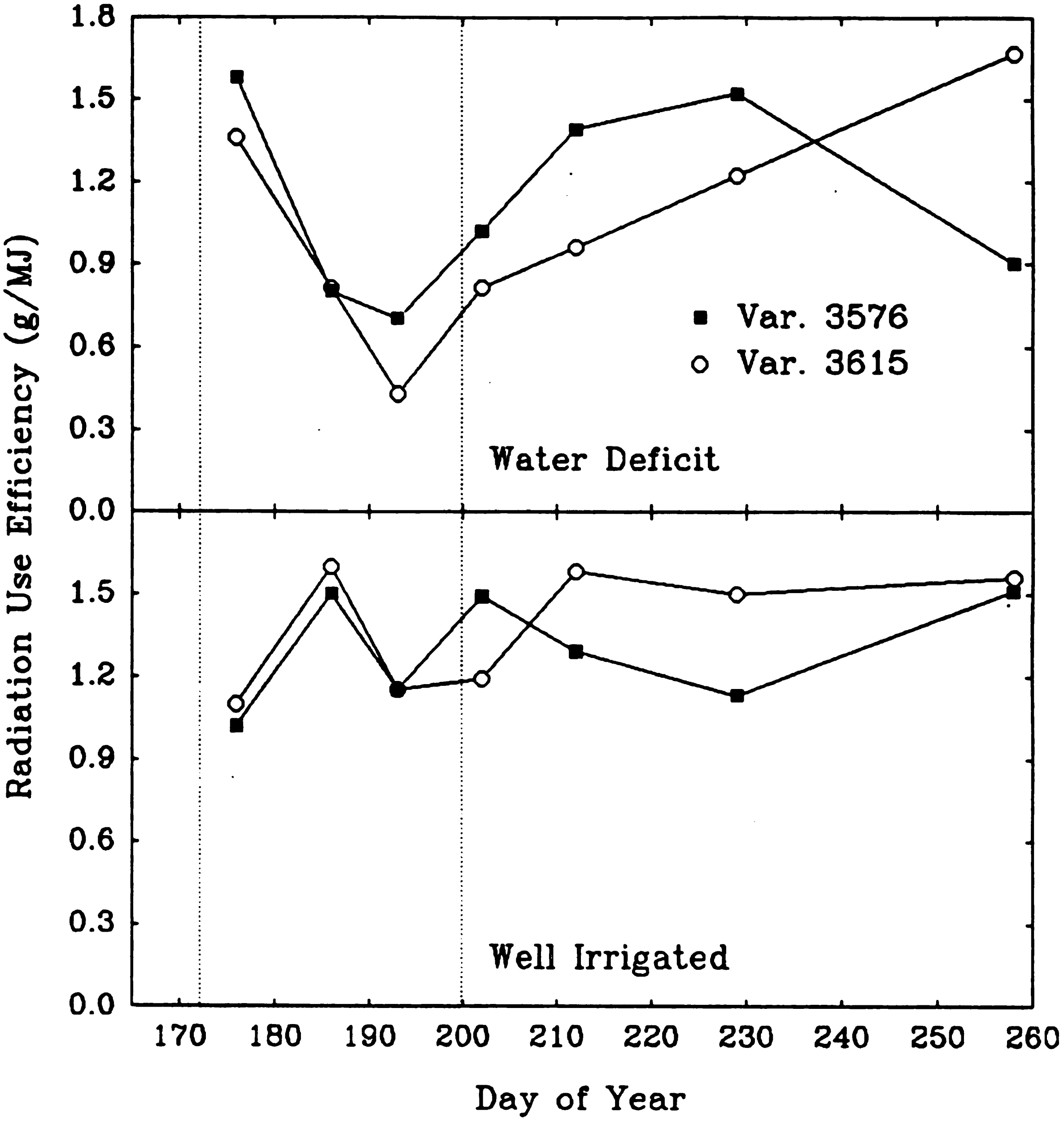

Figure 2.12. Seasonal variation of radiation use efficiency (RUE) for both varieties and treatments during 1991.

increase its RUE.

Plant Leaf Area and Senescence

The soil water deficit during the vegetative phase had a noticeable effect on plant leaf area in both years (Figures 2.13 and 2.14). In 1990, LAI for the water deficit treatment began to diverge from the well-irrigated treatment 7 and 11 days after the irrigation was discontinued for the varieties 3576 and 3615. In 1991, however, both varieties began to diverge from the well-irrigated treatment 6 days after the irrigation was ceased. The exposed LAI was calculated based on the daily average leaf rolling measurements presented in Figure 2.8. In both years, plant leaf rolling contributed significantly to reduce the exposed plant leaf area of the water deficit treatments. In 1991, an increase in the exposed LAI was observed between DOY 189 to 193. This was caused by the low VPD observed during the period (Figure 2.2).

The reduction in plant LAI and exposed LAI of the water deficit treatment was calculated by the integration of LAI curves (Figures 2.13 and 2.14) over the duration of the water deficit period. Although the conditions and the duration of the water deficits were different in both years, a similar reduction in LAI and exposed LAI was observed. In 1991, the LAI of water deficit treatment ranged from 64.4% to 69.6% of the measured LAI for the well-irrigated treatment and, from 68.7% to 73.7% in 1990. The exposed LAI ranged from 41.2% to 42.9% of the well-irrigated treatment in 1991 and from 48.4% to 49.9% in 1990.

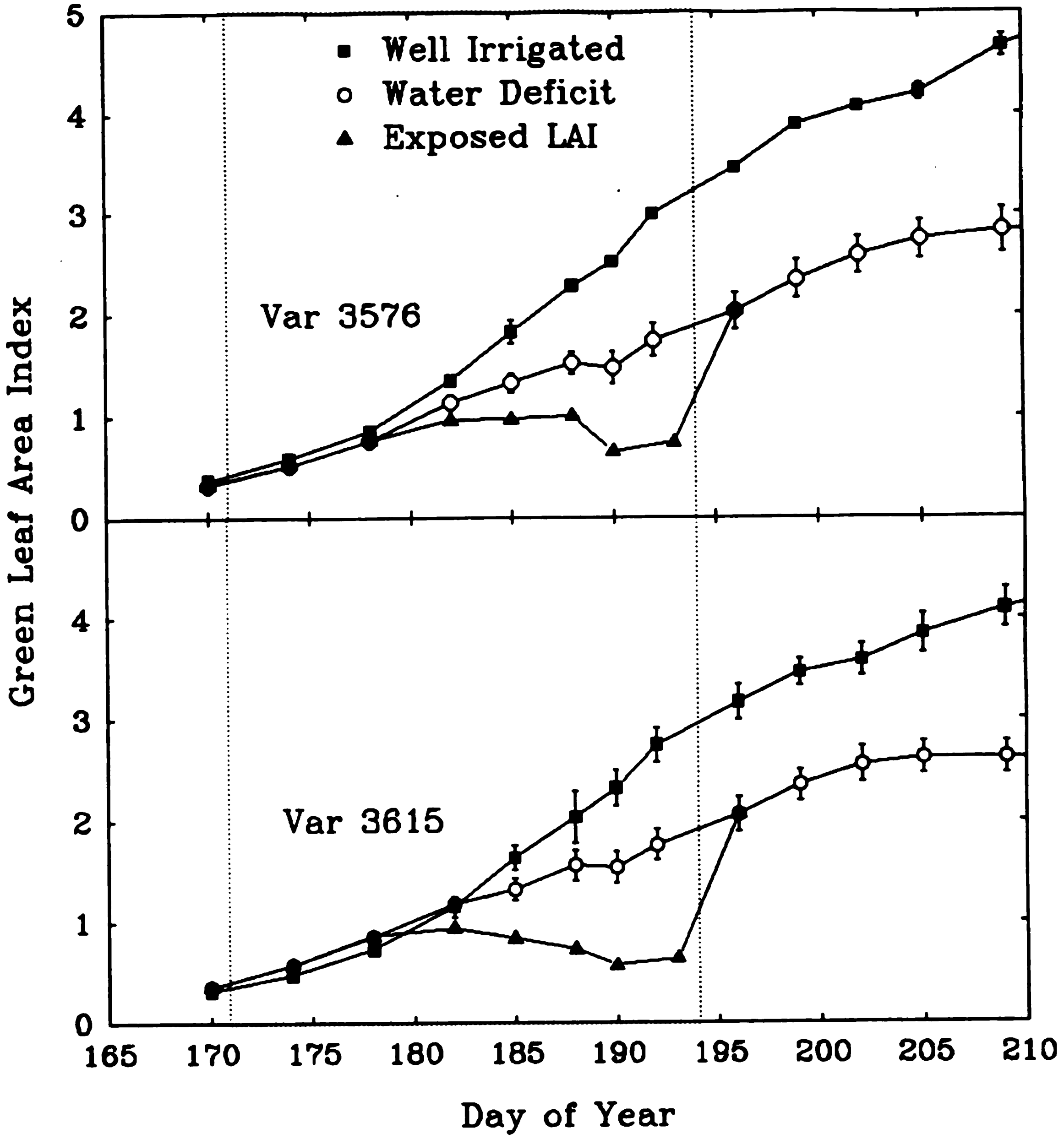

Figure 2.13. Green leaf area index of the well-irrigated treatment, vegetative water deficit and exposed leaf area index of the water deficit treatment for both varieties during vegetative growth in 1990.

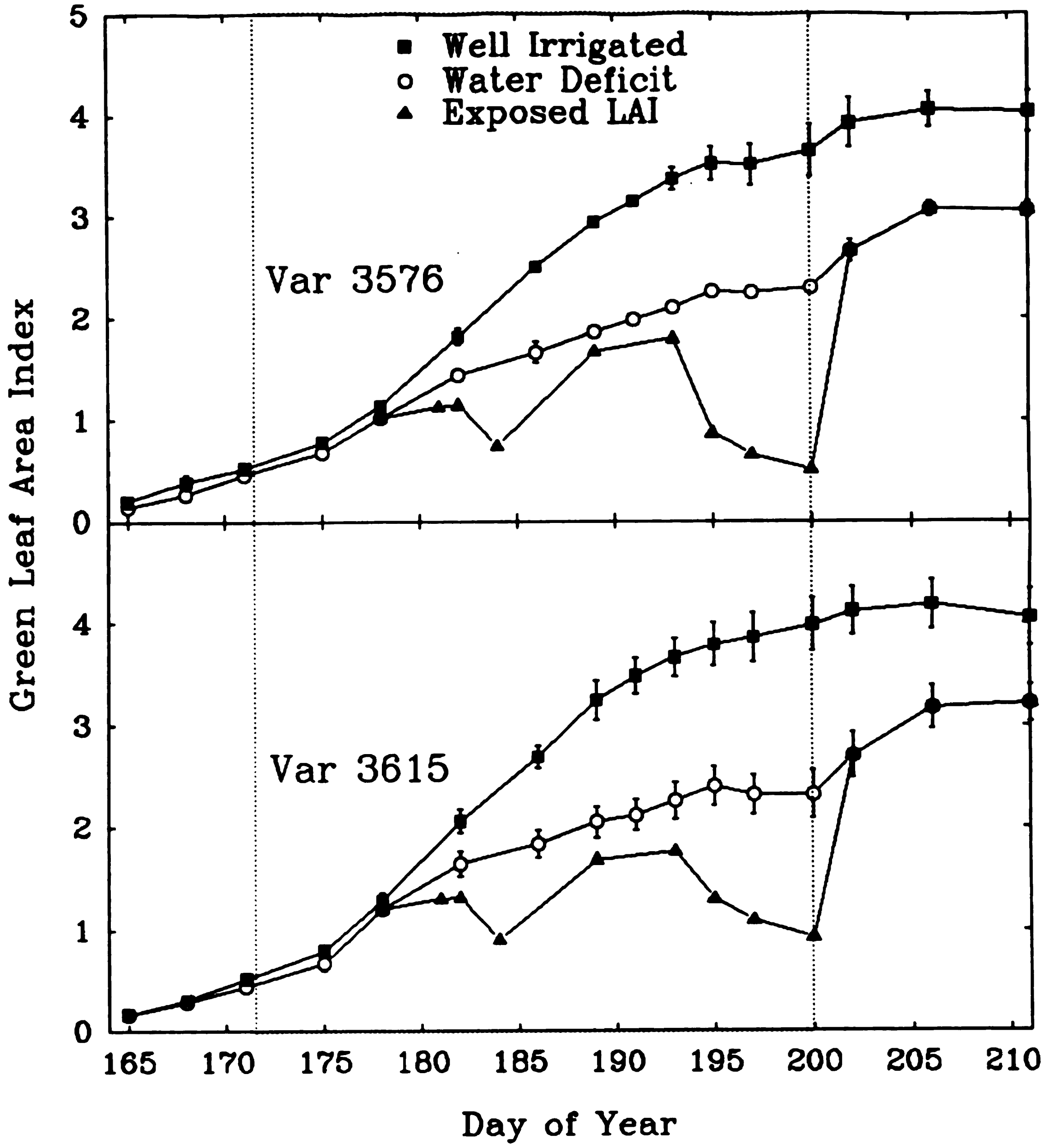

Figure 2.14. Green leaf area index of the well-irrigated treatment, vegetative water deficit and exposed leaf area index of the water deficit treatment for both varieties during the vegetative growth in 1991.

A distinct effect of the water deficit in reducing plant leaf area (leaf elongation) and exposed leaf area was observed between the two varieties. In 1991, the contribution of reduced plant expansion and leaf rolling to diminish the exposed plant leaf area was 30.5% and 26.7% for the variety 3576 and, 35.6% and 17% for the variety 3615 (Figure 2.15). These results indicate that the plant leaf rolling reduced the exposed plant leaf area and, consequently, limited the activity of the leaf elongation mechanism. The rapid development of the water deficit, observed in 1990, caused a different response between the two varieties. The contribution of leaf elongation to reduce LAI was higher for the variety 3576 (31.3% versus 26.3%) with slightly lower leaf rolling (20.3% versus 23.7%) than the variety 3615. Periods of low VPD during water deficit conditions had a more noticeable effect on leaf rolling than plant expansion. At the end of the water deficit period in 1991 (DOY 200), the LAI of the water deficit treatment was 62.7% and 58.1% of the well-irrigated treatment for the varieties 3576 and 3615. The exposed LAI, however, was only 13.7% and 23.3% of the well-irrigated treatment for the varieties 3576 and 3615. The substantial reduction in exposed LAI such as that observed in the water deficit treatment limited leaf area available for photosynthesis, and also reduces transpiration, thereby conserving the limited soil water supply and reducing water requirements for late in the season.

The reduction in plant leaf area by accelerating leaf senescence during 1991 is presented in Figure 2.16. The percentage of plant leaf area senesced progressively increased during the water deficit period for both varieties. A slightly

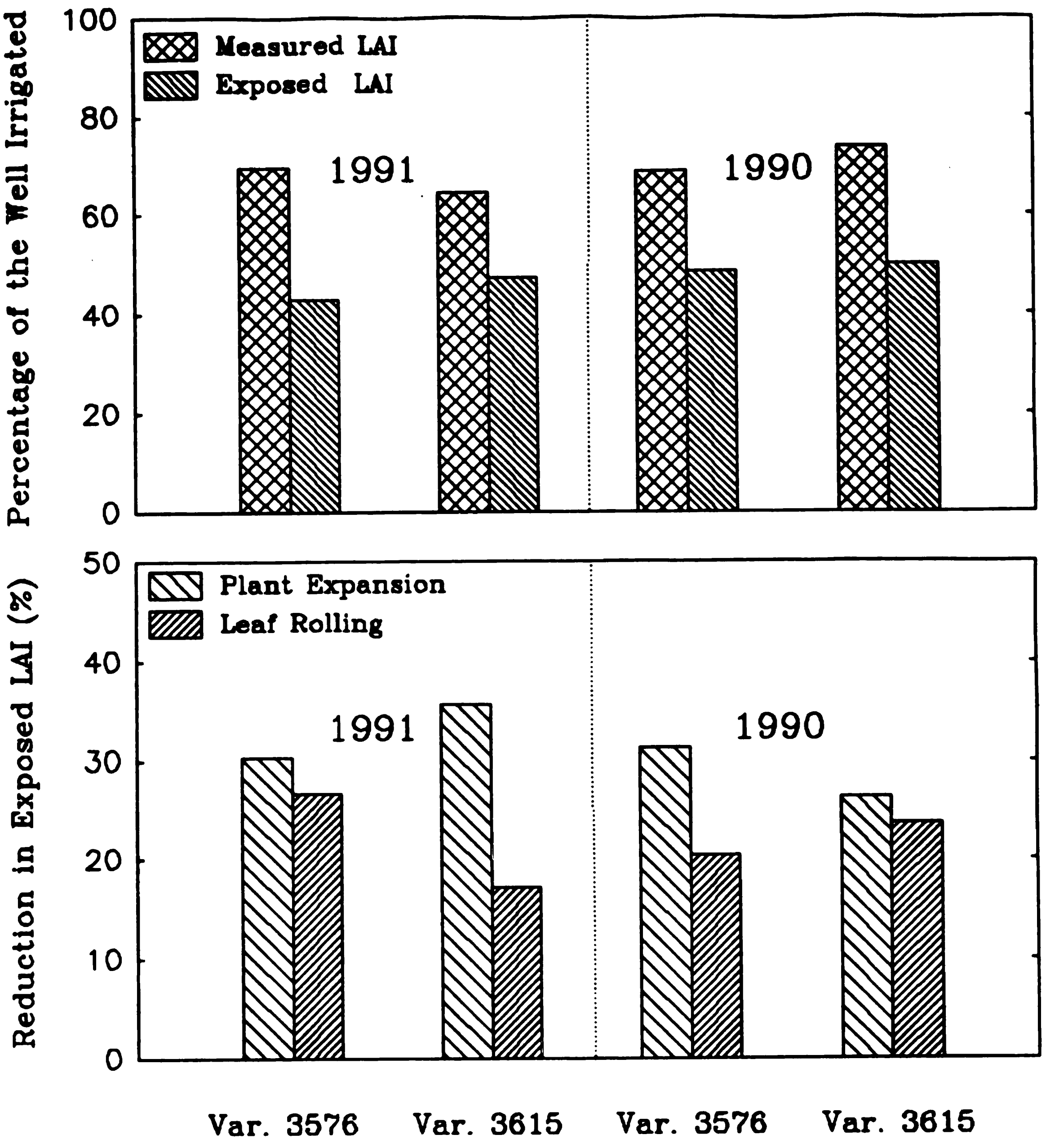

Figure 2.15. Relative effect of the water deficit period imposed in 1990 and 1991 on LAI and exposed LAI of both varieties.

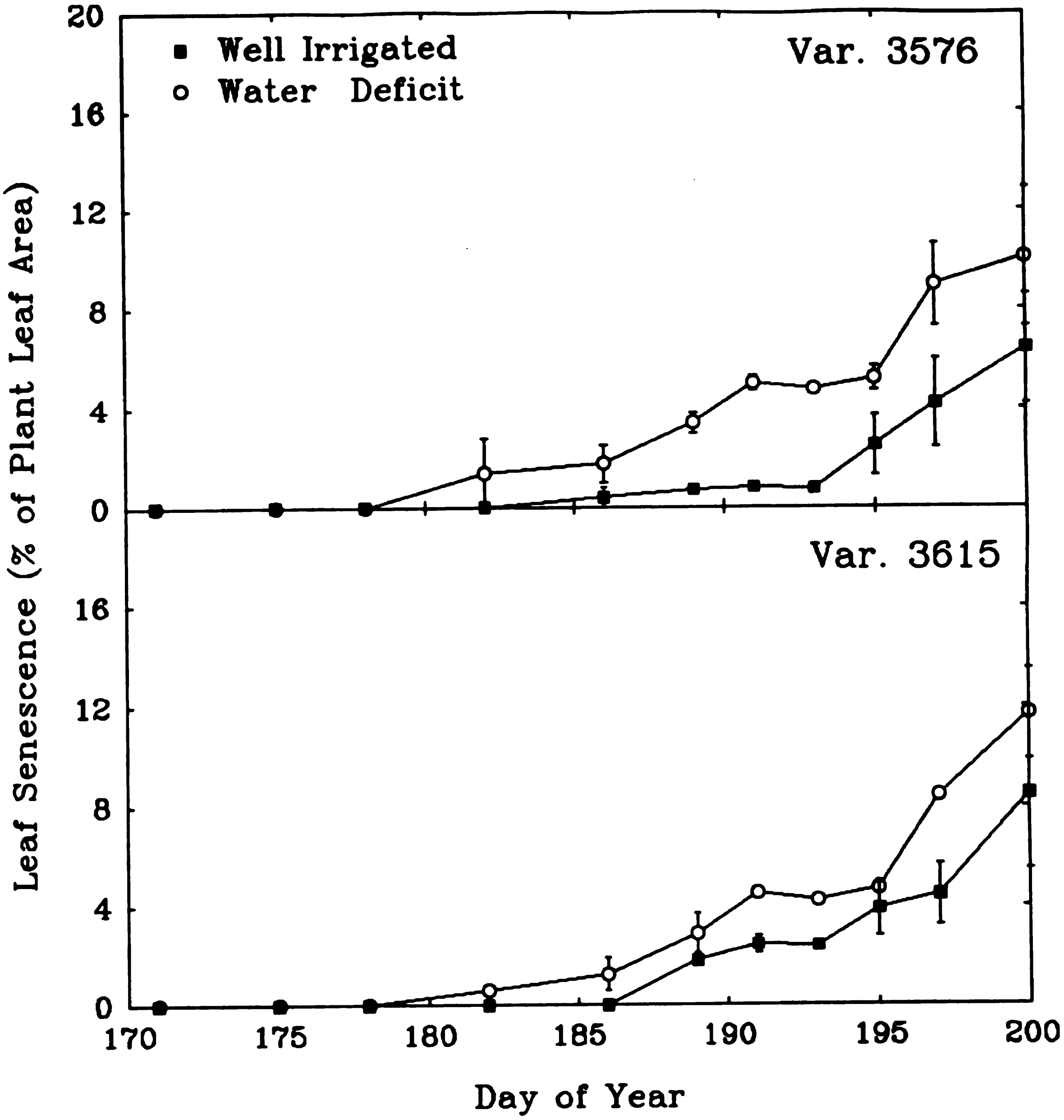

Figure 2.16. Percentage of plant leaf senescence for both treatments and varieties during the vegetative growth in 1991.

higher percentage of leaf senescence was observed at the end of the water deficit period for the variety 3615. A rapid increase in leaf senescence was noted for both varieties as the water deficit became more severe, between DOY 195 and 200, due to low soil water availability associated with high VPD. Many of the lower leaves of maize plants, according to Duncan (1980), are subject to early loss for several reasons. The increasing percentage of leaf senescence observed at the end of the water deficit for the well-irrigated treatment, was probably caused by the low intercepted radiation usually observed for lower leaves in the plant canopy. Although maize leaves are well separated on the stalk ensuring ventilation within the canopy and a minimum of close overlapping (Duncan, 1980), most of the light is intercepted by the top fully expanded leaves resulting in older leaves receiving less light. As a consequence, senescence is increased (Bull and Glasziou, 1980). The main disadvantage of senescence of lower leaves induced by water deficit is that the reduction in leaf area is irreversible, particularly in maize that does not have compensation growth to increase the number of leaves once the deficit is relieved. Thus, the reduction in leaf area can not be recovered if the soil plant water relation returns to more favorable conditions.

Leaf Area adjustments

The relationship between relative plant expansion and leaf rolling with the fraction of plant available water for both varieties during the water deficit period in 1991 is presented in Figure 2.17. The effect of the water deficit on plant expansion

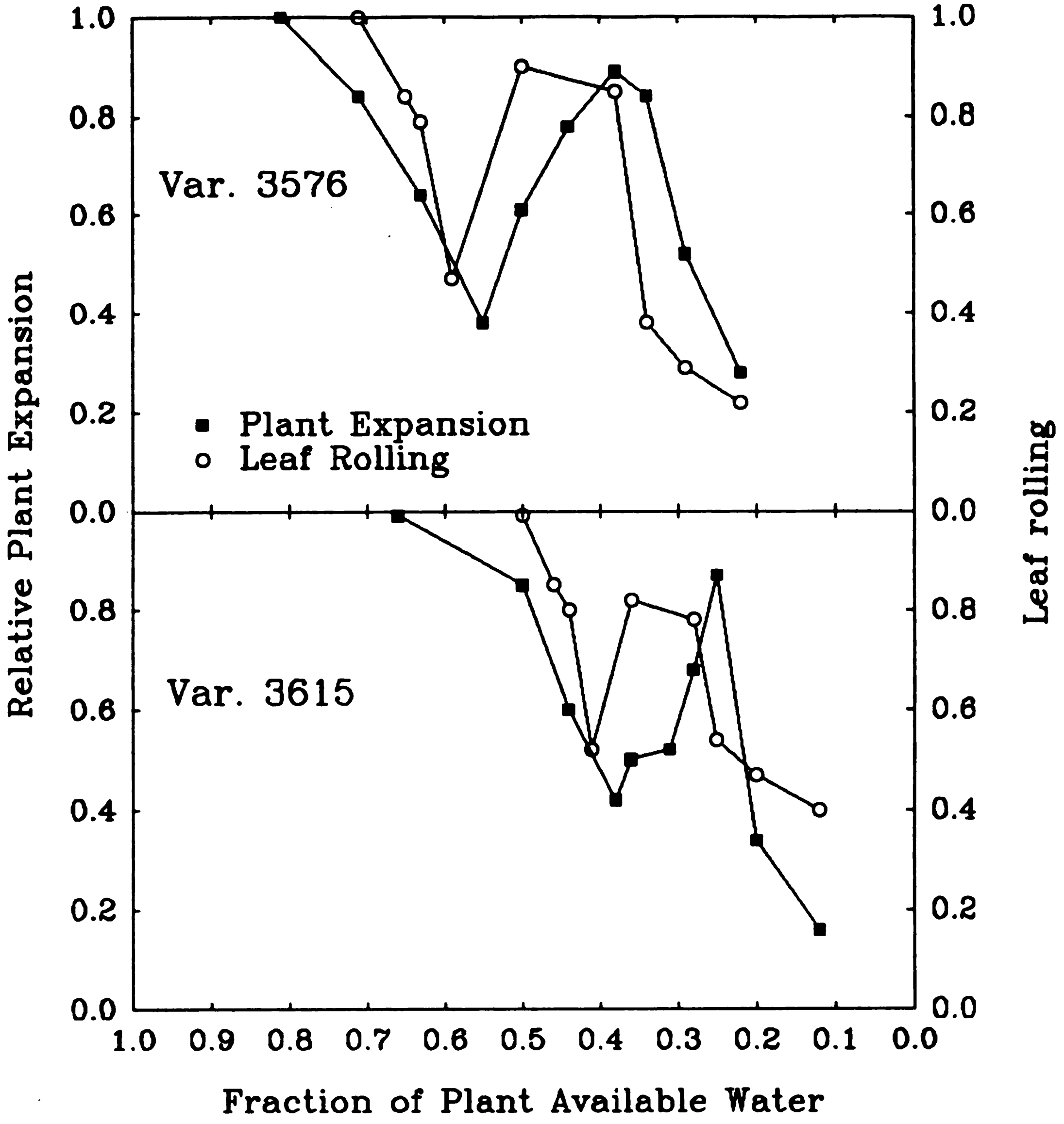

Figure 2.17. Relationship of plant expansion and leaf rolling with the fraction of plant available water for both varieties during the water deficit period in 1991.

began when the fraction of plant available water was between 0.71 to 0.81 and from 0.50 to 0.66. The water deficit effect on the plant leaf rolling began when the fraction of plant available water was between 0.65 to 0.71 and 0.47 to 0.50 for the variety 3576 and 3615. Leaf elongation and leaf rolling mechanisms are turgor pressure dependent and are extremely sensitive to water deficit. This result is in agreement with the slow leaf elongation rates early in the development of the water deficit described by Taiz and Zeiger (1991). The main difference between these two mechanisms is that reduction in leaf elongation causes a permanent reduction in plant leaf area and leaf rolling rapidly recovers on the relief of the stress.

The low VPD observed during the water deficit period caused a marked decrease in plant leaf rolling and a sharp increase in relative plant expansion, although the fraction of plant available water was between 0.38 and 0.55 for the variety 3576 and between 0.25 and 0.38 for the variety 3615. The leaf rolling mechanism reacted more quickly to the period of low VPD than the plant expansion. The plant leaves rehydrated during this period, and as a result leaf growth occurred. Although the relative plant expansion increased, the actual increase in total plant leaf length of plants under water deficit, as well as the well-irrigated treatment, was not significant.

In intermittent water deficit situations such the one observed in 1991, the variety 3576 reduced the exposed plant leaf area by increasing leaf rolling rather than decreasing the rate of plant expansion. The contribution of leaf rolling in the reduction of exposed LAI increased progressively as water deficit intensified, until leaves were rolled during most of the daylight hours. Further increases in leaf rolling were limited due to physical restrictions for the leaves to roll. During the period of low VPD (between DOY 186 to 193), the recovery of the variety 3576 plant expansion rate was quicker and larger than the variety 3615 (Figure 2.7). The leaf rolling mechanism increased the plants' capacity to enlarge the exposed plant leaf area more quickly when either favorable atmospheric conditions occurs or the water deficit was relieved. Once the water deficit was relieved, the variety 3576 rapidly increased its exposed leaf area (Figure 2.14), radiation interception (Figure 2.9) and radiation use efficiency (Figure 2.12). These data indicate that the variety 3576 can increase the production of carbohydrates via plant photosynthesis (enlarging plant leaf area) rapidly soon after the water deficit is alleviated.

The relationship between radiation interception and measured and exposed LAI for the 1991 season is shown in Figure 2.18. At the beginning of the water deficit period similar percentages of radiation interception was observed between the two treatments for both varieties. As the water deficit developed, for similar measured LAI, the radiation interception of both varieties growing under water deficit conditions progressively fell behind the well-irrigated treatment. This gap in radiation interception was caused by leaf movements (leaf rolling and leaf orientation) that changed the size of exposed LAI and, consequently, the radiation interception. Chapter 1 described the changes in leaf rolling and leaf orientation during the vegetative water deficit treatment. A fairly good radiation interception pattern was observed between the two varieties under well-irrigated conditions. A

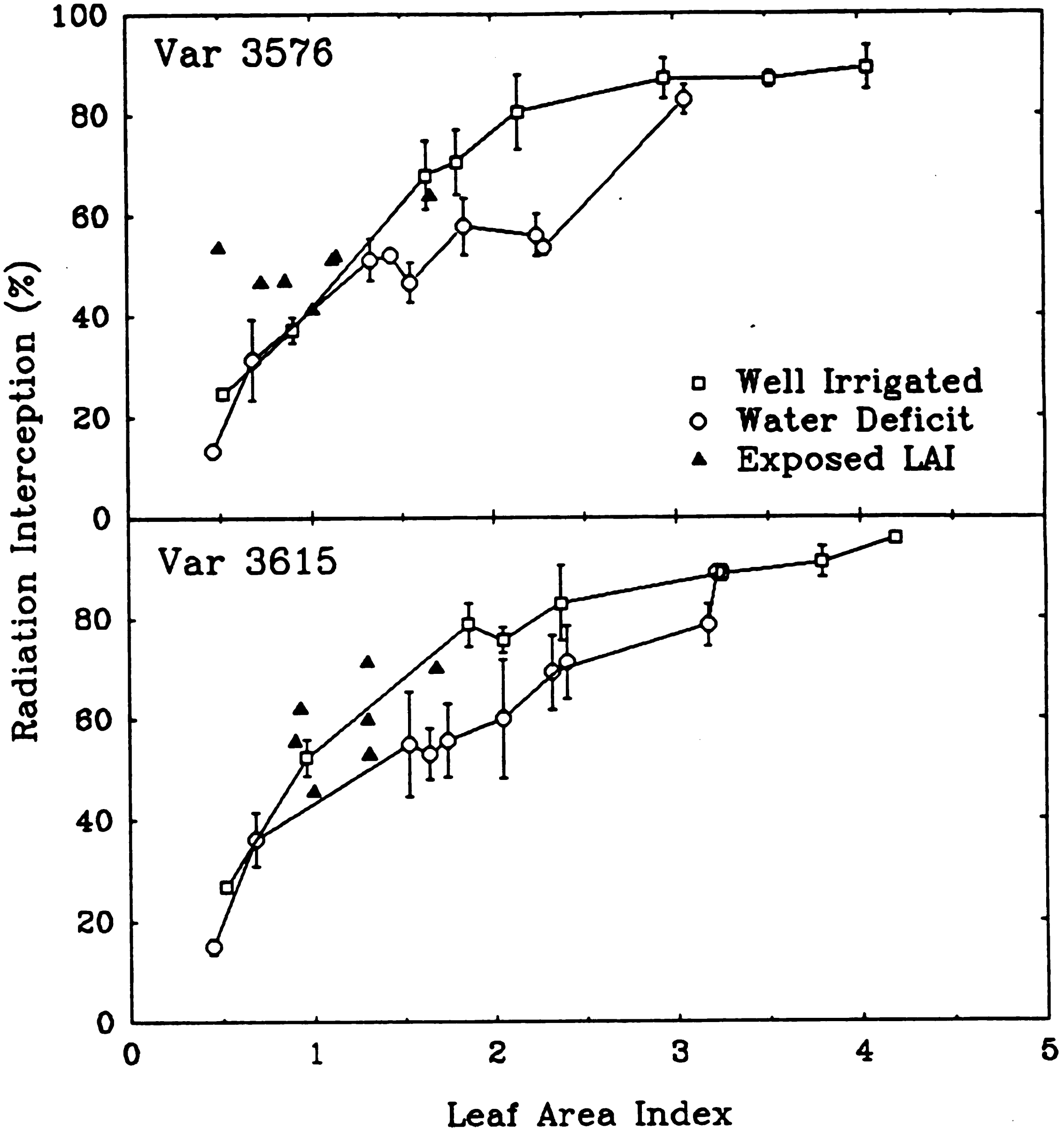

Figure 2.18. Relationship between radiation interception and measured LAI for both treatments and varieties during vegetative growth in 1990.

similar relationship between radiation interception and LAI was reported by Gallo *et al.* (1985); Hatfield *et al.* (1984); and Asrar *et al.* (1984). The radiation interception for both varieties was 87% when the LAI was 3.0.

During the water deficit period a much closer relationship between radiation interception and LAI was obtained when the LAI was transformed into exposed LAI using the daily average leaf rolling measurements (Figure 2.8). The deviation observed was probably caused by changes in leaf orientation during the water deficit period that was not incorporated into the calculation of the exposed LAI.

Conclusions

Leaf area adjustment is a complex phenomenon and distinct mechanisms exist through which varieties may escape or cope with the effects of water deficits. Commonly, at the beginning of a water deficit period, the decrease in cell volume of the expanding part of the leaf results in lower hydrostatic pressure or turgor. The upper part of the leaves lose turgor pressure and the lamina rolls to reduce the exposed leaf area. Subsequently, leaves are orientated more vertically reducing radiation interception. Older leaves are more resistant to leaf rolling and leaf orientation (changes in leaf angle) and they contribute less to the reduction of exposed leaf area. However, if the water deficit becomes more severe, water loss is further reduced by leaf senescence. Maize plants use these mechanisms to cope with water deficit conditions; However, the contribution of each mechanism varies according to the genetic material. This study clearly illustrates the importance of the leaf rolling mechanism in reducing exposed plant leaf area and the intercepted radiation during periods of water deficits. The main advantage of this mechanism is its reversibility, rapidity of leaf recovery when the water deficit is relieved thus, enlarging significantly the photosynthetic surface and the possibility that yield will not be seriously affected.

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CHAPTER 3

Effects of Post-Anthesis Soil Water Deficit on Maize Growth.

I. Leaf Senescence, Leaf Rolling and Radiation Interception.

Abstract

Numerous researchers have investigated the response of crop plants to water deficits and have suggested various mechanisms that may affect crop performance. However, a better understanding of morphological and physiological differences among maize hybrids require additional investigation. The objective of this study was to identify differences in interception of solar radiation, leaf rolling and leaf orientation between two maize varieties with water-limited conditions during post-anthesis growth stage. Pioneer varieties 3576 and 3615 were subjected to two irrigation managements: Well-irrigated and post-anthesis water deficit. The leaf rolling was reduced due to the length and width of the leaf blades. Thus, leaf rolling mainly occurred near the edge of the leaves, limiting further increases in leaf rolling and leaf orientation and, consequently, the reduction in exposed leaf area. A rapid recovery of leaf rolling was observed during early morning hours for the variety 3576. During the water deficit period, a large reduction in LAI was observed for the variety 3615 that, consequently reduced the intercepted radiation.

Introduction

The solar radiation on a canopy from the sun, sky and soil is attenuated as it passes through the vegetation because foliage elements (leaves, stems, flowers, etc.) absorb, reflect, and transmit radiation that they intercept. Clearly, the foliage is exposed to a range of irradiances, varying from near zero to full sunlight depending on the characteristics of the incident radiation and the size, position, orientation, and spectral characteristics of the foliage. Thus, many factors are involved in determining the penetration of radiation into vegetation (Norman, 1980). Leaf area is important in determining the percentage of solar radiation intercepted by a plant and it therefore influences plant growth and final yields (Watson, 1956; Sinclair, 1984). The relation between incident radiation and net photosynthesis by crops depends on the leaf area index and canopy structure (Evans *et al.*, 1975). According to Monteith (1977), crop growth depends on (i) the amount of light intercepted during the growing season and (ii) the efficiency with which intercepted light is used. The amount of intercepted light depends on the seasonal distribution of leaf area which, in turn, depends on temperature and soil water supply, light, photoperiod.

Leaf area maintenance in terminal water deficit conditions has no effect on the total amount of water transpired. However, the water deficit may decrease harvest index if the soil water supply is exhausted before maturity. In intermittent water deficit conditions, leaf area maintenance would improve yield stability due to better radiation interception when water is available (Ludlow and Muchow, 1990). An important consequence of the maintenance of higher leaf areas per plant and higher leaf conductances rate with osmoregulation during water deficit is that plant transpiration also continues at a higher level as the water potential decreases (Wright *et al.*, 1983). The additional dry matter produced with osmoregulation depends upon the additional water that may be extracted from the soil, which is influenced by two factors: (i) the moisture characteristic of the soil, more water would be extracted from a heavier textured soil than a sandy soil with an increase in osmotic adjustments; and (ii) the root length density (Passioura, 1982).

Enhanced leaf senescence is a common effect of drought on crops approaching maturity and may also occur during early stages of growth if the drought is severe (Hall *et al.*, 1979). Senescence is of economic interest since it affects crop production by reducing the active photosynthetic area (Wolfe *et al.*, 1988) and it can provide an adaptative advantage if senescence is accompanied by substantial reduction in transpiration (Hall *et al.*, 1979). Wheat yields were inversely related to the area of leaf senescence after anthesis and senescence was accelerated by plant water deficit (Fischer and Kohn, 1966; Evans *et al.*, 1975).

Physiological aspects of leaf movements and the morphological mechanisms for achieving them have been studied extensively. However, there has been little discussion of the adaptative value of either of these types of leaf movement and the environmental regimes in which natural selection should favor them (Ehleringer and Forseth, 1980). According to Hall *et al.* (1979), leaves that are more parallel to the sun's rays are cooler due to reduced interception of solar radiation. Leaf orientation may be more or less fixed, or may involve complex leaf movements. Leaf movements that result in reduced radiation interception as plant water deficits increase may improve adaptation to semi-arid environments. Leaf movements of Siratro plants growing in water deficit conditions reduce or prevent damage to the photosynthetic system caused by (i) excess of light (photoihibition) intensified by high leaf temperature; and (ii) direct heat damage (Ludlow and Bjorkman, 1984).

Water is extracted from the soil by crops and is evaporated from leaves in proportion to the atmospheric demand. The demand is controlled not only meteorologically, but also by the crop, insofar as the crop canopy affects the net radiation absorbed, crop surface temperature, and surface aerodynamic properties (Robertson, 1991). Many studies have shown that within a crop species, the strongest determinant of the total amount of extraction is the depth of extraction rather than extraction per unit depth, and that is closely linked to crop productivity under water-limiting environments (Hurd, 1974; Rowse and Barnes, 1979; Angus *et al.*, 1983; Squire *et al.*, 1987). According to Ritchie (1981), plant water deficit can be induced (i) by a deficiency of water supply in the root zone, and (ii) by an excessive atmospheric water demand from leaves. The hydraulic resistance to water flow in the plant may limit water uptake by the crop, and this could affect the amount extracted. However, Passioura (1983) also questioned the value of deep roots, because the amount of water transpired to produce carbohydrate necessary for the extra root growth may diminish the extra water gained by deep roots.

The rolling and unrolling movement of mature leaves is presumed to be due to volume changes (loss or gain of water by changes in turgor) in the bulliform cells (Esau, 1977; Duncan, 1980; Bull and Glasziou, 1980; Ellis, 1976; Steponkus *et al.*, 1980). The bulliform cells often become filled with large masses of silica and their outer walls often become thick and cutinized. Consequently, the older leaves are more resistant to rolling. Leaf rolling reduces the effective leaf area (Begg, 1980; Duncan, 1980; Jordan, 1983), the energy load on the plant (Begg, 1980; O'Toole *et al.*, 1979; Jordan, 1983), leaf temperature (O'Toole *et al.*, 1979, Ludlow and Muchow, 1990) and water loss (Oppenheimer, 1960; Austin and Jones, 1975; Turner, 1979). The objective of this study was to identify differences in interception of solar radiation, leaf rolling and leaf orientation between two maize varieties with water-limited conditions during post-anthesis growth stage.

Methodology

This experiment was conducted in 1990 and 1991 at the Kellogg Biological Station, near Kalamazoo, Michigan, under a rain shelter, described by Martin *et al.*, (1988), to prevent rainfall on the experiment.

Spinks loamy sand (mesic Psammentic Hapludalfs) was the soil at the site. The maize varieties, Pioneer 3615 and Pioneer 3576, were planted north-to-south at a high density on May 18 (day of year (DOY) 138) in 1990 and on May 27 (DOY 147) in 1991. Emergence occurred on May 28 (DOY 148) in 1990 and on May 31 (DOY 151) in 1991. Plants were thinned in the seedling stage to a plant density of 7.2 plants/m^2. Weeds were controlled manually during both years. Plot size was 4.6 m x 6.2 m. Maize was planted in six rows, 0.71 m wide, giving two border rows and four main rows in each plot. The experimental layout was a split-plot design, with irrigation treatment as main plot and maize varieties as subplots.

Irrigation water was applied using an overhead Toro FS-LG series sprinkler system, mounted upside down on the trusses of the rain shelter operating with a constant pressure of 103.5 Kg Pa^{-1}, at a rate of approximately 25 mm hr^{-1} (NeSmith *et al.*, 1990). Two irrigation treatments were established: (i) well-irrigated (irrigation was applied to maintain the fraction of plant available water above 0.70); and (ii) anthesis soil water deficit. The water deficit period (period between subsequent irrigations) occurred from DOY 205 to DOY 229 in 1990 and, from DOY 200 to DOY 229 in 1991. The irrigation amounts applied on each treatment in 1990 and 1991 are presented in Figure 3.1.

Before emergence, fertilizer was applied at rates of 60 Kg N ha^{-1} (45-0-0), 200 Kg P ha^{-1} (0-46-0), and 60 Kg K ha^{-1} (0-0-60). Nitrogen was applied at a rate of 100 Kg.ha^{-1} 19 days after emergence (DOY 166) and 17 days after emergence (DOY 168), in 1990 and 1991.

Soon after emergence, four plants per plot were randomly selected and marked for nondestructive measurements throughout the season. Leaf area was

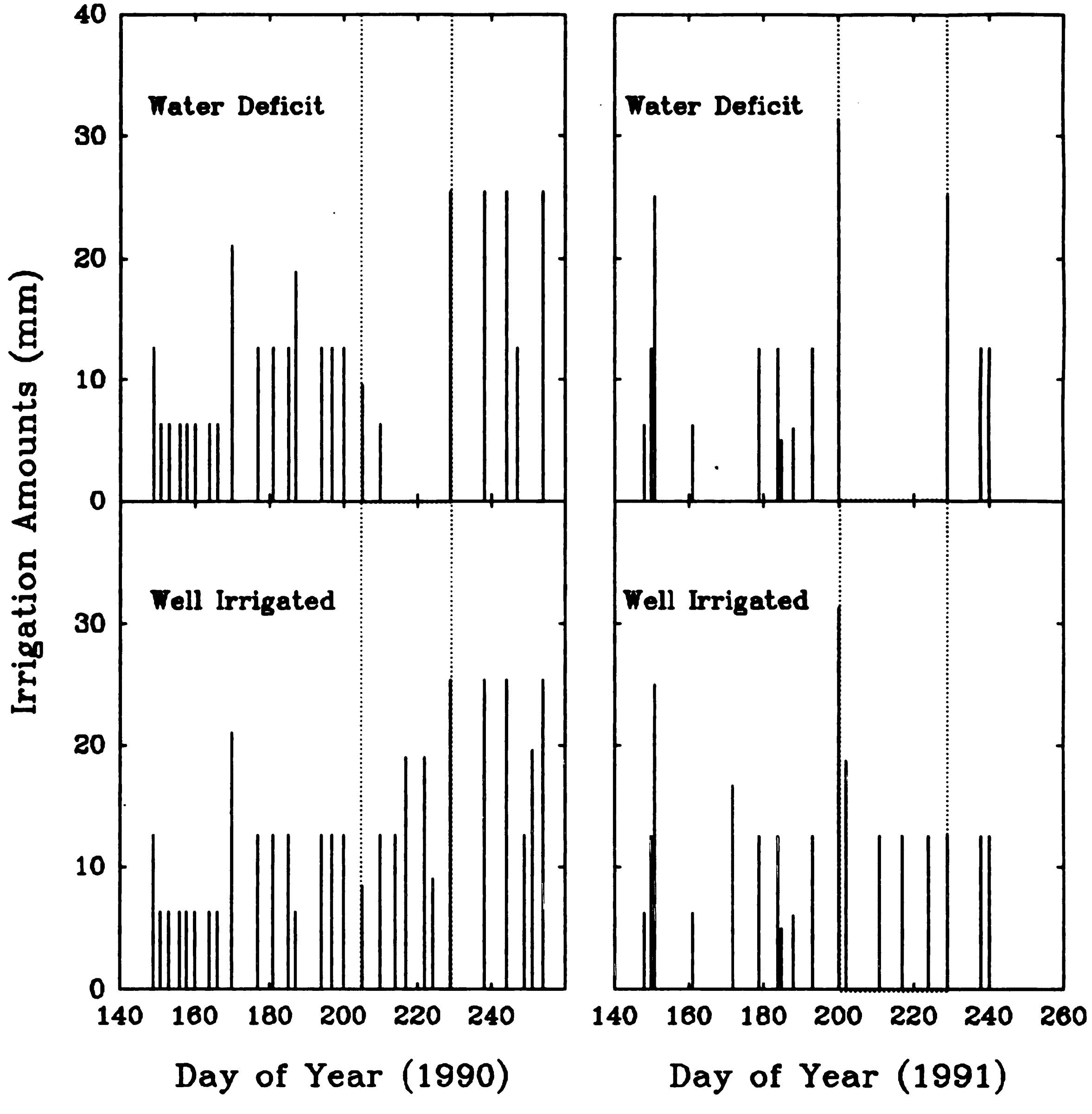

Figure 3.1 Irrigation amounts (mm) applied on each treatment and soil type. The area limited by vertical dotted lines represents the period of post-anthesis soil water deficit.

measured three times a week once the leaves emerged from the whorl until the leaf ligule appeared. The area of each leaf was determined from measurements of leaf length and maximum leaf width multiplied by 0.75 (Stickler *et al.*, 1961).

Leaf rolling and leaf position was measured several times daily and weekly during the water deficit period in four selected plants per plot. In each plant, leaf 13, 15 and 17 were selected to represent the plant leaf rolling and two positions were marked on each leaf (quarter-way and half-way from the tip). A family of individual leaf area curves measured on three different occasions for both varieties during the water deficit period in 1991 are presented in Figure 3.2. The leaf rolling was calculated from the fraction of the rolled leaf width (measured by a caliper) and fully open width. Leaf position was obtained by measuring the vertical and horizontal distances of four marked positions on each leaf (ligule, leaf tip, quarter-way and half-way from the tip). Plant stem and soil surface were the reference points for horizontal and vertical distances.

Photosynthetically active radiation (PAR) interception was measured several times daily in four marked sites in each plot, under clear sky conditions. At ground level, a minimum of three observations were made to compute an individual measurement in each side. A line quantum sensor (Model LI-191SB, Li-cor, Lincoln, NE) was leveled, placed perpendicular to the row direction and positioned so that no shadows from the handle influenced measurement. Canopy incident radiation was measured by placing the line quantum sensor above the crop.

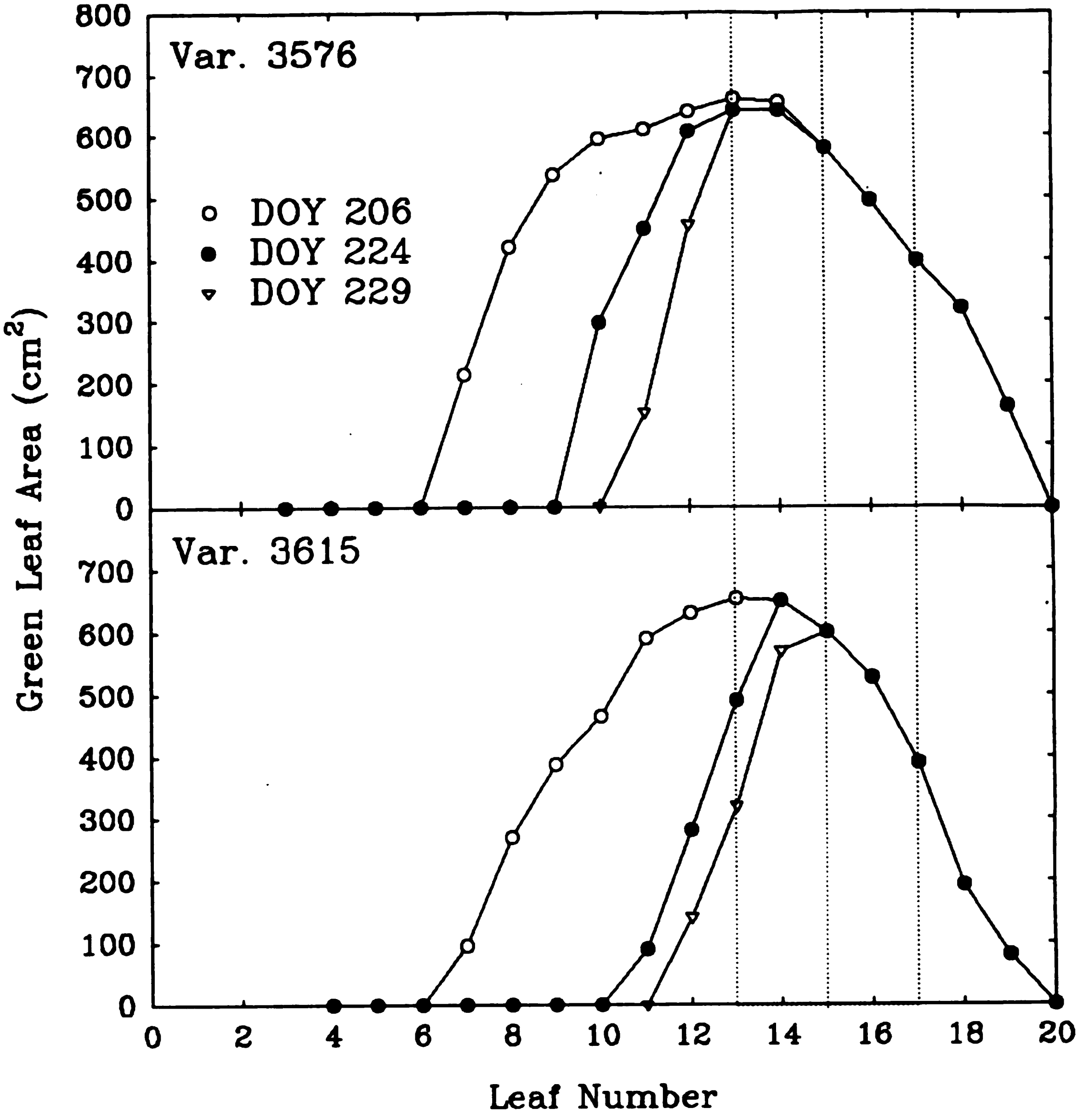

Figure 3.2. Individual leaf area curves on three different occasions for both varieties in 1991. The three vertical dotted lines represent the leaves selected for leaf rolling and leaf orientation measurements.

A minimum data set recorder (Model LI-1200, Li-cor, Lincoln, NE) located outside of the rain shelter was used to record the solar radiation, minimum and maximum air temperature, and rainfall. Daily values of maximum and minimum temperature, solar radiation (MJ/m^2) and vapor pressure deficit of the air (Kpa) for 1990 and 1991 growing seasons are shown in Figures 3.3 and 3.4.

Soil water content was measured by the neutron scattering technique (CPN, Model 503DR). Two access tubes (aluminum, 50 mm i.d.) were seated in the center row of each plot. Readings were made twice a week at 25 cm increments to a depth of 1.5 m. Field measurements of soil water content and neutron counts were used to calibrate neutron counts into volumetric water content. Regression equations, by depth, were determined using only two points: dry point (soil was allowed to dry out); and wet point (soil water content near drained upper limit (DUL)). Soil water content in the 0-12.5 cm and 12.5-25 cm layers was determined by the time domain reflectometry (TDR) technique. Steel rods were installed at each depth leaving 2 cm above the soil surface. Volumetric water content was estimated using the equations described by Topp *et al.*, (1982). Soil water availability in *mm* of equivalent depth was calculated for the top 1.5 m of profile as the difference between volumetric water content of the soil and water content at the lower limit of plant-extractable soil water in the rooting depth.

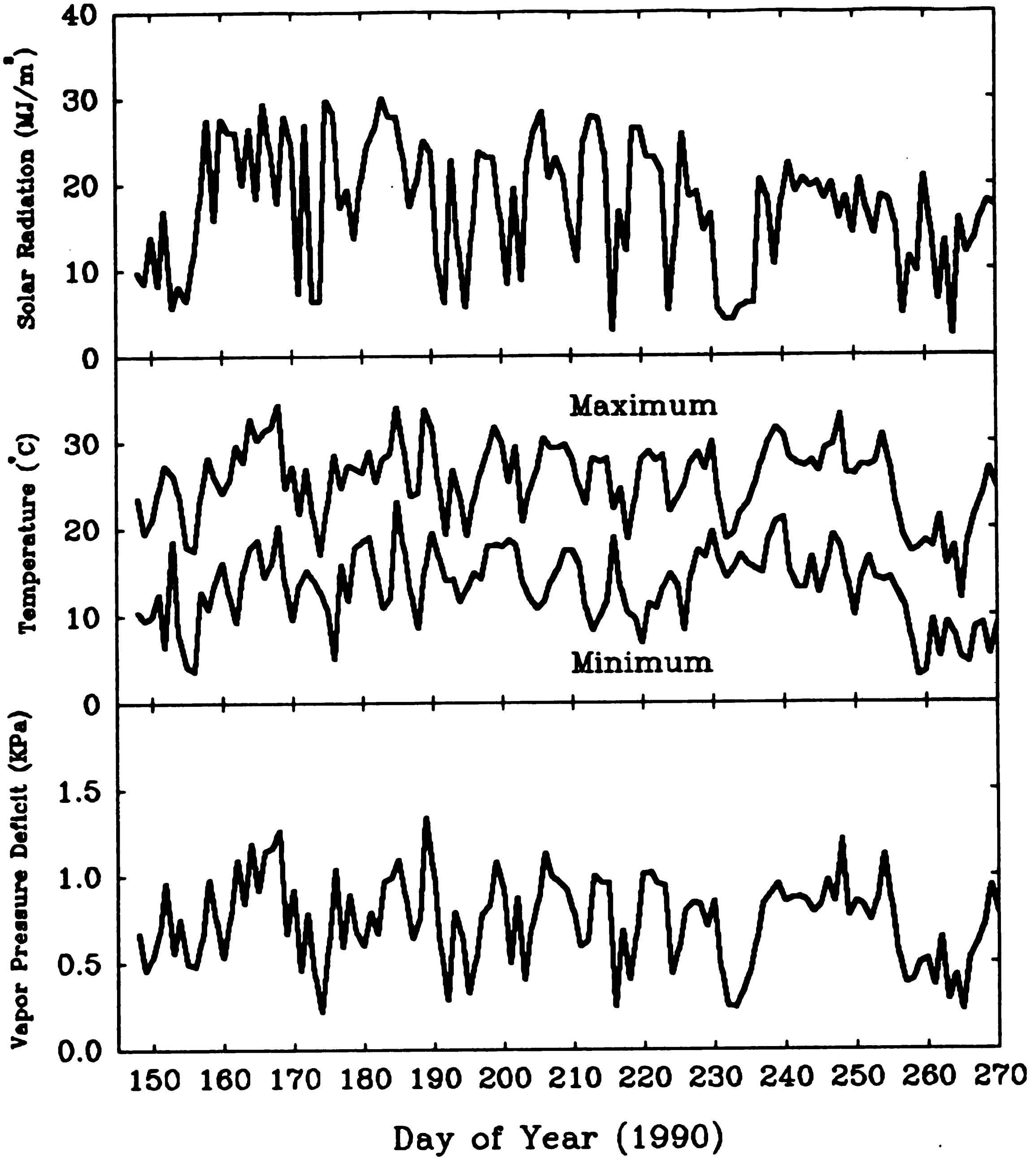

Figure 3.3. Daily incident solar radiation, daily maximum and minimum temperatures and daily vapor pressure deficit during 1990.

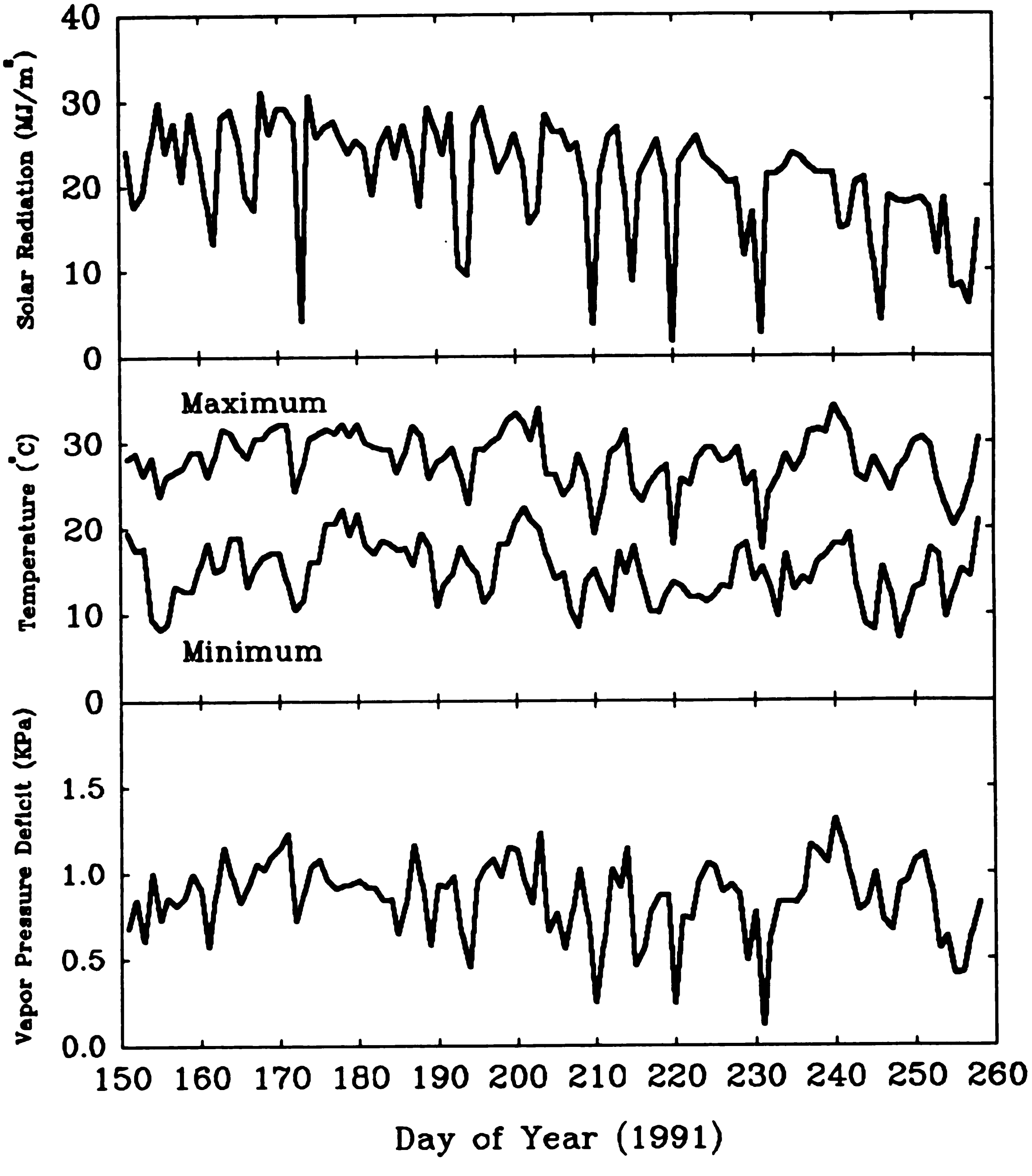

Figure 3.4. Daily incident solar radiation, daily maximum and minimum temperatures and daily vapor pressure deficit during 1991.

Results and Discussions

Weather conditions observed during the experiment in 1990 and 1991 are presented in Figures 3.1 and 3.2. During the water deficit period, from DOY 205 to 229 in 1990 and from DOY 200 to 229 in 1991, similar climatic conditions were observed. The averages of weather conditions during the water deficit periods and the entire growing seasons for both years are presented in Table 3.1.

Table 3.1. Average of daily meteorological variables during the water deficit period and the entire growing season for 1990 and 1991.

	Deficit Period		Growing Season	
Meteorological Variables	**1990**	**1991**	**1990**	**1991**
Solar Radiation (MJ/m^2)	19.93	20.85	17.25	21.05
Minimum Temperature (°C)	12.93	14.44	13.27	15.02
Maximum Temperature (°C)	26.49	27.06	25.40	28.03
Vapor Pressure Deficit (Kpa)	0.79	0.80	0.74	0.86

Water Content and Extraction

The 1991 growing season soil water content on the water deficit and well-irrigated treatments are shown in Figures 3.5 and 3.6 for maize varieties 3576 and

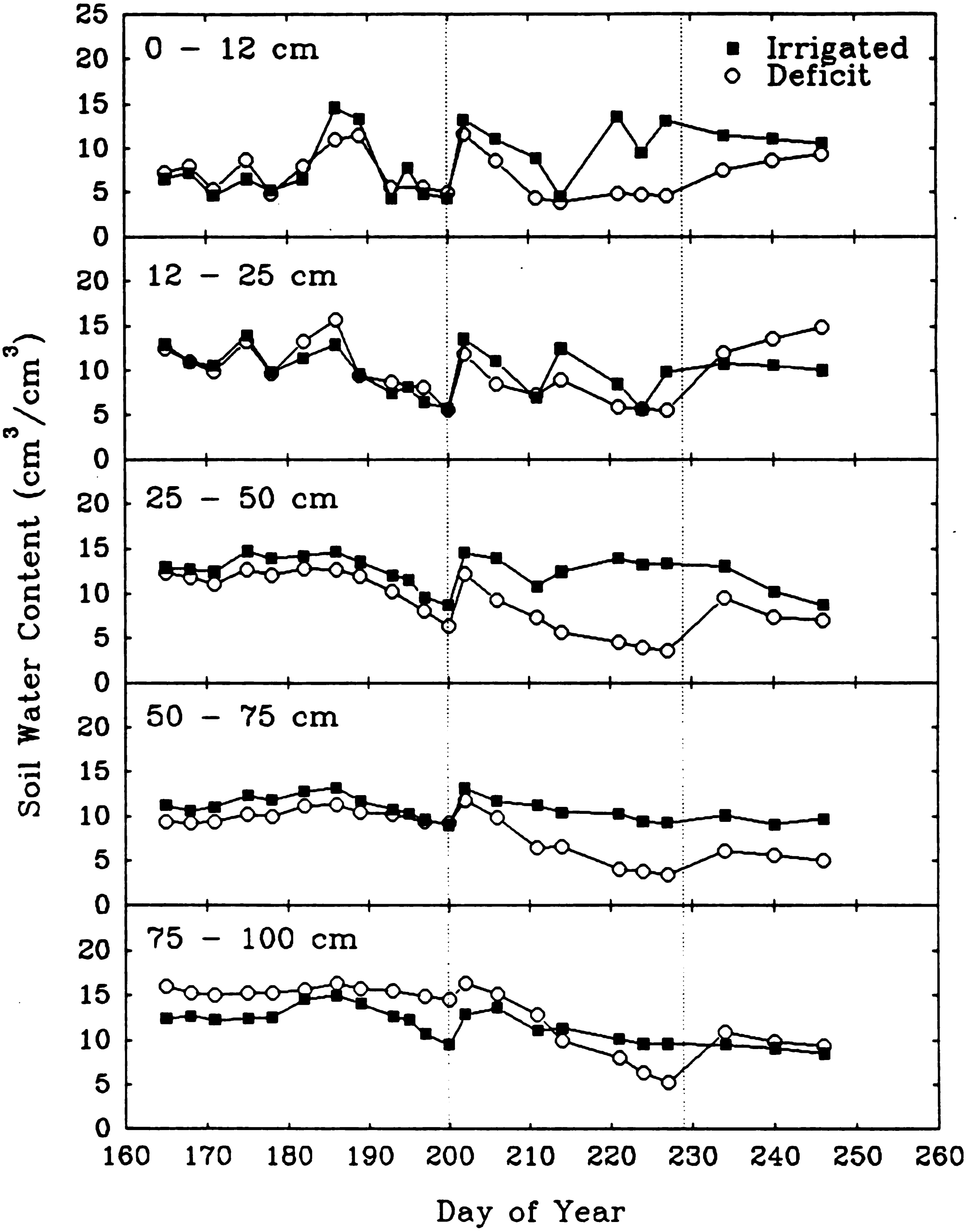

Figure 3.5. Soil water content with depth and time for the variety 3576 in 1991. The area limited by vertical dotted lines represents the period of soil water deficit.

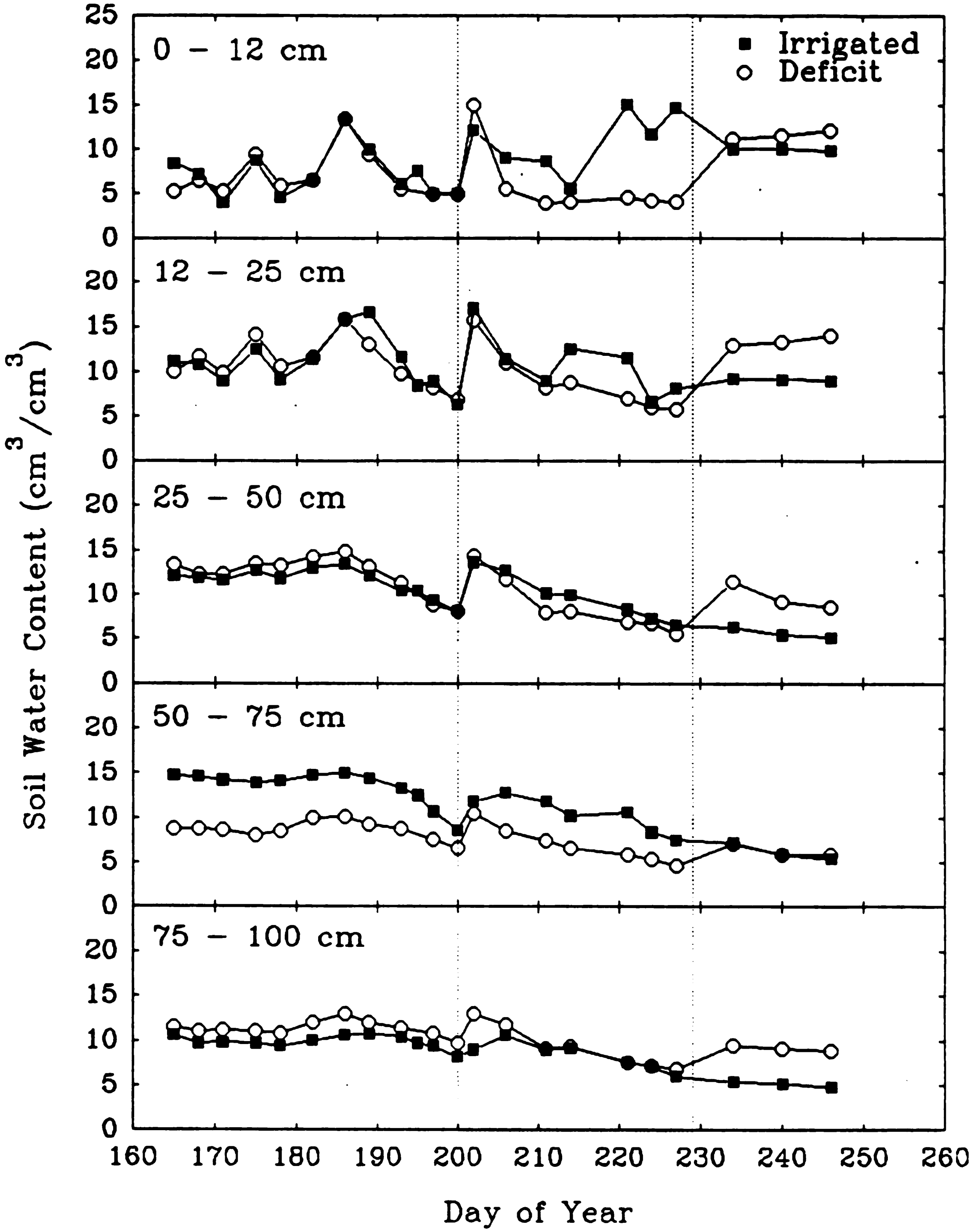

Figure 3.6. Soil water content with depth and time for the variety 3615 in 1991. The area limited by vertical dotted lines represents the period of soil water deficit.

3615, for the upper 75 cm of the soil profile. During the water deficit period a similar pattern of profile drying was observed for the two varieties under water deficit conditions. However, a different pattern was observed for the well-irrigated treatment, especially for the variety 3615 (Figure 3.6). The low values of water content were caused by non-uniform irrigation applications. Although water was applied, it was sprayed near the plot borders adding little or no water on the part of the plot where the soil water measurements were taken. The observed decline in soil water content for both treatments between DOY 193 and DOY 200 was caused by a lack of irrigation due to mechanical problems with the irrigation system. Both varieties showed a rapid decline in soil water content in the top 25 cm of soil profile at the beginning of the water deficit period and, a steady decline in soil water content was observed during the deficit period for the lower layers of soil profile.

The soil water depletion rate (mm/day) at different soil depths during the 1991 water deficit period is shown for both varieties in Figure 3.7. Soon after irrigation was stopped (DOY 200), a rapid increase in the water extraction rate for both varieties, in the upper soil layers (0-25 cm and 25-50 cm) was observed. A slow increase in the extraction rates was observed for the lower depths of the soil profile (50-75 cm and 75-100 cm). As the water deficit developed, little water extraction was observed, for both varieties, near the soil surface (0-25 cm depth) and the water depletion rates for the 25-50 cm and 50-75 cm depths steadily decreased until about the end of the water deficit period. Although during the

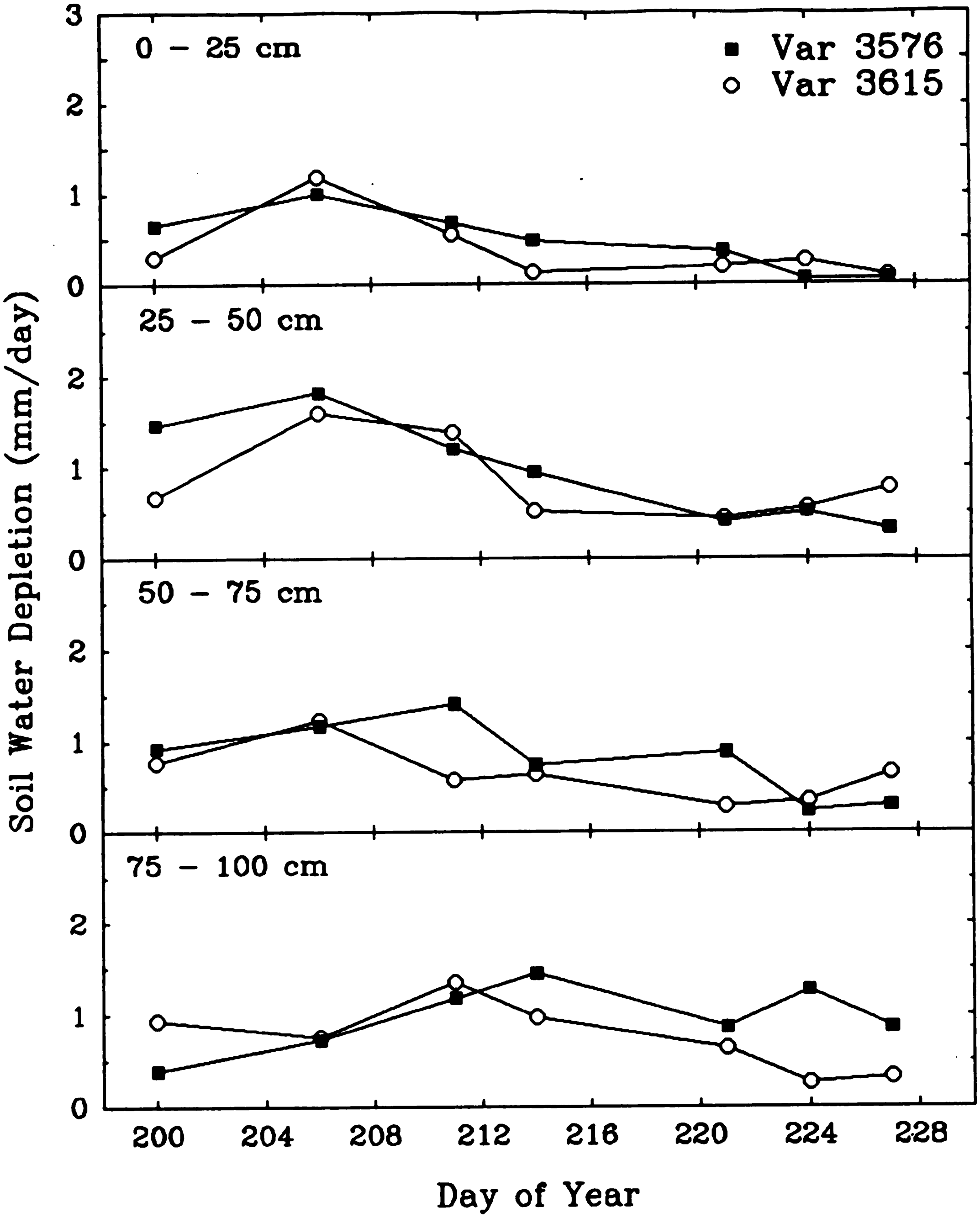

Figure 3.7. Soil water depletion rates with time for both varieties for the top 100 cm of the soil profile during the soil water deficit in 1991.

water deficit period a similar trend in terms of soil water depletion rates was observed for both varieties, the variety 3576 presented higher rates of water extraction than the variety 3615. Near the end of the water deficit period, the maize roots were extracting water mainly from the lower layer of the soil profile. The increased effectiveness of deeper roots of maize as the upper soil layers dried out was demonstrated by Taylor and Klepper (1973).

Soil water availability (*mm*) in the top 150 cm of the soil profile for both treatments and varieties is presented in Figure 3.8. A similar pattern of soil water availability was observed for both varieties in each treatment and, during the water deficit period, the soil water availability declined steadily over time. The observed decline in soil water availability for both treatments between DOY 193 and DOY 200 was caused by a lack of irrigation due to mechanical problems with the irrigation system.

A marked decrease in plant available water from 58.3 mm and 58.8 mm (at DOY 202) to 22.9 mm and 29.7 mm (at DOY 227), was observed during the water deficit period, for the varieties 3576 and 3615. The overall water extraction rate, during the specified period, was 2.33 mm/day and 2.35 mm/day for the variety 3576 and 3615. However, during the second half of the water deficit period, between DOY 211 and DOY 227, the water extraction rate was 1.62 mm/day and 1.17 mm/day for the variety 3576 and 3616. Since soil evaporation depends mainly on the radiation reaching the soil surface when it is wet (Ludlow and Muchow, 1990) and, assuming that during the water deficit period for both varieties, the soil

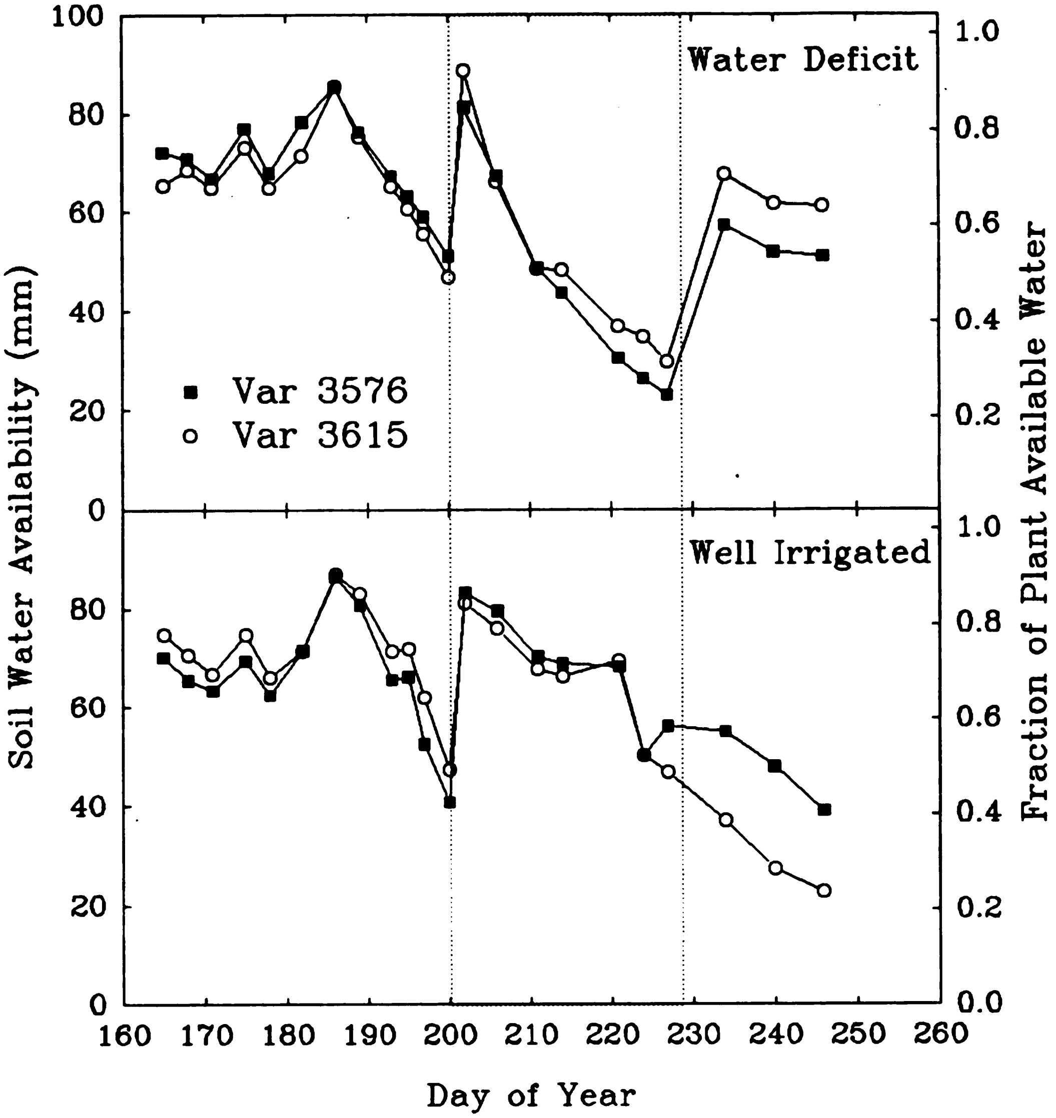

Figure 3.8. Total soil water availability with time for both varieties and treatments for the top 150 cm of the soil profile in 1991. The area limited by vertical dotted lines represents the period of soil water deficit.

surface was dry (low hydraulic conductivity) and the crop canopy was fully covering the ground, the water extraction from the soil profile can be assumed to be approximately equal to the plant transpiration.

These results indicate that during the water deficit period, the amount of soil water extracted was similar for both varieties. The variety 3615 reduced its green LAI earlier than the variety 3576. However, this would only be beneficial in a terminal water deficit situation where the limited supply of water could endure survival and contribute to better crop performance. The variety 3576 has a better performance for intermittent soil water deficit conditions and may contribute significantly to economic yield. A companion paper includes yield results of the current experiment.

At the end of the water deficit period the variety 3576 had less plant available water left in the soil profile (22.9 mm) than the variety 3615 (29.7 mm). Water extraction was occurring mainly in the lower layer of the soil profile, especially for the variety 3576 (Figure 3.7). Although root measurements were not taken in this study, these results imply that variety 3576 had a more dense root system in deeper layers than the variety 3615, thus increasing the amount of water transpired and avoiding a more severe reduction in LAI. According to Ludlow and Muchow (1990), differences in rooting patterns change the amount and timing of water availability to the crop. In a field experiment conducted by Wright and Smith (1983) to determine the morphological and physiological mechanisms responsible for yield differences under water deficit conditions in two sorghum genotypes, they found that the variety that had greater root length densities, especially below 80 cm, extracted more water from deeper layers, maintained higher water use rates during the reproductive period, and had greater yields. Chakravarty and Karmakar (1980), working with several varieties, found that some varieties continued to show increases in root system up to crop maturity, which is contrary to the common idea that cereals suspend root growth after flowering.

Plant Leaf Area

Figures 3.9 and 3.10 present the green leaf area index (LAI) for both treatments and varieties in 1990 and 1991. In both years, during the crop vegetative growth phase, similar LAI were observed for both varieties and treatments. However, a slight difference in LAI was observed in 1991 for the variety 3576. During the water deficit period, the difference in LAI between treatments was larger in 1991 due to the longer imposed water deficit period.

In 1991, a sharp decrease in LAI started (DOY 214) when the total soil water availability fell below 43.7 mm and 48.3 mm (Figure 3.8), for the varieties 3576 and 3615. Although the water extraction rates (Figure 3.7) and plant water availability (Figure 3.8) were similar for both varieties during the water deficit period, the variety 3615 had a larger reduction in LAI than variety 3576. The overall reduction in LAI, at the end of the water deficit period, was 33.4% (from 4.40 to 2.93) and 53.7% (from 3.91 to 1.86) for the varieties 3576 and 3615. A companion paper includes results of leaf senescence of the current experiment. The reduction in

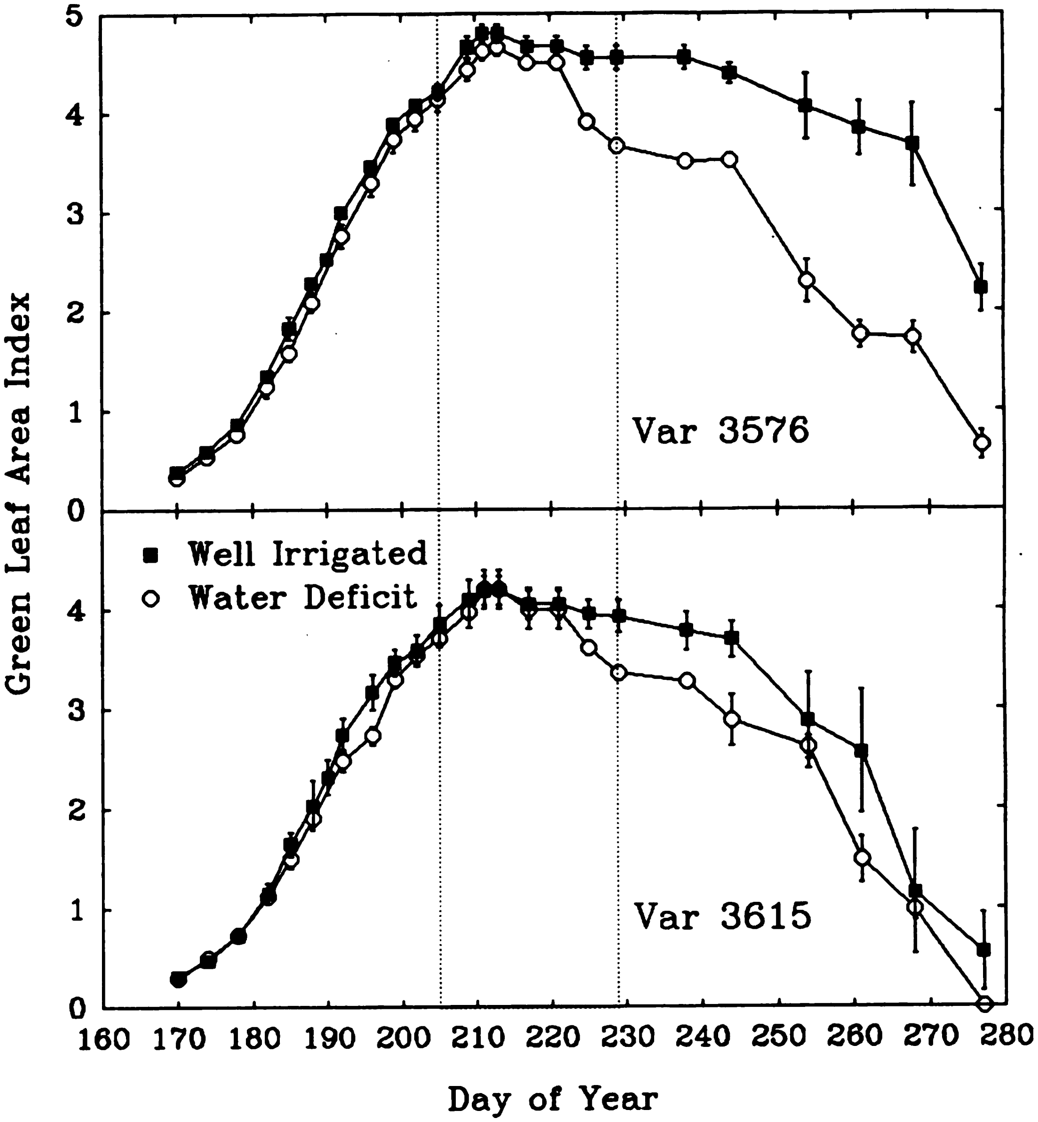

Figure 3.9. Green leaf area index for both treatments and varieties during 1990. The region between the vertical dotted lines indicates the water deficit period.

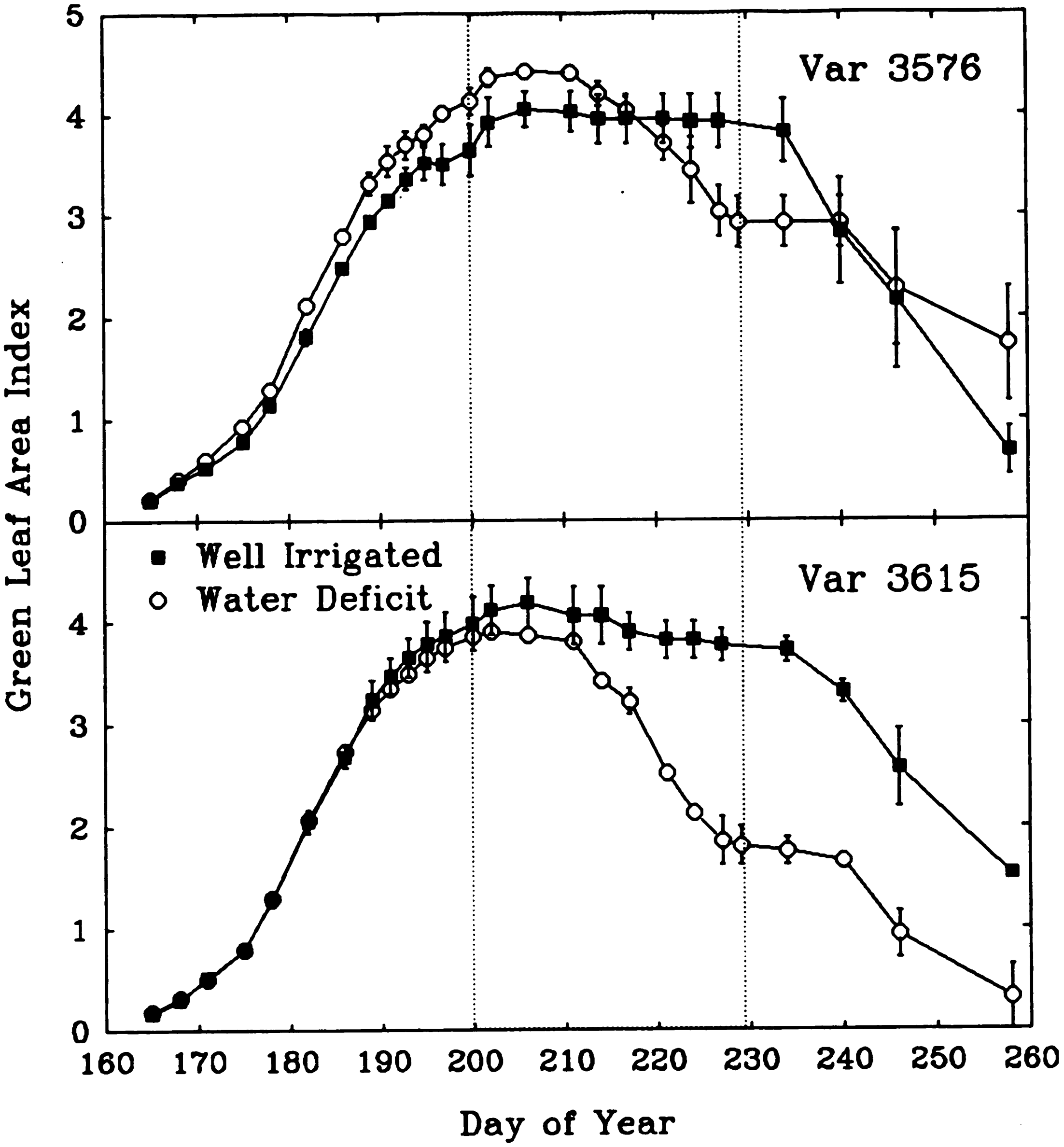

Figure 3.10. Green leaf area index for both treatments and varieties during 1991. The region between vertical dotted lines indicates the water deficit period.

plant LAI by leaf senescence, according to Ludlow and Muchow (1990), is a common response to water deficit.

The sharp reduction in LAI observed for the variety 3615 would be beneficial in terminal water deficit situations. Ludlow and Muchow (1990) indicated that, in terminal water deficits, the maintenance of plant leaf area has little effect on the total amount of water transpired and a larger leaf area only exhausts soil water more rapidly. Leaf area maintenance, such as observed for the variety 3576, probably increased the amount of water transpired during the water deficit period. However, upon the relief of the water deficit it resulted in greater radiation interception and increased the potential to photosynthesis and to produce a higher yield (a companion paper includes results of yields of the current experiment). According to Karami *et al.* (1980) and Wright *et al.* (1983), the maintenance of higher LAI and net photosynthesis per unit of leaf area resulted in higher plant biomass which was associated with osmoregulation during water deficit. The greater leaf area observed for sorghum and wheat resulted from a reduced rate of leaf senescence, especially in the later stages of crop development when water deficit was more severe due to the increased crop water use (Wright *et al.,* 1983).

Radiation Interception

The daily variation of photosynthetically active radiation interception for the variety 3576 and 3615, on three selected days during the 1991 growing season, are presented in Figures 3.11 and 3.12. The effect of the water deficit period on radiation interception was observed, for both varieties, 18 days after the water deficit was imposed (DOY 218). The high values of radiation interception observed for both varieties and treatments, at the beginning of the water deficit period, were caused by the high LAI (Figure 3.10) which provided complete canopy cover. According to Jordan (1983), after effective canopy closure, photosynthesis is no longer dependent upon further increases in LAI, but is most closely correlated with total PAR. As the water deficit became more severe (DOY 223) a marked reduction in radiation interception was observed near solar noon hours for both varieties under water deficit treatment. Although the LAI of variety 3615 was rapidly reduced during the water deficit period (Figure 3.10), a similar reduction of radiation interception was observed near solar noon hours for both varieties. Little change in radiation interception was observed for both varieties grown under well-irrigated conditions during the duration of the water deficit period.

The daily variation of photosynthetically active radiation interception at the end of the water deficit period and eight days after the water deficit was relieved in 1990, is presented in Figures 3.13 and 3.14 for the variety 3576 and 3615. Although the LAI of the variety 3576 (3.66) was slightly higher than the variety 3615 (3.35) at the end of the water deficit period (DOY 228), lower intercepted radiation was observed (61% versus 73%) near solar noon hours (Figures 3.13 and 3.14). On DOY 237, eight days after the water deficit was relieved, both varieties presented lower radiation interception compared to the well-irrigated treatment. This was caused by the permanent reduction in LAI during the water deficit period

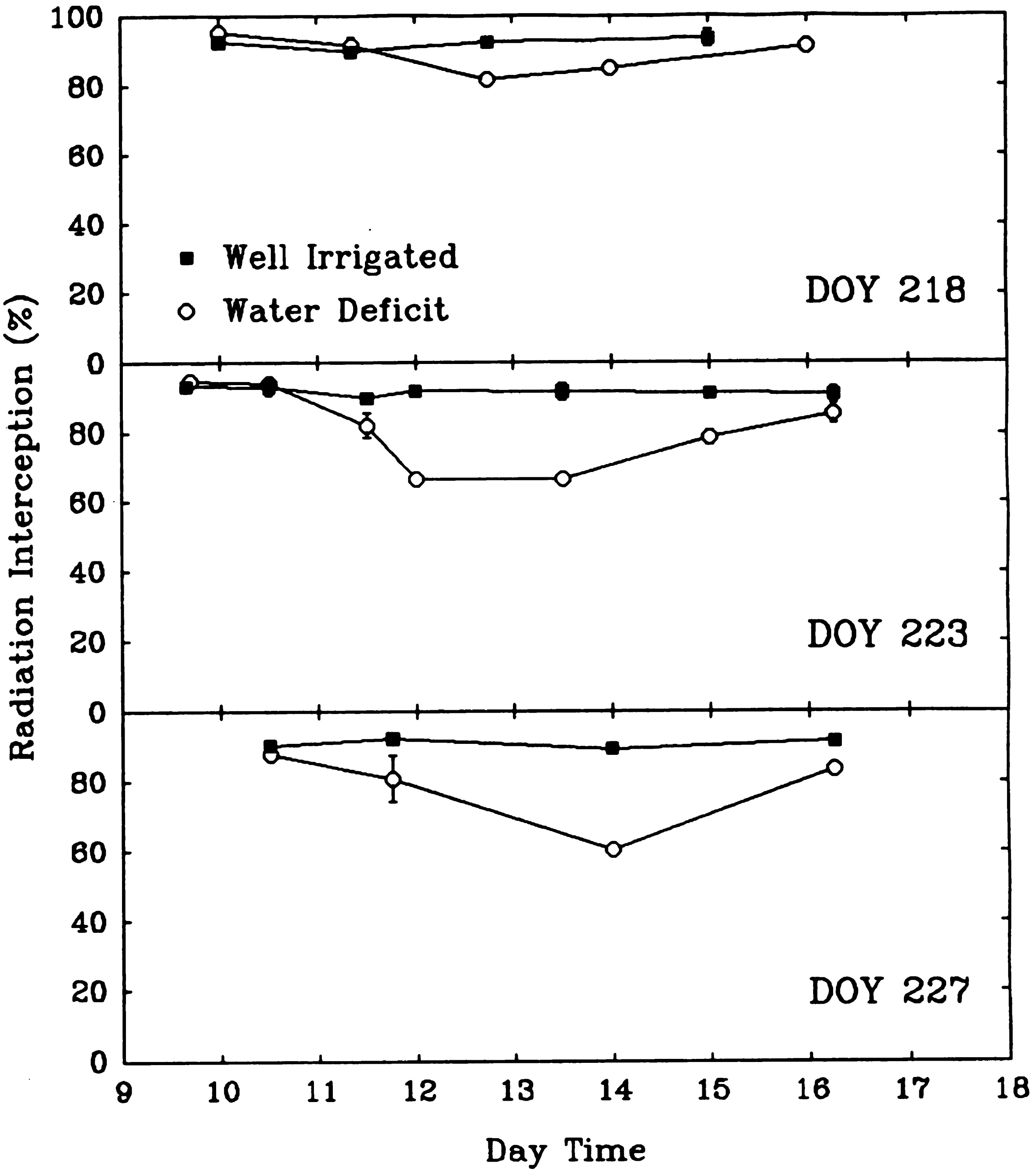

Figure 3.11. Daily variation of photosynthetically active radiation interception of the variety 3576 on three selected days (DOY 218, 223 and 227) in 1991.

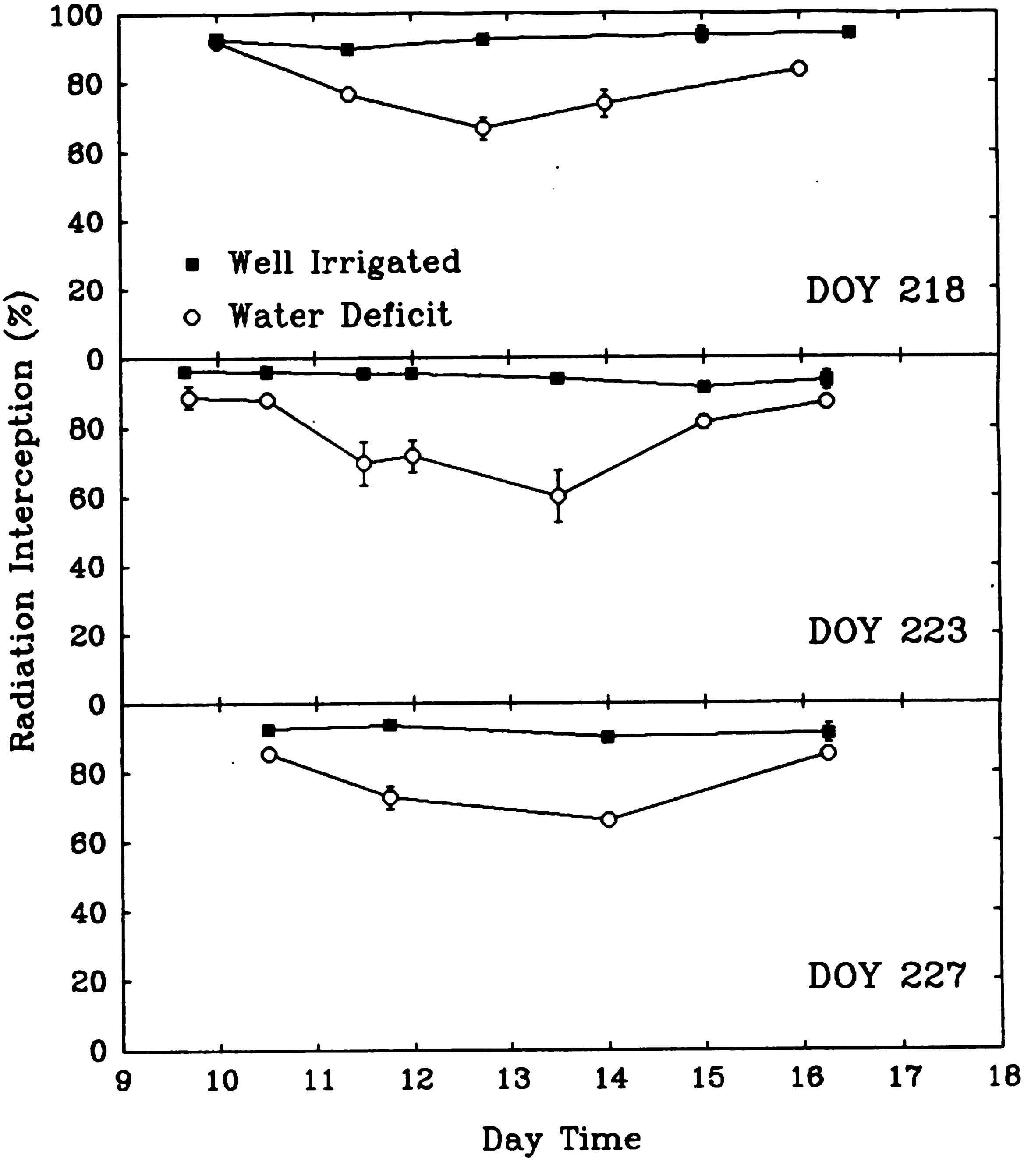

Figure 3.12. Daily variation of photosynthetically active radiation interception of the variety 3615 on three selected days (DOY 218, 223 and 227) in 1991.

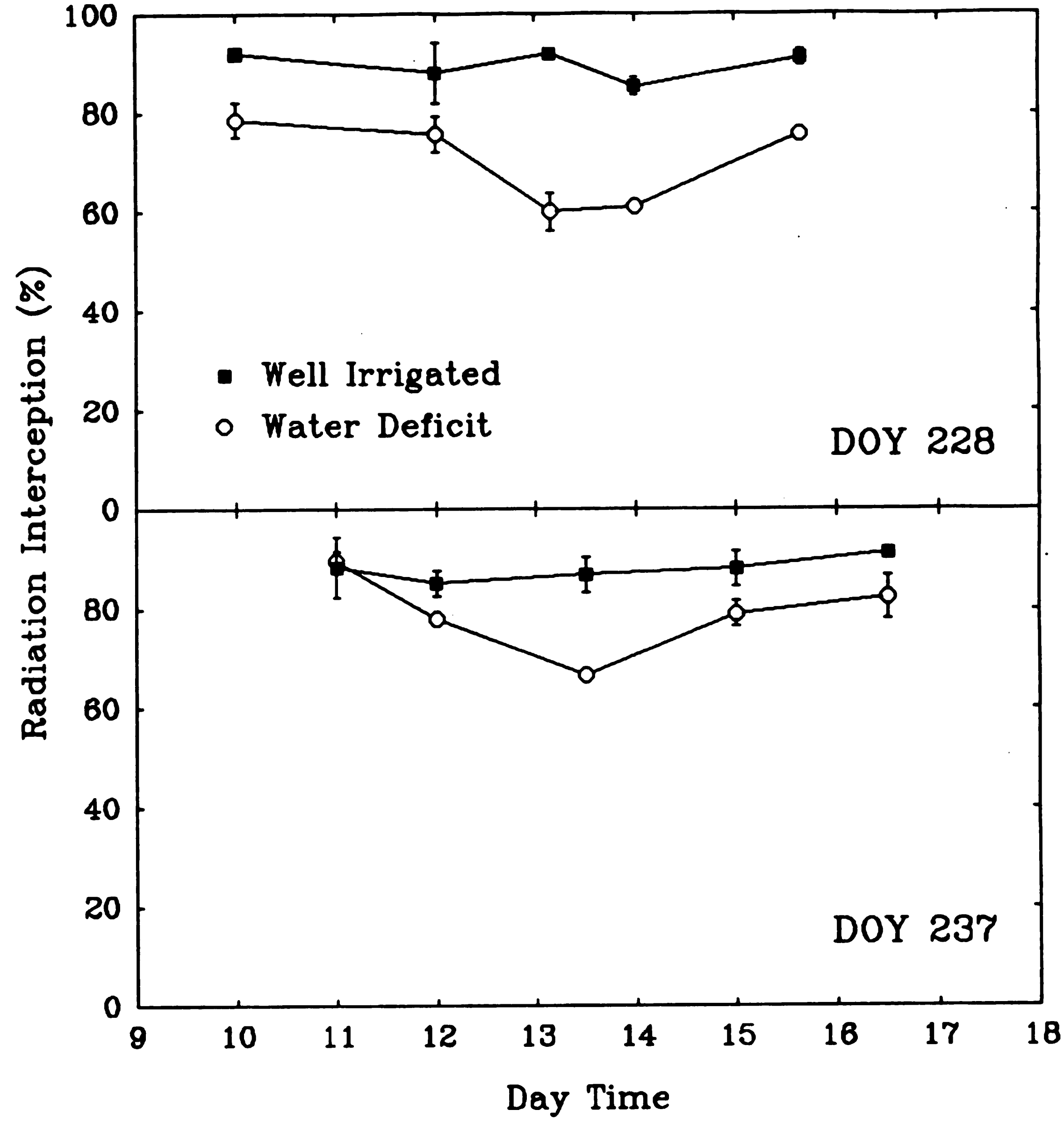

Figure 3.13. Daily variation of photosynthetically active radiation interception of the variety 3576 at the end of the water deficit period (DOY 228) and eight days after the water deficit was relieved (DOY 237), during 1990.

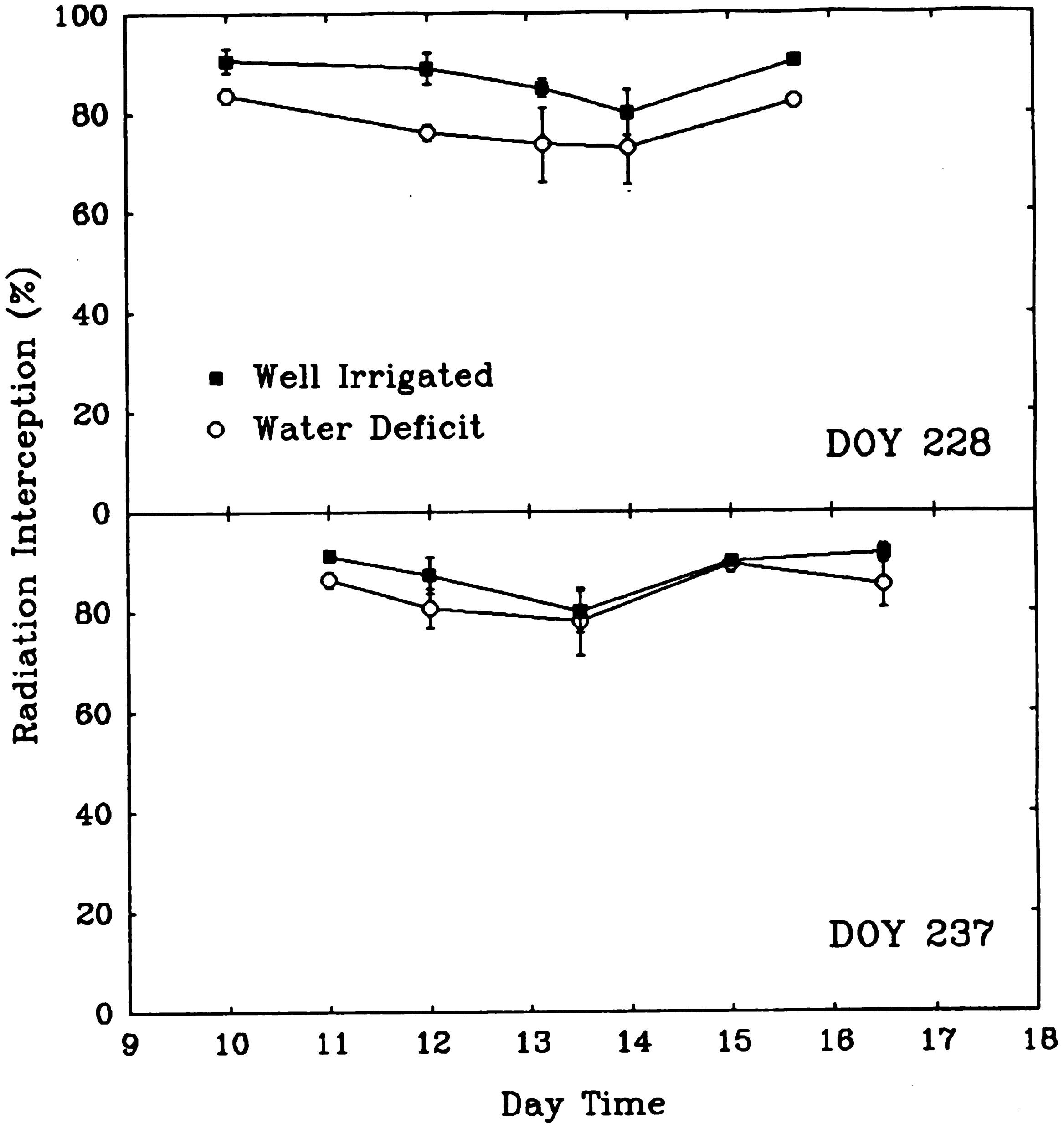

Figure 3.14. Daily variation of photosynthetically active radiation interception of the variety 3615 at the end of the water deficit period (DOY 228) and eight days after the water deficit was relieved (DOY 237), during 1990.

due to leaf senescence. The radiation interception curves tended, in both years, to rise (intercepting more radiation) early in the morning and late in the afternoon because the incident solar radiation had to pass through a more dense crop canopy than during the mid-day hours.

The seasonal variation of radiation interception measured near the solar noon hours in 1991 is presented in Figure 3.15. During the water deficit period, as the water deficit became more severe, radiation interception steadily decreased for both varieties. At the end of the water deficit period, the variety 3576 and 3615, under water deficit conditions, intercepted 67.6% and 66.6% of the radiation intercepted by the well-irrigated treatments, although the LAI of the variety 3576 was 61.9% higher than the variety 3615. The lower radiation intercepted by the variety 3576 compared to its green LAI was because this variety rolled its leaves more effectively than the variety 3615 (Figure 3.16).

Soon after irrigation was resumed (DOY 229) both varieties showed an increase in radiation interception. However, variety 3576 showed a slightly higher increase in radiation interception due to non-occurrence of leaf rolling. The high values of radiation interception observed for the variety 3615 at the end of the water deficit period and for both varieties during the remainder of the growing season, occurred because part of the solar radiation was intercepted by non-green leaves (dead leaves), as the canopy senesced.

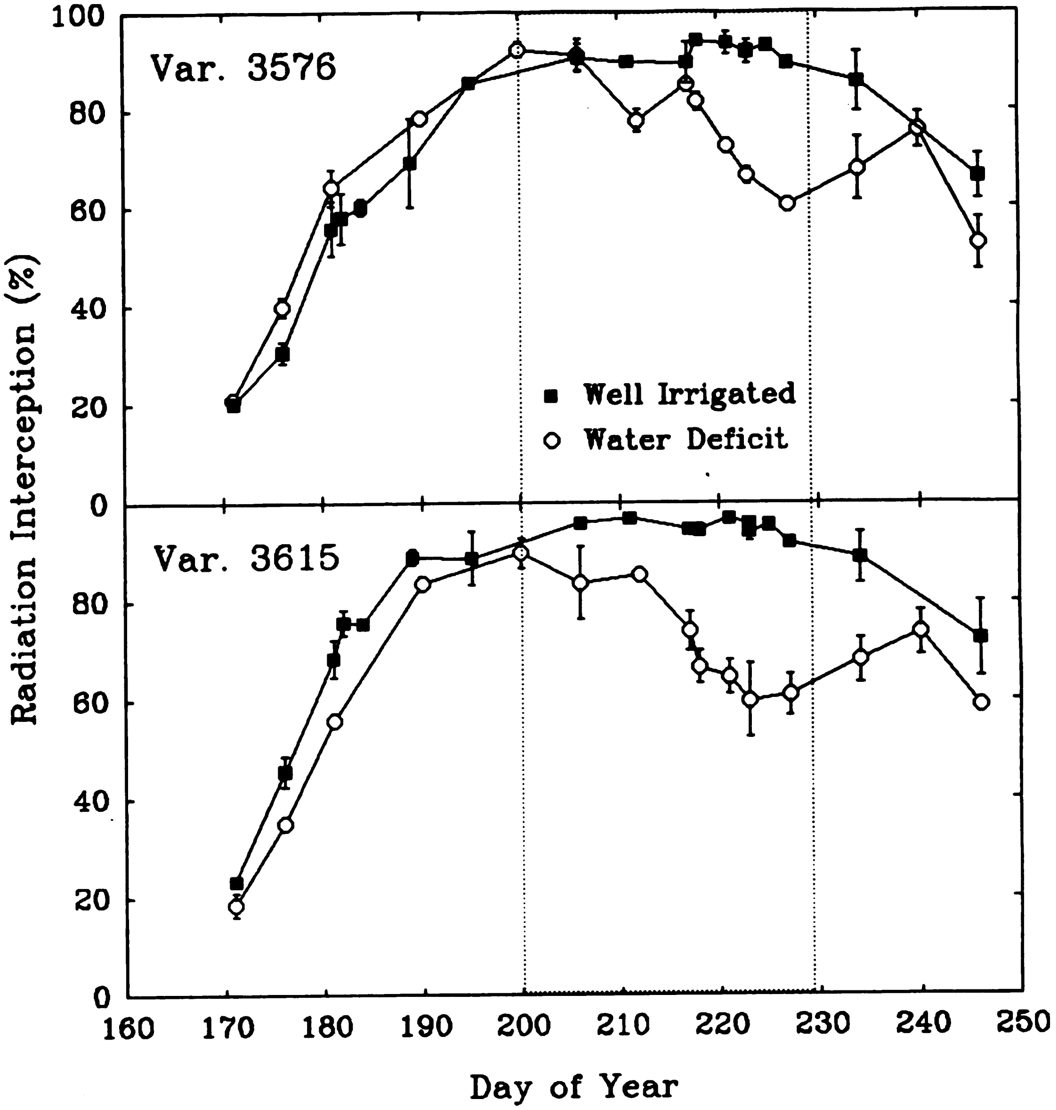

Figure 3.15. Seasonal variation of photosynthetically active radiation interception for both varieties in 1991 as measured near solar noon. The area limited by vertical dotted lines represents the period of soil water deficit.

Leaf Rolling

The daily variation of leaf rolling for both varieties during 1991 is presented in Figure 3.16. A different behavior of daily variation of leaf rolling was observed between the two varieties. As the water deficit became more severe, less daily variation of leaf rolling was observed for the variety 3615 and near the end of the water deficit period (DOY 227) almost no variation in leaf rolling was observed during the day. During the water deficit period the variety 3576 showed a marked reduction in leaf rolling near solar noon hours and little change in leaf rolling was observed in the afternoon hours. As the water deficit became more severe, a progressive increase in leaf rolling was observed toward morning hours and a remarkable recovery of leaf rolling was observed during evening hours. The daily average of exposed leaf blade area (leaf rolling) was 76% on DOY 217 for both varieties and 60.4% and 55.3% on DOY 227 for the variety 3576 and 3615.

These data indicated that the rapid recovery of leaf rolling observed during the evening hours for the variety 3576 increased its photosynthetic capacity early in the morning when VPD is low, water use efficiency is high (Rawson, 1979) and, the photosynthetic efficiency is high. Thus, the rapid recovery of leaf rolling enables the plant to respond rapidly to periods of high VPD, to avoid some of the radiation load, and consequently, reduce plant transpiration. O'Toole and Cruz (1980), working with rice, also found differences in the ability of rice varieties to maintain relatively high leaf water potential, in terms of overnight rehydration (dawn measurements) and the plant capability to maintain leaf water potential during

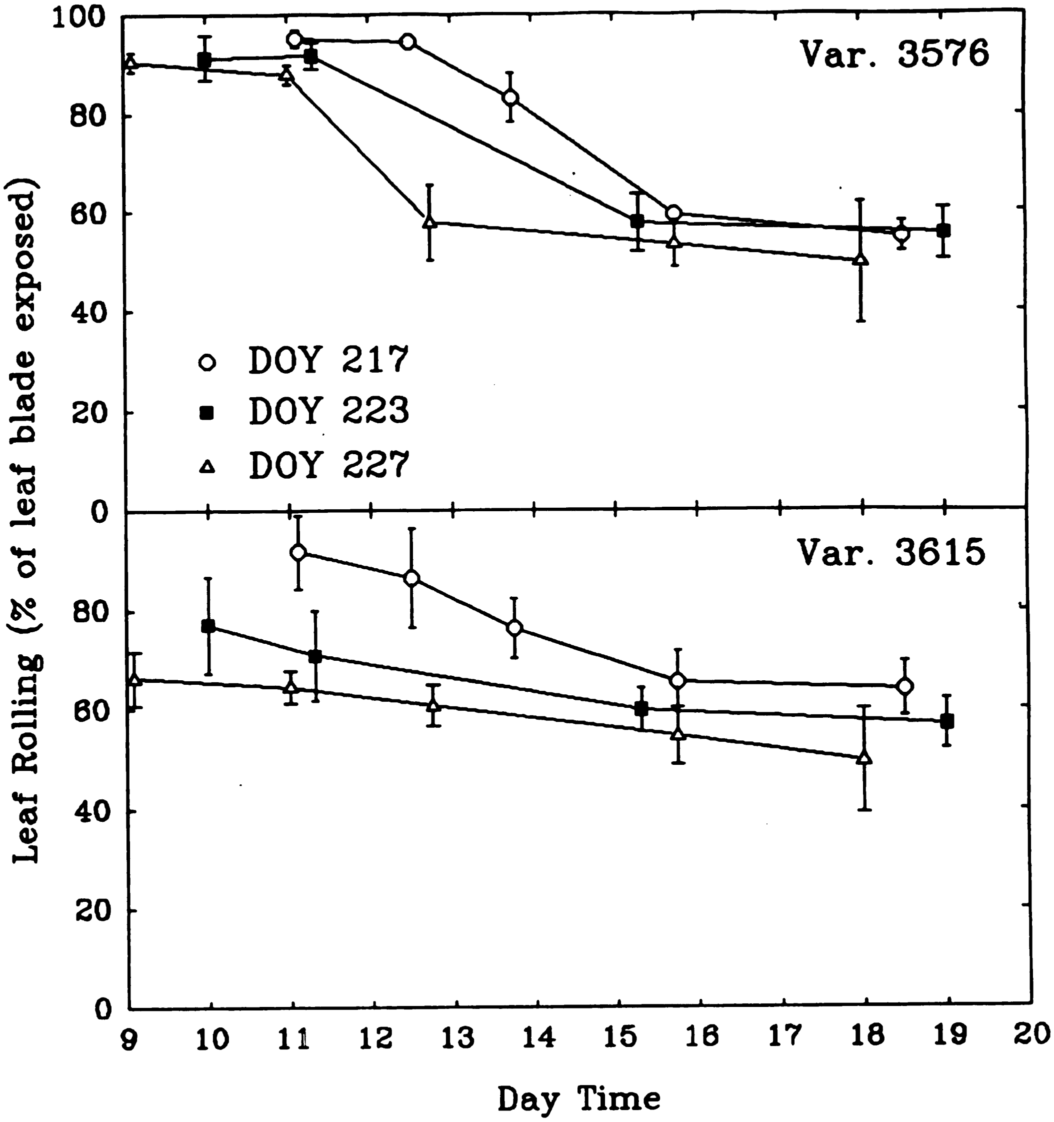

Figure 3.16. Daily variation of leaf rolling for both varieties on three selected days (DOY 217, 223 and 227) during the water deficit period in 1991.

midday periods of peak VPD. Additionally, genetic variability between varieties in terms of plant leaf rolling has been described for grain sorghum (Begg, 1980) and for rice (Turner *et al.,* 1986 and Chang *et al.,* 1974).

A similar pattern of leaf rolling between the two varieties was observed during the water deficit imposed in 1990 (Figure 3.17). A rapid recovery in leaf rolling was also observed for the variety 3576 between 2000 and 2200 hours. A similar overall reduction in the exposed leaf area was observed for the two varieties in both years. In both years, further increases in leaf rolling during the water deficit period were limited due to physical restrictions for leaves to roll. Leaf rolling during the anthesis water deficit period was much less as compared to pre-anthesis water deficit period (described in a companion paper). The main reason for this overall lower leaf rolling (higher leaf area exposed) during anthesis water deficit was because leaves were totally expanded and wider than plant leaves submitted to pre-anthesis soil water deficit.

Leaf Orientation

The daily changes in leaf orientation of leaf 13, 15 and 17 for both varieties on DOY 225 during the 1991 water deficit period is presented in Figure 3.18. Little change in leaf orientation was observed for both varieties during the water deficit period. These results indicate that during anthesis and post-anthesis water deficits, the leaf orientation mechanism contributed the least to the reduction in exposed plant leaf area for both varieties. However, Begg (1980) reported that once the leaf

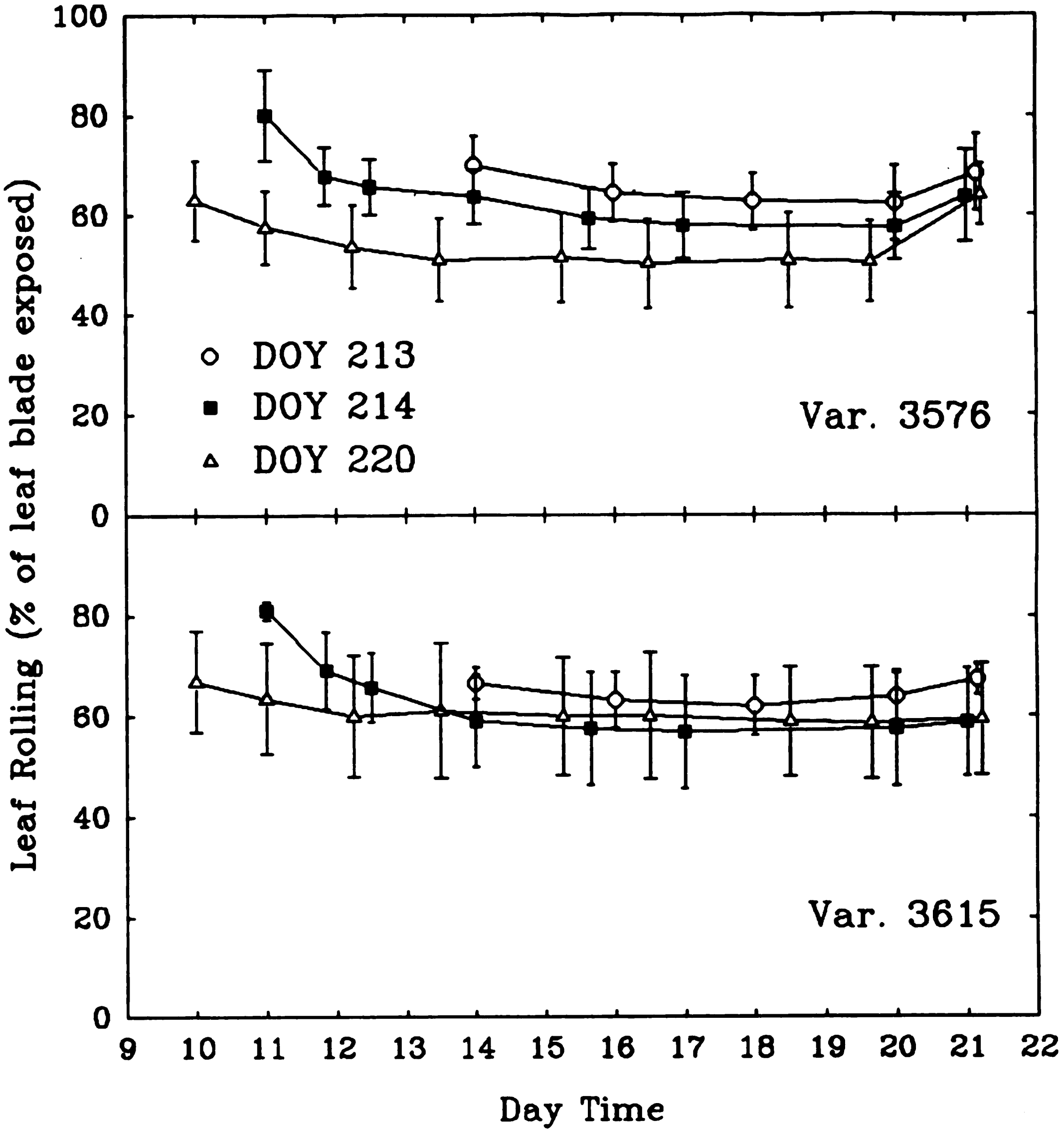

Figure 3.17. Daily variation of leaf rolling for both varieties on three selected days (DOY 213, 214 and 220) during the water deficit period in 1990.

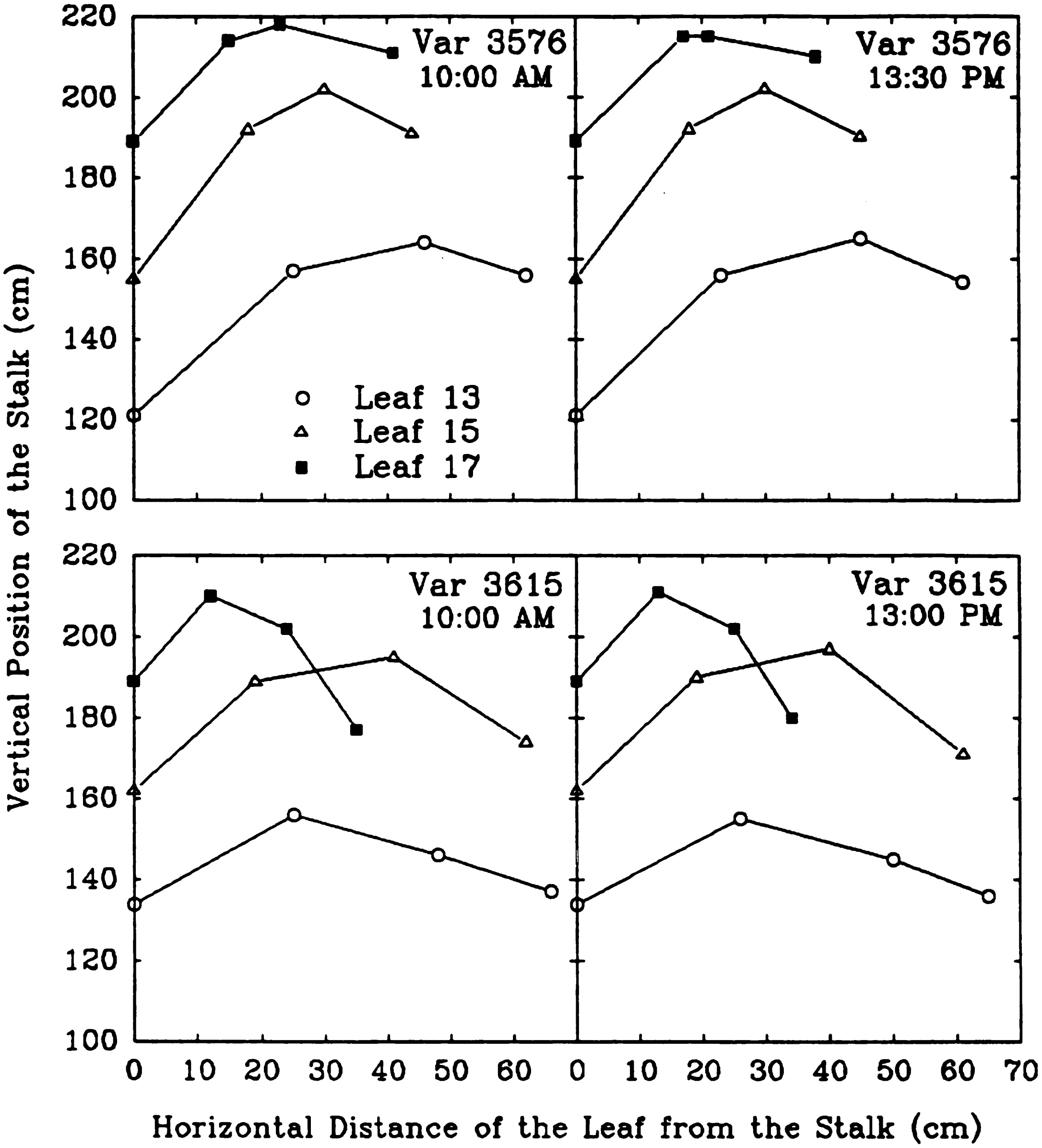

Figure 3.18. Daily variation of leaf orientation for the 13th, 15th and 17th leaves for both varieties in 1991 on DOY 225.

area development was complete, one of the main mechanisms for adapting to water deficit was through changes in leaf angle. He also stated that leaf rolling can be an effective mechanism for reducing the radiation load on water-stressed leaves when less water is available to dissipate energy as latent heat.

Other measurements made during the water deficit period (earlier and later than DOY 225) were not included because no changes in leaf orientation were observed for either variety. Although the leaf rolling increased over time, additional changes in leaf orientation was not observed. The length and width of leaf blades are believed to be the main factor affecting the ability of leaves, under water deficits, to orientate their blade more vertically. Long leaf blades curve downward (Figure 3.18) from about midway along their length. This imposed a physical restriction on the ability of the leaf to roll and, consequently, to orientate the leaf blade more vertically. The leaf rolling in long leaves was also limited by leaf curvature, hence, leaf rolling mainly occurred near the edge of the leaves limiting further increases in leaf rolling.

Conclusions

Although the amount of soil water extracted was similar for both varieties during the water deficit period, the variety 3615 reduced its LAI further than the variety 3576. This large reduction in LAI may be beneficial in a terminal water deficit situation where the limited supply of water may endure plant survival. Though this response can enhance survival by conserving water, it can be detrimental upon the relief of the water deficit if the LAI is reduced too much because radiation interception and transpiration as a proportion of evapotranspiration decreases when LAI decreases. The variety 3576 has a better performance during intermittent soil water deficit conditions and may contribute to better yields. The rapid recovery of leaf rolling during the early morning hours for the variety 3576 may increase its photosynthetic efficiency when VPD is low and water use efficiency is high. Less leaf rolling was observed during post-anthesis water deficits than water deficit imposed during pre-anthesis (described in a companion chapter) because leaves were totally expanded and wider than when the plant was submitted to pre-anthesis soil water deficit. The leaf rolling mainly occurred near the edge of the leaves, limiting further increases in leaf rolling and leaf orientation and, consequently, the reduction in exposed leaf area.

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CHAPTER 4

Effects of Post-Anthesis Soil Water Deficit on Maize Growth.

II. Leaf Area Adjustments and Radiation Interception.

Abstract

Leaf area adjustments during anthesis and post-anthesis soil water deficits are a complex phenomenon and distinct mechanisms exist through which maize varieties may avoid or cope with the effects of water deficits. The objective of this study was to: (i) Identify morphological and physiological differences between two maize hybrids; (ii) Define the relationship between LAI and radiation interception and; (iii) Characterize the sensitivity and quantify the contribution of leaf rolling and leaf senescence to the reduction of plant exposed leaf area. Pioneer varieties 3576 and 3615 were subjected to two irrigation managements: Well-irrigated and post-anthesis soil water deficit. The effectiveness of the leaf rolling mechanism occurred mainly during the beginning of the water deficit period and leaf senescence was activated later when no further reduction in exposed plant leaf area was possible by increasing leaf rolling. Although a similar contribution of the leaf rolling mechanism to the reduction of exposed LAI was observed for both varieties, leaf senescence was triggered earlier for the variety 3615 and a more marked reduction in LAI was observed. The variety 3576 seemed to perform better during intermittent water deficit conditions occurring during the growing season.

Introduction

The growth and duration of green leaf area with the geometry of a crop canopy determines the fraction of solar radiation intercepted by the crop canopy and thereby influences total plant growth and final yield (Dale *et al.*, 1980). Leaf area maintenance in a terminal water deficit situation has no effect on the total amount of water transpired. However, the water deficit may decrease harvest index if the soil water supply is exhausted before maturity. In intermittent water deficit situations, leaf area maintenance would improve yield stability due to a better radiation interception when water is available (Ludlow and Muchow, 1990).

Grain yields in maize have been reported to be especially sensitive to water deficits beginning at silking and continuing through grain filling. The yield is a product of the rate of photosynthesis during the grain filling period multiplied by the duration of the grain filling period, plus the change in labile reserves (Duncan, 1980).

The number of kernels per ear is the most sensitive yield component of maize growth in unfavorable environmental conditions (Claassen and Shaw, 1970; Krishnamurthy *et al.*, 1975; Hall *et al.*, 1981). Water deficit during early grain development affects the number of kernels per ear (Grant *et al.*, 1989). This period, according to Kiniry and Ritchie (1985), is from six to 18 days after silking. Grant *et al.* (1989) stated that water deficit can affect the number of kernels even if adequate pollen is present and adequate fertilization of ovules occurs. The number of kernels per ear and the number of ears that can develop is established at or shortly after pollination. According to Grant *et al.* (1989), the interval when kernel number is more sensitive to water deficit begins two to seven days after silking and ends 16 to 22 days after silking.

The kernels of most varieties are genetically limited as to their maximum weight so the number of kernels available may limit yield regardless of how favorable growing conditions may be subsequent to pollination (Duncan, 1980). According to Claassen and Shaw (1970), water deficit has its greatest effect on kernel weight later in the grain filling period. The photosynthate used for kernel growth may come from both current photosynthesis during the filling period and from labile carbohydrates accumulated earlier in the growth. The remobilization of labile carbohydrates to the kernel during periods of reduced assimilate supply has been emphasized by several researchers (Daynard *et al.*, 1969; Hume and Campbell, 1972; Jurgens *et al.*, 1978). Grant *et al.* (1989) and Jurgens *et al.* (1978) reported that carbohydrate was translocated from the stem and the leaves to the grain even when water deficit limited photosynthesis. Any labile carbohydrate remaining in the maize stalk at grain maturity represents energy fixed by photosynthesis but is not converted into grain and, hence, potential grain yield is not realized.

Senescence is an important development process that has not yet been clearly defined. According to some views this process is under genetic control, but the role of growth regulation and the degree to which environmental factors such as light, temperature, water and nutrients, modify the genetic program is still poorly understood (Nooden, 1980; Thomas and Stoddart, 1980). Water deficit reduces leaf area by accelerating the rate of senescence of older leaves (Fischer and Hagan, 1965; Fischer and Kohn, 1966; Fischer, 1973; Slatyer, 1973; Ludlow, 1975). However, senescence of individual leaves is not seriously altered by water deficits that develop gradually, but rapid development of water deficit may accelerate senescence of lower leaves (Jordan, 1983). Accelerating senescence under post-anthesis water deficit conditions, according to Jordan (1983), is a result of insufficient supply of photosynthate and reduced nitrogen in the presence of a strong reproductive sink.

In the absence of other limiting factors, crop productivity is determined by the absorption of photosynthetic active radiation (PAR) by a crop canopy (Loomis and Williams, 1963; Monteith, 1977; Monteith, 1981; Tollenaar and Bruulsema, 1988; and Ottman and Welch, 1989). Several studies have shown a linear relationship between intercepted radiation and rate of crop biomass production when no other limiting factor affects crop growth. However, Gosse *et al.* (1986) demonstrated that the phase of the crop development affects the relationship. Plant patterns influence the distribution of solar radiation in the canopy as well as the total radiation intercepted by a crop (Ottman and Welch, 1989). In a dense population, light interception occurs mainly in the top part of the canopy (Williams *et al.*, 1965).

Differences in leaf rolling indexes under water deficit conditions provide a sensitive and rapid reversible nonstomatal means for controlling plant water loss (Austin and Jones, 1975). Based on stomatal conductance data, Begg (1980) indicated that leaf rolling precedes the closure of abaxial stomata. However, results from a companion chapter indicate that the leaf rolling was closely related to leaf expansion. The leaf rolling mechanism increased the plant's capacity to enlarge the exposed plant leaf area more quickly when either favorable atmospheric conditions occur or when the water deficit was relieved.

The objective of this study was to: (i) identify morphological and physiological differences between two maize varieties when water deficit was imposed after anthesis; (ii) define the relation between leaf area index and radiation interception; (iii) quantify the contribution of leaf rolling and leaf senescence to the reduction of exposed leaf area and; (iv) characterize the sensitivity of the leaf rolling mechanism and leaf senescence in relation to plant available water.

Methodology

This experiment was conducted in 1990 and 1991 at the Kellogg Biological Station, near Kalamazoo, Michigan, under a rain shelter, described by Martin *et al.* (1988), to prevent rainfall on the experiment.

Spinks loamy sand (mesic Psammentic Hapludalfs) was the soil at the site. Maize varieties, Pioneer 3615 and Pioneer 3576, were planted north-to-south at a high density on May 18 (day of year (DOY) 138) in 1990 and on May 27 (DOY 147) in 1991. Emergence occurred on May 28 (DOY 148) in 1990 and on May 31 (DOY 151) in 1991. Plants were thinned in the seedling stage to a plant density of 7.2 plants/m^2. Weeds were controlled manually during both years. Plot size was 4.6 m x 6.2 m. Maize was planted in six rows, 0.71 m wide, giving two border rows and four main rows in each plot. The experimental layout was a split-plot design, with irrigation treatment as main plot and maize varieties as subplots. Before emergence, fertilizer was applied at rates of 60 Kg N ha^{-1} (45-0-0), 200 Kg P ha^{-1} (0-46-0), and 60 Kg K ha^{-1} (0-0-60). Nitrogen was applied at a rate of 100 Kg ha^{-1} 19 days after emergence (DOY 166) and 17 days after emergence (DOY 168), in 1990 and 1991. Due to the limited space in the rain shelter this experiment was not replicated.

Irrigation water was applied using an overhead Toro FS-LG series sprinkler system, mounted upside down on the trusses of the rain shelter operating with a constant pressure of 103.5 Kg Pa^{-1}, at a rate of approximately 25 mm hr^{-1} (NeSmith *et al.*, 1990). Two irrigation treatments were established: (i) well- irrigated (irrigation was applied to maintain the fraction of plant available water above 0.70); and (ii) post-anthesis soil water deficit. The water deficit period (period between subsequent irrigations) occurred from DOY 205 to DOY 229 in 1990 and, from DOY 200 to DOY 229 in 1991.

Soon after emergence, four plants per plot were randomly selected and marked for nondestructive measurements throughout the season. Leaf senescence was estimated for each leaf by measuring the percentage of leaf that was yellow or necrotic. Measurements of leaf area were taken, approximately three times a week, once the leaves emerged from the whorl until the leaf ligule appeared. The area of each leaf was determined from measurements of leaf length and maximum leaf width multiplied by 0.75 (Stickler *et al.*, 1961). Nondestructive measurements of cob elongation (elongation of husks, cobs and ears) were taken by placing a ruler on the ear node and recording the distance to the top of the husks or ear. Aboveground crop biomass was estimated by harvesting four plants in each plot several times during the growing season. Prior to drying, destructive measurement of ear elongation was taken. In 1990, 20 ears were harvested and 40 ears were harvested in 1991 in each plot. The number of rows, number of kernels, final grain weight and yield were determined.

Plant basis

ear basis

Leaf rolling was measured several times daily and weekly on four selected plants per plot during the water deficit period. In each plant, leaves 13, 15 and 17 were selected to represent the average plant leaf rolling and two positions were marked on each leaf (quarter-way and half-way from the tip). The percentage of leaf rolling (percent of exposed leaf blade) was calculated from the fraction of the rolled leaf width (measured by a caliper) and fully open width. Daily average leaf rolling was calculated by the integration of leaf rolling measurements taken between 0800 hours and 1900 hours. Exposed leaf area index was calculated by incorporating the daily average leaf rolling measurements into plant leaf area index.

Photosynthetically active radiation (PAR) interception was measured in four marked sites per plot, several times daily for several weeks, under clear sky conditions. At ground level, a minimum of three observations were made to compute an individual measurement in each side. The line quantum sensor (Model LI-191SB, Li-cor, Lincoln, NE) was leveled, placed perpendicular to the row direction and positioned so that no shadows from the handle influenced measurement. Canopy incident radiation was measured by placing the line quantum sensor above the crop. The daily average PAR interception was calculated by integration of radiation interception measurements taken between 0900 hours and 1700 hours. Cumulative intercepted PAR was calculated by linear interception of fractional radiation interception between two consecutive measurements multiplied by the daily solar radiation (MJ/m^2). Radiation use efficiency (RUE) for the growing season was calculated as the slope of the linear regression between aboveground biomass and cumulative intercepted radiation with the equation forced through the origin.

A minimum data set recorder (Model LI-1200, Li-cor, Lincoln, NE) located outside of the rain shelter was used to record the solar radiation, minimum and maximum air temperature. Daily values of solar radiation (MJ/m^2), maximum and minimum temperature and vapor pressure deficit of the air for the 1990 and 1991 growing seasons were shown in a companion chapter.

Plant available water was calculated for the top 1.5 m of the profile as the difference between volumetric water content of the soil and water content at the lower limit of plant-extractable soil water in the rooting depth. Fraction of plant available water was calculated by the ratio between the plant available water and the maximum available water within the rooting depth. The drained upper limit and the lower limit soil water contents were assumed to correspond approximately to a soil water potential of 0.01 MPa and 1.5 MPa.

Results and Discussions

During the water deficit periods, from DOY 205 to 229 in 1990 and from DOY 200 to 229 in 1991, similar climatic conditions were observed. The averages of weather conditions during the water deficit periods and the entire growing seasons for both years are presented in Table 4.1.

Leaf Rolling

The daily average values of leaf rolling (percent of leaf blade exposed) for both varieties during 1990 and 1991 are presented in Figure 4.1. In both years, the leaf rolling was similar for the two varieties mainly because the weather conditions were relatively constant and similar during the water deficit periods. Little change in leaf rolling was observed for both varieties, in both years, as the water deficit became more severe. A totally different pattern was observed during water deficit

Table 4.1. Average of daily meteorological variables during the water deficit period and the entire growing season for 1990 and 1991.

	Deficit Period		**Growing Season**	
Meteorological Variables	**1990**	**1991**	**1990**	**1991**
Solar Radiation (MJ/m^2)	19.93	20.85	17.25	21.05
Minimum Temperature (°C)	12.93	14.44	13.27	15.02
Maximum Temperature (°C)	26.49	27.06	25.40	28.03
Vapor Pressure Deficit (Kpa)	0.79	0.80	0.74	0.86

imposed during the vegetative stage (chapter 2). For the older leaves, additional increases in leaf rolling was limited by physical restrictions for the leaves to roll. Leaves were totally expanded and wider than leaves submitted to vegetative stage soil water deficit (described in chapter 1). Thus, leaf rolling occurred mainly near the edge of the leaves and long leaf blades curve downward from about midway along their length limiting further increases in leaf rolling and, consequently, the reduction of exposed plant leaf area. Leaf rolling causes a reduction in exposed LAI and, as a consequence, reduces plant transpiration between 50% and 70% (Oppenheimer, 1960) and increases water use efficiency (Johns, 1978).

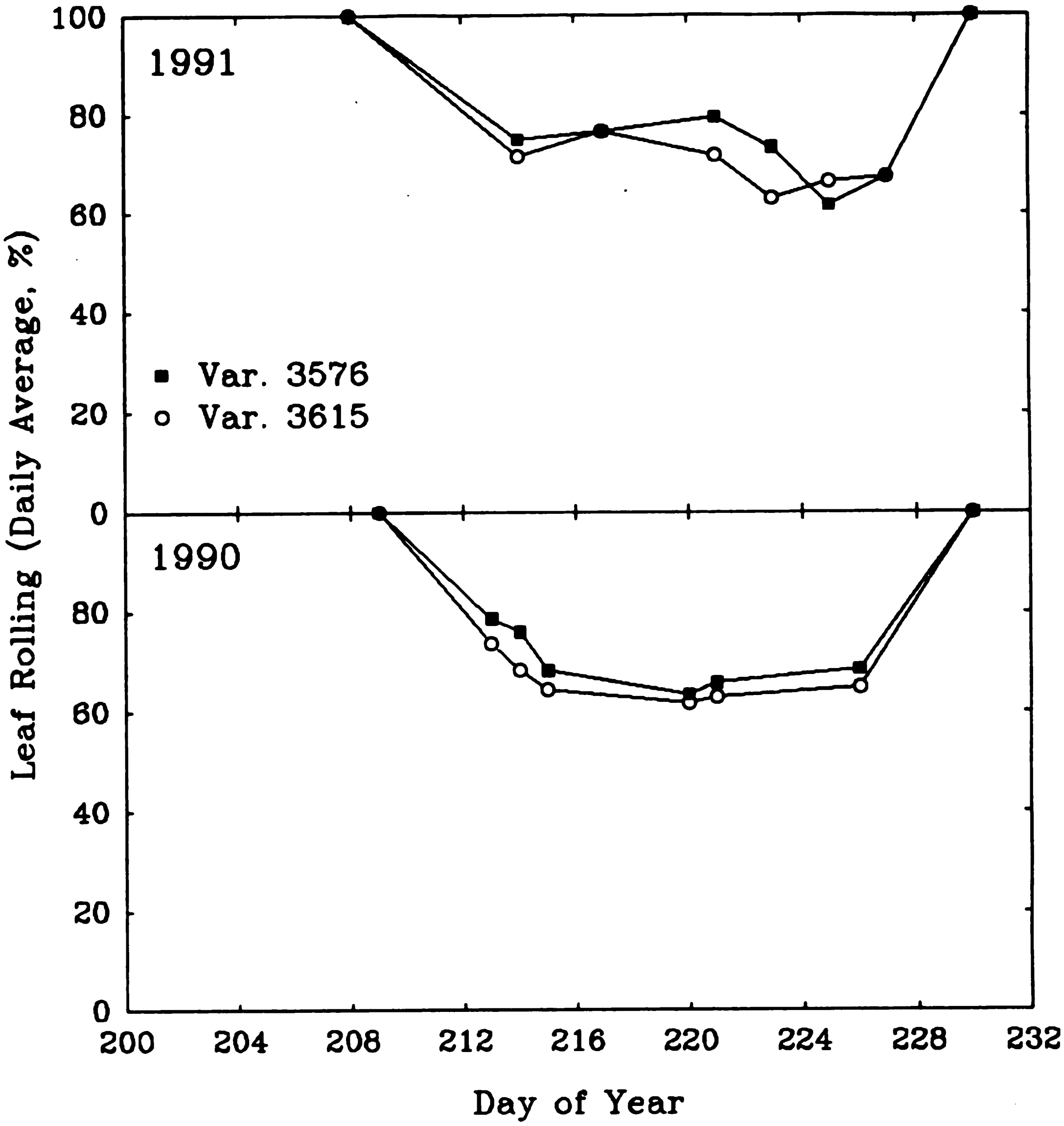

Figure 4.1. Daily average of leaf rolling (percentage of leaf blade exposed) for both treatments during 1990 and 1991 post-anthesis soil water deficits periods.

Radiation Interception

The seasonal variation of radiation interception (daily average) during 1991 is presented in Figure 4.2. A slight decrease in radiation interception was only observed for both varieties 15 days after the water deficit was imposed. During the water deficit period a greater reduction in radiation interception was observed for the variety 3615. This was caused mainly by a reduction in green leaf area due to accelerating leaf senescence. Soon after the irrigation was resumed (DOY 229) both varieties showed an increase in radiation interception. This was caused by the non-occurrence of leaf rolling (both varieties had a similar percentage of leaf rolling). However, the variety 3576 showed a slightly higher increase in radiation interception due to enlargement of the exposed LAI in a larger number of leaves than the variety 3615. This rapid increase of exposed LAI and resumption of crop growth is of major importance for the plants to recover from water deficit periods (Bull and Glasziou, 1980). Non-green leaves (senesced leaves) were attenuating a large fraction of the measured radiation interception. This was not quantified in this experiment.

The radiation interception at different heights above the soil surface for both varieties and treatments on DOY 223, in 1991, is shown in Figure 4.3. Three measurements were taken for each 25 cm height increment up to 200 cm. The radiation intercepted by the variety 3576 and 3615 above the ear level (average ear height was 120 cm above the soil surface) was 74.7% and 76.9% for the well-irrigated treatment and, 61.1% and 61.8% for the water deficit treatment.

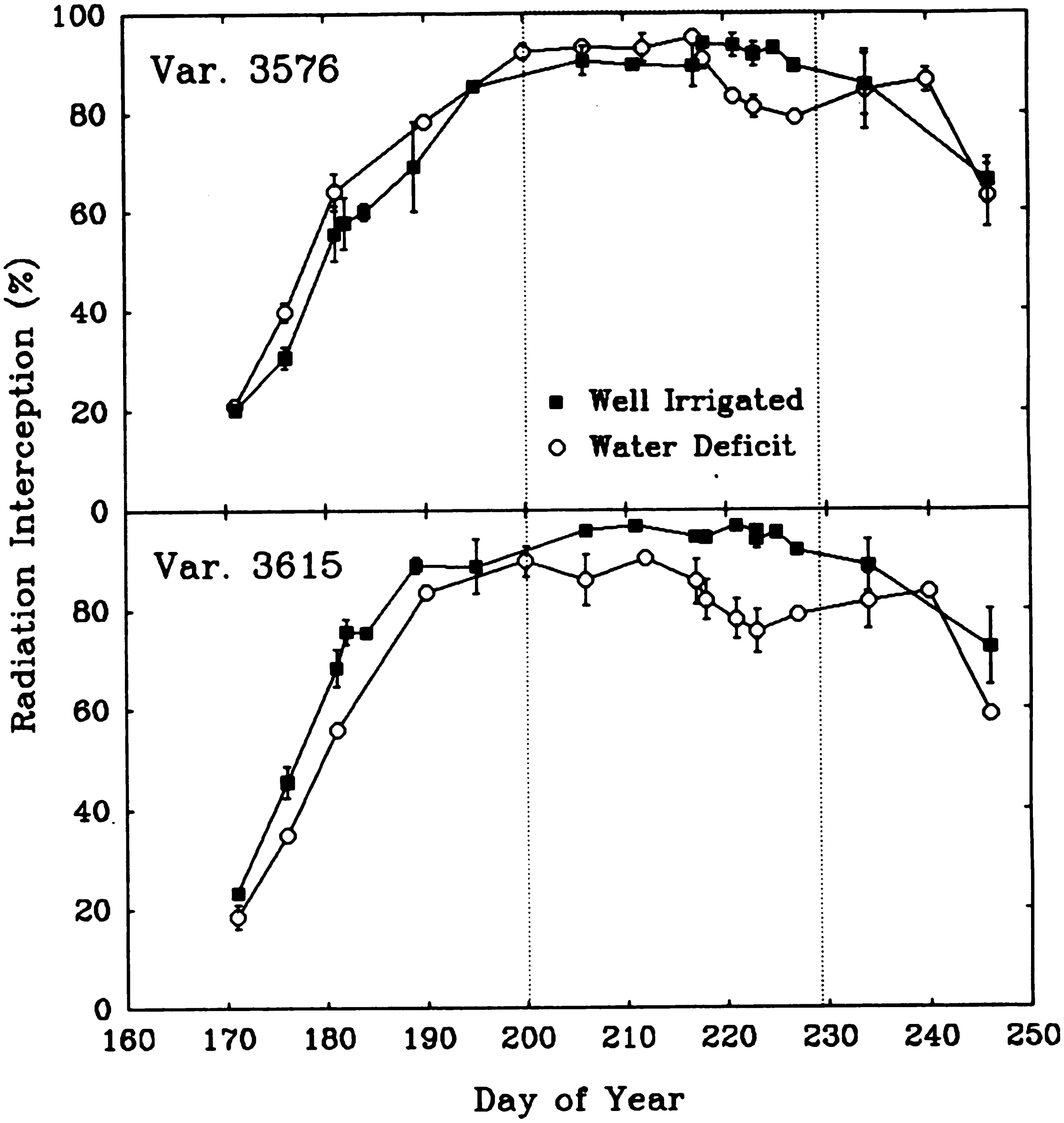

Figure 4.2. Daily average of radiation interception for both treatments and varieties during 1991. The area limited by vertical dotted lines represents the period of post-anthesis soil water deficit.

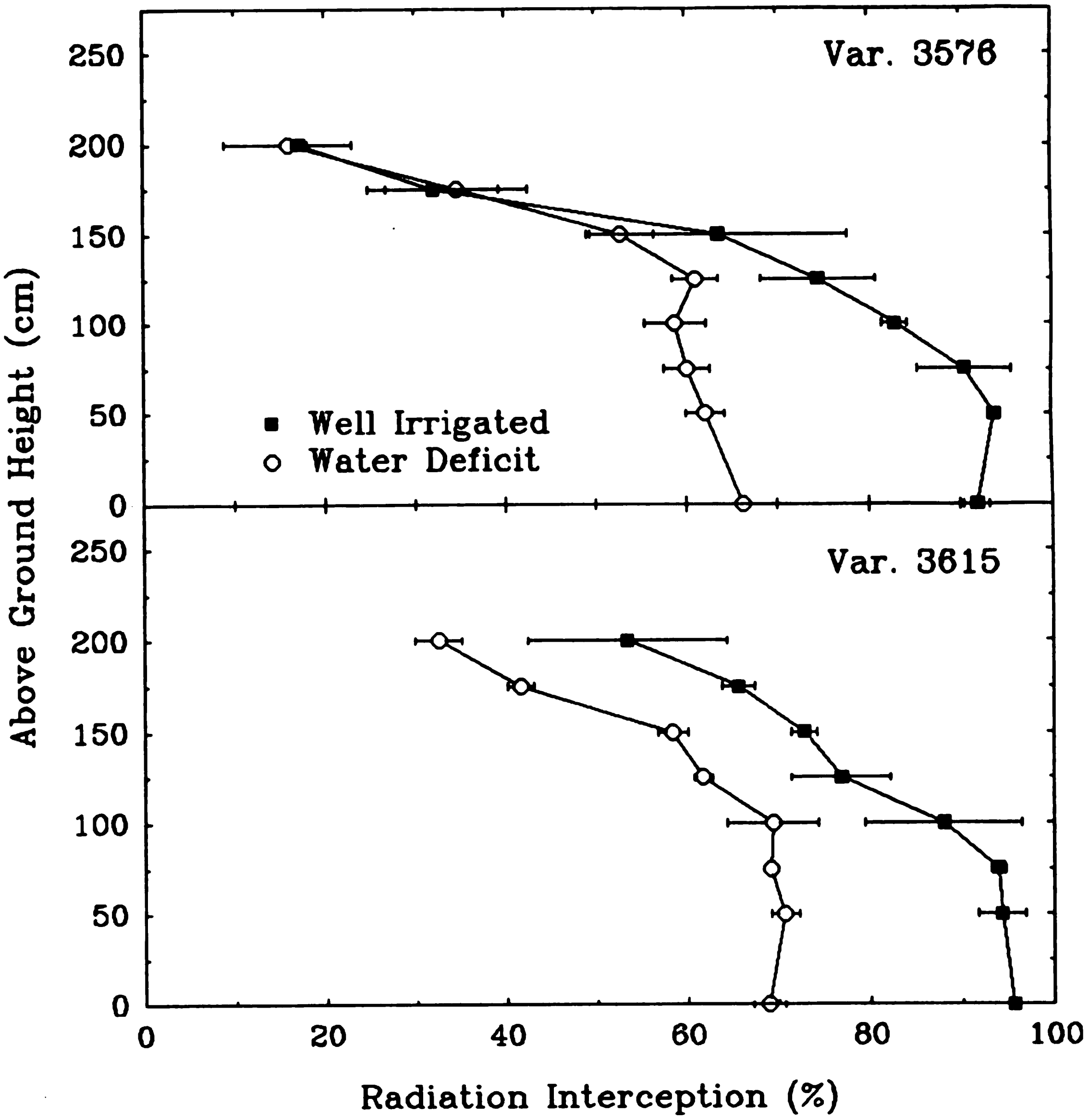

Figure 4.3. Radiation interception at different heights above the soil surface for both varieties and treatments on DOY 223 during 1991.

The cumulative vertical distribution of leaf area on DOY 223 is presented in Figure 4.4. Above leaf node 12 (equivalent to 53.2% of the maximum LAI produced) the variety 3576 had similar amounts of leaf area compared to the well-irrigated treatment. The variety 3615, however, had similar values for leaf area above leaf node 13 (equivalent to 41.8% of the maximum LAI produced) compared to the well-irrigated treatment. Under soil water deficit conditions, leaves below leaf node 8 and 11 were totally senesced for the varieties 3576 and 3615. The well-irrigated treatment, however, showed leaf senescence below leaf node 7 and 9 for the varieties 3576 and 3615.

These results indicate that the radiation interception observed for the variety 3576 above 125 cm (leaf node 12) was mainly caused by plant leaf rolling rather than differences in green leaf area or leaf senescence. However, for the variety 3615, the differences in radiation interception observed above 140 cm (leaf node 13) was not only due to differences in plant leaf rolling but also due to differences in the overall plant heights. Plants of the variety 3615 grown in well-irrigated conditions were 22 cm taller than plants grown under water deficit conditions. Additional investigation is needed to separate the radiation intercepted between green leaves and senesced leaves. On DOY 223, the percentage of green leaf area was reduced by 27% and 19.8% for the variety 3576 and 49.2% and 37.7% for the variety 3615, compared to the maximum LAI produced and the LAI of the well-irrigated plants.

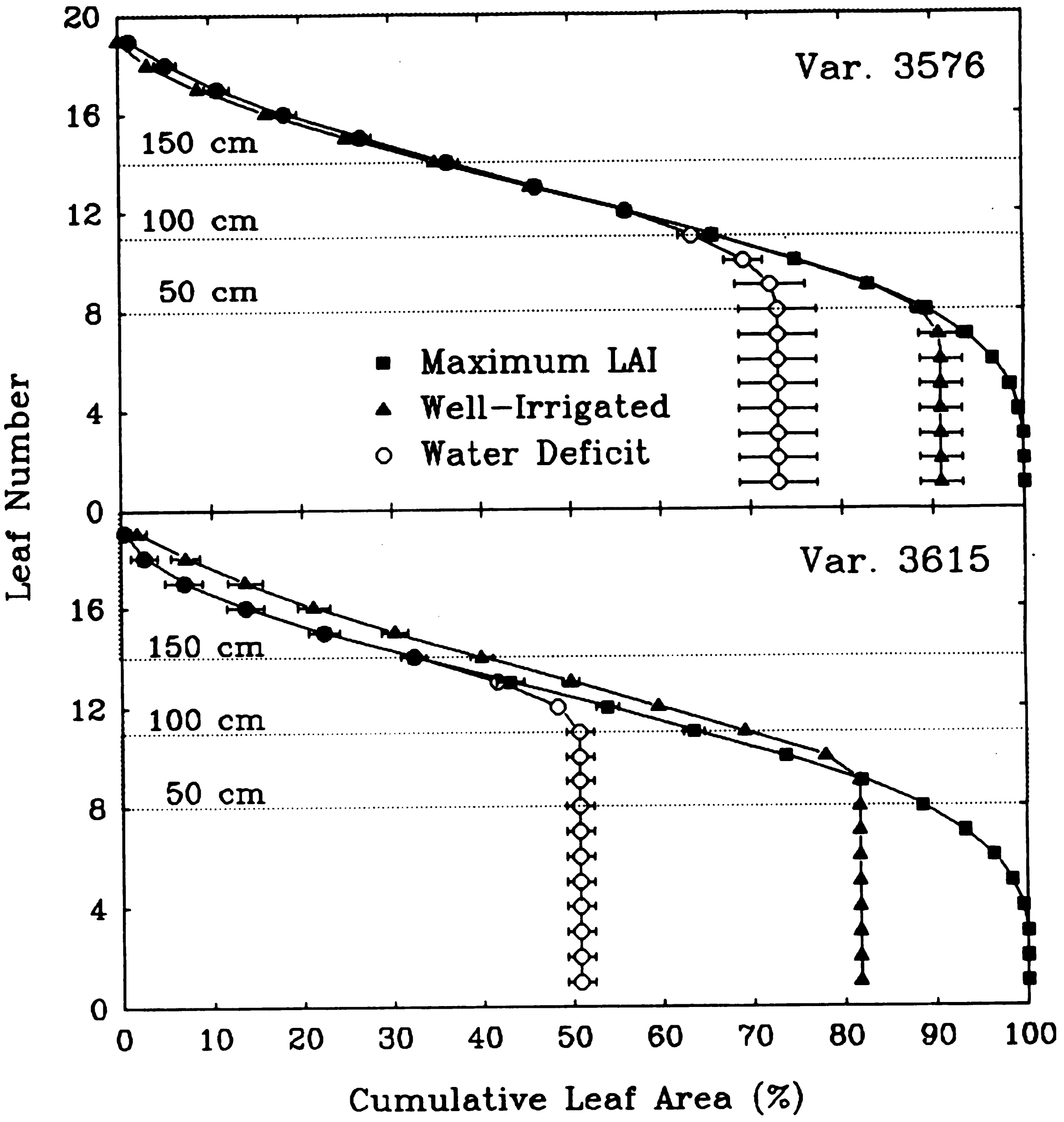

Figure 4.4. Cumulative vertical distribution of plant leaf area on DOY 223 for both varieties and treatments in 1991. The horizontal dotted lines indicate 50 cm increment of the plant height.

Plant Biomass Accumulation

The seasonal variation of aboveground biomass accumulation for both varieties during 1991 is shown in Figure 4.5. Aboveground biomass accumulation for the variety 3615 began to decline in relation to the well-irrigated treatment for the variety 3615 shortly after the water deficit was imposed. Less reduction in plant biomass was observed for the variety 3576 during the water deficit period. At the end of the water deficit period (DOY 229), the aboveground biomass production of the water deficit treatment was 74.8% and 54.2% of the well-irrigated treatment for the variety 3576 and 3615. After the water deficit was relieved, both varieties increased aboveground biomass accumulation and, at harvest, the water deficit treatment produced 87.4% and 61.8% of the aboveground biomass of the well-irrigated treatment, for the variety 3576 and 3615. According to Steven *et al.* (1983), daily dry matter production has been described as a function of the total incident solar radiation, the proportion of solar radiation intercepted, and the efficiency of conversion of solar radiation to photosynthates. Additionally, several previous reports have indicated that dry matter accumulation ceased due to impairment of photosynthesis under water deficit conditions during grain filling (Jurgens *et al.*, 1978; McPherson and Boyer, 1977; Westgate and Boyer, 1985).

The relationship between aboveground biomass and cumulative intercepted radiation is presented in Figure 4.6. The radiation intercepted by the variety 3576 and 3615 during the entire growing season was 99.1% and 88.3% of the radiation intercepted by the well-irrigated treatment. Radiation use efficiency (RUE) was

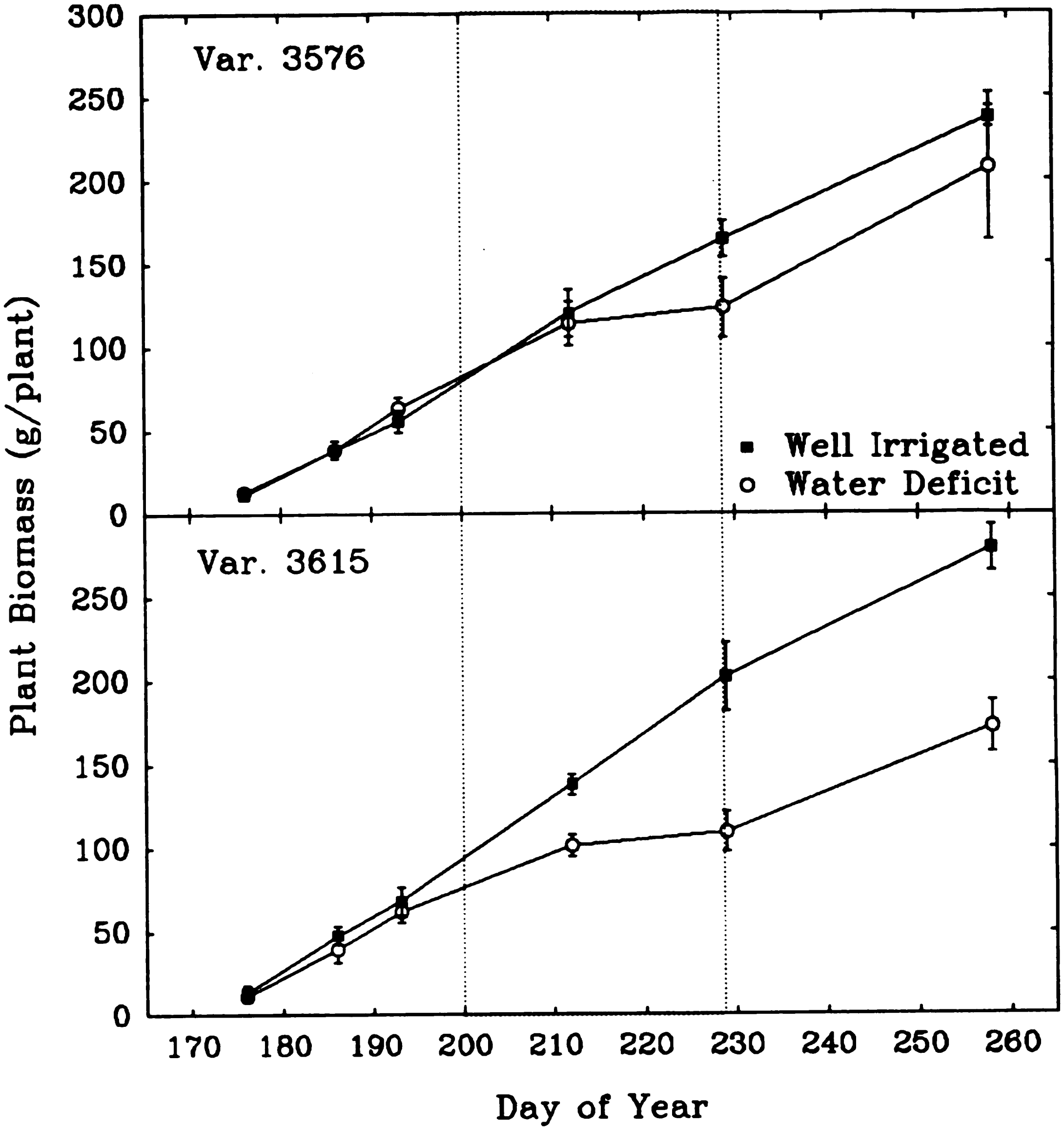

Figure 4.5. Aboveground biomass for both treatments and varieties in 1991. The area limited by vertical dotted lines represents the period of vegetative soil water deficit.

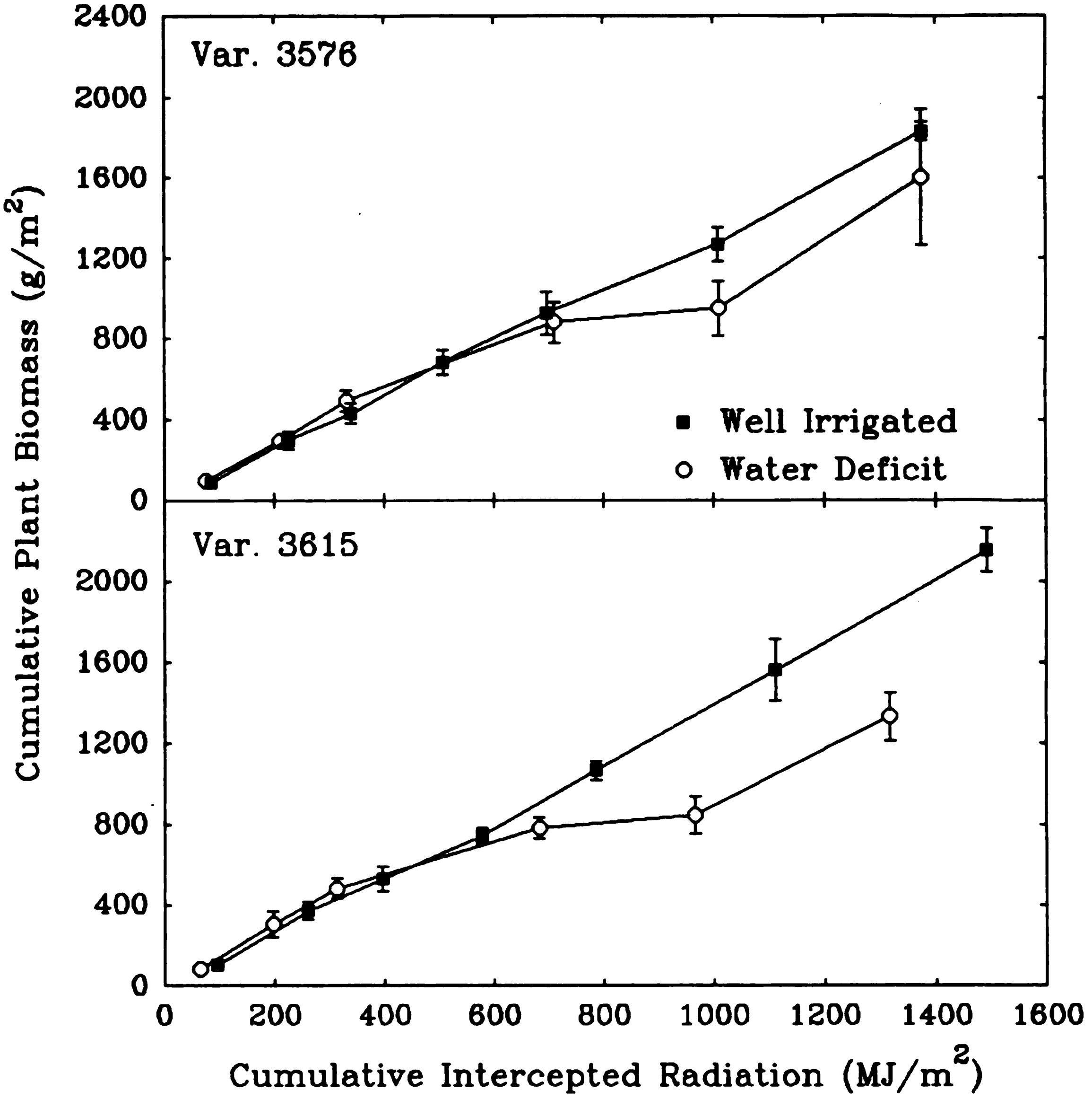

Figure 4.6. Relationship between aboveground biomass and cumulative intercepted radiation in 1991.

higher for both varieties grown under well-irrigated conditions (Table 4.2) and the post-anthesis water deficit caused differences in RUE between the two varieties.

Table 4.2. Total intercepted radiation, radiation use efficiency (RUE) and above-ground biomass for both treatments and varieties in 1991. Values in brackets are percentages of the well-irrigated treatment.

Treatment	**Variety**	**Intercepted Radiation**	**Biomass Production**	**RUE**	R^2
Water Deficit	3576	1364.4 (99.1)	1604.1 (87.7)	1.16 (88.5)	0.953
	3615	1318.0 (88.3)	1328.6 (61.8)	1.01 (72.1)	0.931
Well Irrigated	3576	1376.7	1830.0	1.31	0.998
	361~~6~~5	1491.9	2151.0	1.40	0.996

The lower value of RUE for the variety 3615 was mainly caused by the larger reduction in its LAI compared to variety 3576. This reduction in plant leaf area reduced the plant photosynthetic area and, consequently, the capacity of the plant to increase the production of photosynthates after the water deficit was relieved. The relatively high value of total intercepted radiation observed for the variety 3615 was mainly caused by radiation being intercepted by non-green leaves (senesced leaves).

The low values of RUE observed for both varieties, grown under water deficit conditions, and the discrepancy in RUE observed between the variety 3576 (1.16 g/MJ) and the variety 3615 (1.01 g/MJ) during the growing season may be explained by the lower values of RUE observed during the water deficit period and after the water deficit was relieved (Figure 4.7). A marked drop in RUE was observed for both varieties during the water deficit period and at the end of the water deficit period (DOY 229) the RUE was approximately 0.23 g/MJ for both varieties. After the water deficit was relieved, the variety 3615 showed a much slower recovery of RUE compared to the variety 3576. The reasons for this slower recovery of RUE for the variety 3615 may be explained by its lower LAI and the radiation intercepted by non-green leaves (senesced leaves). The linear relationship between aboveground biomass accumulation and intercepted radiation, observed for both varieties under well-irrigated conditions (1.31 g/MJ and 1.40 g/MJ for the variety 3576 and 3615), corresponds with results obtained by Monteith (1981); Gallagher and Biscoe (1978); Sibma (1977). Monteith (1977) found that the production of biomass by barley, potatoes, sugar beet, and apples is strongly correlated with intercepted radiation and the RUE was approximately 1.4 g/MJ for all crops. Muchow (1985) found that for grain sorghum under non-stressed conditions a typical value for RUE is 1.25 g/MJ.

The variety 3576 had better crop performance than the variety 3615 during the post-anthesis water deficit period and after the water deficit was relieved. This was mainly due to less reduction in its LAI by leaf senescence during the water

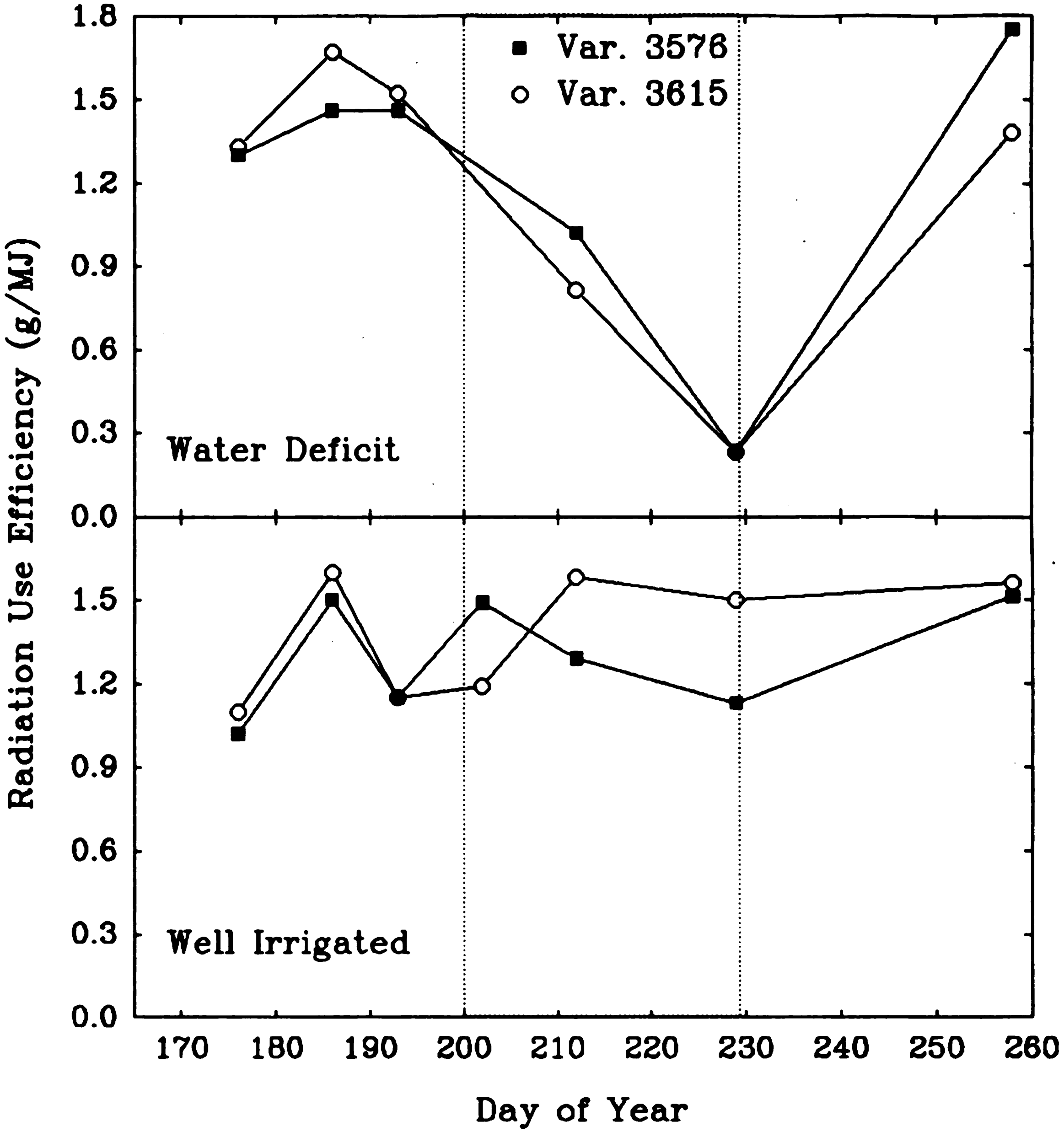

Figure 4.7. Seasonal variation of radiation use efficiency (RUE) for both varieties and treatments during 1991.

deficit period. According to Watson (1956) and Sinclair (1984), leaf area maintenance is important in determining the percentage of solar radiation intercepted by the canopy and it therefore influences plant growth and final yields.

Plant Leaf Area and Senescence

The water deficit had a marked effect on plant leaf area in both years (Figures 4.8 and 4.9). In 1990, the green LAI for both varieties, under water deficit conditions, began to decrease 15 days after irrigation was discontinued. However, in 1991 a reduction in green LAI for both varieties started about 11 days after irrigation was ceased. The exposed LAI was calculated based on leaf rolling measurements (daily average) presented in Figure 4.1. The reduction in plant LAI and exposed LAI of the water deficit treatment was calculated by the integration of LAI curves over the duration of the water deficit period.

Leaf rolling markedly contributed to the reduction in exposed plant leaf area of the water deficit treatments in both years. The exposed LAI ranged from 65.6% to 74.2% of the well-irrigated treatment in 1991 and from 62.9% to 69.8% in 1990. Although similar reduction in exposed LAI was observed for both varieties in each year, a distinct effect of the water deficit in reducing plant leaf area (leaf senescence) and exposed LAI was observed between the two varieties. In 1991, the contribution of leaf senescence and leaf rolling to the decrease in exposed plant leaf area was 10.9% and 14.9% for the variety 3576 and, 20.5% and 13.9% for the variety 3615 (Figure 4.10). In 1990, however, the contribution of plant leaf

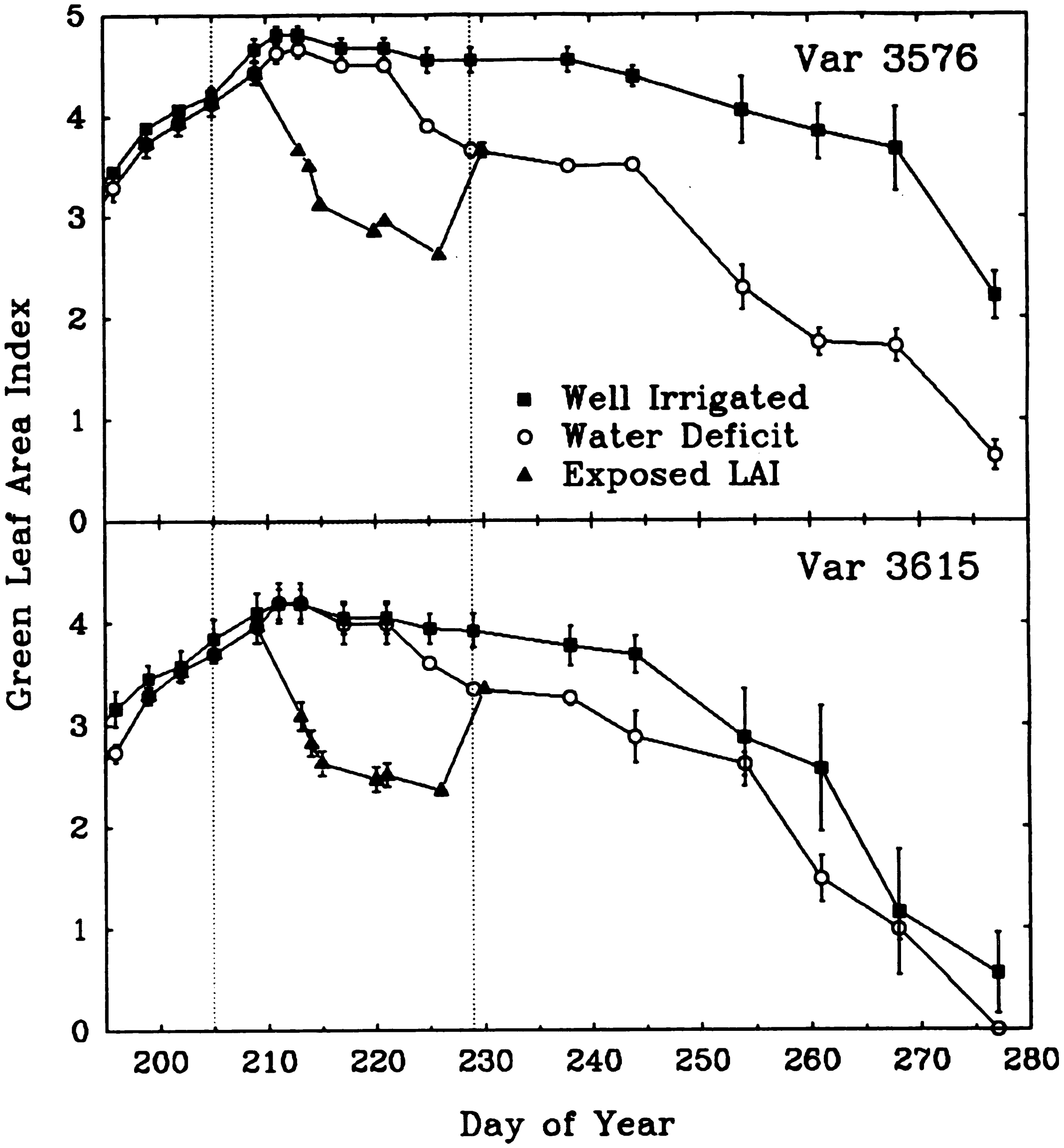

Figure 4.8. Green leaf area index of well-irrigated treatment, post-anthesis soil water deficit and exposed leaf area index of the water deficit treatment for both varieties during 1990.

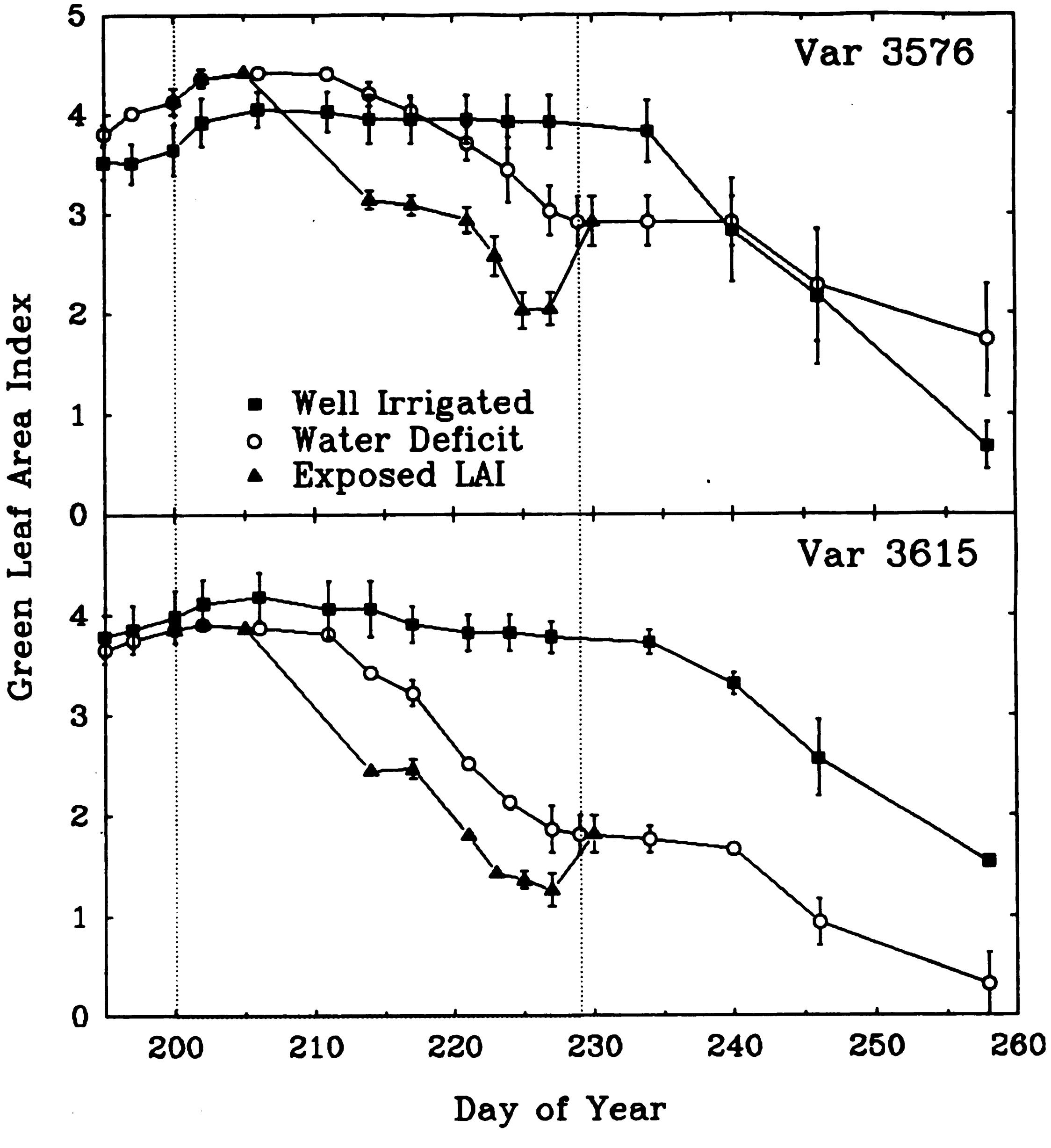

Figure 4.9. Green leaf area index of well-irrigated treatment, post-anthesis soil water deficit and exposed leaf area index of the water deficit treatment for both varieties during 1991.

rolling to the reduction in exposed LAI was greater, between 20.4% and 23.3%, than the contribution of leaf senescence (between 3.7% and 6.6%). The duration of the water deficit period in 1990 (five days shorter than 1991) reduced the effectiveness of the leaf senescence mechanism and consequently, less permanent reduction in green plant leaf area was observed.

At the end of the water deficit period (DOY 229) imposed in 1991, the LAI of the water deficit treatment was reduced in 33.6% and 53% of the LAI measured at the beginning of the water deficit period for the varieties 3576 and 3615. The exposed LAI, however, was only 44.6% and 31.8% of the green LAI measured at the beginning of the water deficit period. The substantial reduction in exposed LAI for the variety 3576 without accelerating leaf senescence was beneficial in intermittent water deficit situations. This variety had a larger green LAI with the onset of precipitation or irrigation, hence, maintaining its photosynthetic capacity. The rapidity of resumption of crop growth was of major importance when water deficits were severe during the growing season, and this capacity of recovery was not necessarily only associated with retention of a green leaf area canopy (Bull and Glasziou, 1980). Experiments indicated that dry matter accumulation may be reduced by the impairment of photosynthesis under water deficit conditions (Jurgens *et al.*, 1978; McPherson and Boyer, 1977; Westgate and Boyer, 1985).

These results indicate that the plant leaf rolling mechanism reduced the exposed LAI and, consequently, limited the reduction of plant leaf area by accelerating leaf senescence. A similar contribution of the leaf rolling mechanism

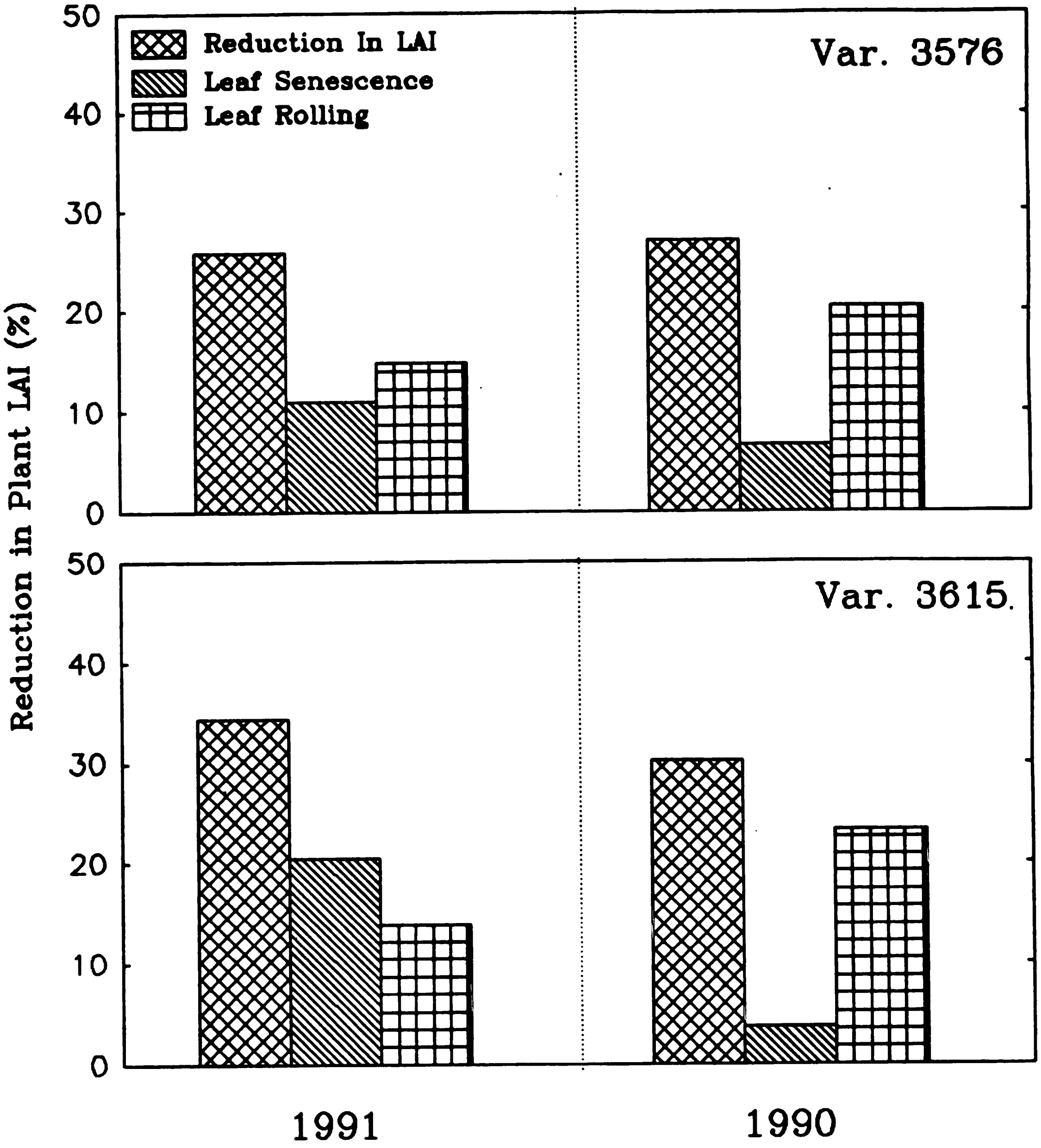

Figure 4.10. Effect of the water deficit period imposed in 1990 and 1991 on leaf rolling and leaf senescence response of both varieties.

was observed for pre-anthesis soil water deficit when reduction of the overall plant expansion was minimized (Chapter 2). During post-anthesis soil water deficit periods, the effectiveness of the leaf rolling mechanism occurred mainly during the beginning of the water deficit period and the leaf senescence mechanism was activated later when no further reduction in exposed LAI was possible by increasing leaf rolling.

The reduction in plant leaf area by accelerating leaf senescence during 1990 and 1991 is presented in Figures 4.11 and 4.12. In 1991, a rapid increase in leaf senescence was noted for both varieties as the water deficit became more severe, between DOY 211 and 214. This increase was caused by the low soil water availability associated with no further reductions in exposed LAI by leaf rolling. Water deficits reduce plant leaf area by accelerating the rate of leaf senescence of older leaves (Fisher and Hagan, 1965; Fischer and Kohn, 1966; Fischer, 1973; Slatyer, 1973; Ludlow, 1975). A similar pattern of leaf senescence was observed in 1990 for both varieties, except that the leaf senescence was less due to a shorter water deficit period. The disadvantage of accelerating leaf senescence with water deficit is the permanent reduction in plant leaf area, particularly after plant anthesis when the reduction in leaf area can not be recovered if a more favorable soil water conditions return late in the season.

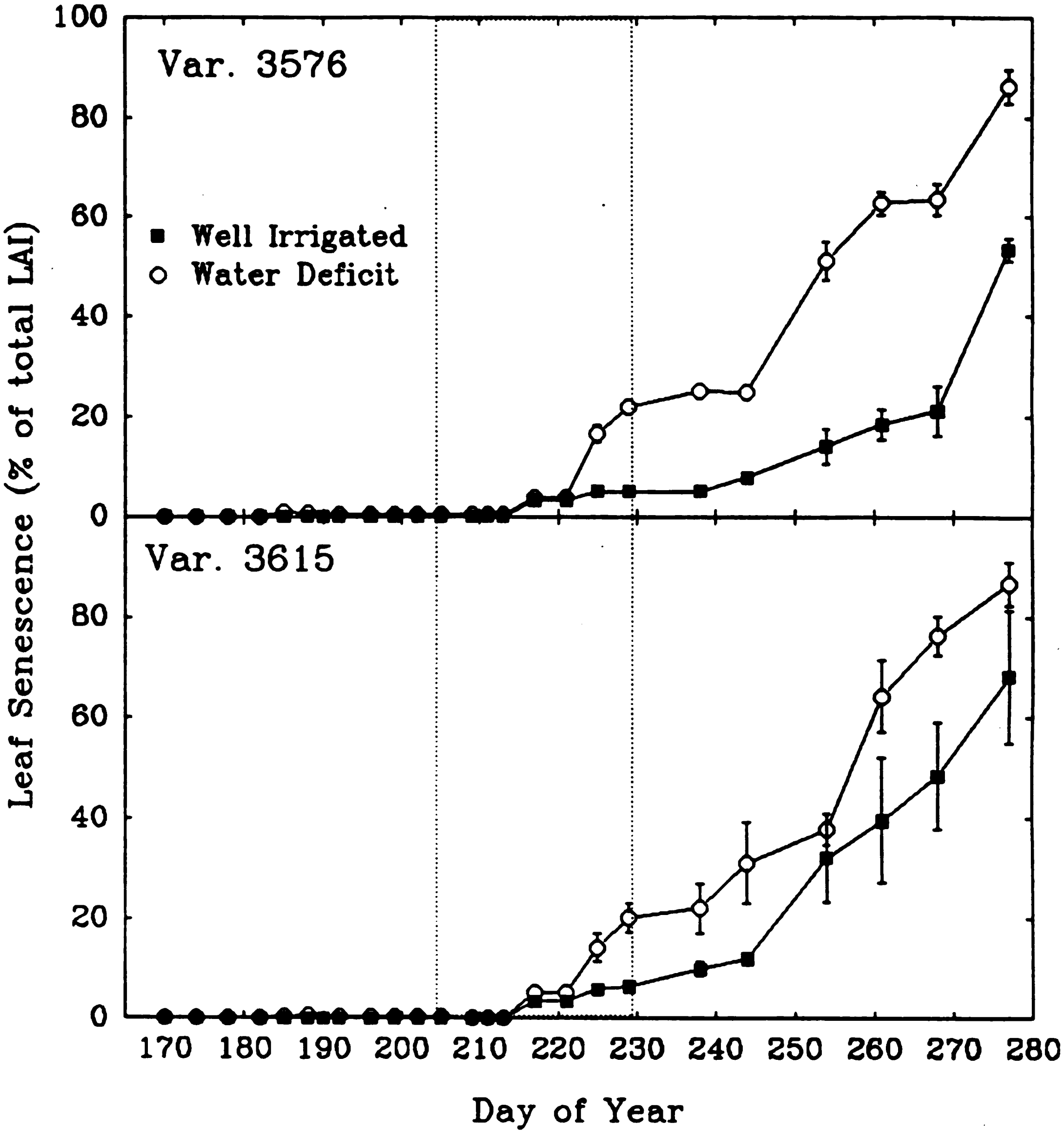

Figure 4.11. Percentage of plant leaf senescence for both treatments and varieties during 1990. The area limited by vertical dotted lines indicates the water deficit period.

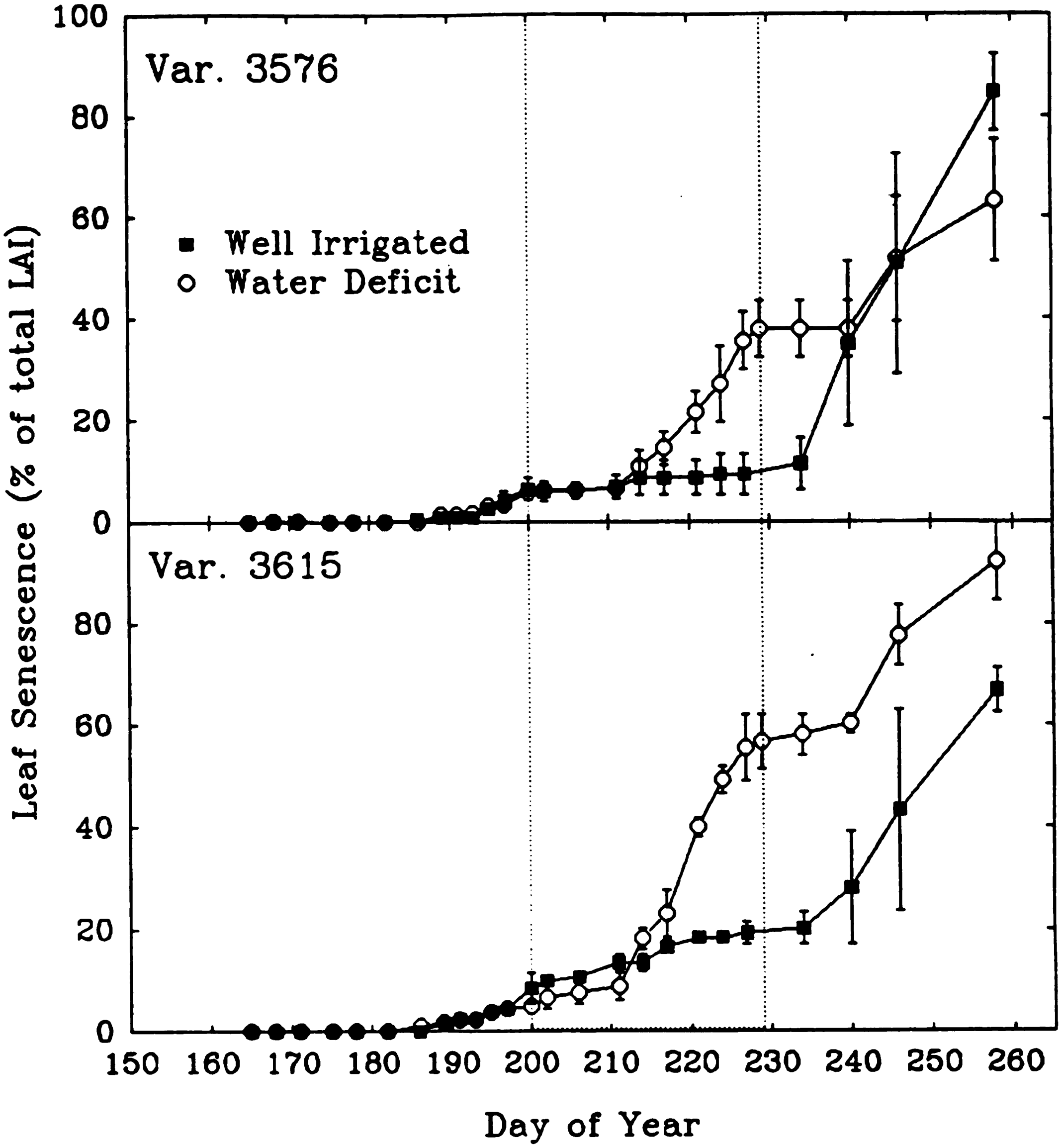

Figure 4.12. Percentage of plant leaf senescence for both treatments and varieties during 1991. The area limited by vertical dotted lines indicates the water deficit period.

Leaf Area Adjustments

The relationship between the fraction of total plant leaf area (difference between the maximum LAI produced and leaf senescence) and leaf rolling with the fraction of plant available water for both varieties during the water deficit period in 1991 is presented in Figure 4.13. The effect of the water deficit on leaf rolling began when the fraction of plant available water was below 0.61 and 0.64 for the variety 3576 and 3615. Leaf senescence, however, began when the fraction of plant available water fell below 0.51 and 0.54 for the variety 3576 and 3615. A rapid reduction in the fraction of total plant leaf area (leaf senescence) was observed for the variety 3615 as the water deficit became more severe. Hence, the beginning of the leaf senescence was delayed by 0.10 of the fraction of plant available water for both varieties. Values of fraction of plant available water below 0.30 are normally reported as the threshold to enhance leaf senescence (Grant *et al.*, 1989; Rosenthal *et al.*, 1987). During pre-anthesis soil water deficit (described in Chapter 2) a delay of 0.37 and 0.25 of the fraction of plant available water was observed between the activation of the leaf rolling and leaf senescence for the varieties 3576 and 3615. Although similar decreases in the fraction of plant available water was observed for both varieties during the post-anthesis soil water deficit period, the variety 3615 reduced its green LAI more rapidly than the variety 3576.

The reduction of plant active photosynthetic area by accelerating leaf senescence is one of the morphological adaptations that occurs after full leaf area development is achieved (Begg, 1980; Ludlow, 1975; Wolfe *et al.*, 1988). These

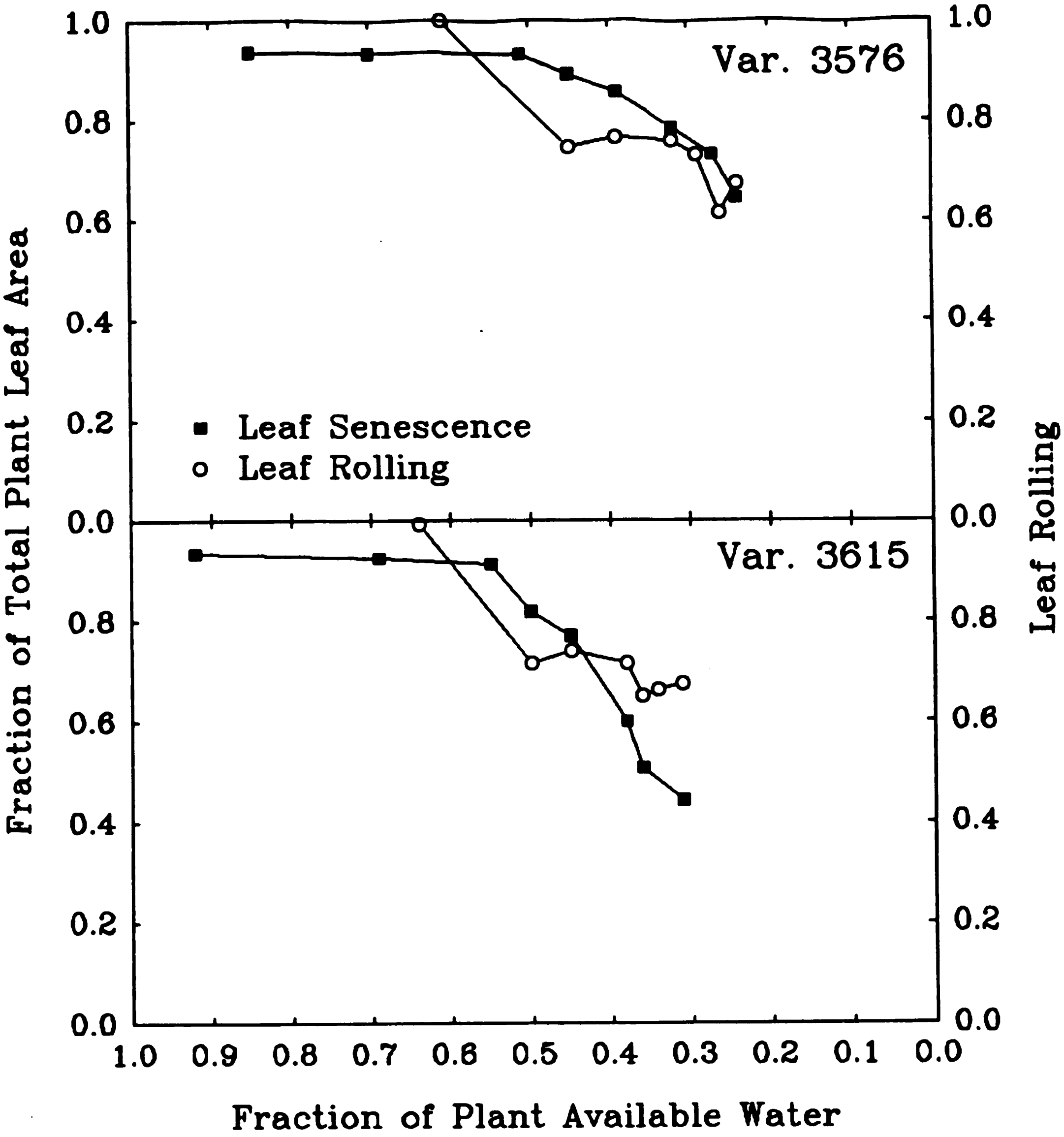

Figure 4.13. Relationship of the fraction of total plant leaf area (leaf senescence) and leaf rolling with the fraction of plant available water for both varieties during the water deficit period in 1991.

data indicate that the variety 3615 triggers the leaf senescence mechanism earlier than variety 3576 regardless of the time of occurrence of the water deficit period. This indicates that the variety 3576 may be better adapted to intermittent water deficit conditions during the growing season.

The term, osmotic adjustments, is widely used to describe osmoregulation in response to water deficit in higher plants where it is also used to describe changes in solute content after recovery from water deficit. The rapidity of the water deficit development appears to affect the crop response in terms of leaf senescence. Thus, leaf area duration of individual leaves is not seriously altered by water deficits that develop gradually or plants that have a higher osmoregulation capacity. According to Jones (1979), the stomata provide control of water loss, and consequently, of plant stress and the plant's ability to adapt to changing conditions. The three possible ways in which stomatal behavior can enhance drought resistance include: (i) conservation of limited supply of water; (ii) prevention of potential damaging plant water deficit; and (iii) maximization of total assimilation with the available water.

The relationship between radiation interception and measured and exposed LAI for the 1991 season is presented in Figure 4.14. Although a marked change in measured and exposed LAI was observed for both varieties during the water deficit period, little change in radiation interception was noted. Part of the radiation was intercepted by senesced leaves. At the end of the water deficit period, a slight increase in radiation interception was observed for both varieties because the non-

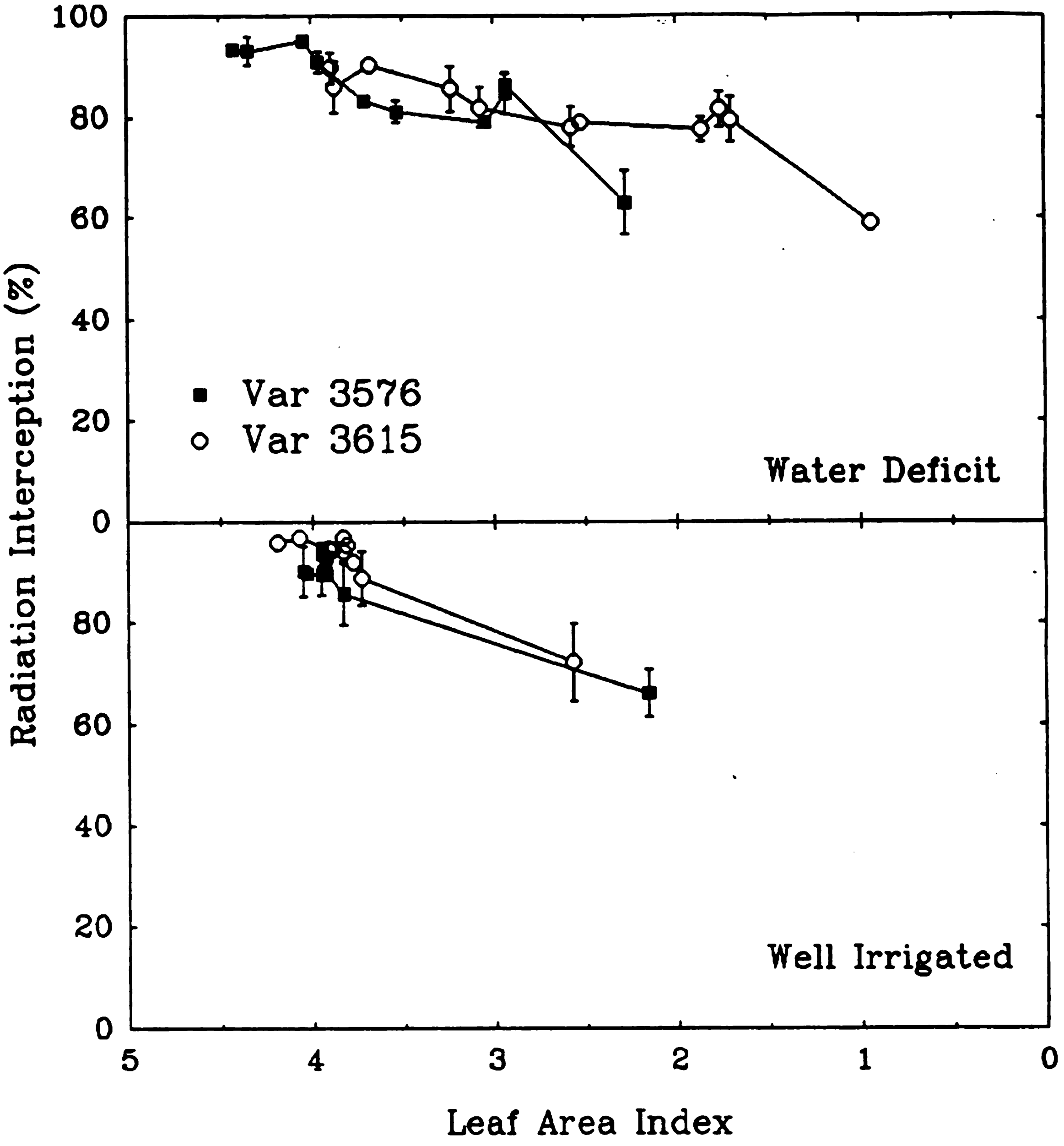

Figure 4.14. Relationship between radiation interception and measured LAI for both treatments and varieties during post-anthesis soil water deficit in 1991.

occurrence of leaf rolling after the irrigation was reapplied. Less reduction in measured LAI during the water deficit period was observed for the variety 3576 as compared to the variety 3615. On the other hand, under well-irrigated conditions, little change in radiation interception and measured LAI was observed, except near crop maturity when a rapid increase in leaf senescence decreased the green LAI and, consequently, decreased the radiation interception for both varieties.

Despite the similar water deficit conditions experienced for both varieties in 1991 (described in Chapter 3), a different crop performance was observed. Mechanisms that reduce plant photosynthesis and growth may also be beneficial under water deficit conditions if they result in an increase in water use efficiency and enable sufficient soil and plant water conservation to provide some reproductive or economic yield. Mechanisms such as stomatal conductance, leaf rolling, leaf orientation, leaf area maintenance may all enable plant survival through plant adjustments to water deficit conditions and water conservation for late stages of growth where the yield components are more sensitive to water deficits.

Ear Elongation and Weight

The ear and cob elongation for both treatments and varieties during 1991 are presented in Figure 4.15. Ear elongation of the water deficit treatment began to differ from the well-irrigated treatment, between two and 12 days after the water deficit was imposed for the variety 3615. For variety 3576, however, ear elongation began to differ between 12 and 17 days after the water deficit was imposed. A

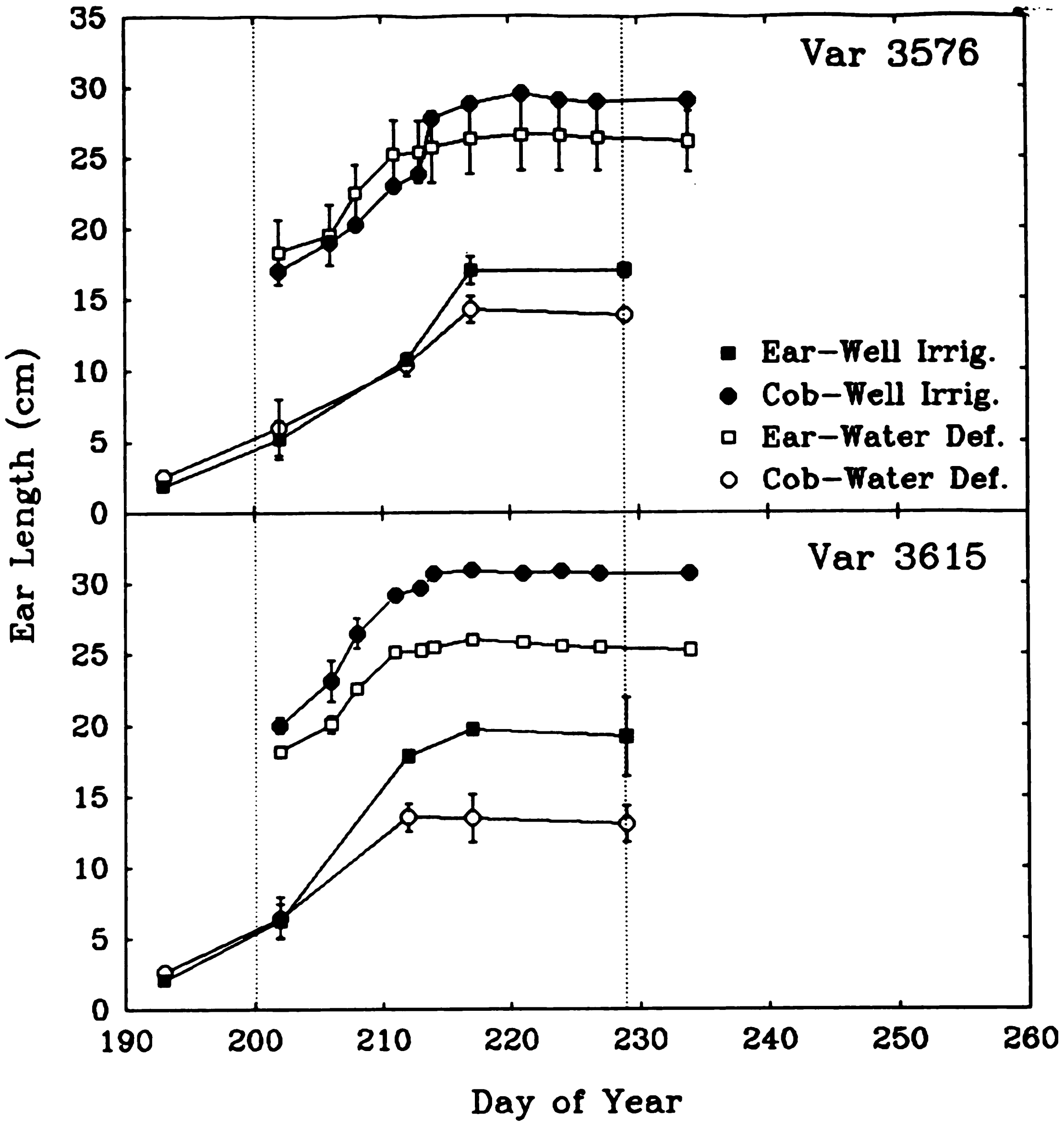

Figure 4.15. Expansion of maize ears and cobs for both treatments and varieties during 1991. The area limited by vertical dotted lines represents the duration of water deficit period.

greater reduction in the total length of the ear was observed for the variety 3615 as compared to the well-irrigated treatment. A similar trend was observed for cob elongation for both varieties in each treatment.

Although non-destructive measurements are often described as more accurate in estimating rates of crop growth, measurements of cob elongation was not as sensitive as ear elongation. The main reason was because the measurements of cob elongation started when the length of the cob was about 15 to 20 cm. Cobs and ears are protected by husks and are involved by the ear leaf ligule and, once the cob emerged from ear leaf ligule, the measurements started. Although measurements of ear elongation are preferable to cob elongation, cob elongation can easily provide a rapid non-destructive indication of the severity of the water deficit imposed during anthesis and grain filling periods. The final length of the cob and husks were reduced by the water deficit for both varieties.

Cumulative ear weight for both treatments and varieties during 1991 are presented in Figure 4.16. A marked reduction in the overall ear weight gain was observed for the variety 3615 during the water deficit period. At the end of the water deficit period (DOY 229), the weight of individual ears of the water deficit treatment was reduced by 38.5% and 66.7% compared to the well-irrigated treatment, for the varieties 3576 and 3615. The substantial reduction in the weight of the ears such as that observed for the variety 3615 during the water deficit period drastically reduced crop yield. At maturity, however, the weight of individual ears of the water deficit treatment was reduced by 26.6% and 47.3% as compared

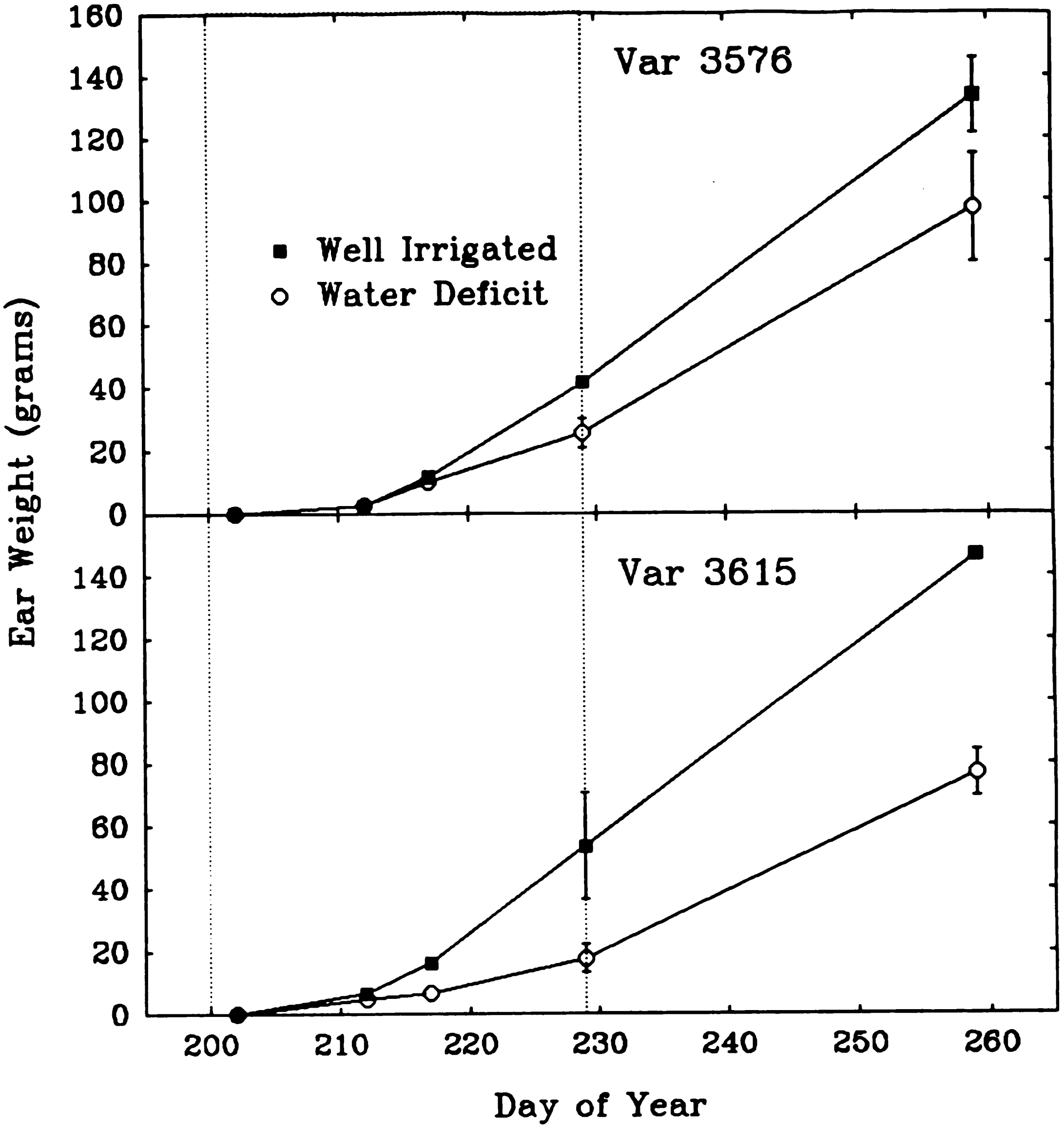

Figure 4.16. Cumulative ear weight of maize ears for both treatments and varieties during 1991. The area limited by vertical dotted lines represents the duration of water deficit period.

to the well-irrigated treatment for the varieties 3576 and 3615.

Grain Yield and Yield Components

Harvest data for both varieties and treatments during 1990 and 1991 is presented in Table 4.3. In 1991, the water deficit period reduced the grain yield by 28.3% and 44.9% for the variety 3576 and 3615 in relation to the well-irrigated treatment. In 1990, however, the reduction in yield was 84.5% and 80.9% for the variety 3576 and 3615 compared to the well-irrigated treatment. Although the water deficit imposed in 1990 was shorter as compared to 1991's water deficit, the water deficit occurred during anthesis. According to Begg and Turner (1976) water deficits that develop during or shortly after anthesis are considered the most devasting to crop yields, especially for determinate species such as maize. In 1991, the reduction in grain yield of the variety 3576 was mainly caused by a reduction in the number of kernels per ear and the kernel weight. However, for the variety 3615, the number of kernel rows per ear was also reduced. Grain weight reductions due to defoliation stress has been attributed to decreased rate of grain filling, shortened duration of grain filling, and combinations of both (Hanway, 1969; Jones and Simmons, 1983; Tollenaar and Daynard, 1978). A similar trend was observed in 1990 for both varieties.

A marked reduction in the number of fertilized kernels was observed in 1990 for both varieties. The reduction in grain number due to water deficits during anthesis has been attributed, in part, to poor synchronization in emergence of

Table 4.3. Yield and yield components for both varieties and treatments during 1990 and 1991. Values between parenthesis are standard errors.

Treatment	Variety	Yield	Number of Rows	Number of Grains	Kernel Weight
					kg/ha
grams					
		1991			
		Kg ha^{-1}			g/seed
Well-Irrigated	3576	7927.2 (413.4)	15.65 (0.26)	431.3 (14.7)	0.26 (0.01)
	3615	7570.4 (312.9)	15.33 (0.36)	445.0 (13.6)	0.24 (0.01)
Water Deficit	3576	5686.0 (881.4)	17.00 (0.45)	349.3 (31.5)	0.19 (0.02)
	3615	4167.0 (849.8)	11.43 (0.67)	260.6 (51.2)	0.19 (0.01)
		1990			
Well-Irrigated	3576	7844.4 (267.6)	16.20 (0.20)	362.5 (16.6)	0.30 (0.01)
	3615	10442.9 (724.8)	14.80 (0.33)	512.8 (24.5)	0.28 (0.01)
Water Deficit	3576	1219.5 (122.2)	13.25 (0.75)	90.5 (11.95)	0.20 (0.02)
	3615	2000.4 (631.85)	10.70 (1.76)	72.2 (43.13)	0.15 (0.02)

male and female flower components (Freier *et al.*, 1984; Hall *et al.*, 1982; Herrero and Johnson, 1981). This may be caused by the earlier application of the water deficit period as compared to 1991. The number of kernel rows was more affected for the variety 3615 in both years. The effect of water deficits extending into the grain filling period has been shown to be the time when grain weights are most reduced by water deficits (Grant *et al.*, 1989; Jurgens *et al.*, 1978; NeSmith, 1990; Westgate and Boyer, 1985).

Conclusions

Plant responses to post-anthesis soil water deficit are complex phenomena and several mechanisms exist by which maize plants alleviate the effects of water deficits. During the post-anthesis soil water deficit period, the effectiveness of the leaf rolling mechanism occurred mainly during the beginning of the water deficit period and leaf senescence was activated later when no further reduction in exposed plant leaf area was possible by increasing leaf rolling. The effect of water deficit on leaf rolling began when the fraction of plant available water was below 0.61-0.64 for both varieties. Leaf senescence, however, began when the fraction of plant available water fell below 0.51-0.54. Although similar reduction in exposed LAI was observed for both varieties in each year, a distinct effect of the water deficit in reducing green leaf area (leaf senescence) and exposed LAI was observed between the two varieties. Similar contributions of leaf rolling to the reduction of exposed LAI were observed for both varieties. However, leaf senescence was triggered earlier for the variety 3615 and a more marked reduction in green LAI was observed. The greater reduction in plant leaf area for the variety 3615 reduced the plant photosynthetic area and the radiation intercepted and, consequently, lowered the capacity of this variety to increase the production and allocation of photosynthates after the water deficit was relieved. These results indicate that the variety 3576 may be better adapted to intermittent water deficit conditions during the growing season.

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CHAPTER 5

Responses of Maize Plants, Grown on a Loam Soil, to a Terminal Water Deficit Imposed During Vegetative Growth Stage.

Abstract

Different criteria have been used to determine the timing and duration of water deficits. Despite the abundant literature on water deficit effects on crop growth and development, few studies have investigated the sensitivity of the indicators of soil water status among different soils. The objective of this study was to: (i) identify differences in interception of solar radiation and leaf area development between two maize varieties; and (ii) to analyze the intensity of the water deficit in maize growth. Pioneer varieties 3576 and 3615 were subjected to two irrigation managements: well-irrigated and terminal soil water deficit. Results of this study indicate that water deficits imposed during the vegetative growth in plants grown on a large quantity of stored water have little effect on plant elongation and crop growth. Crop performance during the vegetative growth was more closely linked to the amount of soil available water than to the fraction of plant available water. Radiation interception during crop vegetative growth was independent of the soil water deficit in the loamy textured soil under conditions of relatively low VPD. Aboveground crop biomass accumulation was reduced when the total amount of plant available water was lower than 35 mm.

Introduction

Different criteria have been used to determine the timing and duration of water deficits. Despite the abundant literature available about water deficit effects on crop growth and development, few studies have investigated the sensitivity of the indicators of soil moisture status among different soil types. Much attention has been given to the problems associated with the evaluation of the limits of soil water availability and the root growth dynamics. However, considerations about the total amount of plant water available in the soil profile to affect plant growth and development have received little attention. According to Ritchie (1981), the fraction of plant available water above 0.70 is usually assumed to cause little or no effect on plant transpiration and plant growth. Values about 0.50 have been reported (Rosenthal *et al.*, 1987) to cause a significant reduction in leaf expansion rates and values below 0.30 are normally reported as the range where no significant leaf expansion occurs and leaf senescence is enhanced (Grant *et al.*, 1989).

Soil water available to plants is influenced by several mechanisms associated with water uptake (depth of the root system, root density and homogeneity, distribution, and permeability) and soil characteristics (available water, water movement, soil impedance). These factors, combined with evaporative demand, determine the plant water status and are associated with plant water conservation mechanisms (stomatal resistance, leaf rolling, leaf orientation, leaf area and overall canopy architecture). Furthermore, plant sensitivity to water deficit depends on the plant's stage of growth and development. Plant available water and fraction of available water have been used as indicators of soil water deficits (Denmead and Shaw, 1962; Ritchie *et al.*, 1972; Meyer and Green, 1980; Rosenthal *et al.*, 1987). These water deficit indicators have advantages over other water deficit factors because they are primarily dependent on water use rates and physical properties of the soil (Ritchie *et al.*, 1972).

According to Jordan (1983) the gradual development of water deficit by plants growing in most field situations allows slow and continual adjustments in physiological processes. These adjustments are eventually manifested as alterations in growth and development. Osmotic adjustments result from accumulation of solutes within the cell allowing turgor driven processes, such as expansion growth and stomatal opening to continue at a reduced rate at lower soil water contents (Turner and Jones, 1980 and Morgan, 1984). According to Ludlow and Muchow (1990), under increasing soil dehydration, differences in the rooting pattern may change the amount and timing of water availability to crops. As the water deficit becomes more severe, rates of carbon use for cell expansion and maintenance fall, but cell expansion is more severely affected. The decline in growth components results from reduced photosynthate production during water deficit periods (Jordan, 1983).

Water deficits reduce plant leaf area by accelerating the rate of senescence of older leaves (Fischer and Hagan, 1965; Fischer and Kohn, 1966; Fischer, 1973; Slatyer, 1973; Ludlow, 1975). The senescence of individual leaves is not seriously altered by water deficits that develop gradually, but rapid development of water deficit may accelerate senescence of lower leaves (Jordan, 1983). Water deficit during vegetative development affects leaf growth components (total number of leaves, leaf elongation and senescence), and therefore reduces the plant leaf area (Rosenthal *et al.*, 1987). According to Claaseen and Shaw (1970), and Denmead and Shaw (1960) the primary influence of water deficit on the reduction of grain yield was caused by the reduced leaf size, particularly during the crop establishment when there is incomplete light interception (Begg, 1980), rather than changes in the net assimilation rate.

The objective of this study was to: (i) identify differences in interception of solar radiation and leaf area development between two maize varieties, and (ii) to analyze the intensity of the water deficit in maize growth. Research has shown that any water deficit occurring during the growth and development of maize results in a loss of grain yield. The magnitude of the reduction depends on the stage of crop development, duration, intensity, soil type, and the susceptibility of the maize variety to water deficit.

Methodology

This experiment was conducted in 1990 and 1991 at the Kellogg Biological Station, near Kalamazoo, Michigan. A rain shelter, described by Martin *et al.*, (1988), was used to prevent rainfall on the experiment.

Kalamazoo loam (mesic Typic Hapludalfs) was the soil at the site. Maize varieties, Pioneer 3615 and Pioneer 3576, were planted north-to-south at a high density on May 18 (day of year (DOY) 138) in 1990 and on May 27 (DOY 147) in 1991. Emergence occurred on May 28 (DOY 148) in 1990 and on May 31 (DOY 151) in 1991. Plants were thinned in the seedling stage to a plant density of 7.2 plants/m^2. Weeds were controlled manually during both years. Plot size was 4.6 m x 6.2 m. Maize was planted in six rows, 0.71 m wide, giving two border rows and four main rows in each plot. The experimental layout was a split-plot design, with irrigation treatment as main plot and maize hybrids as subplots.

Irrigation water was applied using an overhead Toro FS-LG series sprinkler system, mounted upside down on the trusses of the rain shelter operating with a constant pressure of 103.5 Kg.Pa^{-1}, at a rate of approximately 25 mm.hr^{-1} (NeSmith *et al.*, 1990). Two irrigation treatments were established: (i) well-irrigated (irrigation was applied to maintain the fraction of plant available water above 0.70); and (ii) terminal water deficit. The water deficit period (period between subsequent irrigations) occurred from DOY 171 and from DOY 172 to grain harvest in 1990 and 1991. The irrigation amounts applied on each treatment in 1990 and 1991 are presented in Figure 5.1.

Before emergence, fertilizer was applied at rates of 60 Kg N ha^{-1} (45-0-0), 200 Kg P ha^{-1} (0-46-0), and 60 Kg K ha^{-1} (0-0-60). Nitrogen was applied at a rate of 100 Kg ha^{-1} 19 days after emergence (DOY 166) and 17 days after emergence (DOY 168), in 1990 and 1991.

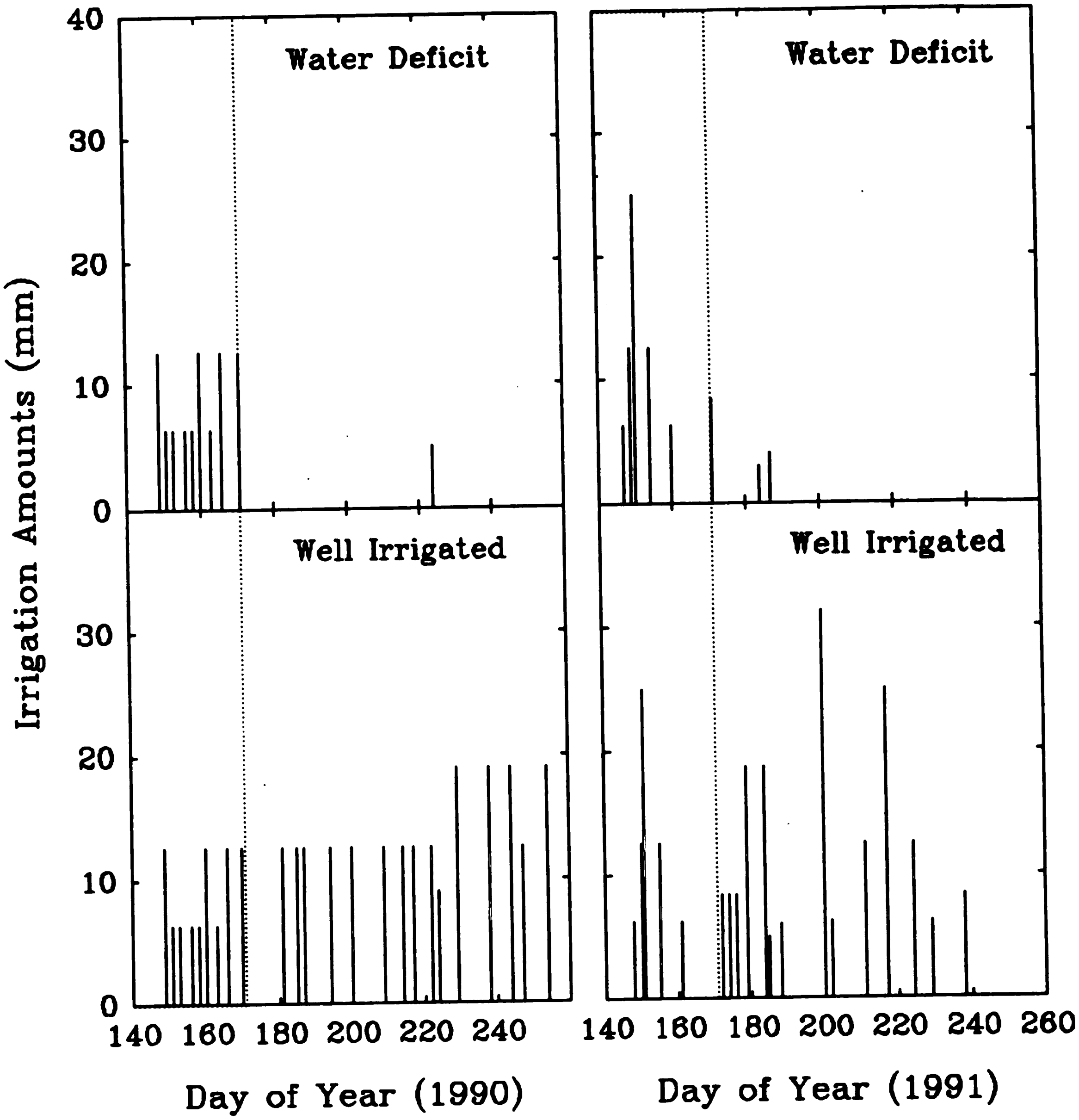

Figure 5.1 Irrigation amounts (mm) applied on each treatment in 1990 and 1991. The area limited by vertical dotted lines represent the period of vegetative soil water deficit.

Soon after emergence, four plants per treatment were randomly selected and marked for nondestructive measurements throughout the season. Leaf area were measured three times a week once the leaves emerged from the whorl until the leaf ligule appeared. The area of each leaf was determined from measurements of leaf length and maximum leaf width multiplied by 0.75 (Stickler *et al.*, 1961).

Photosynthetically active radiation (PAR) interception was measured several times daily in four marked sites in each plot, under clear sky conditions. At ground level, a minimum of three observations were made to compute an individual measurement in each side. The line quantum sensor (Model LI-191SB, Li-cor, Lincoln, NE) was leveled, placed perpendicular to the row direction and positioned so that no shadows from the handle influenced measurement. Canopy incident radiation was measured by placing the line quantum sensor above the crop.

A minimum data set recorder (Model LI-1200, Li-cor, Lincoln, NE) located outside of the rain shelter was used to record the solar radiation, minimum and maximum air temperature and rainfall. Vapor pressure deficit of the air (VPD) was calculated as the difference between the saturation vapor pressure, e_s (minimum temperature used as dew point temperature) and the actual vapor pressure, e_a (the drying power of the air was assumed to be the daily average temperature). Daily values of maximum and minimum temperature, solar radiation (MJ/m^2) and vapor pressure deficit of the air (KPa) for 1990 and 1991 growing seasons are shown in Figures 5.2 and 5.3.

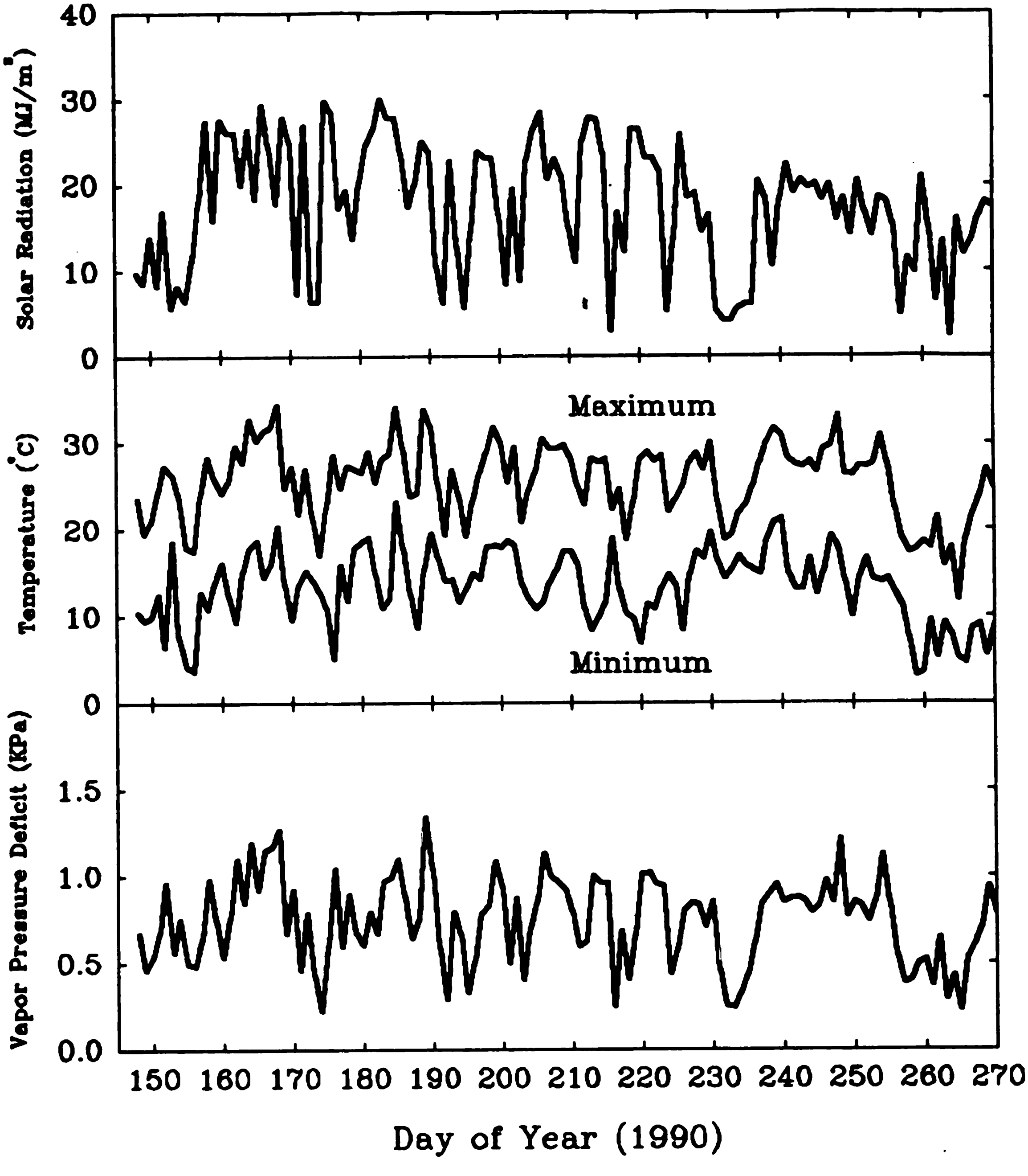

Figure 5.2. Daily incident solar radiation, daily maximum and minimum temperatures and daily vapor pressure deficit during 1990.

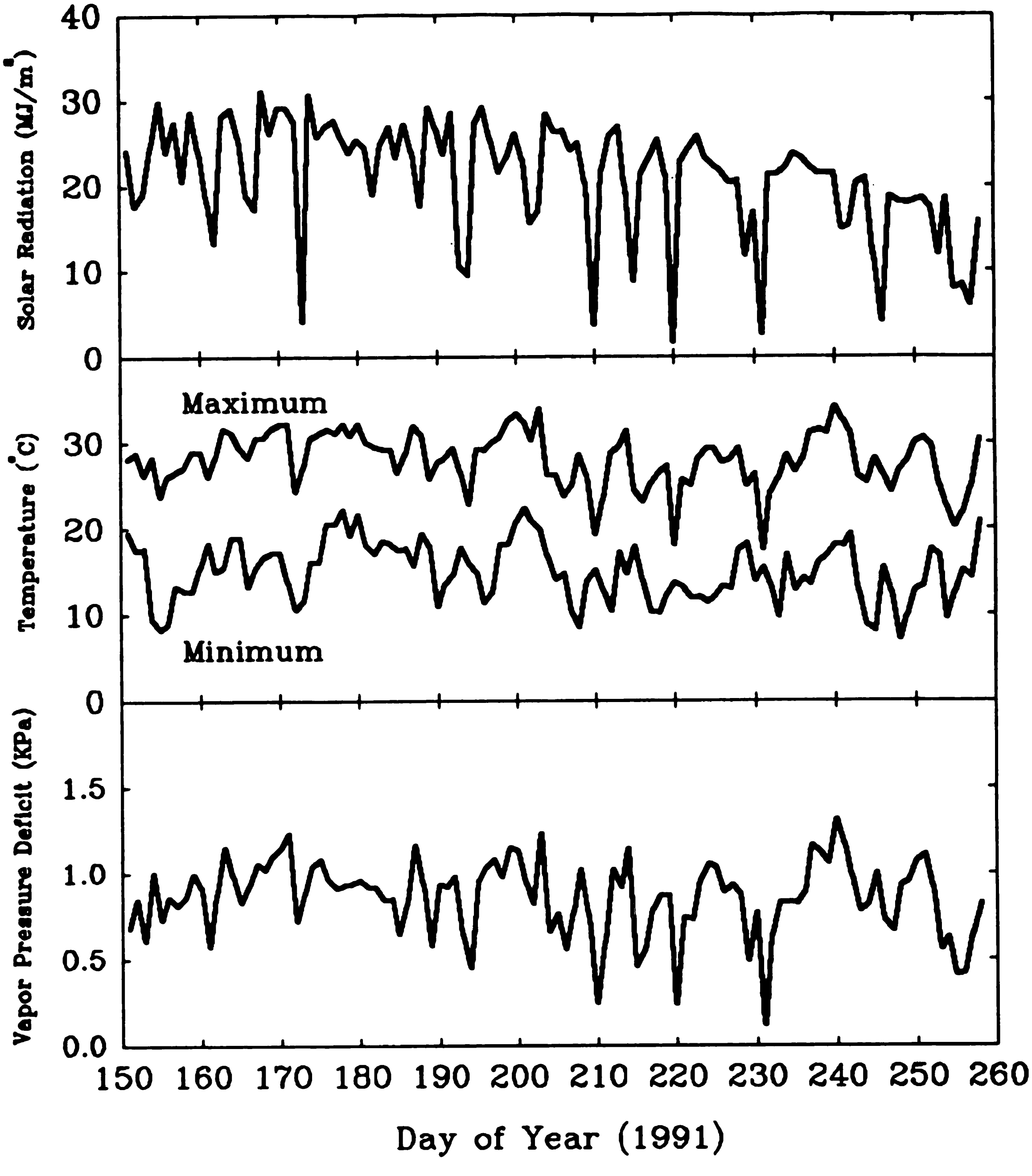

Figure 5.3. Daily incident solar radiation, daily maximum and minimum temperatures and daily vapor pressure deficit during 1991.

Soil water content was measured by the neutron scattering technique (CPN, Model 503DR). Two access tubes (aluminum, 50 mm i.d.) were seated in the center row of each plot. Readings were made twice a week at 25 cm increments to a depth of 1.5 m. Field measurements of soil water content and neutron counts were used to calibrate neutron counts into volumetric water content. Regression equations, by depth, were determined using only two points: dry point (soil was allowed to dry for 85 days); and wet point (soil water content near saturation). Soil water content in the 0-12.5 cm and 12.5-25 cm layers were determined by the time domain reflectometry (TDR) technique. Steel rods were installed at each depth leaving 2 cm above the soil surface. Volumetric water content was estimated using the equations described by Topp *et al.*, (1982).

Soil water availability in *mm* of equivalent depth and plant available water was calculated for the top 1.5 m of profile, as the difference between volumetric water content of the soil and water content at the lower limit of plant-extractable soil water in the rooting depth. The fraction of plant available water was calculated by the ratio between plant available water and the maximum plant available water in the rooting depth.

Results and Discussions

Weather conditions observed during the experiment in both years are presented in Figures 5.2 and 5.3. During the duration of the terminal water deficit period, from DOY 171 in 1990 and from DOY 172 in 1991 to the grain harvest, different weather climatic conditions were observed. The mean daily incident radiation was 17.73 MJ/m^2 and 20.32 MJ/m^2, the mean daily minimum temperature was 14.42 °C and 15.01 °C, the mean daily maximum temperature was 26.29 °C and 27.84 °C and, the average vapor pressure deficit of the air was 0.74 KPa and 0.91 KPa for 1990 and 1991.

Soil Water Extraction

The 1991 season soil water contents are presented in Figures 5.4 and 5.5 for variety 3576 and 3615, for the upper 75 cm of the soil profile. A similar pattern of soil profile drying was observed for both varieties during the water deficit treatment. A very different pattern was observed for the well-irrigated treatment, especially for the variety 3615 (Figure 5.5). The low values of water content were caused by non-uniform irrigation applications. Although water was applied, it was sprayed near the plot borders adding little or no water on the part of the plot where the soil water measurements were taken.

Soil water depletion rate (mm/day) during the crop vegetative growth in 1991 water deficit period is shown for both varieties in Figure 5.6. A noted increase in water extraction from the layer 25-50 cm depth began about 10 days after the water deficit was imposed (DOY 172). A steady soil water extraction was observed for both varieties in this layer until DOY 200 (near the end of the plant vegetative growth). The nearly steady water extraction from this layer was due to

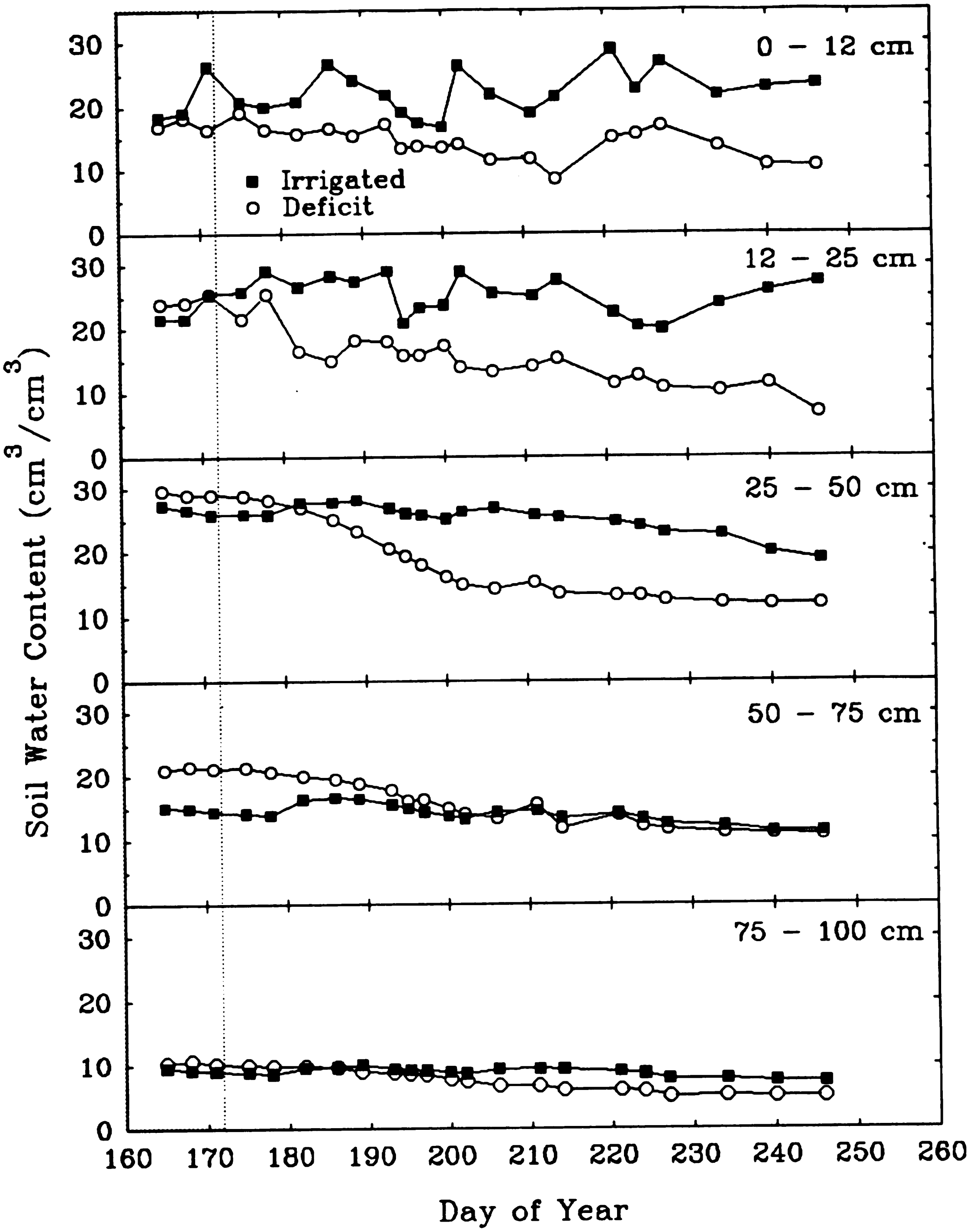

Figure 5.4. Soil water content with depth and time for the variety 3576 in 1991. The area limited by vertical dotted lines represents the period of soil water deficit.

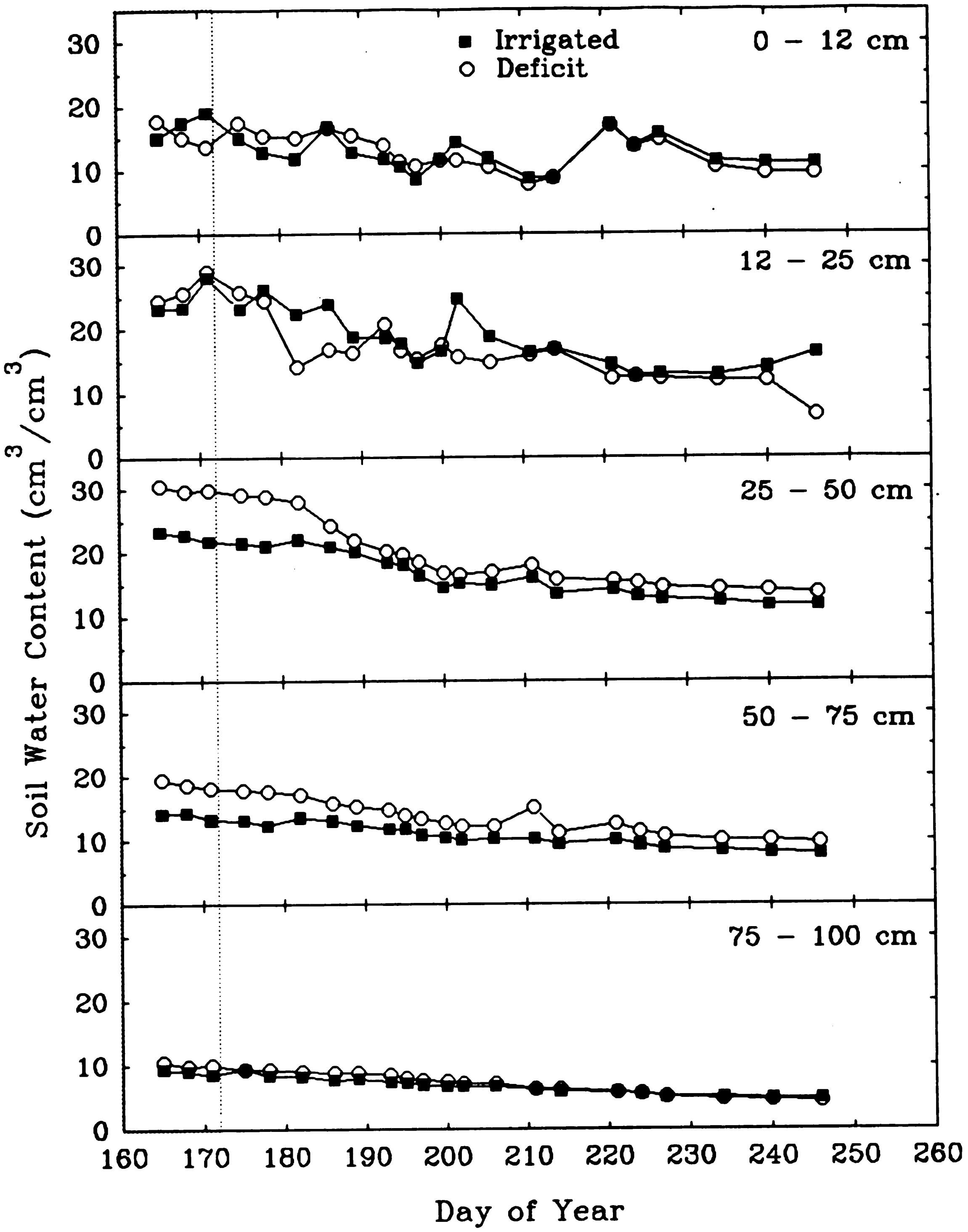

Figure 5.5. Soil water content with depth and time for the variety 3615 in 1991. The area limited by vertical dotted lines represents the period of soil water deficit.

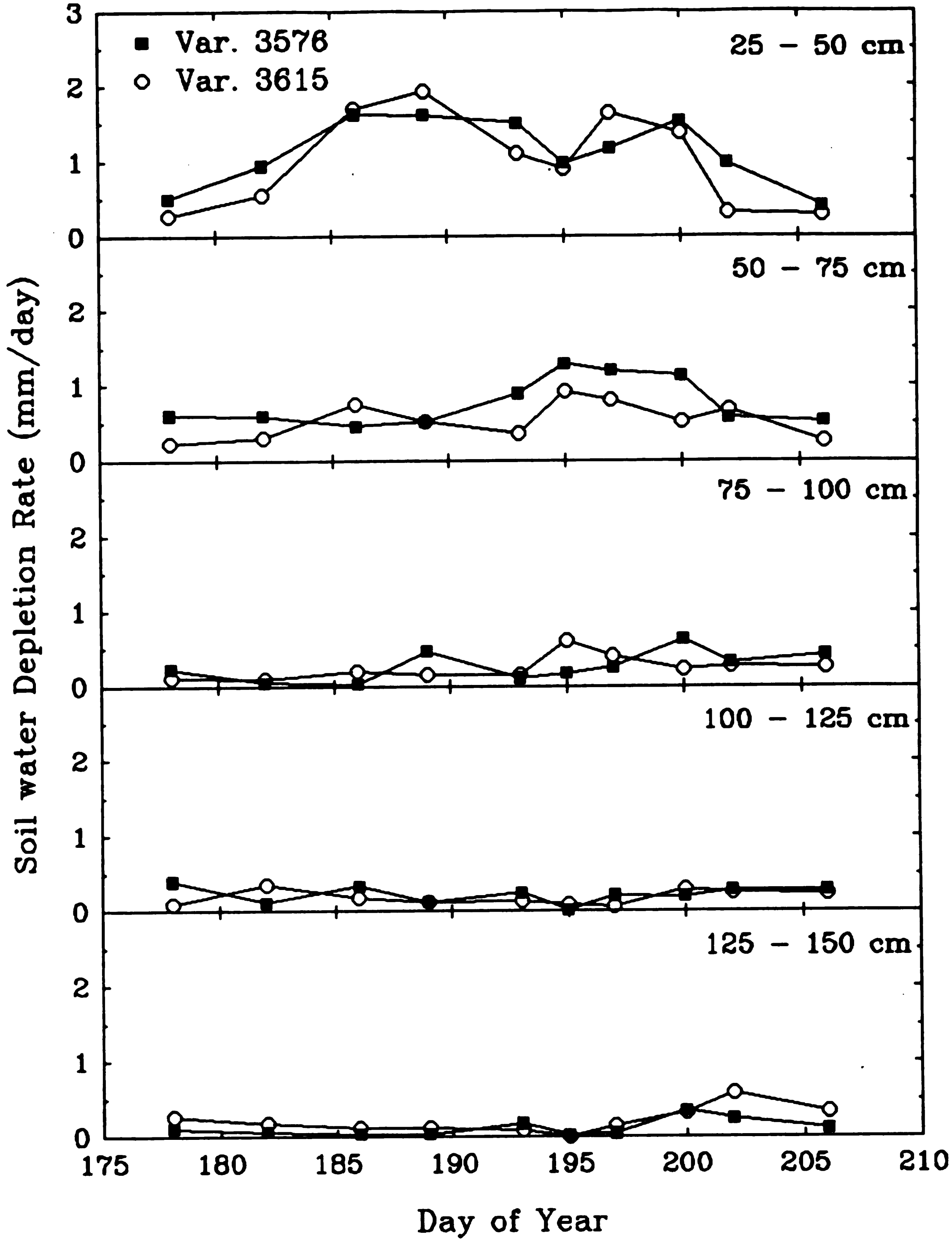

Figure 5.6. Soil water depletion rates with time for both varieties for the top 150 cm of the soil profile during the soil water deficit in 1991.

its higher clay content which provided additional soil water storage. This layer was almost depleted of its available water at the end of vegetative growth. An increase in water extraction rates for the layers 50-75 cm and 75-100 cm depths was only observed after the decline in soil extraction of the adjacent upper layer (25-50 cm depth). By the end of the crop vegetative growth (DOY 200) a marked increase in water extraction was noted in the lower layers of the soil profile (125-150 cm depth). No difference in the soil water extraction pattern was observed between the two varieties during the vegetative growth. The descent of the extraction front can be delayed on soils of high available water content (Meinke *et al.*, 1990). According to ODA (1987), the extraction front is in someway slightly sensitive to the balance between soil water supply and evaporative demand and, the extraction front can be faster on sand soil or in environments where the VPD is high.

At the end of the crop cycle (DOY 246) very little available water was left in the soil profile (less than 10 mm). During the vegetative crop growth no indication of plant water deficit was noted on either variety. On the other hand, the water deficit period imposed in the Spinks soil (discussed in the previous chapter) from DOY 171 to 200 caused a large reduction in plant growth. The total amount of water extracted from the Kalamazoo soil profile between DOY 176 and DOY 200 was 71.2 mm and 71.8 mm for the variety 3576 and 3615. During the specified period (24 days), rates of soil water extraction were 2.97 mm/day and 2.99 mm/day for the maize variety 3576 and 3615. The cause of discrepancy of the soil water deficits between the two soil types was due to the higher soil water availability in the Kalamazoo soil that provided enough water to both varieties during vegetative growth. Gardner (1960) showed theoretically that on soils with high available water contents, the critical values of fraction of plant available water should be smaller than on soils with low available water.

Soil Water Availability

Soil water availability and fraction of plant available water of the top 150 cm of the soil profile for both treatments and varieties are presented in Figure 5.7. During the water deficit period the soil water availability declined steadily over time. Fraction of plant available water has been largely used as an indicator of the plant moisture status (Denmead and Shaw, 1962; Ritchie *et al.*, 1972; Meyer and Green, 1980; Rosenthal *et al.*, 1987; Ritchie and Amato, 1990). The plant available water for plants depends of the soil physical properties and the distribution and activity of the plant root system. Frequently, however, for clay soils and loam soils, the index of water deficit does not always reflect the actual plant water status and, consequently, the crop performance. According to Rosenthal *et al.*, (1989), the critical fraction of plant available water varies with the level of VPD. In their crop growth model when the evaporative demand is high (7 mm/day) the critical value is 0.30 but if the demand is only 2 mm/day the critical value is 0.17. However, many crop growth models assume that transpiration is able to meet demand until 0.30 of the fraction of the available water is remaining in the root zone (Sinclair, 1986).

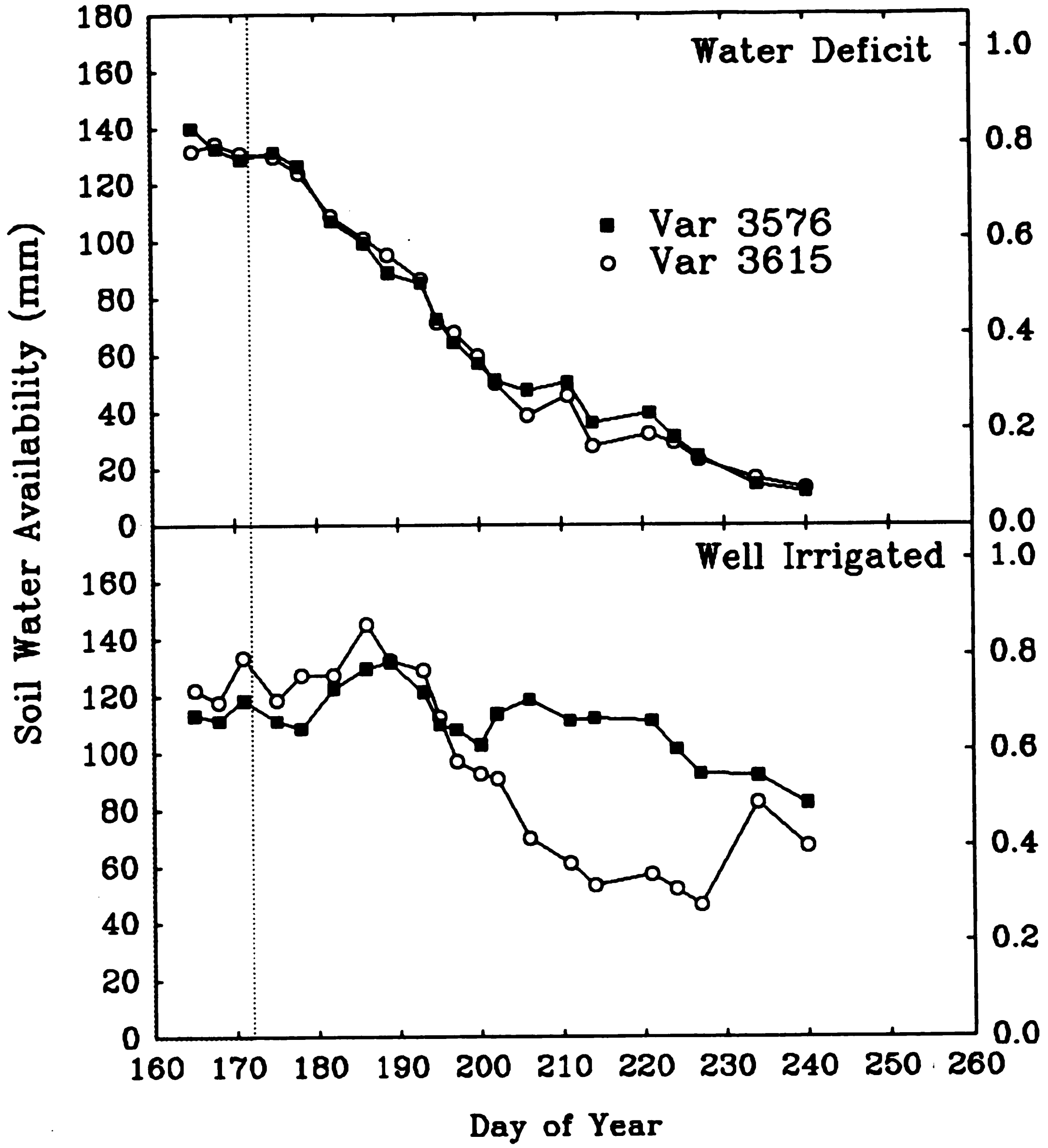

Figure 5.7. Total soil water availability with time for both varieties and treatments for the top 150 cm of the soil profile in 1991. The area to the right of the vertical dotted line represents the period of water deficit.

The crop performance during the vegetative growth stage was more closely linked to the amount of soil available water than to the fraction of plant available water. During vegetative growth no significant changes in plant leaf area was noted for either variety, although the fraction of plant available water showed a marked decrease from 0.80 (at the beginning of the drying period, DOY 172) to 0.23 and 0.28 (at the end of the vegetative growth, DOY 206), for the varieties 3576 and 3615 (Figure 5.7). In the same period, the total amount of soil available water decreased from 129 to 47 mm and from 131 to 39 mm, for the variety 3576 and 3615. In a similar experiment conducted by Robertson (1991), the slowing of sorghum leaf expansion, grown in clay soil, began when the fraction of plant available water in the root zone was below between 0.35-0.30.

Plant Leaf Area and Senescence

The LAI for both treatments and varieties during 1990 and 1991 are shown in Figures 5.8 and 5.9. Little treatment effect was observed between the two varieties during the crop vegetative growth stage during either years. A marked decrease in LAI was observed in both years after the silking for both varieties under the imposed soil water deficit. In 1991, a sharp decline in LAI was only noted when the total soil water availability fell below 38 mm (DOY 212) and 35 mm (DOY 222) for variety 3576 and 3615. This decline in LAI was caused by a rapid increase in leaf senescence (Figure 5.10). The variety 3576 senesced its leaves earlier than the variety 3615 although both had the same amount of available water

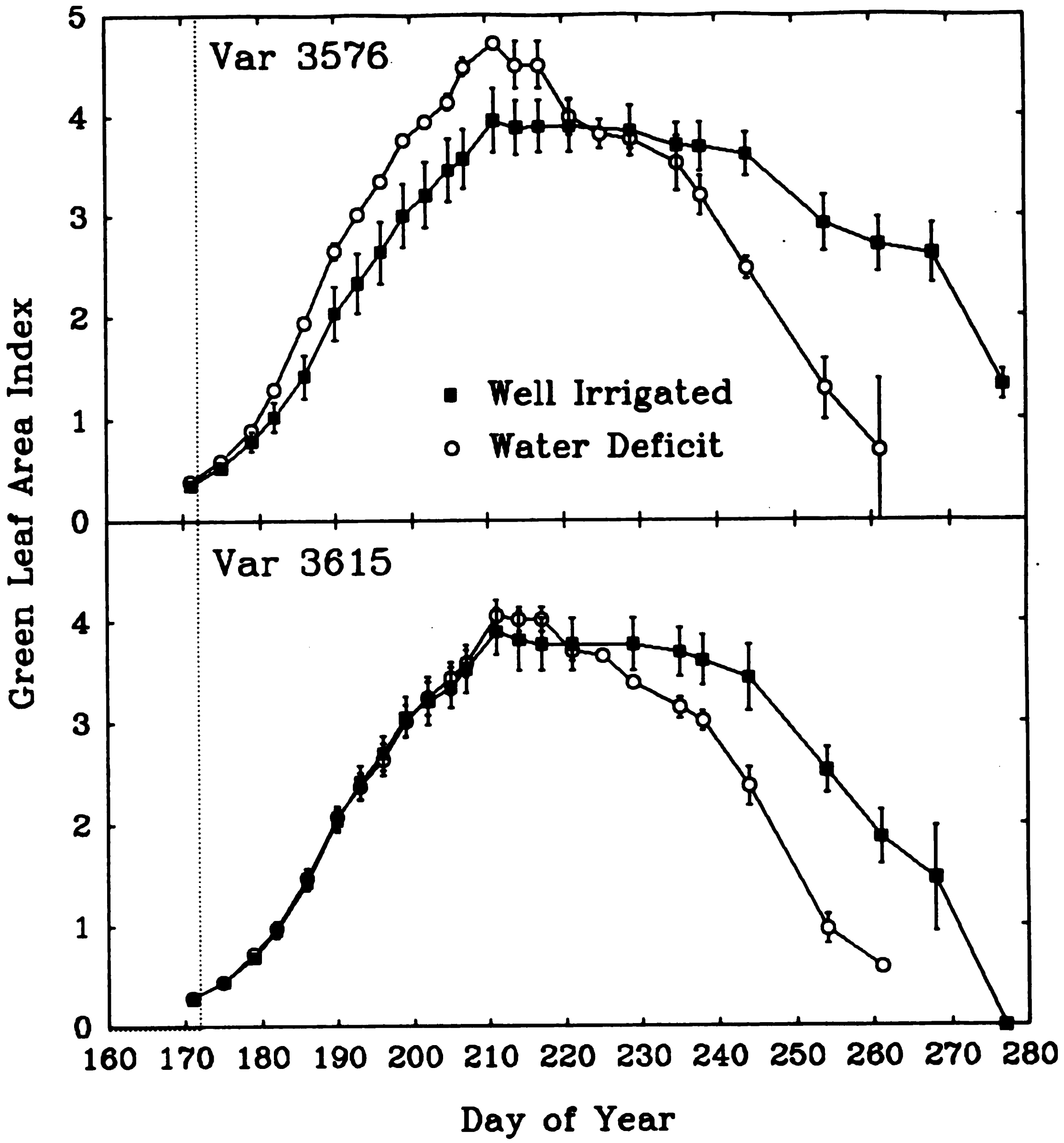

Figure 5.8. Green leaf area index for both treatments and varieties during 1990. The area to the right of the vertical dotted line indicates the water deficit period.

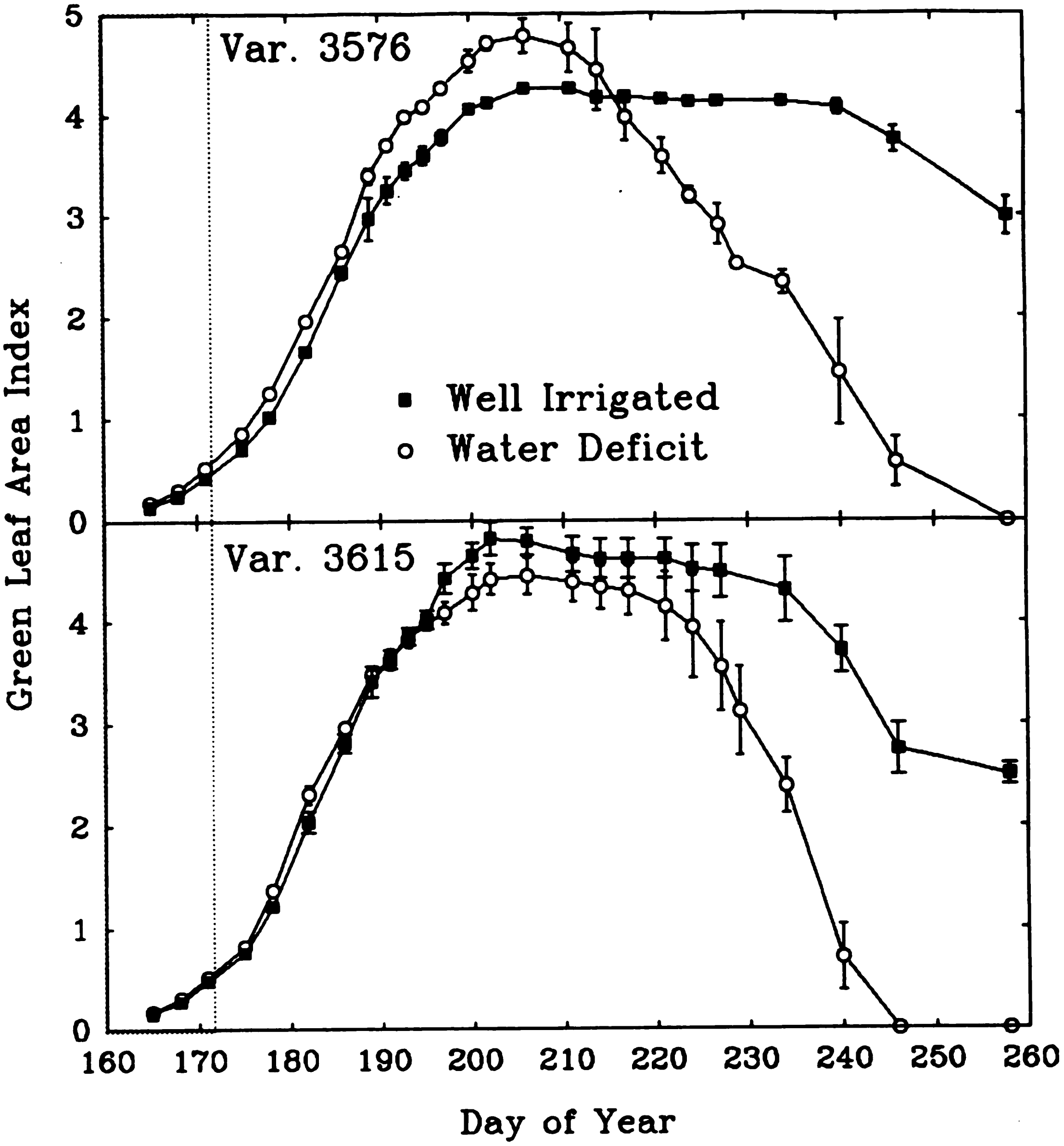

Figure 5.9. Green leaf area index for both treatments and varieties during 1991. The area to the right of the vertical dotted line indicates the water deficit period.

(Figure 5.7) and a similar plant leaf area (Figure 5.9). A similar pattern of leaf senescence was observed near the crop maturity for both varieties. Jordan (1983) noted that sorghum that received irrigation early in the season and developed a large LAI showed a greater leaf senescence during subsequent water deficit than plants with lower initial leaf area.

The leaf senescence was enhanced on DOY 212 and DOY 222 for the varieties 3576 and 3615 where the fraction of plant available water was about 0.18 for both varieties. Values below 0.30 are normally reported as the threshold to enhance leaf senescence (Grant *et al.*, 1989; Rosenthal *et al.*, 1987). However, Robertson (1991) also found a remarkably low fraction of plant available water (0.14) at which the leaf senescence began.

The reduction of the plant active photosynthetic area by accelerating leaf senescence is one the morphological adaptations that occurs after the full area development is achieved (Begg, 1980; Ludlow, 1975; Wolf *et al.*, 1988). Water deficits that develop after anthesis appear to elicit a more drastic response in terms of leaf senescence (Fischer and Kohn, 1966). However, according to Wilson and Allison (1978), the leaf area duration of individual leaves is not seriously altered by water deficits that develop gradually. Rapid development of water deficits, however, may accelerate lower leaf senescence.

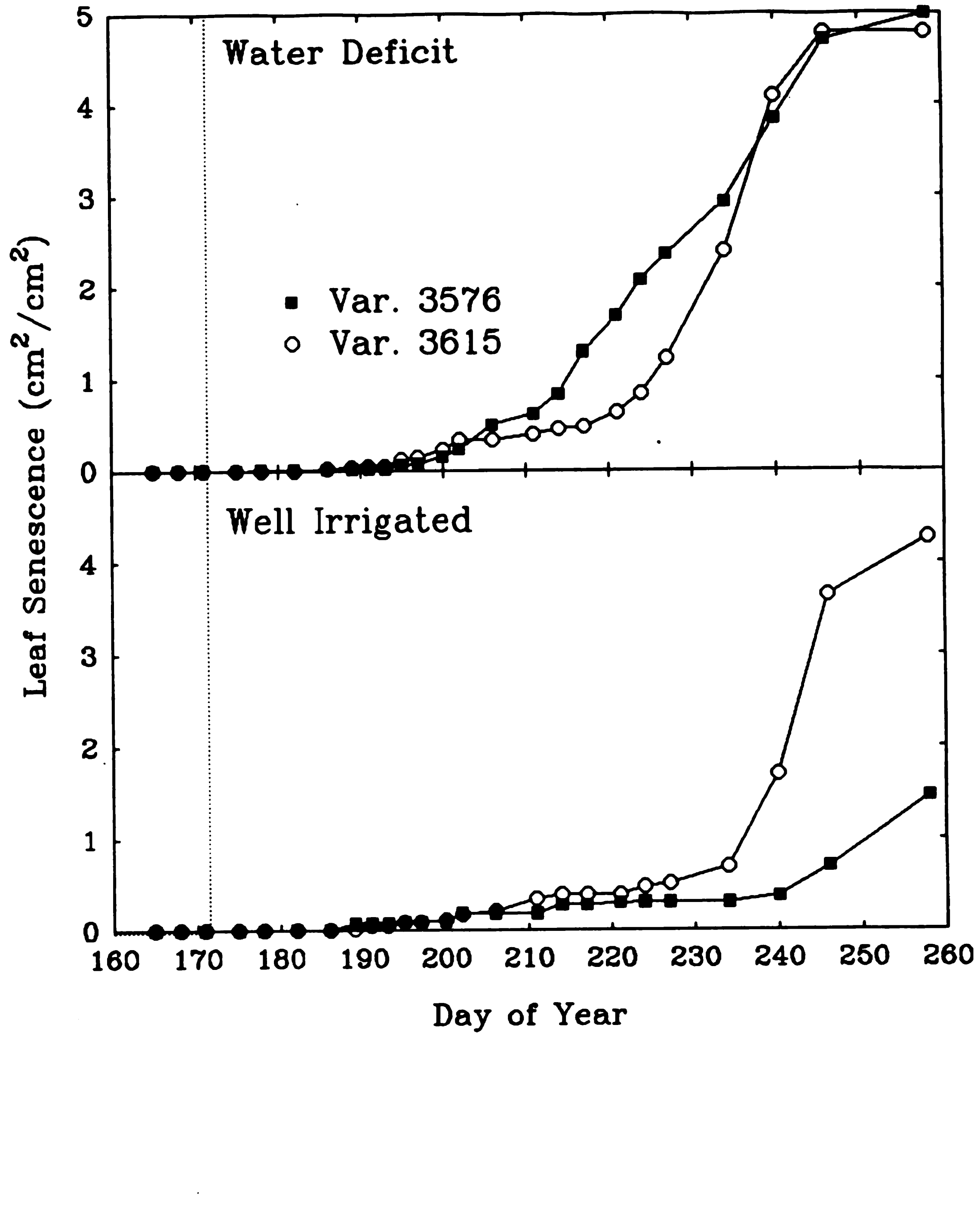

Figure 5.10. Leaf senescence for both treatments and varieties during 1991. The area to the right of the vertical dotted line represents the water deficit period.

Plant Growth and Leaf Elongation

Accumulative plant leaf length for both treatments and varieties during 1990 and 1991 are shown in Figures 5.11 and 5.12. In both years, neither treatment differences nor variety differences were observed. The variety 3576 under the water deficit treatment showed a larger total leaf length than the well-irrigated treatment. This difference in the total leaf growth was due to different LAI between treatments (Figures 5.8 and 5.9).

Figures 5.13 and 5.14 delineate leaf length for a single leaf growing during 1991, for the variety 3576 and 3615. These data indicated that duration of growth was not altered by the water deficit. A slight reduction in the final leaf length was observed for the variety 3576 during the water deficit. Acevedo *et al.* (1971) also found that a mild water deficit did not influence the final leaf size.

The level of water deficit that results in a reduction in growth varies with the conditions under which the plants are grown. The data of McCree and Davis (1974) and Watts (1974) indicate that leaf expansion continues day and night at the same rate, despite the diurnal change in leaf water potential from -1 to about -8 bars. This probably arises partly from the turgor pressure maintenance of the expanding leaves during most of the day. Plants grown in Kalamazoo soil probably recovered their turgor pressure during the night even when the water deficit was relatively severe.

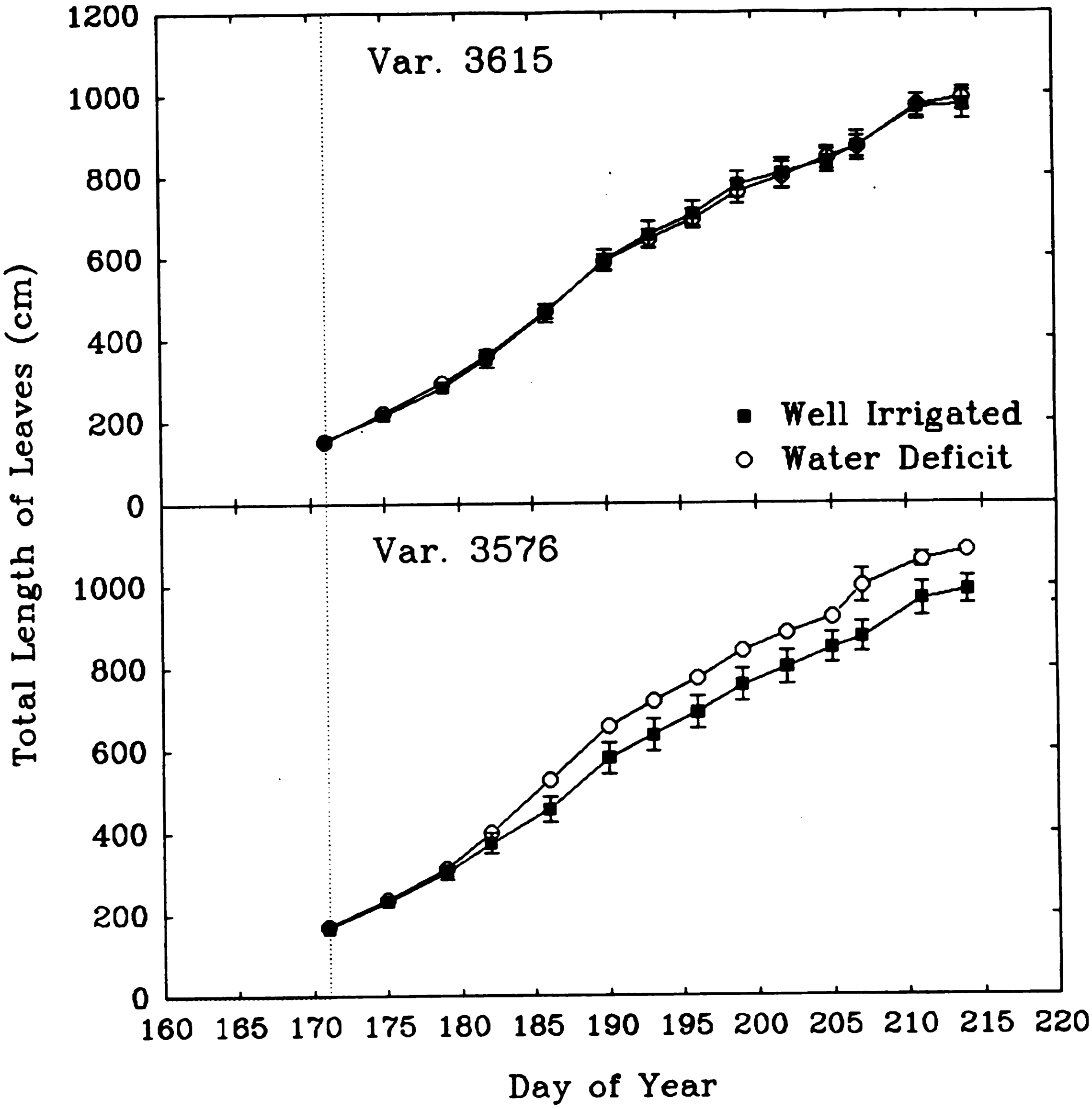

Figure 5.11. Cumulative leaf length for both treatments and varieties during vegetative growth in 1990. The area to the right of the vertical dotted line represents the water deficit period.

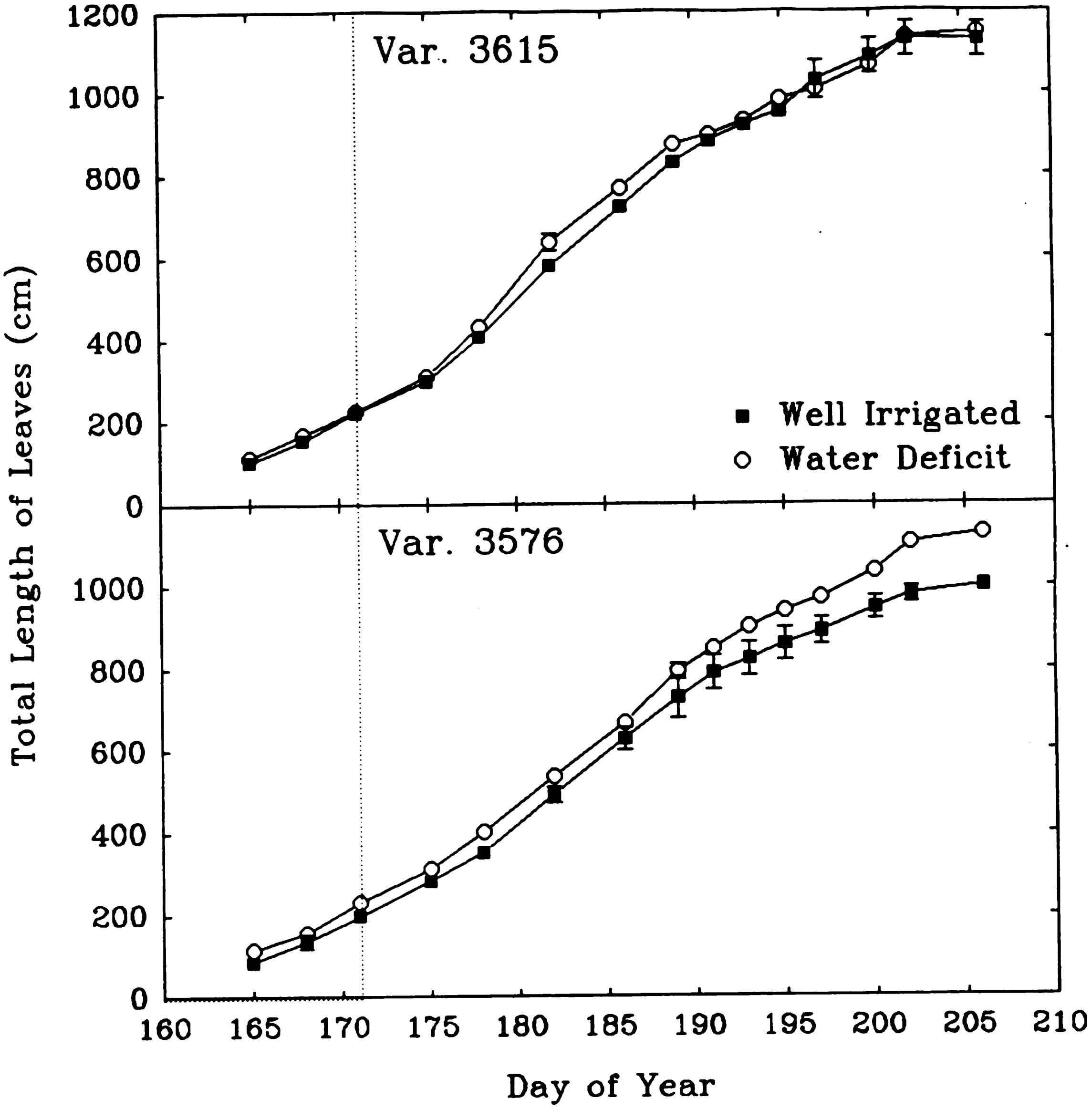

Figure 5.12. Cumulative leaf length for both treatments and varieties during vegetative growth in 1991. The area to the right of the vertical dotted line represents the water deficit period.

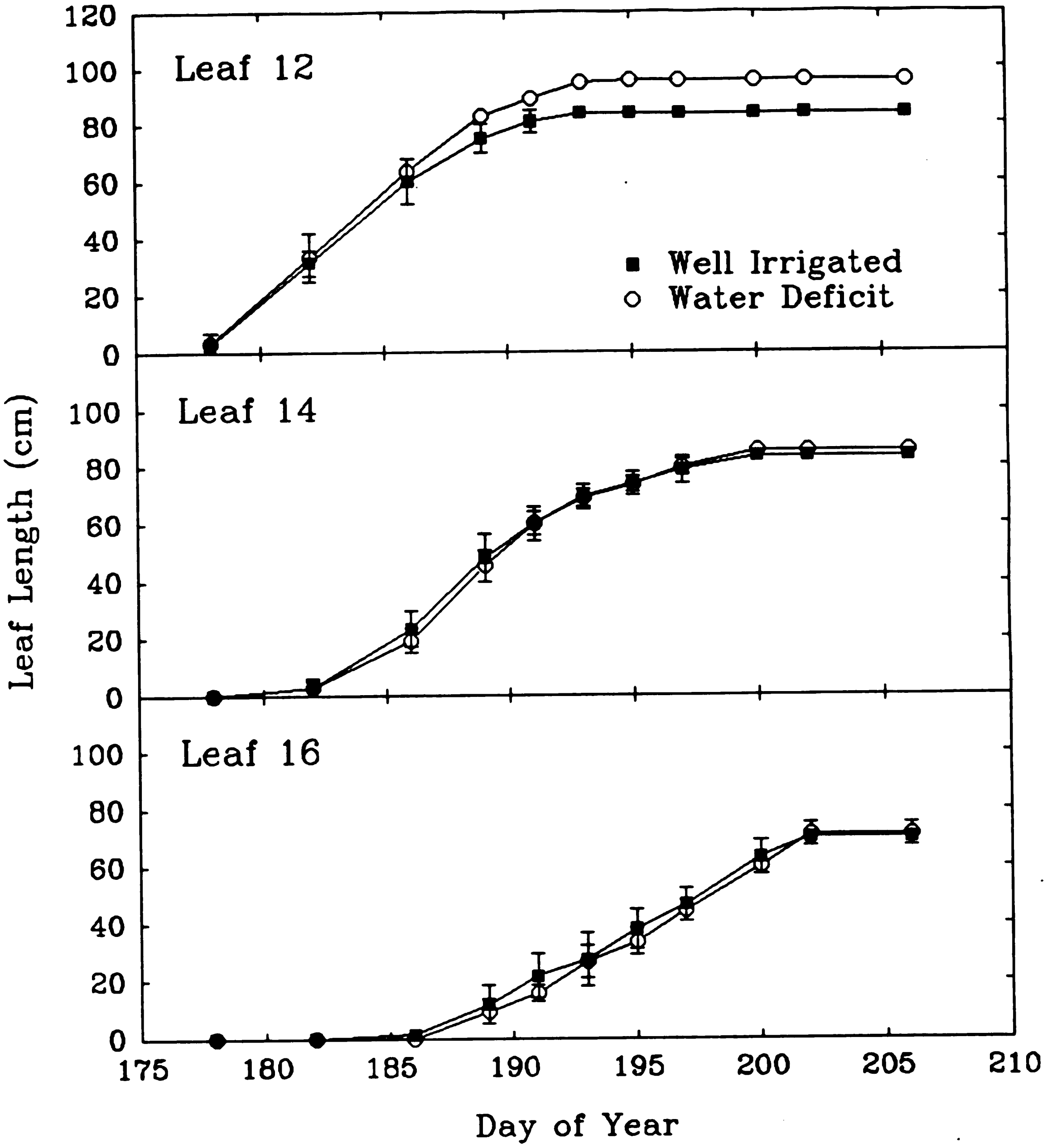

Figure 5.13. Elongation of individual leaf blades for both treatments of variety 3576 during the water deficit period in 1991.

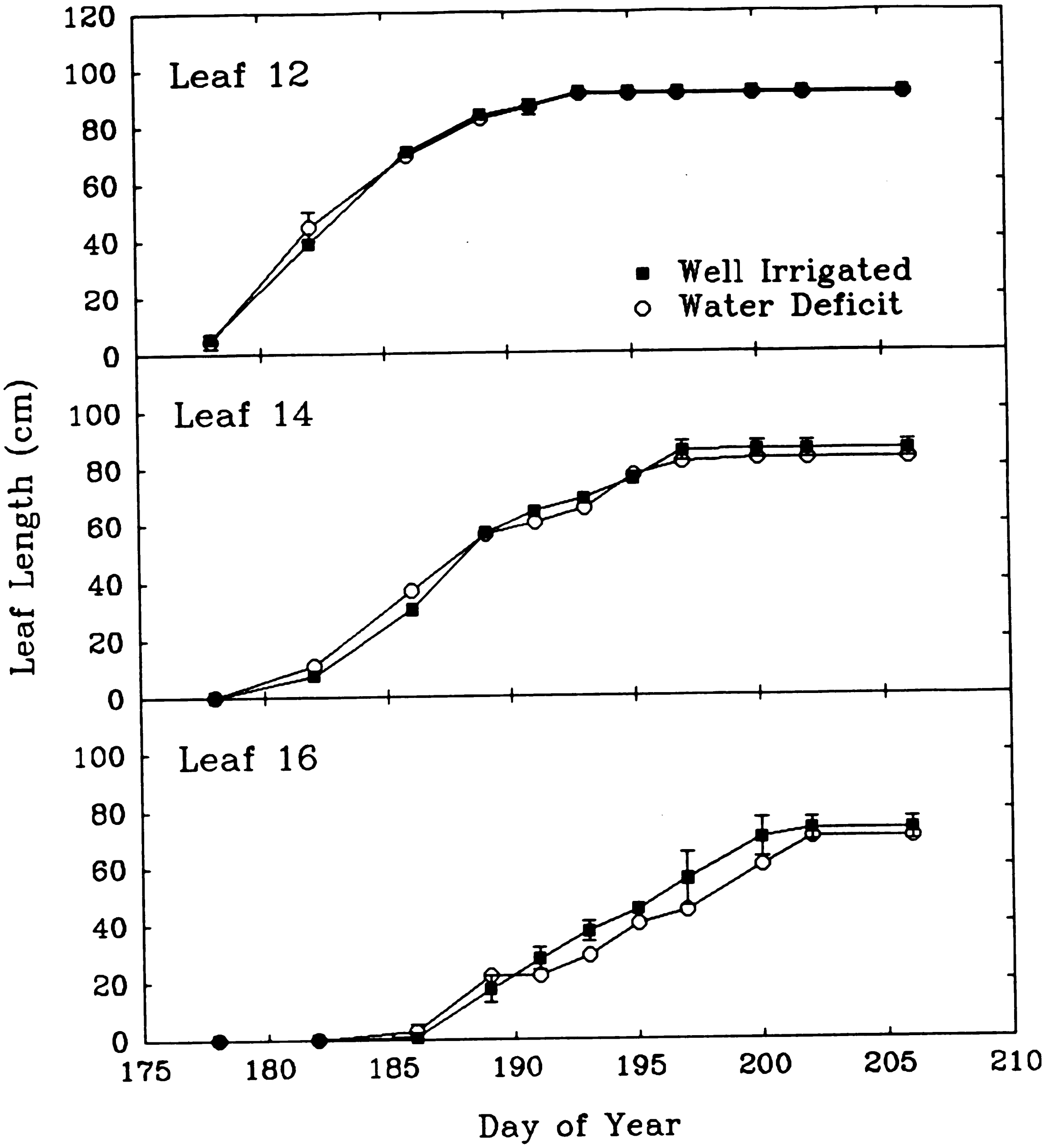

Figure 5.14. Elongation of individual leaf blades for both treatments of variety 3615 during the water deficit period in 1991.

Radiation Interception

The daily variation of photosynthetically active radiation interception on three selected days during vegetative growth in 1991 are presented in Figures 5.15 and 5.16, for the variety 3576 and 3615. For 1990, the radiation interception for both varieties and treatments on DOY 183 is shown in Figure 5.17. In both years, at the start of the water deficit period no difference in radiation interception between the two varieties was observed, except for the maize variety 3576 on DOY 181. The difference noted was due to a difference in LAI between treatments rather than any treatment effect.

The radiation interception slightly decreased for both varieties under water deficit conditions at the end of the crop vegetative growth (DOY 200). Although the variety 3576 growing under water deficit had a larger LAI (Figure 5.9), the radiation intercepted was lower than the well-irrigated treatment. The discrepancy between LAI and radiation interception occurred because the variety 3576 started to roll its leaves. No measurements of leaf rolling were taken during this period because the leaf rolling was not observed in the majority of the plants and leaves, and the leaf rolling pattern was not consistent over time.

The seasonal variation of radiation interception measured near solar noon hours in 1991 is shown in Figure 5.18. A marked shift in the amount of radiation interception between treatments was noticed for both varieties at the end of vegetative growth (DOY 206). The lower radiation intercepted by the water deficit treatment was due not only to the leaf rolling but also to the lower green leaf area

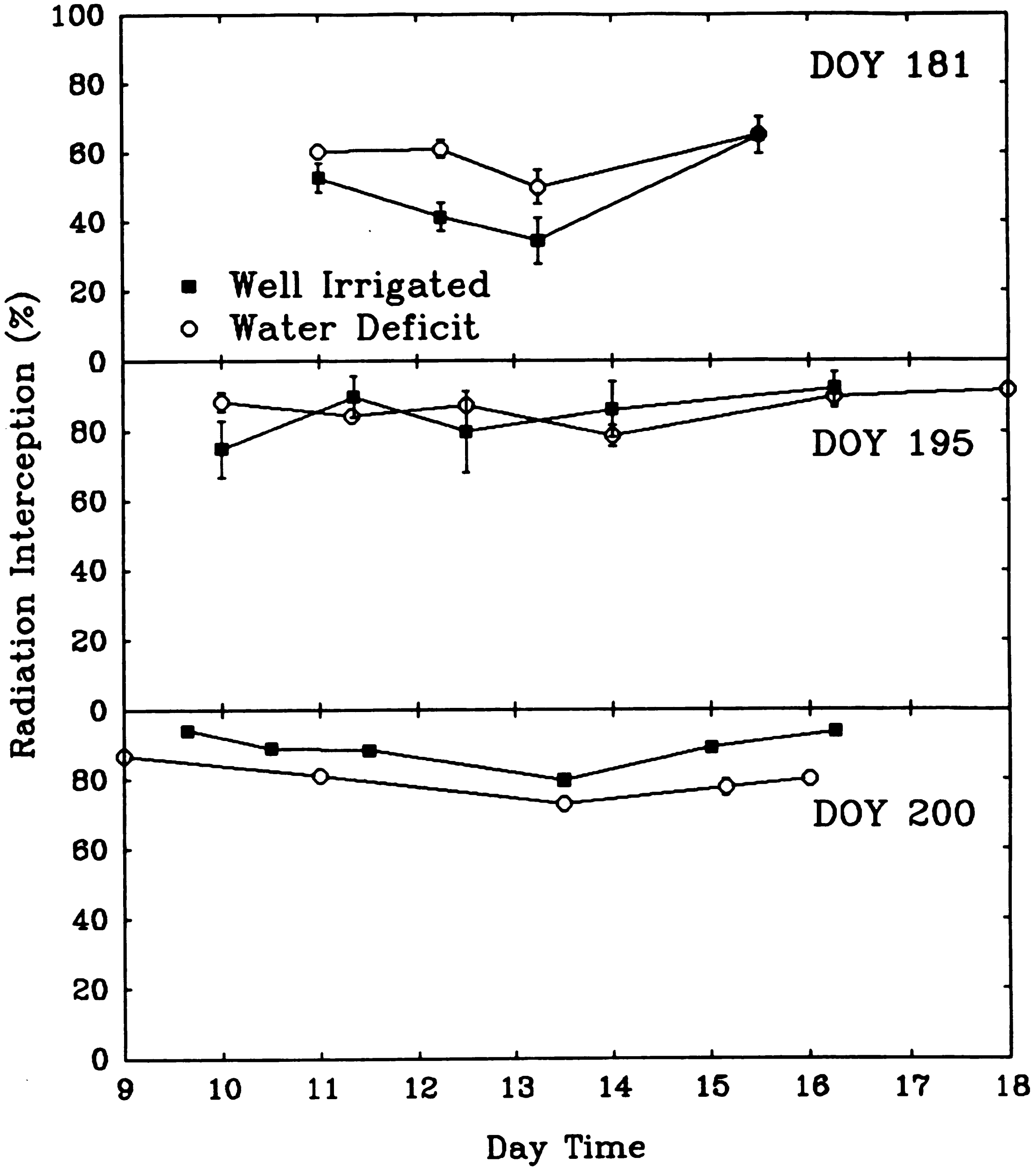

Figure 5.15. Daily variation of photosynthetically active radiation interception of the variety 3576 on three selected days (DOY 181, 195 and 200) in 1991.

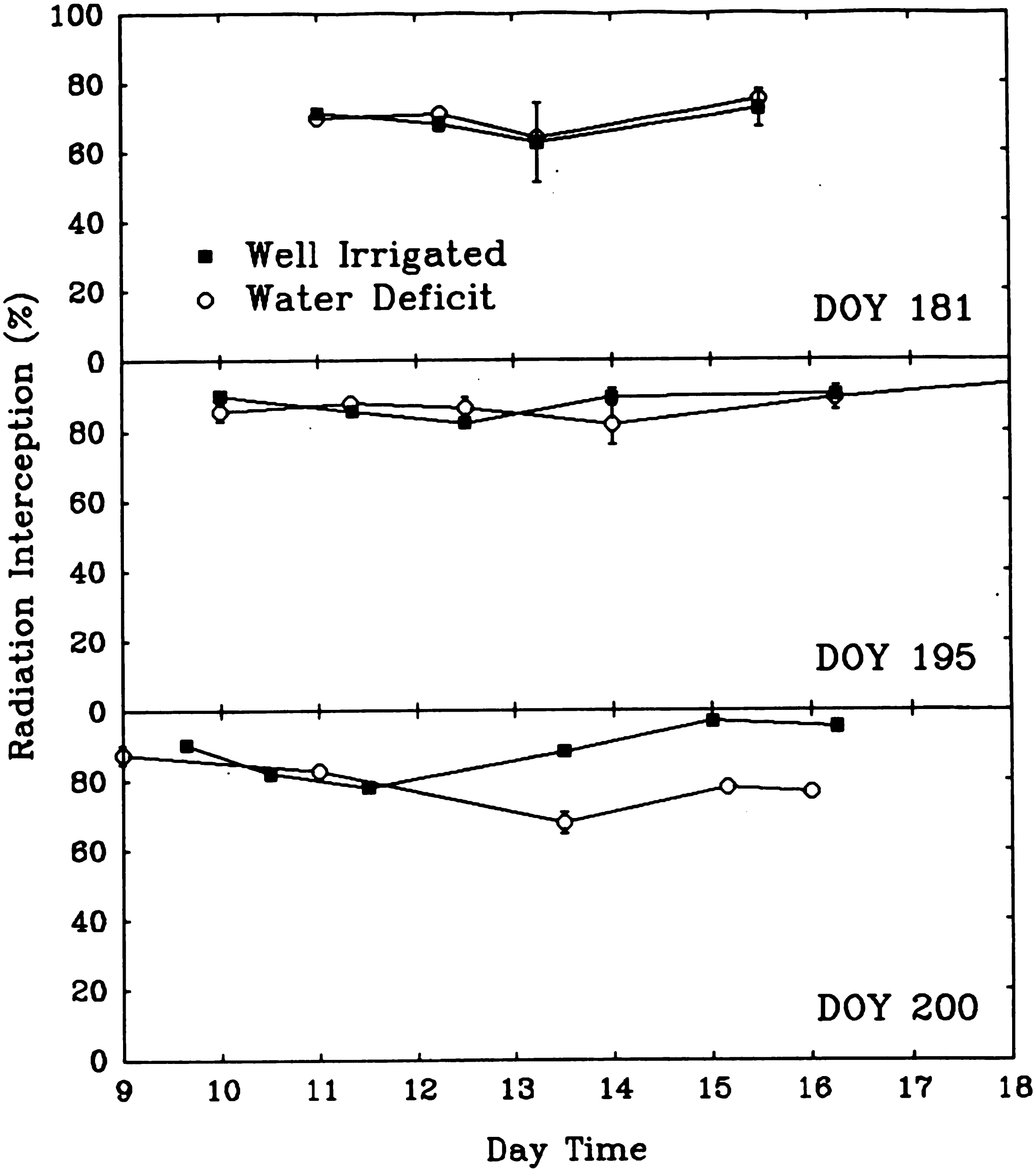

Figure 5.16. Daily variation of photosynthetically active radiation interception of the variety 3615 on three selected days (DOY 181, 195 and 200) in 1991.

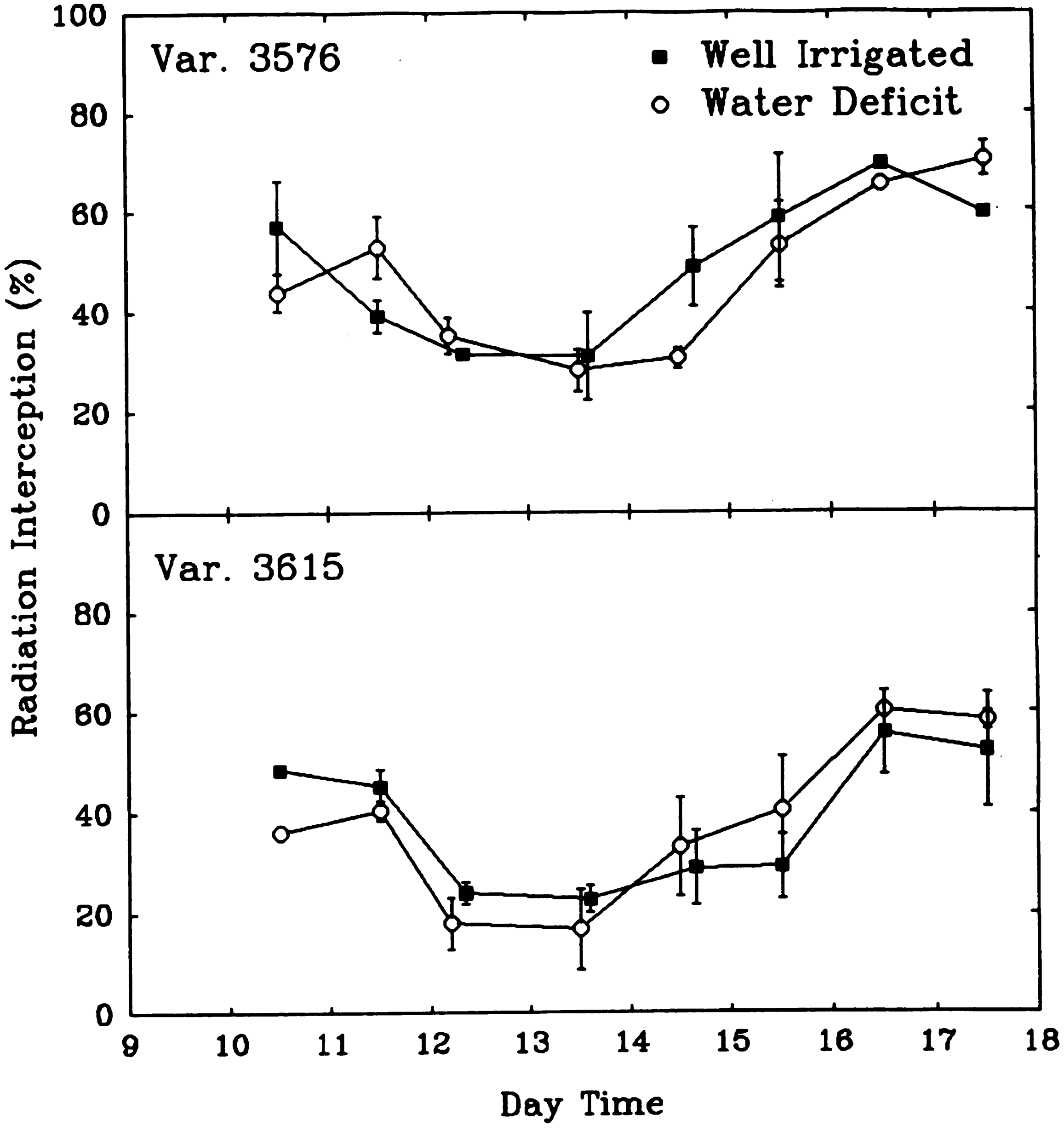

Figure 5.17. Daily variation of photosynthetically active radiation interception of the two varieties on the DOY 181 in 1990.

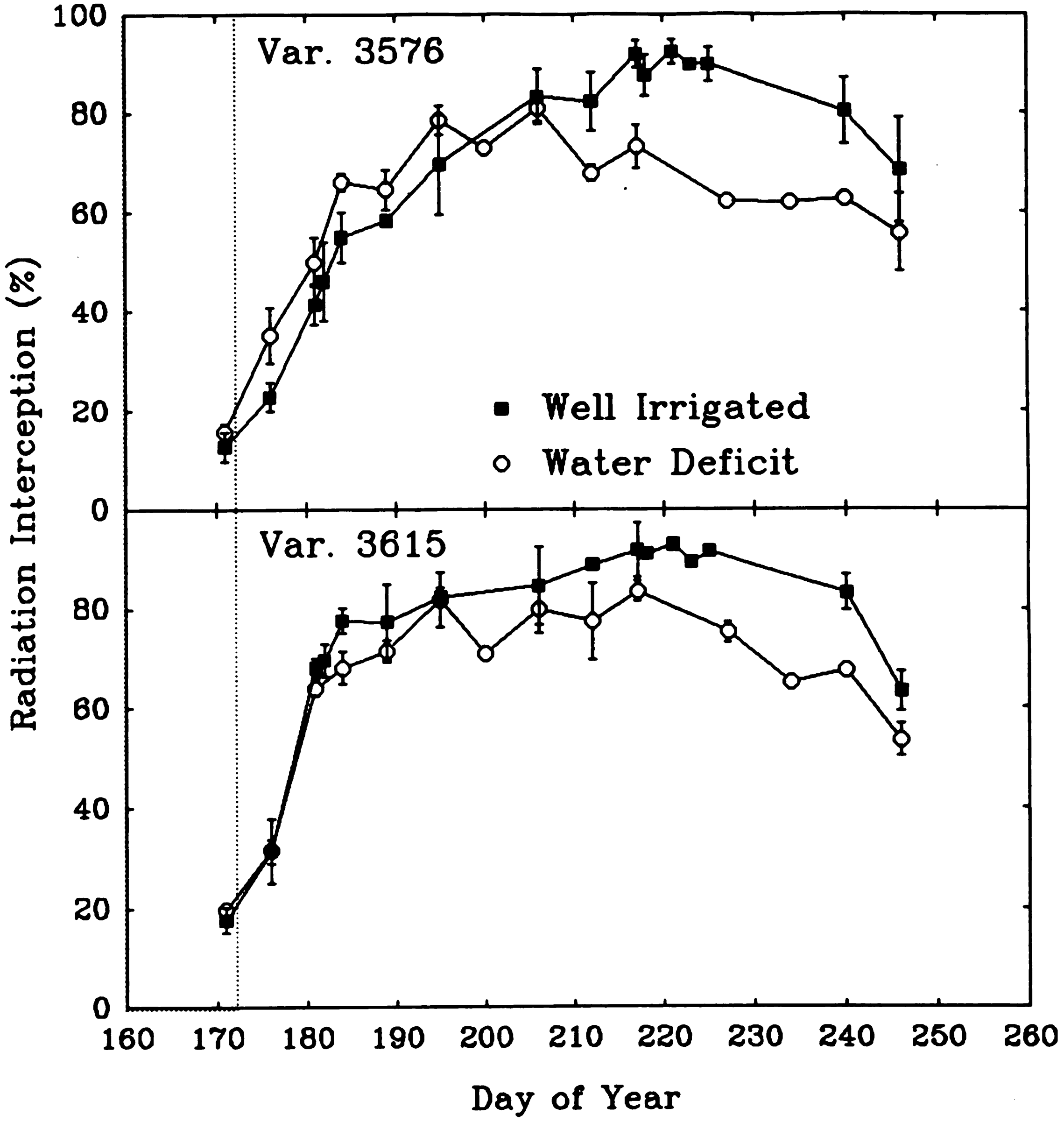

Figure 5.18. Seasonal variation of radiation interception for both maize varieties in 1991 as measured near solar noon. The area to the right of the vertical dotted line represents the water deficit period.

caused by leaf senescence.

Plant Biomass Accumulation

The seasonal variation of aboveground biomass accumulation for both varieties during 1991 is shown in Figure 5.19. Aboveground biomass accumulation began to decline in relation to the well-irrigated on DOY 202 and DOY 212 for the variety 3576 and 3615. At harvest (DOY 258), the aboveground production of the water deficit treatment was 56.2% and 56.3% for the variety 3576 and 3615. After plant anthesis (DOY 206), little increase in aboveground biomass accumulation was observed for both varieties. According to Steven *et al.* (1983), daily dry matter production has been described as a function of the total incident solar radiation, the proportion of solar radiation intercepted, and the efficiency of conversion of solar radiation to photosynthates. Several reports have indicated that biomass accumulation ceased due to impairment of photosynthesis under water deficit conditions during grain filling (Jurgens *et al.*, 1978; McPherson and Boyer, 1977; Westgate and Boyer, 1985).

The relationship between aboveground biomass accumulation and cumulative intercepted radiation for both varieties and treatments is presented in Figure 5.20. The radiation intercepted by the variety 3576 and 3615 under water deficit conditions during the entire growing season was 92.4% and 89.5% of the radiation intercepted by the well-irrigated treatment. A large proportion of the radiation was being intercepted by non-green leaves (senesced leaves). A linear

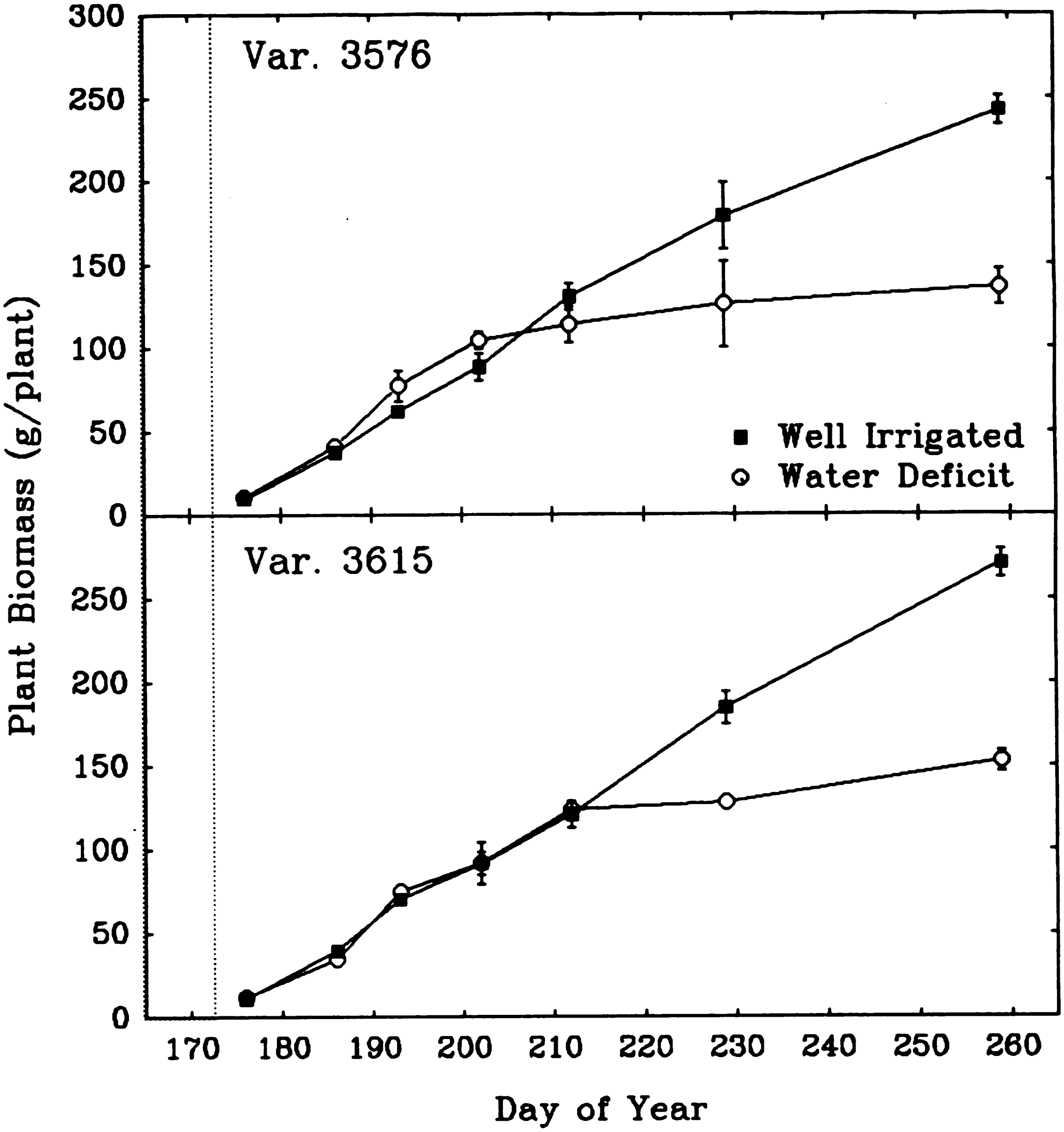

Figure 5.19. Aboveground biomass for both treatments and varieties in 1991. The area to the right of the vertical dotted line represents the water deficit period.

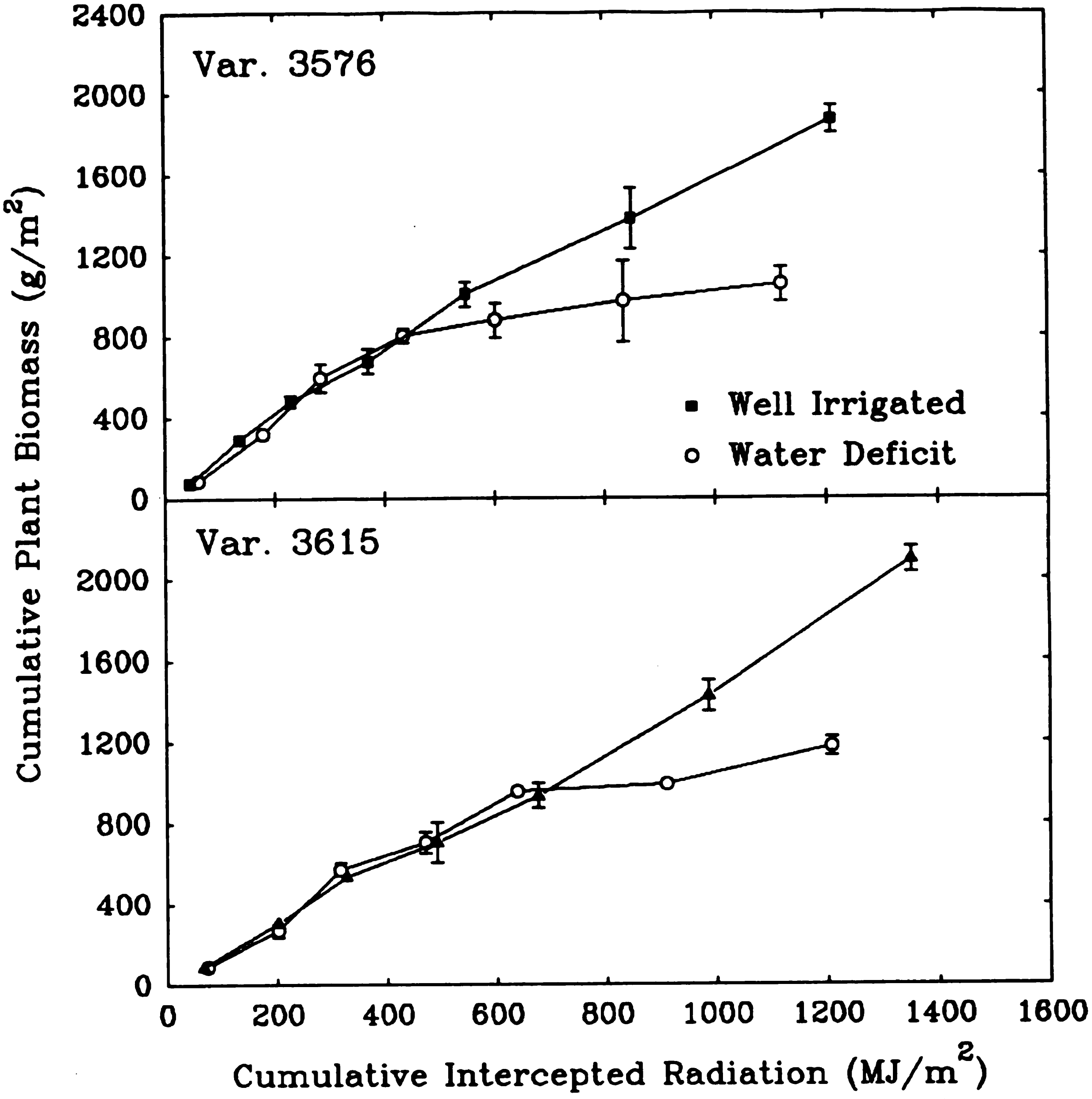

Figure 5.20. Relationship between aboveground biomass accumulation and cumulative intercepted radiation for both varieties and treatments in 1991.

relationship was observed for both varieties under well-irrigated conditions between biomass accumulation and intercepted radiation. These results correspond with results obtained by Monteith (1981); Gallagher and Biscoe (1978); Sibma (1977).

Radiation use efficiency (RUE) was higher for both varieties grown under well-irrigated conditions (Table 5.1). The water deficit imposed during the vegetative growth caused a marked reduction in RUE (Figure 5.21) for both varieties near the end of the vegetative growth (DOY 202). The lower values of RUE observed for the variety 3576 after plant anthesis was mainly caused by the larger reduction in its LAI compared to variety 3615 (Figure 5.9). This reduction in plant leaf area reduced the plant photosynthetic area and, consequently, the capacity of the plant to increase the production of photoassimilates. A marked drop in RUE was observed for both varieties during the grain filling period and, at harvest the RUE was 0.28 g/MJ and 0.64 g/MJ for the variety 3576 and 3615.

Conclusions

During the vegetative crop growth no indication of plant water deficit such as reduction in leaf elongation, leaf rolling or leaf senescence was noted on either variety. Plants were grown on a large quantity of stored water at the beginning of the water deficit. This higher soil water availability in the Kalamazoo soil combined with the relative low VPD provided enough water to both varieties during the

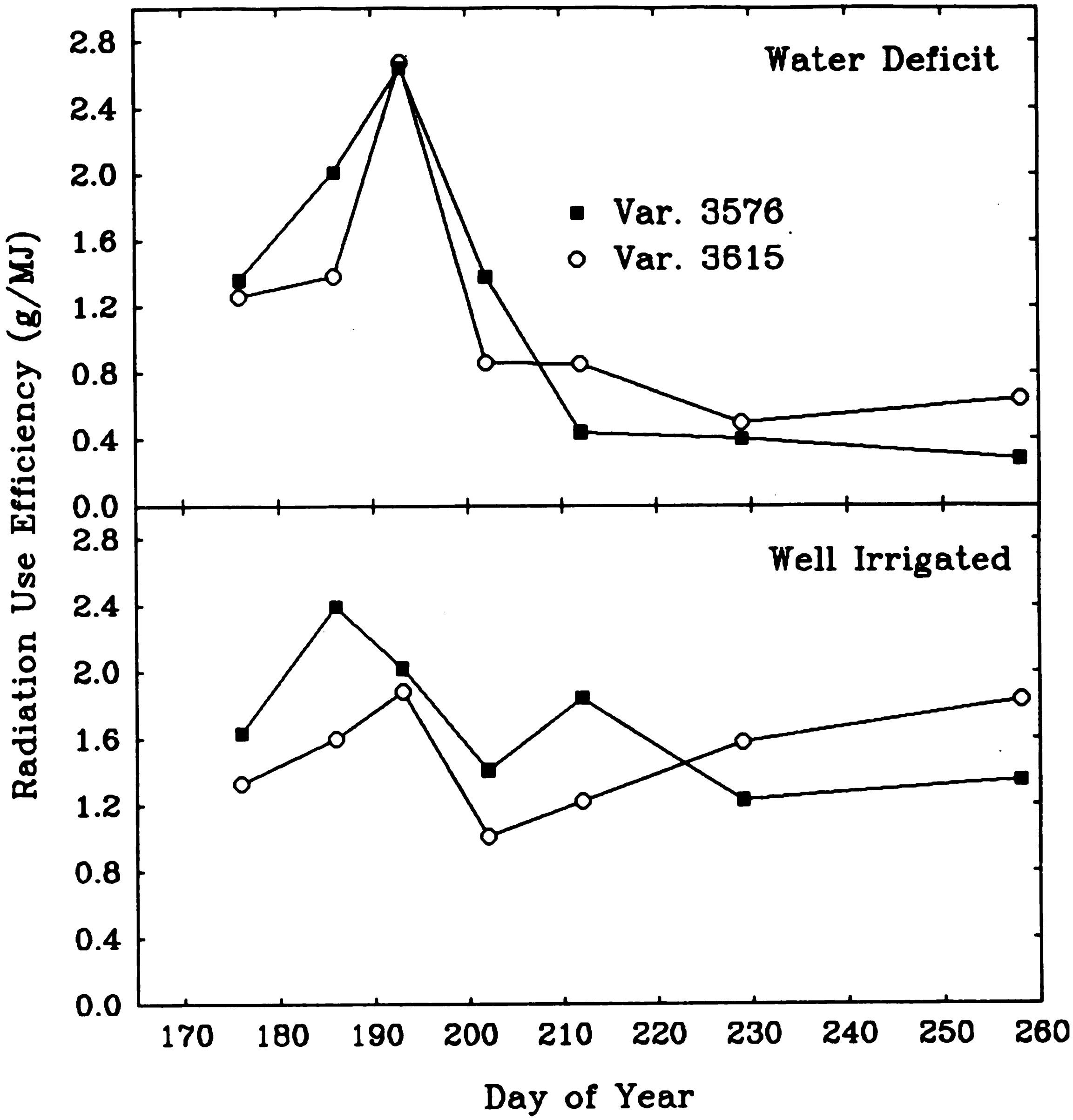

Figure 5.21. Seasonal variation of radiation use efficiency (RUE) for both varieties and treatments during 1991. The area to the right of the vertical dotted line represents the water deficit period.

Table 5.1. Total intercepted radiation, radiation use efficiency (RUE) and above ground biomass for both treatments and varieties in 1991. Values in brackets are percentages of the well-irrigated treatment.

Treatment	Variety	Intercepted Radiation	Biomass Production	RUE	R^2
Water Deficit	3576	1121.9 (92.4)	1051.2 (56.2)	1.18 (72.8)	0.653
	3615	1209.0 (89.5)	1176.2 (56.3)	1.14 (76.5)	0.819
Well Irrigated	3576	1214.2	1868.9	1.62	0.981
	3615	1351.4	2088.4	1.49	0.994

vegetative growth. Plant leaf senescence was enhanced for both varieties, after flowering, where the fraction of plant available water was about 0.18 for both varieties. Results of this experiment demonstrate that maize performance during vegetative growth in a loamy textured soil is more closely linked to the amount of soil available water in the rooting zone than to the fraction of plant available water. Radiation interception during crop vegetative growth is independent of the soil water deficit in a loam textured soil under conditions of relatively low VPD. Leaf senescence was enhanced, aboveground biomass accumulation and radiation use efficiency (RUE) was reduced when the amount of soil available water is lower than 35 mm.

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CHAPTER 6

Predicting Radiation Interception and Exposed Plant Leaf Area Using a Modified CERES-Maize Model

Abstract

A simplified model for calculating the intercepted photosynthetically active radiation and the exposed plant leaf area to incident radiation is needed to eliminate the necessity for determining the detailed plant foliage characteristics required in many light interception and crop growth models. The objective of this study was to modify the CERES-Maize model to predict the daily fraction of radiation intercepted by maize plants grown under a variety of soil water deficit conditions through the estimation of the exposed plant leaf area. The version 2.1 of the CERES-Maize model was used to simulate the effects of water deficit periods on maize light interception and leaf area adjustments. Modifications in the CERES-Maize model enabled the model to predict intercepted photosynthetically active radiation of maize plants growing in different soil water conditions. The modified model can be used to simulate the fraction of plant leaf area that is exposed to the incident solar radiation. The model slightly under-predicted aboveground biomass accumulation. Additional adjustments in plant biomass production is needed to validate the model against more plant biomass field data.

Introduction

Radiation incidence on a canopy from the sun, sky, and soil is attenuated or extinguished as it passes through the vegetation because foliage elements (leaves, stems, flowers, etc.) absorb, reflect, and transmit radiation that they intercept. Clearly the foliage is exposed to a range of irradiances, varying from near zero to full sunlight depending on the characteristics of the incident radiation and the size, position, orientation, and spectral characteristics of the foliage. Thus, many factors are involved in determining the penetration of radiation into vegetation (Norman, 1980).

Leaf area index (LAI) and distribution of leaf area within a corn canopy are major factors determining total light interception, which affects photosynthesis, transpiration, and dry matter accumulation (Pearce *et al.*, 1967; Lieth and Reynolds, 1984). The LAI is often an input for, or is calculated in, crop yield models (Reetz, 1976; Coelho and Dale, 1980), and can be used to estimate the absorption of photosynthetically active radiation (PAR) (Linvill *et al.*, 1978; Gallo *et al.*, 1985). Beer's law described the relationship between intercepted radiation and leaf area index (Asrar *et al.*, 1984; Hipps *et al.*, 1983; and Norman, 1980).

Solar radiation is the source of energy for photosynthesis, the initial process that green plants use to convert CO_2 and water into simple sugars. Other plant processes convert these initial products of photosynthesis into dry matter including carbohydrates, proteins, and oils. Solar radiation is available as the source of energy for plants only when it interacts with leaves. In a healthy crop adequately supplied with water, the production of dry matter is proportional to the solar radiation intercepted by the canopy. Thus, the important components of growth and yield are the amount and duration of green leaf surface available for photosynthesis (Brown and Blase, 1968; Dale, 1977).

According to Norman (1991) the mass of dry matter produced per unit of absorbed PAR could be termed as dry matter light-use efficiency. This term involves maintenance and growth respiration, which may not directly depend on light, and photosynthesis, which does not directly depend on light interception. Estimates of radiation use efficiency (RUE), for corn grown under field conditions, vary between 2.9 (Williams *et al.*, 1965), 3.2 (Yao, 1980), 3.8 (Sivakumar and Virmani, 1984), and 4.4 g/MJ of intercepted PAR (Griffin, 1980).

The response of leaf photosynthesis to light, systematically investigated in many laboratory studies, provides a basis for simple models of crop production in relation to solar radiation. The response of photosynthesis to temperature and water deficit has also been examined, mainly in terms of stomatal behavior. However, because the physiological basis of these responses is not fully understood, photosynthesis models incorporating the temperature or water potential of leaf tissues rely heavily on empiricism and lack generality (Monteith, 1977).

A simplified model for calculating the intercepted PAR and the exposed plant leaf area to incident radiation is needed to eliminate the necessity for determining the detailed plant foliage characteristics required in many light interception and crop growth models. According to Norman (1980), solar azimuth and zenith angles, spectral properties of canopy elements, LAI, leaf angle distribution, leaf size and shape, and leaf movements due to wind, wilting, and phototropism influence the interception of radiation by vegetation.

The objective of this study was to modify and validate the CERES-Maize model, using a simple approach, to predict the daily fraction of radiation intercepted by maize plants grown under a variety of soil water deficit conditions through the estimation of the exposed plant leaf area.

Methodology

The version 2.2 of the CERES-Maize model described by Jones and Kiniry (1986) was used to simulate the effects of water deficit periods on maize light interception and leaf area adjustments. The maize growth subroutine was modified to predict plant leaf rolling, radiation interception and radiation use efficiency.

Water Deficit Factor

A soil water deficit factor for rolling (SWDFR) was incorporated in the model to predict plant leaf rolling. This factor takes into account the shortage of water to the root system (determined by the soil water conditions) and atmospheric water demand (determined by the state of the atmosphere) as follows:

$$SWDFR = 0.667 \times \frac{TRWU}{EO} \tag{6.1}$$

where TRWU is the maximum possible water uptake from the soil profile calculated in the WATUP subroutine and EO is the potential evapotranspiration estimated as a function of temperature and radiation. The potential evapotranspiration is calculated in the POTEV subroutine. When the ratio between TRWU and EO is lower than 1.5 the conditions for leaf rolling are met. SWDFR is a zero-to-unity factor and it is set to 1.0 when the ratio between TRWP and EO is larger than 1.5. SWDFR values of 1.0 correspond to negligible soil water deficit so that plant growth occurs at a potential growth rate and leaf rolling does not occur.

Predicting Plant Leaf Rolling

Daily average plant leaf rolling was estimated from the SWDFR values. The leaf rolling index (LRI) during the ISTAGE 3 (tassel initiation to end of leaf growth and silking) was calculated by the following equation:

$$LRI = 0.20 + 0.60 \times SWDFR \tag{6.2}$$

During the ISTAGE 4 (silking to beginning of effective grain filling period) or ISTAGE 5 (effective grain filling period) the LRI is calculate as:

$$LRI = 0.54 + 0.34 \times SWDFR \tag{6.3}$$

The model also calculates the average of the current day's LRI and the LRI of the two previous days (AVEGLRI) as follow:

$$AVEGLRI = \frac{LRI_{Day-2} + LRI_{Day-1} + LRI_{Day}}{3} \tag{6.4}$$

When AVEGLRI is lower or equal to 0.85, the LRI is used in the model to reduce the exposed plant leaf area. Thus, the model activates the leaf rolling mechanism when soil water conditions, combined with atmospheric evaporative demand, occur for two consecutive days.

Predicting Radiation Interception

The LRI and LAI were used to estimate the exposed plant leaf area index (ELAI) and, therefore, to calculate the radiation intercepted by the crop canopy. The ELAI represents the reduction of LAI due to plant leaf rolling.

$$ELAI = LRI \times LAI \tag{6.5}$$

The fraction of the photosynthetic active radiation (FRACPAR) intercepted by the crop canopy was calculated using the following expression.

$$FRACPAR = 0.98 \times (1.0 - e^{-0.74 \times ELAI}) \tag{6.6}$$

This equation implies that the crop radiation interception obeys Beer's Law; The extinction coefficient is 0.74 and the constant 0.98 indicates that 2% of the incident radiation is not attenuated by the crop foliage.

The PCARB equation (potential plant biomass production, g/plant) in the model was modified to include FRACPAR as follow:

$$PCARB = 5.0 \times FRACPAR \times 0.50 \times SOLRAD \tag{6.7}$$

where SOLRAD is the daily incident solar radiation (MJ/m^2), the constant 0.5 implies that 50% of the incident solar radiation is PAR and, 5.0 g/MJ is the maximum plant biomass production per MJ of intercepted PAR under non-deficit conditions.

The fraction of intercepted radiation (INTCPAR) and cumulative PAR intercepted (CUMPAR) was calculated during the growing season as:

$$INTCPAR = 0.50 \times SOLRAD \times FRACPAR \qquad (6.8)$$

$$CUMPAR_{Day} = CUMPAR_{Day-1} + INTCPAR \qquad (6.9)$$

Predicting Radiation Use Efficiency

The daily radiation use efficiency (RUE) was calculated by the following expression:

$$RUE = \frac{BIOMASS}{INTCPAR} \qquad (6.10)$$

where the BIOMASS is the daily aboveground plant biomass produced in g/m^2 and INTCPAR is the PAR intercepted in MJ/m^2.

The seasonal RUE was calculated by the ratio of the cumulative aboveground plant biomass and cumulative intercepted radiation:

$$RUE = \frac{CUMBIOMS}{CUMPAR} \qquad (6.11)$$

Leaf Senescence

The equations that estimate plant leaf senescence in the model were modified according to the crop's stage of development. The effect of soil water deficit on leaf senescence during vegetative growth was calculated as:

$$SLFW = 0.97 + 0.03 \times SWDF1 \qquad (6.12)$$

where SLFW is the zero-to-unity factor for leaf senescence due to water deficit conditions and SWDF1 is the soil water deficit factor used to predict reductions in plant photosynthesis and transpiration. A small reduction in plant leaf area by leaf senescence is expected for water deficits that occur during the plant vegetative growth (Chapter 2). The leaf senescence mechanisms occur when no further increase in plant leaf rolling is feasible and, consequently, leaf senescence is enhanced (Chapter 2). During pre-anthesis soil water deficit conditions, the model reduces the exposed plant leaf area by increasing leaf rolling and then reduces plant leaf area by increasing leaf senescence. During post-anthesis, however, less leaf rolling is expected (Chapter 4). Leaf senescence is an effective mechanism by which plants reduce the plant leaf area. Thus, SLFW was enlarged as compared to the pre-anthesis equation:

$$SLFW = 0.94 + 0.06 \times SWDF1 \qquad (6.13)$$

Results and Discussions

Field results measured in 1991 and described in Chapters 1 through 4 were used to compare the model predictions. The model simulates results of plant leaf area, exposed LAI, fractional radiation interception, plant biomass, radiation interception and radiation use efficiency for the pre-anthesis soil water deficit, post-anthesis soil water deficit, and well-irrigated treatment.

Plant Leaf Area

The seasonal measured and predicted plant leaf area for all treatments is presented in Figures 6.1. A fairly good prediction of plant leaf area was observed for the well-irrigated treatment. A slight over prediction was observed during the water deficit for the pre-anthesis soil water deficit. The model is unable to track the reduction in LAI at the beginning of the water deficit period. This, according to Ritchie (1993, personal communication), may be caused by the feed-forward process in which plants are receiving signals from the roots to reduce plant growth before any detectable difference in shoot water relations is observed. Root signals are not yet incorporated into the CERES family of models. During post-anthesis

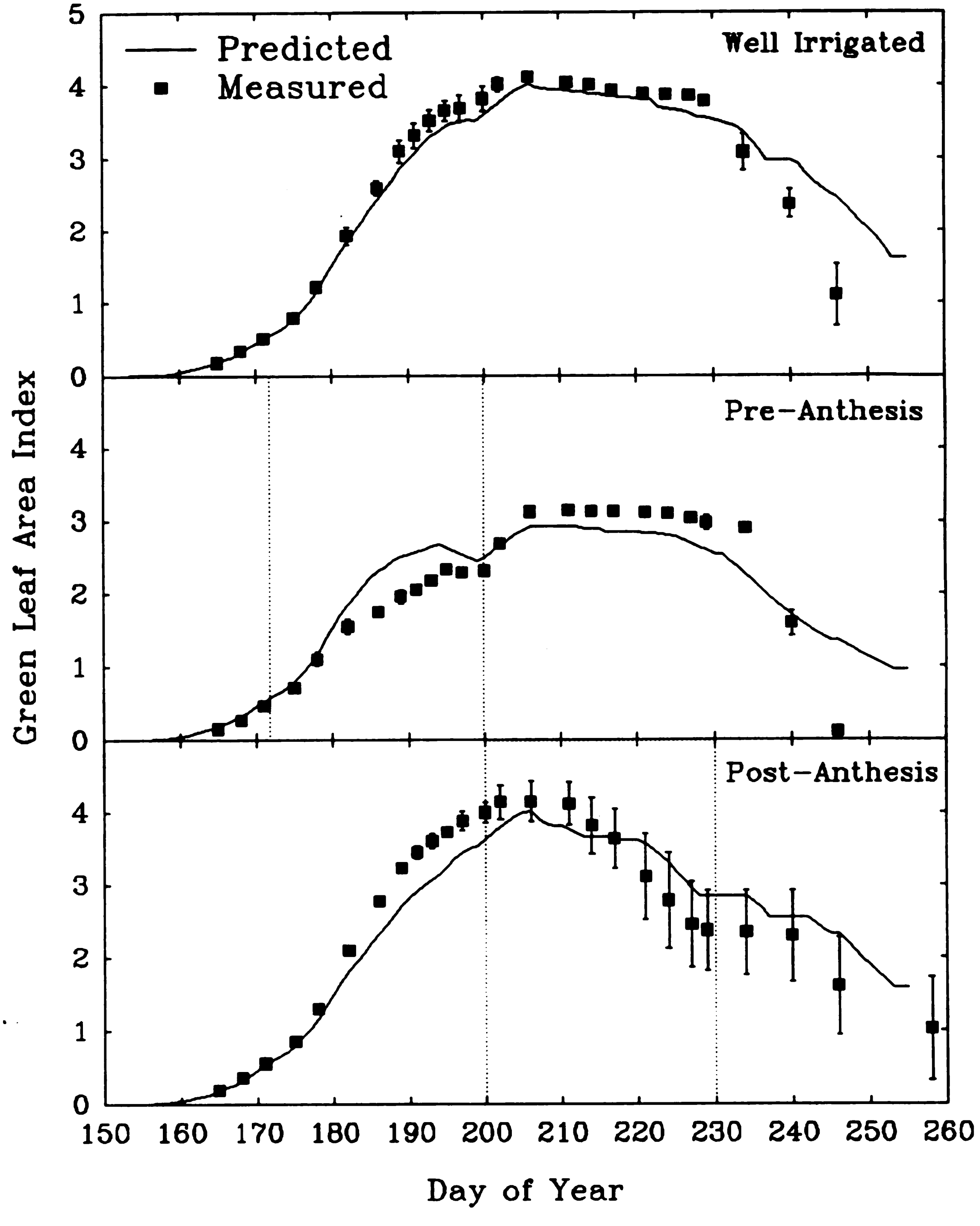

Figure 6.1. Predicted and measured green leaf area index for all treatments. The regions between the vertical dotted lines indicate the water deficit periods.

soil water deficit the modified model yielded good predictions with a slight over prediction of the green LAI at the end of the water deficit period. Although the model leaf senescence was increased, the model predictions of leaf maintenance and senescence require further adjustments and validation against field data. The green LAI during the water deficit period was reduced 43.4% and 29.1% for the measured LAI and predicted LAI.

The good agreement between measured and modeled LAI indicates that the modified model was responsive to periods of water deficit that may occur during plant growth. According to Arkin *et al.* (1976), to determine the amount of PAR intercepted by the corn canopy, the leaf area per plant must be known, since the amount of intercepted radiation is primarily dependent on leaf area.

The exposed LAI was calculated based on the daily average leaf rolling measurements described in Chapters 2 and 4. The predicted ELAI was calculated according to procedures described in Equations 6.2 through 6.5. Figures 6.2 and 6.3 present the predicted and measured ELAI for the pre-anthesis and post-anthesis soil water deficit. The modified model accurately predicted the ELAI during pre-anthesis soil water deficits. The model can also track increases in ELAI during the water deficit period (pre-anthesis soil water deficit). The reduction in ELAI measured at the beginning of the water deficit period was not mimicked by the modified model. This was caused by the feed-forward process. During post-anthesis soil water deficit the model slightly over predicted the ELAI. However, when the water deficit became more severe model predictions were closer to the

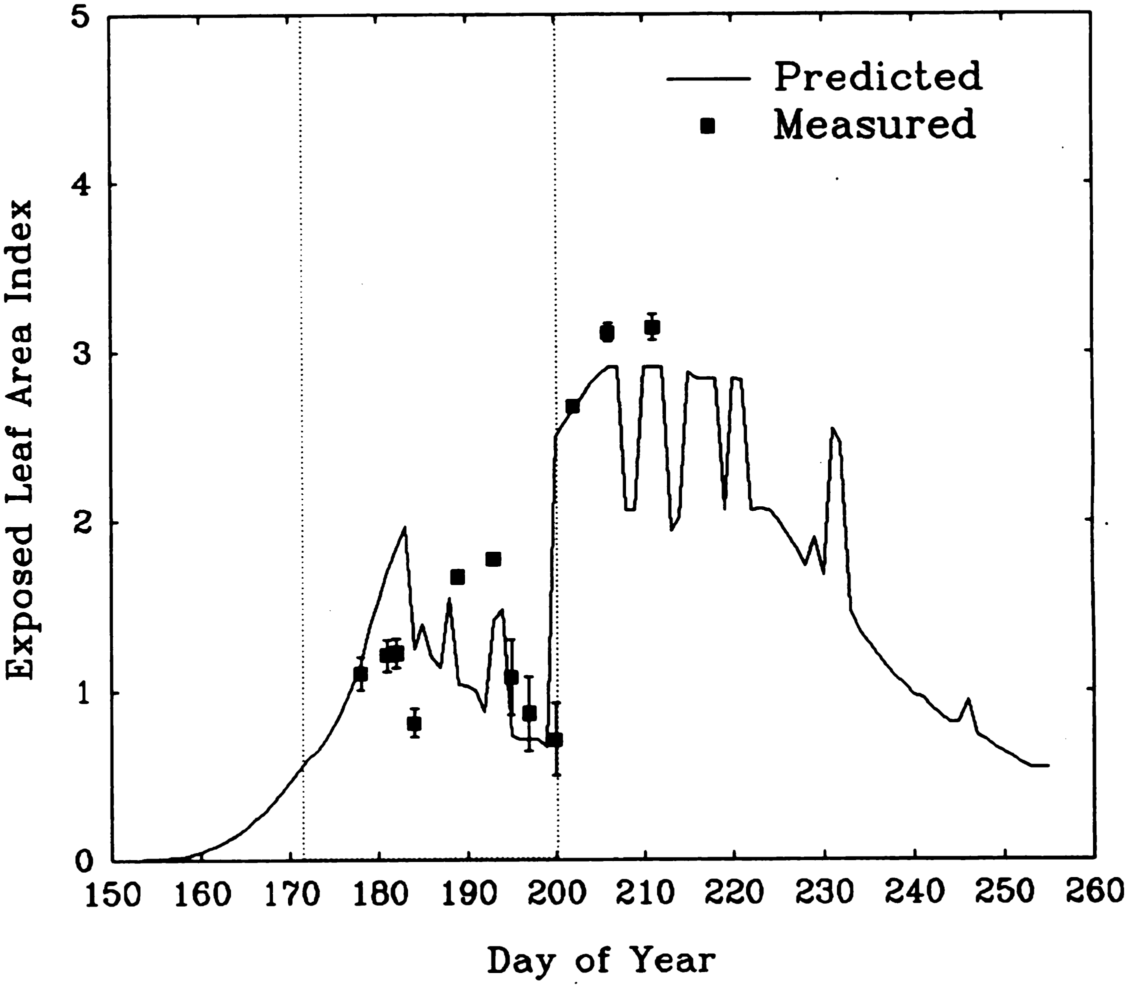

Figure 6.2. Predicted and measured exposed leaf area index for the pre-anthesis soil water deficit. The area limited by vertical dotted lines represents the soil water deficit period.

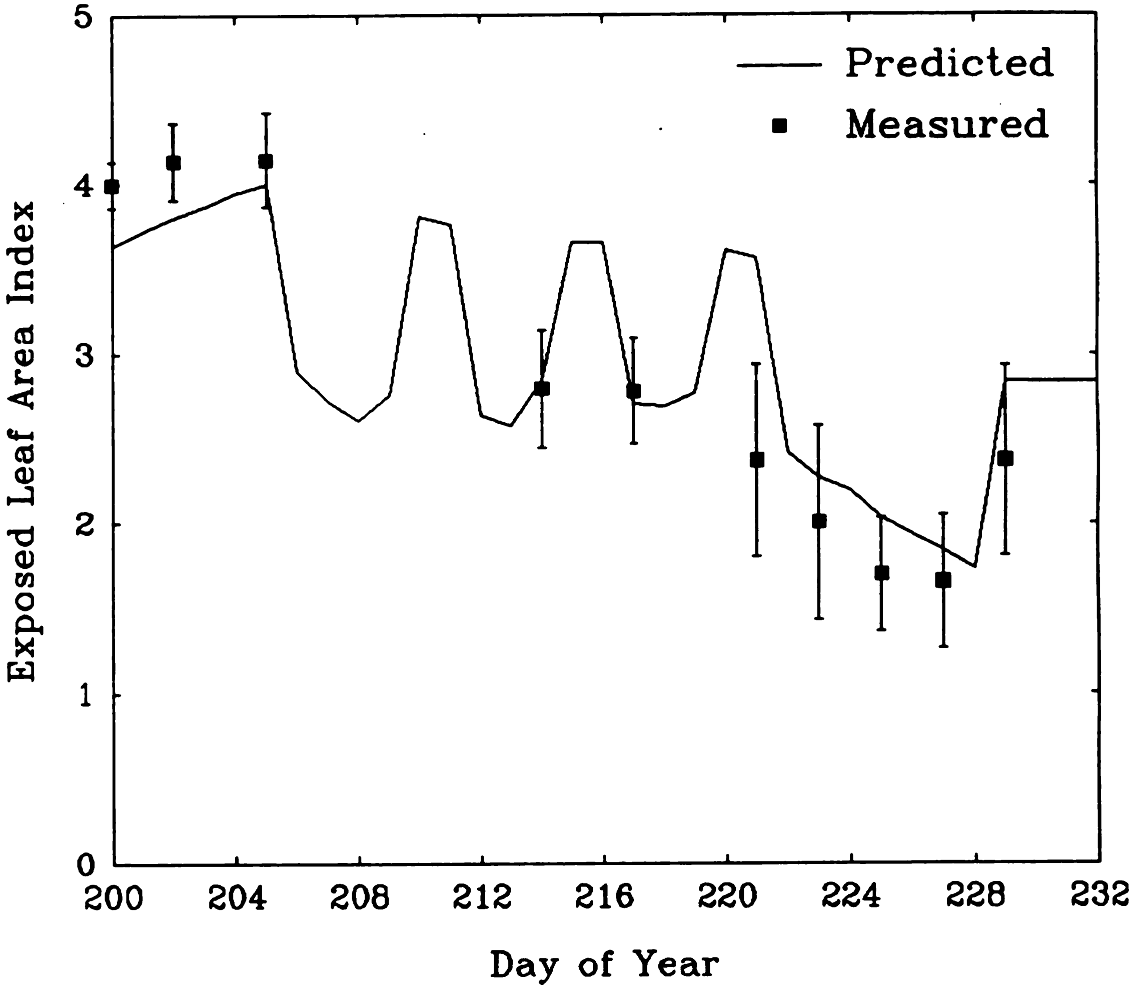

Figure 6.3. Predicted and measured exposed leaf area index for the post-anthesis during the post-anthesis soil water deficit.

measured ELAI.

These result indicate that the modified CERES-Maize model can be used to simulate the fraction of plant leaf area that is exposed to the incident solar radiation. The model does not simulate ELAI for the well-irrigated treatment because the soil water deficit factor for rolling (SWDFR), described in Equation 6.1, was larger than unity. This indicates that the soil water conditions and atmospheric evaporative demand were above the plant's threshold for leaf rolling.

Radiation Interception

The seasonal variation of the measured fractional radiation interception (daily average) and predictions of the modified model for all treatments is presented in Figures 6.4. The modified model predicted the fraction of the radiation intercepted by the crop canopy very well, especially for the well-irrigated treatment. The unexpected downturns observed during the plant vegetative growth for the well-irrigated and post-anthesis treatments were caused by malfunction of the irrigation system (described in Chapters 1 and 3). The model is able to track short periods of soil water deficit especially when plant canopy if fully expanded.

The measured and predicted results of the CUMPAR intercepted (MJ/m^2) for all treatments is presented in Figure 6.5. For all conditions the modified model yielded excellent predictions. These results clearly indicate that the modifications included in the CERES-Maize model enables the model to predict the intercepted radiation of maize plants growing in different soil water conditions.

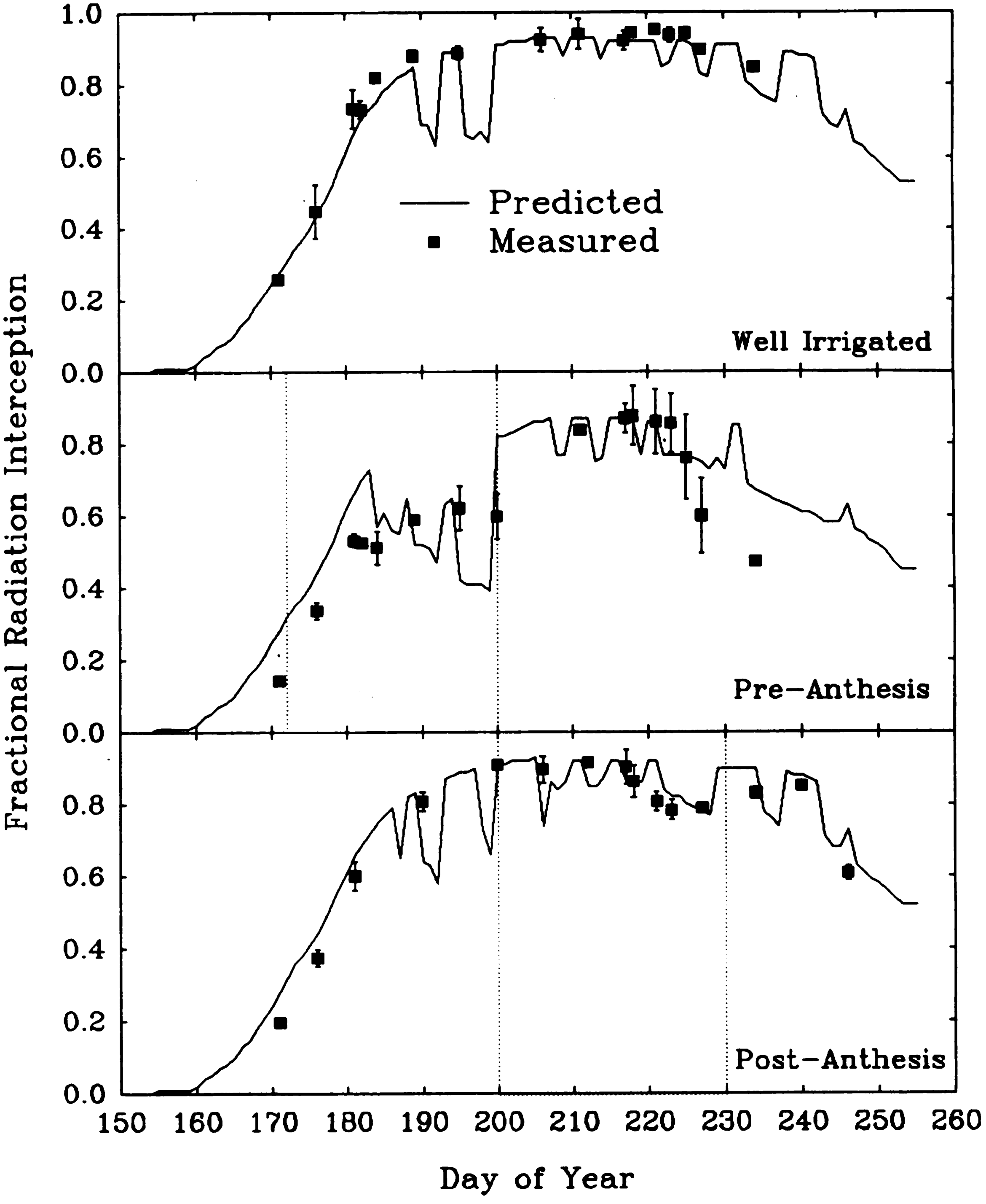

Figure 6.4. Predicted and measured fraction of radiation interception for all treatments. The areas limited by vertical dotted lines represent the periods of soil water deficit.

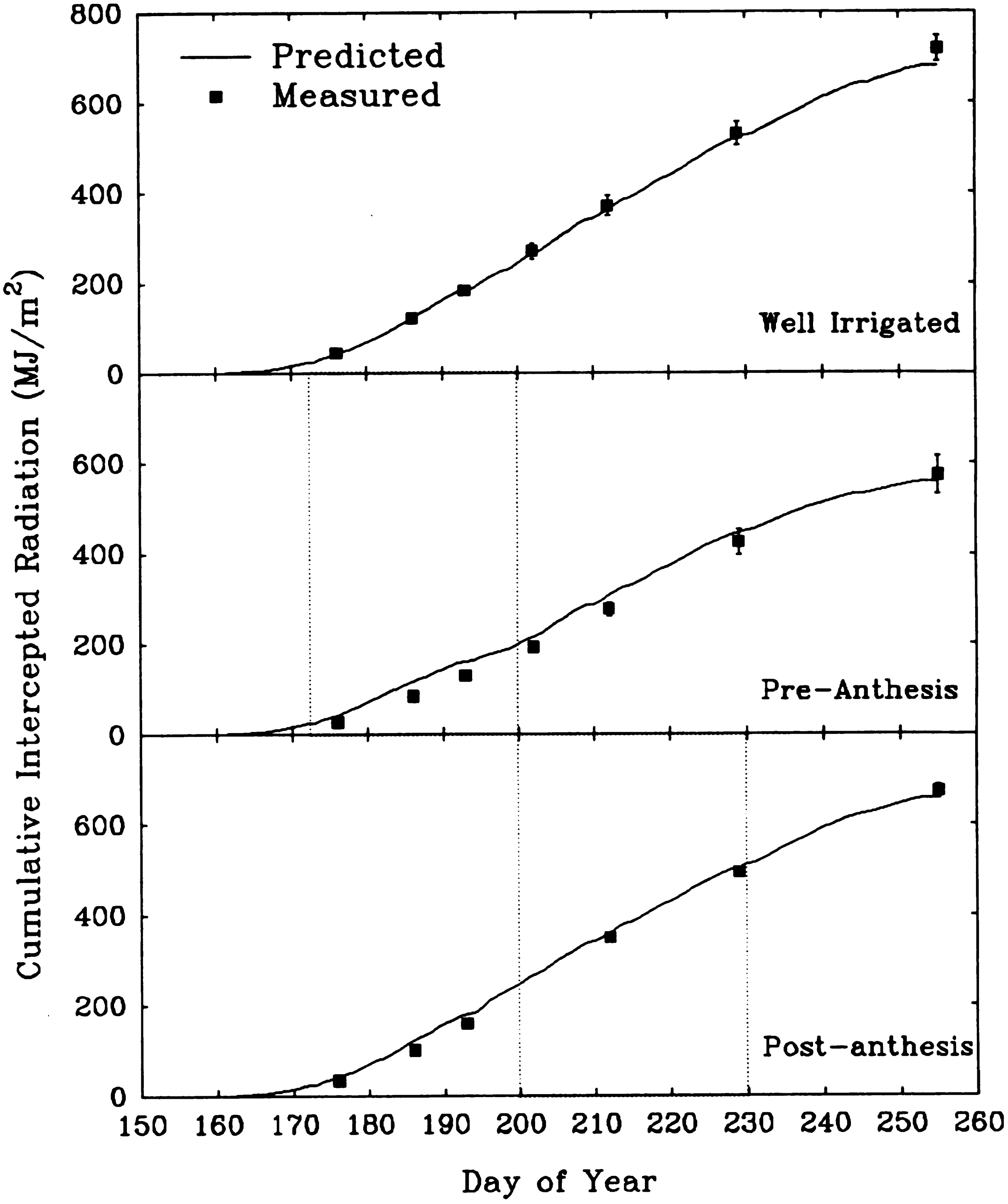

Figure 6.5. Predicted and measured cumulative intercepted radiation for all treatments. The areas limited by vertical dotted lines represent the water deficit periods.

The relationship between fractional radiation interception and exposed leaf area index is presented for all treatments in Figure 6.6. Based on the calculated exposed leaf area, the modified model predicted very well the fractional PAR intercepted by the canopy. A slight deviation was noted for the post-anthesis soil water deficit. The measured values were slightly off mainly because a fraction of the intercepted radiation was intercepted by non-green leaves (senesced leaves) as described in Chapter 4. Gallo *et al.* (1985) described the differences observed in the relationship between plant leaf area and radiation interception before and after silking as being due to the absorption of PAR by nongreen vegetation after silking as senescence occurs.

Additional factors may account for differences between intercepted radiation and plant leaf area. According to Arkin *et al.* (1976), leaves on the plant overlap one another and neighboring plants may shade one another. Thus, not all of the plant's leaf area is actually intercepting radiation. Shading in the plant canopy is dynamic and changes with the sun's altitude and azimuth, and with plant size. Gallo and Daughtry (1986) show that changes in leaf orientation during senescence resulted in increased total intercepted radiation. However, results presented in Chapter 3 indicate little change in leaf orientation during anthesis or the grain filling period.

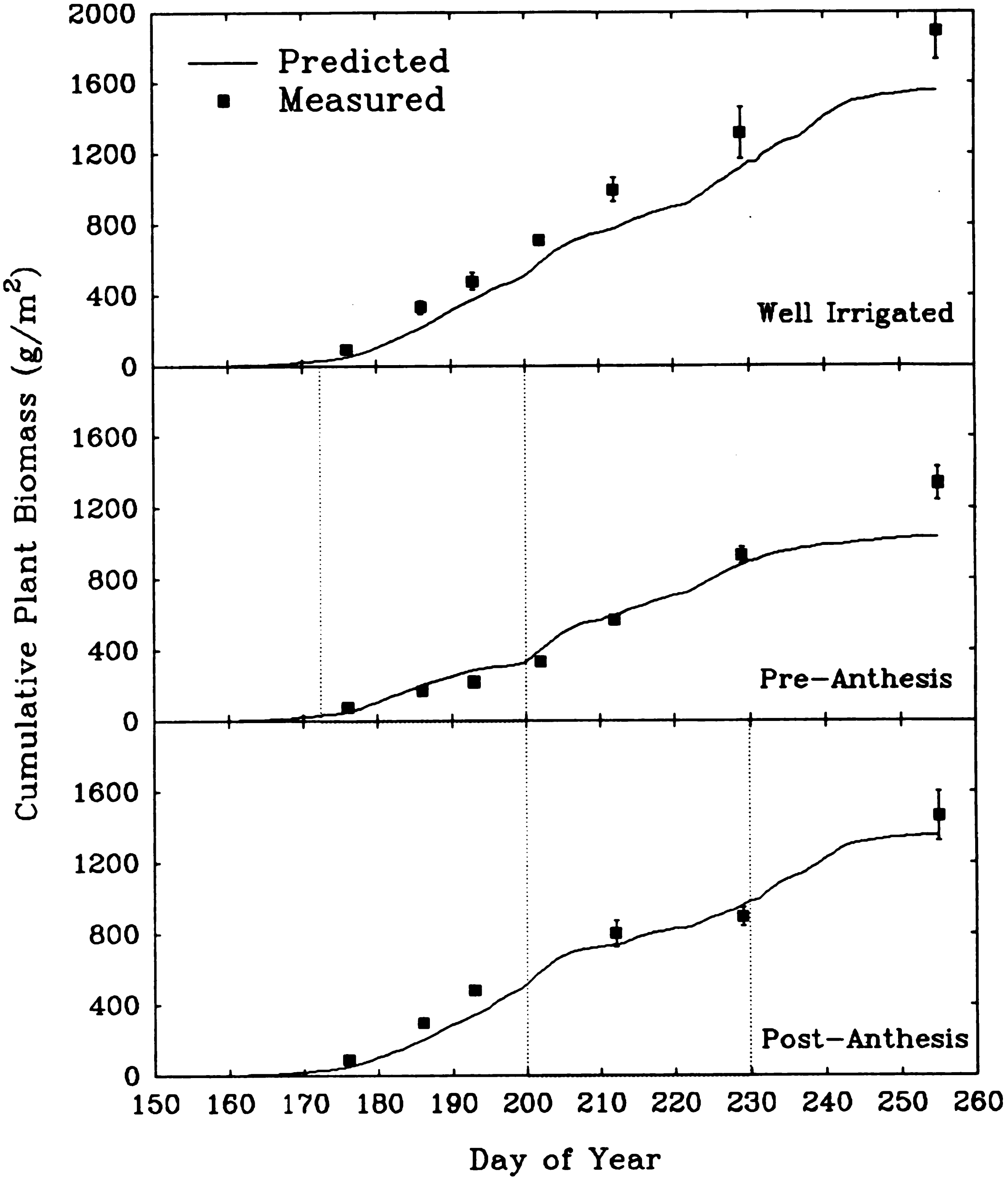

Figure 6.6. Predicted and measured relationship between radiation interception and exposed leaf area index for all treatments.

Plant Biomass Accumulation

Results of the measured (described in Chapters 2 and 4) and predicted aboveground biomass accumulation for all treatments are presented in Figure 6.7. The modified model slightly under-predicted aboveground biomass accumulation, especially late in the season. However, the model was sensitive to both periods of soil water deficit. Additional adjustments in plant biomass production were not carried out due to the limited number of aboveground biomass measurements taken. The model needs to be validated with more field measured plant biomass production.

The relationship between cumulative aboveground biomass and cumulative PAR intercepted is presented in Figure 6.8 for all treatments. The modified model yielded excellent predictions for the pre-anthesis soil water deficit. The model under-predicted the cumulative plant biomass for the well-irrigated treatment although the predicted cumulative PAR intercepted was fairly good. The literature shows that the rate at which arable crops accumulate dry matter during early growth is proportional to the rate at which radiant energy is absorbed by the canopy (Monteith, 1977; Gallagher and Biscoe, 1978; Sibma, 1977).

For the post-anthesis soil water deficit, the modified model under-predicted the aboveground biomass early in the season and predicted very well late in the growing season. Daily plant biomass production has been described as a function of the total incident solar radiation, the proportion of the solar radiation intercepted, and the efficiency of conversion of solar energy to phytomass (Steven *et al.*, 1983).

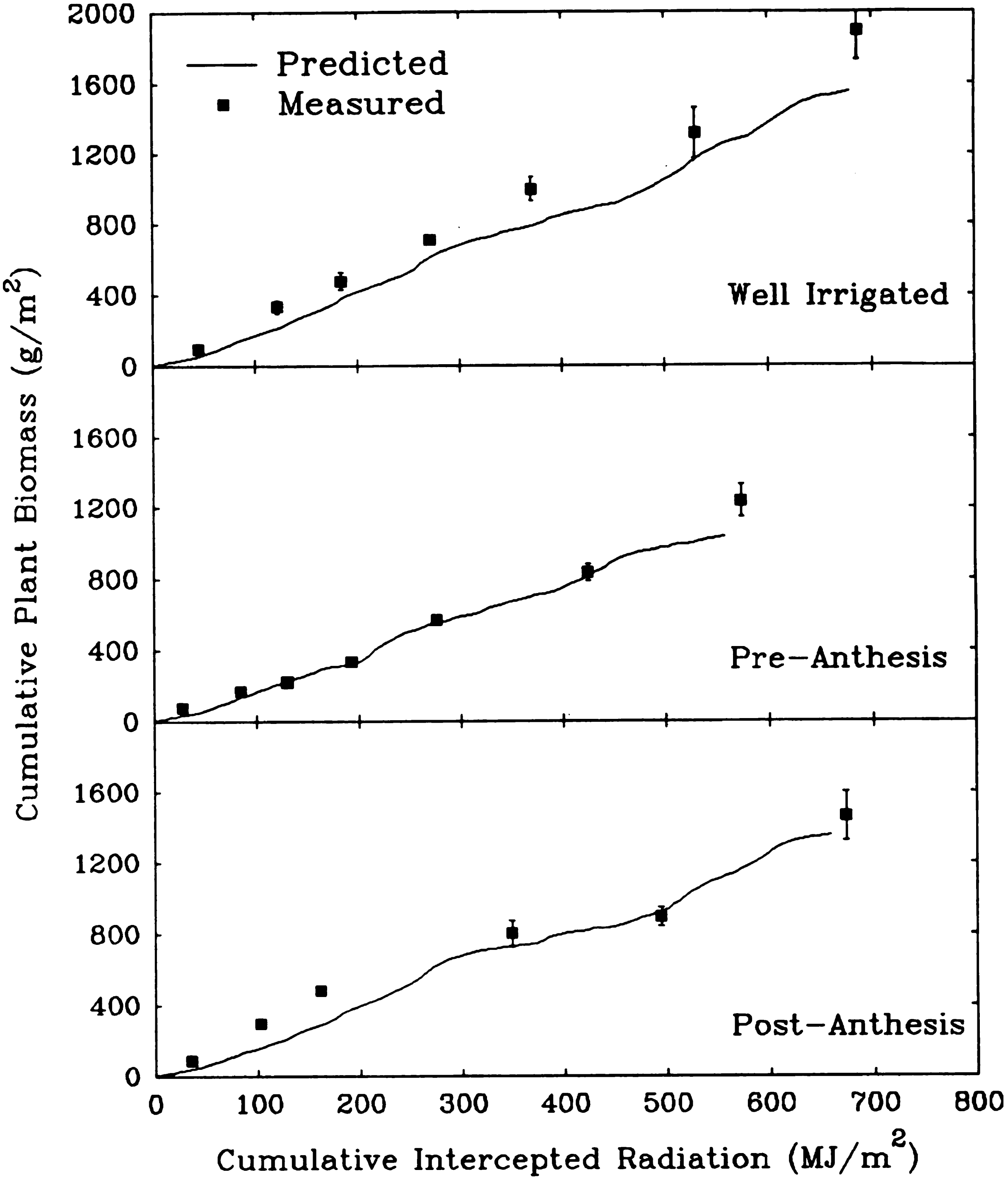

Figure 6.7. Predicted and measured aboveground plant biomass for all treatments. The areas limited by vertical dotted lines represent the water deficit periods.

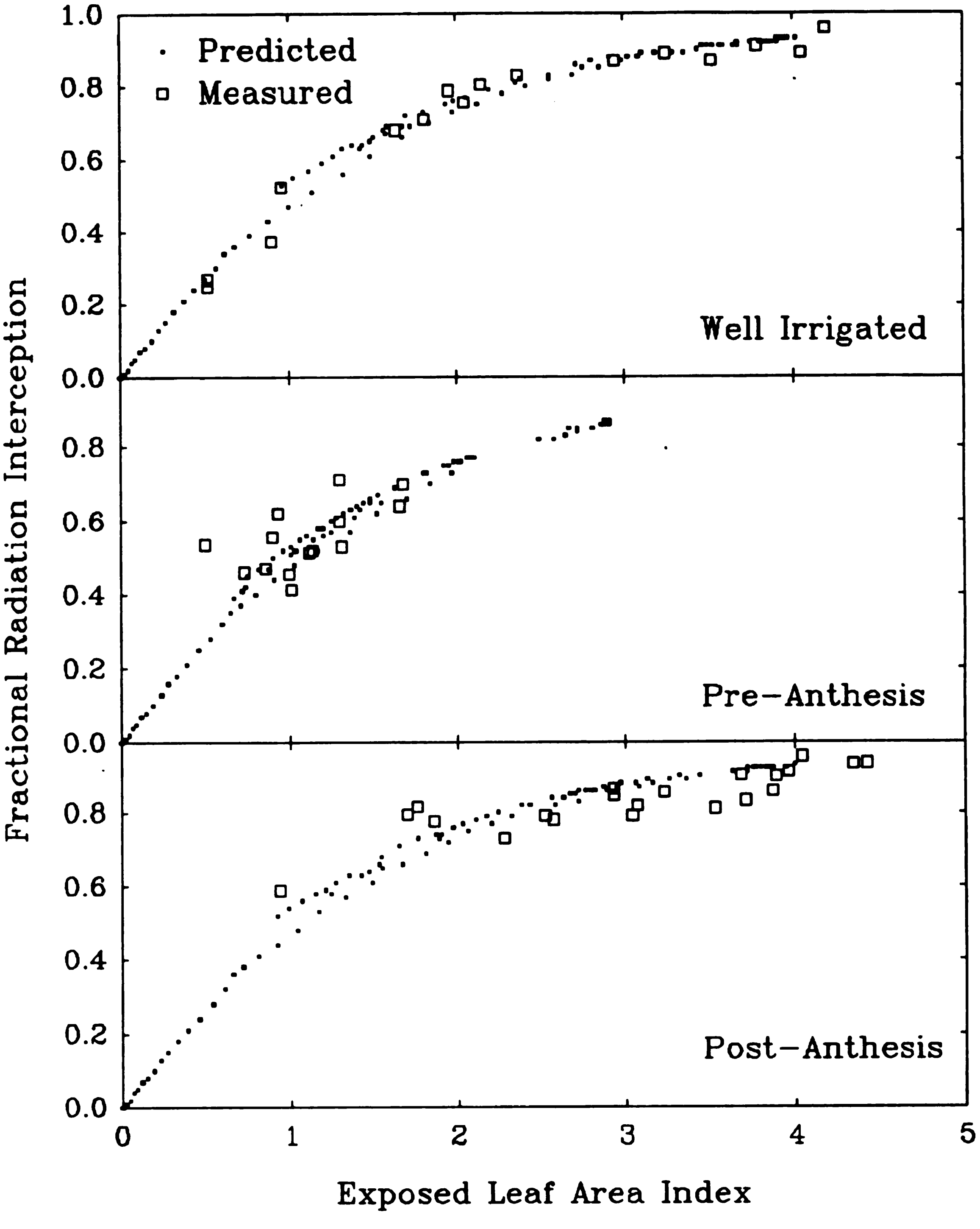

Figure 6.8. Predicted and measured relationship between aboveground plant biomass and cumulative intercepted radiation for all treatments.

Blackman and Black (1959) concluded that under conditions where growth is not restricted by temperature or by supplies of nutrients or water, maximum production of dry matter per unit area is limited by leaf area index and the amount of solar radiation.

Radiation Use Efficiency

Figures 6.9 and 6.10 present the daily values of radiation use efficiency (g/MJ) for the pre-anthesis and post-anthesis soil water deficits. The radiation use efficiency of the pre-anthesis soil water deficit began to diverge from the well-irrigated treatment nine days after irrigation was discontinued. Near the end of the water deficit period, radiation use efficiency was about 49.4% of the RUE predicted for the well-irrigated treatment. The average radiation use efficiency was 1.91 g/MJ and 2.22 g/MJ for the water deficit and well-irrigated treatments.

The RUE for post-anthesis soil water deficit treatment began to diverge from the well-irrigated treatment about four days after irrigation was discontinued. Lower values of RUE were observed during the water deficit period compared to the well-irrigated treatment. The seasonal average RUE was 2.03 g/MJ for the post-anthesis soil water deficit and 2.22 g/MJ for the well-irrigated treatment. A reduction in about 50% of the RUE observed for the well-irrigated treatment was also observed for the post-anthesis water deficit treatment.

The field measured results of RUE were not included in this comparison due to the limited number of aboveground plant biomass measurements taken during

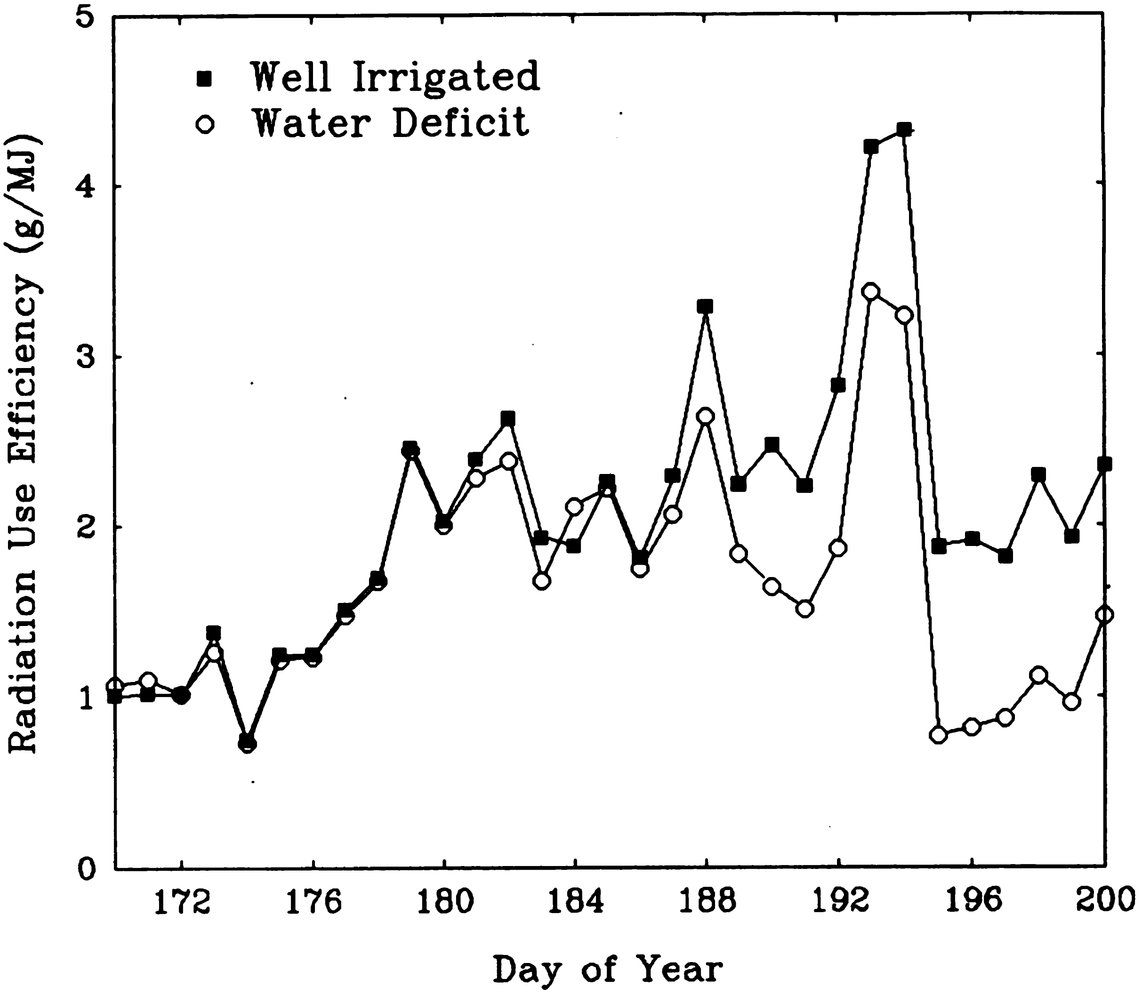

Figure 6.9. Predicted and measured variation of radiation use efficiency for the pre-anthesis soil water deficit and well-irrigated treatment during the water deficit period.

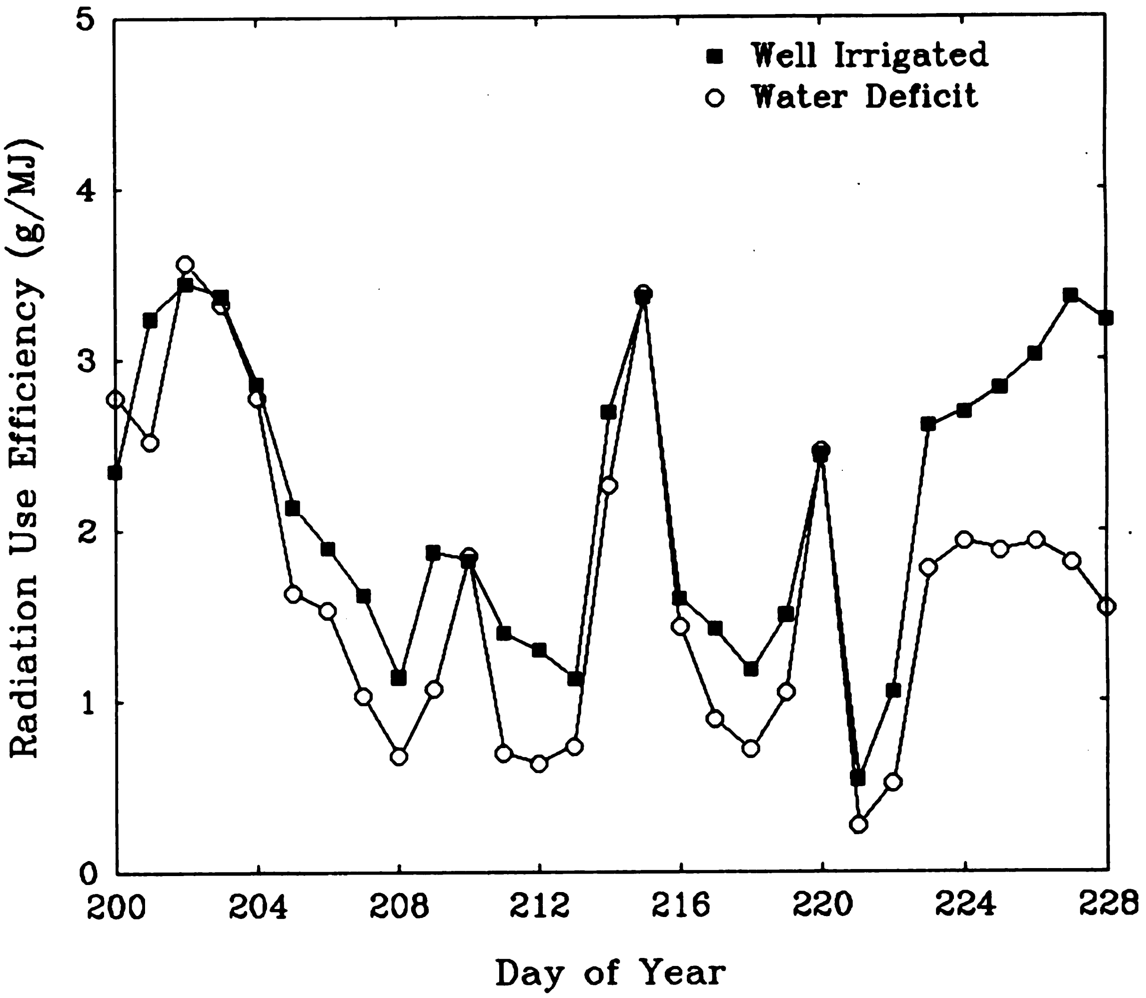

Figure 6.10. Predicted and measured variation of radiation use efficiency for the post-anthesis soil water deficit and well-irrigated treatment during the water deficit period.

the growing season. However, the measured seasonal average of RUE was 2.21 g/MJ, 2.26 g/MJ and 2.71 g/MJ for the pre-anthesis, post-anthesis and well-irrigated treatments. The lower RUE values predicted by the modified model was mainly caused by the overall under-prediction of aboveground biomass in all treatments (Figure 6.7). Monteith (1977) described a seasonal canopy RUE value of 2.8 g/MJ (intercepted PAR) based on aboveground data from apple, barley, sugar beet, and potato. Gallagher and Biscoe (1978) found a seasonal value of 3.0 g/MJ (intercepted PAR) for wheat and barley, including roots and shoots. However, Muchow and Coates (1987) determined seasonal sorghum RUE between 2.1 and 2.4 g/MJ (intercepted PAR).

The reduction in the seasonal average RUE caused by the water deficit period was 14% and 18.5% for the measured and predicted RUE compared to the well-irrigated treatment. During post-anthesis water deficit a reduction of 16.6% and 8.6% was observed for the measured and predicted RUE compared to the well-irrigated treatment.

Conclusions

The modifications included in the CERES-Maize model enables the model to predict the intercepted radiation of maize plants growing in different soil water conditions. Results indicate that the modified CERES-Maize model can be used to simulate the fraction of plant leaf area that is exposed to the incident solar radiation. The model was responsive to periods of water deficit that may occur during plant growth and the model slightly under-predicts the aboveground biomass early in the season and predicts very well late in the growing season. The CERES-Maize model, developed thus far, simulated accurately the intercepted photosynthetically active radiation. The model performed satisfactorily for a variety of soil water conditions. Prediction differences between measured and predicted results were considered excellent. However, additional adjustments in plant biomass production need to be carried out against more field data.

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Conclusion and Recommendations

The complexity of the different mechanisms interaction that maize plants use to escape or cope with the effects of water deficits was illustrated in this experiment. The reduction in leaf expansion during water deficits causes a reduction in plant leaf area and less radiation is intercepted by the crop canopy. As a consequence, the total plant assimilation is reduced. The reduction of maize canopy radiation interception due to vegetative stage soil water deficit is mainly due to slower leaf area expansion and the increase in leaf rolling. Expanding leaves (younger leaves) more easily changed leaf orientation during water deficit periods than totally expanded leaves (shorter leaves).

Leaf area adjustment is a complex phenomenon and distinct mechanisms exist through which maize varieties may escape the effects of water deficits. Commonly, at the beginning of a water deficit period, the decrease in cell volume of the expanding part of the leaf results in lower hydrostatic pressure or turgor and, consequently, reducing plant leaf area. Turgor pressure is also lost in the expanded part of the leaf and the lamina rolls to reduce the exposed leaf area. Subsequently, leaves are orientated more vertically reducing radiation interception. The main advantage of this mechanism is its reversibility, rapidity of leaf recovery when the water deficit is relieved, thus enlarging significantly the photosynthetic surface and the possibility that yield will not be seriously affected.

Plant responses to post-anthesis soil water deficit are complex phenomena and several mechanisms exist by which maize plants alleviate the effects of water deficits. Less leaf rolling was observed during post-anthesis water deficits than water deficit imposed during pre-anthesis. Leaves were totally expanded and wider than when the plant was submitted to pre-anthesis soil water deficit. The leaf rolling mainly occurred near the edge of the leaves, limiting further increases in leaf rolling and leaf orientation and, consequently, the reduction in exposed leaf area. The effectiveness of the leaf rolling mechanism occurred mainly during the beginning of the water deficit period and leaf senescence was activated later when no further reduction in exposed plant leaf area was possible by increasing leaf rolling. The effect of water deficit on leaf rolling began when the fraction of plant available water was below 0.61-0.64. Leaf senescence, however, began when the fraction of plant available water fell below 0.51-0.54.

Different criteria have been used to determine the timing and duration of water deficits. The vegetative soil water deficit imposed in plants grown on a large quantity of stored water (Kalamazoo soil) have limited effect on plant elongation and crop growth. The crop performance during the vegetative growth was more closely linked to the amount of soil available water than to the fraction of plant available water. Plant senescence was enhanced for both varieties, after flowering, where the fraction of plant available water was about 0.18 (35 mm of soil available water) for both varieties.

The modifications included in the CERES-Maize model enables the model to predict the intercepted radiation of maize plants growing in different soil water conditions. CERES-Maize model can be used to simulate the fraction of plant leaf area that is exposed to the incident solar radiation. Differences between measured and predicted results were considered excellent. However, additional adjustments in plant biomass production need to be carried out against field data.