Water stress effects on biomass production and partitioning in processing tomatoes

By

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B.S. (University of Nairobi, Kenya) 1978.
M.S. (University of Nairobi, Kenya) 1981.

Dissertation

Submitted in partial satisfaction of requirements for the degree of

Doctor of Philosophy

in

Ecology

in the

1985

GRADUATE DIVISION

of the

University of California

Davis

Approved:

Committee in Charge

Deposited in the University Library_____
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To my brothers, Dr. Jak Sijenyi and Martin Okech,

whose brilliance and hard work gave me the

initial academic challenge

and

To a very dedicated teacher, Tobias Otieno Maluga,

formerly of Nyawanga Primary School, who

first advised me 17 years ago to aim

at getting a doctorate degree.

ACKNOWLEDGEMENTS

I wish to express special thanks to my major professor, Dr. T.C. Hsiao for the very enlightening advice and criticisms he offered to me during all stages of this work. I gained tremendously from his indepth knowledge in plant water relations and scientific writing. His suggestions have added a great deal to the quality of this paper but I remain responsible for any mistakes, errors, or other inadequacies that may be found in this work. I am also thankful to Dr. T. De Jong and Dr. J.D. Hewitt for the advice I received from them during my research and particularly for reading the drafts for this paper. I benefitted a lot from their criticisms.

Special thanks are due to my good friend, Miss Eda Lim who assisted me selflessly during my research and also typed and editted parts of this paper. I am also indebted to Miss Cathy Wranovics for typing sections of this paper, to Bruce Lampinen for creating a good working atmosphere in the laboratory, to Jorge Bolanos and Tony Matista for maintaining the gas exchange systems and to all other members of Dr. Hsiao's laboratory for their help and good working relations.

Lastly I wish to thank all other people who helped me in one way or another during the period of this work.

Abstract

Experiments were conducted at the University of California, Davis field station. Soils were deep silty loam with high water storage capacity. Water stress effects on vegetative and reproductive growth, canopy light conversion efficiency and single leaf photosynthesis of tomato, cultivar U.C. 82B were investigated under different irrigation regimes. Irrigation treatments were: well irrigated (I) and non-irrigated (NI). Treatment NI received no more irrigation after the sixth leaf stage and thus depended largely on water stored in the soil.

There was little or no difference in leaf water potential between I and NI through most of the season. Single leaf photosynthetic rate also showed little response to irrigation treatments. However, withholding irrigation caused marked depression on canopy expansion. Non-irrigated plots had much smaller canopies and the resulting incomplete ground cover greatly reduced biomass accumulation. A linear relationship was found between cummulative intercepted radiation and biomass accumulation. The slope of this line is an expression of canopy photosynthetic efficiency. Water stress reduced this parameter but this effect was much less than the reduction of canopy expansion suggesting that water stress depressed biomass accumulation largely through its effects in inhibiting canopy growth rather than canopy photosynthetic efficiency.

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There was little or no difference in leaf water potential between I and NI through most of the season. Single leaf photosynthetic rate also showed little response to irrigation treatments. However, withholding irrigation caused marked depression on canopy expansion. Non-irrigated plots had much smaller canopies and the resulting incomplete ground cover greatly reduced biomass accumulation. A linear relationship was found between cummulative intercepted radiation and biomass accumulation. The slope of this line is an expression of canopy photosynthetic efficiency. Water stress reduced this parameter but this effect was much less than the reduction of canopy expansion suggesting that water stress depressed biomass accumulation largely through its effects in inhibiting canopy growth rather than canopy photosynthetic efficiency.

Generally water stress depressed vegetative growth but enhanced or had no effect on reproductive growth. Water stressed plants had higher fruit set on early flower trusses. They also had higher coefficient of biomass partitioning into fruits through most of the season but the duration of biomass accumulation into fruits was reduced. Prevention of fruit development by continuous flower removal failed to stimulate canopy growth in water stressed plants suggesting that the preferential partitioning of biomass into fruits may not be explained by simple competition for assimilates.

Due to depression of canopy expansion, water stressed plants may be limited by vegetative sinks and this could ultimately lead to photosynthetic inhibition. Removal of all fruits depressed photosynthesis presumably through sink limitation and the mechanism involved was apparently similar to that reported for water stress limitation on photosynthesis. It is thus suggested that effect of water stress on photosynthesis could be operating through sink limitation.

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SECTION I

General Introduction

In the world of ever increasing population, there is an urgent demand to achieve a matching growth in food production. The use of artificial fertilizers has, in the past, produced a steady increase in world food supply, mainly through increase in yield per unit land. Recent data, however, suggest that we may be approaching another yield plateau. In the next decade the pressure to keep on expanding the total area of land under cultivation will increase, pushing agriculture into less favorable areas. There is, therefore, an urgent need to further our understanding of crop responses to the marginal environments in order to maximize production.

Outside the polar areas, water availability is the most important single environmental factor restricting the range of agricultural production. Of course, drought can be, and has been alleviated by irrigation. The increasing cost of irrigation together with the limited supply of good quality water have, however, created the need to improve crop water use efficiency. Much research has gone into the study of crop water relationships. The literature available on this subject, however, reveals that field crops, particularly cereals and, to some extent, cotton and grain legumes have received much more attention than vegetable

crops. The reasons for this disparity are probably to be found in the fact that vegetables are traditionally consumed as fresh produce where fresh juicy quality associated with high irrigation levels is an advantage. With the expansion of the processing industry, however, production of vegetables and particularly tomatoes, has become a field practice with emphasis on biomass yield.

Tomato, a crop which was first domesticated in Mexico, is the world's most widely grown vegetable after potato. Plant explorers have found wild relatives of the tomato in environments as diverse as the tropical rain forests of South America and the arid regions of Mexico. Certainly there is a gene pool that can be utilized to develop drought resistant cultivars. Work hitherto conducted in tomato water relations have been mainly geared towards irrigation management and results typically show that tomato yield is sensitive to water stress. I believe these should be considered as preliminary studies directed towards understanding of current cultivars. We cannot expect crops developed for high moisture conditions to always perform well under drought. However, we can use information gathered from present cultivars to chart a direction for future improvement. Ecophysiological work is needed to examine and integrate various responses of the plant to water stress so the information can be incorporated in programs directed at the development of drought resistant

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tomatoes.

Much improvement in crop productivity has been derived from increase in harvest index rather than photosynthesis. There is, thus an impetus for studying partitioning of biomass in crops. Some literature on crop-water relations indicate that various phenological stages and plant parts exhibit different degrees of sensitivity to moisture stress, suggesting an influence of water stress on biomass partitioning. In tomatoes, water stress often influences earliness, total solute content of fruits, root/shoot ratio and other partitioning phenomena. The objective of this study was to take a critical look at some of these partitioning phenomena arising from water stress and assess their implications in yield of tomatoes under limited moisture. The tomato has only been used as a model crop and it is hoped that results emanating from this study will add to our understanding of general crop water relations and crop adaptation to marginal moisture conditions.

SECTION II

Literature Review

This section discusses literature regarding the effect of water stress on crop yield. Development of crop water deficits and its effects on biomass accumulation and partitioning are reviewed. The last part of this section deals with the effect of sink limitation on photosynthesis, as assimilate accumulation following water stress could account, at least partly, for water stress induced photosynthetic depression (Barlow and Boersma 1976).

Development of crop water deficits in the field

Plant water deficits develop when transpiration exceeds absorption rate. In a normal day, a plant goes through a diurnal cycle consisting of a period of increasing internal water deficits when transpiration is greater than absorption, followed by a late afternoon recovery period when absorption is greater than transpiration (Kramer, 1937; Slatyer, 1967). This cycle develops irrespective of soil moisture status as long as transpiration occurs for at least part of the day. Thus water stress is a relative term which depends on the degree and duration of internal water deficits.

The progression of long term plant water deficits has

been analysed by Slatyer (1967). It essentially begins with the daily cycle but as soil water potential drops, the plant not only experiences lower water potential but the recovery phase also takes longer. Ultimately, the plant water deficits get so severe that the plant will die if no irrigation or rain occurs. This simple model may be complicated by a number of factors that are important in the long term development of plant water deficits under field conditions. First, it has been observed that water stress inhibits shoot more than root growth so that the shoot-root ratio is increased (Bradford and Hsiao, 1982). Such a response reduces transpiration surface relative to the water absorbing surface and thus improve the plant water economy. Occasionally there is an absolute increase in root biomass in plants under mild water stress (Sharp and Davies, 1979). Moreover, within the drying soil itself roots grow faster in wet than dry portions of the profile (Portas and Taylor, 1976). Klepper et al. (1973) and Taylor and Klepper (1974) reported a shift in rooting pattern of cotton in such a way that rooting density increased with depth while the opposite was true for the irrigated treatment. Salter (1954) reported a similar shift in glasshouse tomatoes. Enhanced root growth in deeper, wetter soil layers would increase the root area effectively involved in water uptake and thus reduce the rate of progression of plant water stress. Other acclimatory responses such as increase in pubescence (Ehleringer, 1980), parahelionastic leaf movements (Mooney et al., 1977) and stomatal closure may also complicate the

long term trend of development of plant water deficits.

Relationship between leaf and soil water potentials

In studies of plant water relations, soil moisture potential has often been used as an index of plant water stress. However, little relationship exists between leaf water potential and soil water potential (Slatyer, 1967). For a plant to extract water from the soil, it must have a water potential lower than that of the soil. This difference depends on the evaporative demand (or vapor pressure deficit), the extent to which a plant can cope with the demand and the water conducting properties of the soil and the plant (Gardner and Nieman, 1964). Rudich *et al* (1981) obtained results which suggest that hourly changes in the leaf water potential of tomato plants were strongly correlated with changes in vapour pressure deficit (VPD). At any one VPD level, however, leaf water potential will be positively correlated with soil water potential. As soil water potential falls, soil hydraulic conductivity declines rapidly so that lower root and leaf water potentials are required to sustain transpiration rate at desired level.

Soil water potential also represents the upper possible limit of recovery by the plant during the night (Slatyer, 1967; Turner and Begg, 1981). However, it has been observed (e.g. Cary and Wright, 1971; Klepper *et al.*, 1973) that plant and soil moisture potentials do not

equilibrate overnight even under conditions where dew formation preclude night time transpiration. The existence of soil-root interface and internal plant resistances dictate that leaf water potential will lag behind soil water potential in the recovery process. Moreover, Boyer (1974) found that plant resistance to water flow increases markedly as absorption decreases when the leaf approaches saturation. Lack of equilibration could also be caused by plant expansive growth (Molz and Boyer, 1978).

Canopy development and biomass production

The rate and extent of crop growth is postulated to depend on amount of light intercepted and the canopy light conversion efficiency. Several workers (e.g. Monteith, 1977; Shible and Weber, 1966; Williams et al. 1965) have reported significant linear relationship between the total light intercepted and crop aboveground biomass accumulated over specific time intervals in various field crops. A typical annual crop has a small canopy early in the season and absorbs only a part of the incident photosynthetic radiation. Hsiao (1982) has theorized that at this stage, canopy light interception is the main factor limiting productivity and that growth should follow first order kinetics, being proportional to the initial biomass and exponential with time. However, experimental data bearing on this point are limited. Once a crop has achieved full canopy cover, the efficiency of light utilization (biomass

produced per unit light absorbed or intercepted) controls biomass accumulation rate and, if light conditions do not change, crop growth rate should remain constant as reported by Williams et al. (1965) for maize. It is hence suggested that further increase in leaf area index (LAI) beyond full canopy cover is unnecessary and may actually be undesirable as it only leads to more shading of the lower leaves and increased respiratory load on the plant system (see Gifford and Jenkins, 1982). The knowledge that shaded lower canopy leaves tend to shift their light compensation point downwards and stay in positive carbon balance (McCree and Troughton, 1966; King and Evans, 1967) and that photosynthetic activity of leaves decreases with age (Catsky et al., 1976) may, however, suggest that there would be some benefits derived from increased leaf formation even after full canopy. Absence of such leaf growth may result in rapid decrease in crop growth rate as efficiency of uppermost leaves falls with age.

Effects of water stress on canopy development

Bradford and Hsiao (1982) pointed out that crop canopy growth is very sensitive to water stress. This is probably due to high sensitivity of expansive growth to plant water deficits (Boyer, 1968). Hsiao (1973) concluded that cell expansive growth appears to be more sensitive to water stress than other physiological processes. The sensitivity of canopy development to water stress may have important

implications for crop productivity. Small reductions in growth rates in the early growth stage due to water stress would, because of the the exponential nature, compound with time into large reductions in biomass production (Bradford and Hsiao, 1982). The ecological implications of canopy response to water stress remain to be analysed. Studies are needed to look at the adaptive importance of this response and how it can be incorporated in crop management practices under conditions of water stress.

The mechanisms underlying the sensitivity of expansive growth to water potential are not well understood. Lockhart (1965) defined a relation between cell expansion rate and turgor pressure:

$$dV/Vdt = E_g (\Psi_p - \Psi_{p,th})$$

where V is the cell volume, dV/Vdt is the relative rate of increase in cell volume, E_g is gross extensibility of the cell wall, Ψ_p is turgor pressure (or pressure potential) and $\Psi_{p,th}$ is the threshold turgor pressure below which no expansion occurs. Green *et al.* (1971) reported results which, in general, support the Lockhart equation. Based on this relationship, water stress induced inhibition of expansive growth may result from decrease in extensibility, decrease in turgor pressure or increase in threshold turgor pressure.

Turgor pressure can be readily reduced by water

stress. Relationships between water content and leaf water potential (e.g. Tyree and Hammel, 1972) show that a small reduction in water content is usually associated with a large fall in turgor pressure. Because only the turgor above the threshold is effective in expansive growth and the threshold is high (Green et al., 1971), inhibition of growth by water stress has been considered in terms of turgor reduction (Hsiao, 1973; Hsiao et al., 1976a). Recently, however, some work has been reported which shows that while expansive growth depends on having some minimum turgor pressure, the relationship is complex depending on the age of the tissue and its past history (Kramer, 1983). For example, Bunce (1977) found a linear relationship between elongation rate and turgor in soybean leaves but leaves in drier field environment required less turgor for elongation than those grown in the more humid growth chamber. Wenkert et al. (1978) concluded that turgor pressure is not the primary factor limiting leaf growth within the daily range of water potential in the field. In growth chamber, Michelena and Boyer (1982) and Van Volkenburgh and Boyer (1985) reported that withholding water from maize plants inhibited leaf elongation even though enough solutes accumulated in the elongating region to maintain virtually constant turgor. Van Volkenburgh and Boyer (1985) found that while growing tissues of well watered plants excreted protons into the apoplastic space, this acidification was inhibited in tissues exposed to water stress. Wall acidification has been reported to enhance expansive growth

by increasing cell wall extensibility (Hsiao and Bradford, 1983; Rayle and Cleland, 1977). In the case of water stress it is not clear if reduction in wall acidity could account for all growth inhibition; and a possible effect of an undetected small drop in turgor is not ruled out. There is clearly a need for more research to investigate the primary mechanism responsible for expansive growth reduction in plants.

Effect of water stress on biomass partitioning

High crop yield depends on biomass production and partition in a manner that maximises economic harvest. Partitioning is dependent on the allocation of current assimilates and mobilisation of stored assimilates to metabolic sinks. A good partitioning strategy should ensure plant survival, allow for agronomic management practices (e.g. reduce crop lodging and hence facilitate mechanical harvesting) and maximise the proportion of total biomass deposited in the plant parts that constitute yield. Under conditions of soil moisture deficits, water acquisition could be the single most important factor influencing yield. In this section crop partitioning strategies that influence crop yield under water stress are discussed. The effect of water stress on phloem transport process appears to be small (Slatyer, 1973; Wardlaw, 1968) and is not included in this discussion.

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Root growth: Roots constitute an important sink for assimilates. Soil water deficits affect root growth in a number of ways. Generally growth rate of roots decreases with increasing degree of water deficits (Portas and Taylor, 1976). However, root growth in each soil layer appears to be independent of moisture content in other soil layer. As a result, growth may stop in roots ramifying into upper dry soil layers but continue in those penetrating wet zones of the profile (McWilliam and Kramer, 1968; Klepper et al., 1973). Arnon (1975) noted that roots grow towards water in the soil provided the distance from the water is small.

Water stress usually depresses shoot growth to a relatively greater extent than root growth so that the overall root/shoot ratio is increased (Begg and Turner, 1976; Davis, 1942; Harris, 1914; Hsiao, 1973; Martin, 1940). Situations have also been reported where mild water stress induced absolute increase in root growth (Doss et al, 1960; Hsiao and Acevedo, 1974; Sharp and Davies, 1979). It should be added that root/shoot ratio at any point in time portrays both the proportion of assimilates allocated to roots and the rate of turnover of roots relative to shoot (Fischer and Turner, 1978). Sharp and Davies (1979) observed that, as water stress developed, an increase in root/shoot ratio started about the same time as a decrease in leaf elongation rate.

Both a greater density of roots and increased rooting depth are morphological adaptations to water deficits which facilitate better extraction of soil water and maintainance of high plant water status. Salter (1957) commented that wet soil regimes led to shallow rooting in contrast to deeper development of roots under dry conditions. Work with broad beans (Kausch, 1955 cited in Salter and Goode, 1967) showed that when the plant was grown in sodium chloride or sucrose solutions of of decreasing water potential, the growth of lateral roots was retarded before that of tap root. Likewise Lundkvist (1955) (see Salter and Goode, 1967) showed that tap root constituted a larger proportion of total root length under conditions of water stress. Development of deep root systems would be a useful adaptive feature if water is available in the deeper soil layers. Hurd (1968; 1974) showed that deeper rooting varieties of wheat yielded better under drought stress.

Reproductive growth and development: Due to differences in life history, reproductive growth in annual crops responds to water stress in a slightly different way from perennials (Fischer and Turner, 1978). This discussion will be limited largely to the response of annual crop plants but examples from annual wild plants will also be used where necessary. There is much in literature relating overall crop yield to water stress (see Salter and Goode, 1967) but data are limited on the detailed dynamics of responses of the various stages of reproductive growth.

Response of flower initiation to water stress seems to be complicated. Severe early water stress has been shown to delay (Marc and Palmer, 1976) or have no effect (Mott and McComb, 1975) on flower initiation. Flowering is generally hastened slightly by mild water stress (Turner and Begg, 1977) but has been found to be unaffected in some desert ephemerals (Mott and McComb, 1975). Angus and Moncur (1977) found that, in wheat, flowering was hastened by mild water stress but there was developmental retardation in plants which had been heavily stressed, the retardation being commensurate with the duration of severe stress. Water stress during fruit set and fruit filling will usually accelerate fruit maturation (Clarkson and Russell, 1976; El Nadi, 1974) although some exceptions have been observed among wild species (Mott and McComb, 1975). Salter (1958) noted that water stress shortened fruit growth period in tomatoes.

It is frequently reported that the the number of fruits per plant is the yield component most sensitive to water stress and such observations are used to support the idea that pollination is easily inhibited by stress (see Salter and Goode, 1967). The evidence, however is confusing, particularly when based on harvest-time data without consideration of changes throughout the season. Water stress developing slowly during crop growth have no effect on tomato fruit set in the studies of Cannell and

Asbell (1974) and of Haghighi (1980). When plants are well supplied with water early during reproductive phase, subsequent stress will increase shedding of flowers and developing fruit (El Nadi, 1969; also see Hearn, 1980) and reduce yield. Severe water stress has been reported to inhibit pollination but mild stress of the order usually encountered under field conditions has little effect (Hsiao, 1982). Wudiri (1980) found that water stress had little effect on pollen viability in tomato. A liberal water supply early during flowering can also increase shedding of young bolls in cotton (Stockton et al., 1961; Hearn, 1975) apparently by stimulating internal competition between vegetative and reproductive growth (Hearn, 1980). Fruit shedding during severe water stress is possibly also induced by source limitation.

Following fruit set fruit growth becomes an increasingly strong sink for current assimilates, and a large proportion of the total assimilation over the fruit growth period goes to the fruit (Hurd, 1979; Johnson and Moss, 1976). Growing fruits or seeds may also receive some carbon through remobilisation of assimilates stored in the plant before the onset of fruit growth (e.g. Bidinger, 1977, see Fischer and Turner, 1978). Water stress during fruit growth not only increases the proportion of current assimilates translocated to the seed (Johnson and Moss, 1976) but also increases remobilisation of assimilates stored prior to fruit growth (Boyer, 1976; Constable and

Hearn, 1978; Passioura, 1976). Individual fruit growth was found to be insensitive to water stress (Salter, 1958). In cotton, water stress increased the number of early bolls (Hearn, 1975). The duration of fruit growth is, however, often curtailed (Salter, 1958). There is need to further study the interactions between biomass allocation and duration of reproductive growth under water stress.

Whole season partitioning of assimilates into fruits manifests itself in the harvest index (HI). Where water stress develops early or is mild and evenly distributed over the whole season, HI is unaffected (de Wit, 1958, see Fischer and Turner, 1978; Haghighi, 1980). Considering the influence of water stress on assimilate allocation into fruits and duration of reproductive growth as discussed earlier, there is need to study the trend of proportion of total biomass allocated to fruits throughout the reproductive phase. Severe plant water deficits concentrated around flowering or in the fruit filling stage can reduce HI remarkably (see Fischer and Turner, 1978; Salter and Goode, 1967).

Sink Limitations on Photosynthesis.

Effect of sink/source ratio on photosynthesis: It has been observed that reduction of sink-source ratio often inhibits photosynthetic rate (Neales and Incoll, 1968). The rate of photosynthate export from source leaves to sinks is

thought to be important in regulating the CO_2 assimilation rate in the source leaf. If rates of export are so low assimilates accumulate in the source leaf, photosynthesis will be inhibited. Hence, changes such as inhibited translocation and reduced sink demand have frequently (Guinn and Mauney, 1980; Lenz, 1978; Neales and Incoll, 1968) but not always (see Geiger and Giaquinta, 1982) been shown to lead to lower photosynthetic rates.

Much of the literature indicates that reduction of fruit load on a plant depresses leaf photosynthetic rates. For example, Setter *et al.* (1980a) found that complete de-podding of soybean produced up to 70% reduction in CO_2 exchange rate. Similarly Loveys and Kriedemann (1974) observed about 50% decrease in photosynthesis following defruiting of grape vines. These results may be interpreted in terms of sink source relationships (Neales and Incoll, 1968). It would appear that reduction of sink/source ratio leaves source leaves with excess assimilates which accumulate in the leaf tissues and effect negative feed-back upon biochemical processes of photosynthesis. Work reviewed by Geiger and Giaquinta (1982), however suggest that the mechanisms involved in these responses are complex and that assimilate accumulation in leaves *per se* does not always cause depression in photosynthesis. Situations have also been reported where the onset of fruiting *per se* led to an increase in photosynthetic rate. Chalmers *et al.* (1975) found that photosynthesis increased as the rate of fruit

growth increased in peaches but again decreased when the fruits were harvested. They explained their results on the basis that accumulation of assimilate in leaves before rapid fruit growth and after harvest limited photosynthesis. Flinn (1974) observed that presence of fruits enhanced photosynthetic rates in adjacent leaflets. The possibility that fruits produce some photosynthetic stimulators has been discussed by Guinn and Mauney (1980).

Mechanisms of sink limitation on photosynthesis: The mechanisms involved in the inhibition of photosynthesis by fruit removal are not well understood. The end product inhibition hypothesis (Guinn and Mauney, 1980; Herold, 1980; Neales and Incoll, 1968) has dominated the literature for over a century (Neales and Incoll, 1968) yet, although a number of workers (e.g. Kriedemann *et al*, 1976; Loveys and Kriedemann,1974; Setter *et al*, 1980b) have reported increase in carbohydrate concentration in leaves following defruiting, the biochemical processes that would lead to such a feed-back have not been well established (Geiger and Giaquinta, 1982; Herold, 1980). Certain phosphorylated sugars such as fructose-1,6-diphosphate, glucose-1,6-diphosphate, glucose-6-phosphate and 3-phosphoglcerate have been shown to competitively inhibit RUBP-carboxylase activity (see Guinn and Mauney, 1980). Sucrose, glucose and fructose, however, had no appreciable effect. Accumulation of non-phosphorylated sugars may inhibit photosynthesis by

sequestering inorganic phosphate (Pi) (Herold et al, 1976) thereby interfering with triose-Pi translocator. Deficiency of Pi has been shown to depress photosynthesis (Terry and Ulrich, 1973). The sequestration of Pi by sugars could explain the inhibition of photosynthesis by applied sugar solutions (Moore et al, 1973).

The chloroplast membrane is impermeable to sucrose (see Geiger, 1979). It is therefore more difficult to conceive a mechanism by which sucrose which is formed outside the organelle could inhibit photosynthesis. Herold (1980) noted that increased levels of sucrose in the cytoplasm, when sink activity is reduced, could lead to increased concentration of triose phosphate (TP) from mass action or feed-back inhibition of enzymes. Another possibility is the inhibition of sucrose phosphate phosphatase by sucrose (Hawker, 1967). In this case accumulation of sucrose phosphate will be accompanied by lowered concentration of Pi and increased concentration of TP in the cytoplasm. For further details on possible sucrose mediated mechanisms the reader is referred to Herold (1980). In intact plants, correlations between sucrose accumulation and decreased rate of photosynthesis are tenuous (Neales and Incoll, 1968; Herold, 1980). Furthermore, the importance of sucrose concentration in sink-source interactions is complicated by the paucity of knowledge concerning the distribution of sugar between cytoplasm and vacuole and the extent of interspecific

variation (Herold, 1980).

Because starch is insoluble in water, most of the proposed mechanisms for feed-back inhibition by starch are based on physical rather than biochemical effects (Neales and Incoll, 1968). Guinn and Mauney (1980) have summarized these mechanisms to include binding of Mg^{2+} ions, interference with light transmission, increased distance for CO_2 diffussion and physical damage to chloroplasts.

Since the review by Neales and Incoll (1968) a number of workers have shown that defruited plants often have lower leaf epidemal conductance (g_e) (Koller and Thorne, 1978; Kriedemann et al, 1976; Lenz, 1978; Loveys and Kriedemann, 1974; Setter et al, 1980a; 1980b). Similar reduction in g_e has been observed following inhibition of phloem transport in girdling experiments (Setter et al, 1980a; Azcon-Bieto, 1983). Setter et al (1980a) reported that the reduction in photosynthetic rate was in direct proportion to decrease in g_e and hence suggested that the non-stomatal factors may be unimportant. Azcon-Bieto (1983), on the other hand, found that the reduction in g_e following girdling had little or no effect on intercellular CO_2 concentration (C_i) and attributed the decrease in photosythetic rate to non stomatal factors. It should be mentioned that Setter et al (1980a) did not measure C_i therefore their findings do not necessarily contradict those of Azcon-Bieto.

The depression in g_e following defruiting or leaf girdling has drawn attention to the possibility of hormonal involvement in these processes. Kriedemann et al (1976); Loveys and Kriedemann (1974); and Setter et al (1980a) reported that reduction in g_e was associated with increase in abscisic acid (ABA) and phaseic acid (PA). Detailed kinetics involved in ABA and PA increase g_e decrease and decrease in photosynthesis are, however, not known. Results reported by Azcon-Bieto (1983) indicate that decrease in g_e, which probably arise from increased ABA production, is of little consequence with respect to photosynthetic depression following sink manipulation. Possible role of ABA and PA in influencing non stomatal components is certainly worth investigating.

The literature discussed above shows that the feed-back hypothesis is still in an equivocal position because a direct biochemical explanation of the processes involved is lacking. However, there is so much evidence connecting accumulation of assimilates to decrease in photosynthetic rate that the feed-back hypothesis can not be disregarded. Evidently more biochemical studies are needed. Geiger and Giaquinta (1982) discussed hormone mediated control as possible and probably more explicable alternative to direct product regulated feedback mechanism. To my knowledge, the hormonal control is not any better established. The influence of ABA has only been linked to reduction in g_e as

discussed earlier. Hence, in the absence of significant stomatal effect (Azcon-Bieto, 1983), the role of ABA remains questionable. The possible involvement of other hormones has been considered (see Guinn and Mauney, 1980) but no direct link has been established between production of hormones in the sink, translocation to the source and subsequent response of the source (see Herold, 1980).

SECTION III

Effect of Water Stress and Flower Removal on Tomato Canopy Development and Growth.

Introduction

The rate and extent of plant growth depend on the amount of light intercepted by the crop, the efficiency of utilization of the absorbed light and the photosynthetic duration of the crop canopy. Water stress may influence plant growth through its effects on one or all of these parameters. Under field conditions of deep soil with high water holding capacity, water stress develops gradually and the plant has opportunity to develop acclimation mechanisms for survival. The result is that severe internal water stress may not develop until later in the season and any growth reduction will only be effected by those physiological parameters that are most sensitive to mild water stress. In many crop plants expansive growth appears to be the process most sensitive to mild water stress (Hsiao, 1973) with the result that reduced canopy cover characterises initial stages of plant water deficit (Bradford and Hsiao, 1982). An understanding of the pattern of canopy development is therefore important in the study of crop-water relationships under field conditions.

The growth pattern of an annual crop stand follows a

sigmoidal curve. Hsiao (1982) has defined the growth stages as: canopy cover limited (exponential), light limited (linear), and senescence phases. In terms of crop production, and given a crop of particular canopy architecture, there is little that can be done to improve the light limited phase short of increasing the photosynthetic rate per unit light intercepted. Literature summarized by Gifford and Evans (1981) reveals that attempts to increase photosynthetic rate have met with little success. However, a linear relationship exists between total light intercepted and total biomass accumulated during the season (Monteith, 1977; Shibbles and Weber, 1966; Williams et al, 1965). Hence we can maximize production by hastening the achievement of full canopy cover.

Water stress limits the rate of leaf area development and hence will reduce the rate of achievement of full canopy. Moreover, due to the exponential manner of growth in the phase before full canopy, a small reduction in leaf area development and biomass accumulation rate will be compounded over time leading to a markedly smaller biomass later in the season (Bradford and Hsiao, 1982). Conversely, a process which hastens leaf area development in the exponential phase will lead to compounded growth advantage during this phase which may be realised throughout the rest of the season. Total (Murneek, 1926) or partial (Salter, 1958) deflowering has been reported to stimulate leaf

growth. Increase in leaf area that accompanies such leaf growth would be expected to enhance plant growth if it stimulates the rate of achievement of full canopy. Theoretically, increase in leaf area resulting from deflowering would bring no growth advantage if both control and deflowered plants already have full canopy cover. Murneek (1926), Salter (1958) and Hurd et al (1979) showed that increased leaf growth following deflowering never produced corresponding increase in above ground biomass. There was increase in vegetative growth but this only compensated for the forfeited fruit growth so that the total above ground biomass was not affected. Canopy size measurements were not reported in these studies. However, judging from biomass data, it is likely that the increase in leaf area never produced corresponding increase in canopy size.

In this study both canopy development and biomass accumulation were studied under two irrigation treatments. The objective was to examine the effects of water stress on canopy development and growth and the influence of deflowering on these parameters in a processing tomato cultivar which, at commercial density, starts flowering at a canopy cover of less than 10 per cent.

Materials and methods

Tomatoes (Lycopersicum esculentum), cultivar UC 82B, a determinate processing cultivar, was subjected to two

different levels of irrigation and flower removal (deflowering). The studies were conducted at the experimental farm of the University of California at Davis during the summers of 1983 and 1984. The procedure of 1983 season is described here. No deflowering was done in 1984. Other experimental procedures were similar in both years unless stated otherwise. The soil was a deep profile of Yolo silt loam with an average *in situ* field capacity of about 30 per cent by volume. The experiment was laid out in a completely randomised split plot block design with 3 replications. Only 2 replications were used in 1984. Each block consisted of two sprinkler lines 15 meters apart bearing sprinkler risers at 9.2 meter intervals. This sprinkler arrangement provided approximately even distribution of water between the sprinkler lines and a zone beyond the reach of the sprinklers for dry treatment. Between the wet and dry treatment areas was an irrigation gradient zone. In order to achieve uniformity, irrigation was restricted as much as possible to calm periods of the day when there was little or no wind. Catch cans placed along the irrigation gradient from wet to dry parts of the block revealed a good linear relationship between the distance from the sprinkler line and the amount of water applied (Figure 1). Using catch can data the irrigation gradient zone was further divided into three watering levels during 1984 season. These received equivalent of 60, 25, and 15 per cent of of the control irrigated treatment.

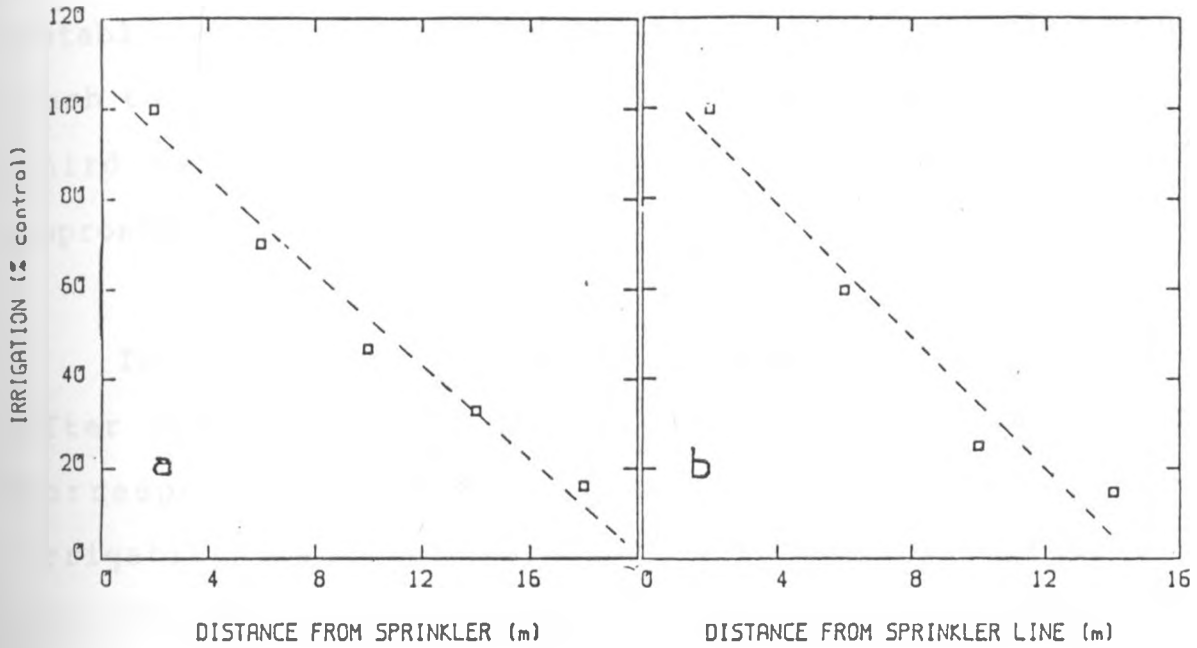

Fig 1. Water applied in relation to distance from the sprinkler in 1983 (a) and 1984 (b). Each point represents a mean of 4 replications taken on different irrigation occasions.

The plot size was 30m x 10m but each plot was divided into two subplots measuring 15m x 10m. Nitrogen, in the form of NH_4NO_3, was applied to the plots before planting at a rate of 170 Kg ha^{-1}. Double row planting with 0.75m between rows was done on 1.5m wide beds and the seedlings emerged after about 10 days. The field was given light but frequent sprinkler irrigations during the period of crop establishment to ensure a good crop stand without adding too much to the soil water reserve. Thinning was done in the third week after emergence to an intra-row spacing of approximately 30 cm.

Irrigation and deflowering treatments started 28 days after emergence (DAE) in 1983 and 34 DAE in 1984. This corresponded to the beginning of flowering phase. Irrigation treatment was applied to the main plots and deflowering was performed on subplots. No more water was applied to the dry (or non-irrigated) plots after the beginning of the treatments so that the crop depended wholly on soil moisture reserves. Approximately 50 mm of water was applied to the wet (or irrigated) treatments weekly. Deflowering treatment involved removal of all fully open flowers once each week throughout the growing season so that fruit formation was prevented. The deflowered plants were compared to fruited (or non-deflowered plants). Hence we had a 2 x 2 factorial structure with the treatments:

(i) Irrigated fruited (IF),

(ii) Irrigated deflowered (IDF),

(iii) Non-irrigated fruited (NIF),

(iv) Non-irrigated deflowered (NIDF).

Volumetric soil moisture content down to 240 cm was monitored using neutron probe moisture sensor (Campbell pacific Nuclear Corp. model 503) which had been calibrated on the local soil. These measurements were taken one day prior to the day of irrigating the wet treatment on several occasions during the season, that is, when the wet treatments were at their driest in each irrigation cycle.

To monitor growth pattern, 1.52 m^2 sample (composite of two 0.76 m^2 subsamples, each derived from 1 m row lenth) of above ground plant material was harvested periodically from each replicate and separated into leaves, stems, petioles and fruit. The vegetative parts were dried in forced draft oven at 70° C for 4 days. Fruit was sliced into halves or quarters, depending on the size, spread out in single layer and oven dried at the same temperature as vegetative parts but over a period of one week. In 1983 fresh leaf area was determined prior to drying using an electronic area meter (Li-cor Inc, Lincoln Nebraska).

The pattern of canopy development was determined through measurement of canopy light interception. A photosynthetically active radiation (PAR) sensor, 1 m long, (Li-Cor Inc, Lincoln Nebraska) was used to measure the percentage of light intercepted by the plant canopy. The

measurements were taken at or around solar noon when sun was directly overhead so that the percent light intercepted was a good indicator of percent crop canopy cover. Six such measurements were taken per replication each time.

Once during peak canopy cover (on 75 DAE) in 1983 and on four occasions in 1984, canopy light interception measurements and above ground biomass samples were taken along a gradient of decreasing irrigation from a sprinkler line (Fig 1). The objective of this operation was to study the trend of canopy size and biomass accumulation associated with relatively small differences in irrigation.

Leaf water status was determined using a pressure chamber (Soil Moisture Equipment Corporation, Santa Barbara, California). Only uppermost, fully expanded and fully exposed leaves were sampled and their water potential was taken as indicator of leaf water status. Normally four leaves were sampled per replication. To avoid loss of water after the leaf was excised, each leaf was wrapped in a moist piece of cheese cloth immediately prior to sampling and was placed in pressure chamber so wrapped. The cheese-cloth was wetted frequently with water then sqeezed hard to remove free water before use. All leaf water potential measurements were done around midday which corresponded to 1200-1400 Pacific Standard Time (PST) on clear cloudless days.

Measurements of steady state midday leaf net photosynthetic rates were performed on several occasions during the 1983 season on treatments IF and NIF. During 1984 season such measurements were done along irrigation gradient. The measuring equipment consisted of a clamp on photosynthetic cup (1.8 cm^2 in area) connected to a portable differential infrared gas analyser for CO_2 (Binos, Leybold-Heraeus, West Germany) in an open system. Only the youngest fully expanded and fully exposed leaves were used. The leaves were held perpendicular to incident sunlight. Air from a tank with CO_2 concentration of about 340 ppm was passed over the leaf at a rate of 8.3 ml s^{-1} until steady state CO_2 differential was obtained. Humidity and temperature were not controlled but each measurement took approximately half a minute only so that there was little heat build-up in the leaf cup. The leaf cup was designed to facilitate high velocity flow of air passing over the leaf (elliptical in shape; 3 cm x 0.6 cm with the long side being in the direction of flow, and minimal depth) so that, although it was not fitted with air fans for boundary layer control, the boundary layer resistence was small (0.03 s mm^{-1}, Jorge Bolanos. Personal communication). Three to four leaves were sampled in each replication.

Results

Soil moisture content: The soil moisture depletion

pattern is shown in fig 2. These measurements were taken one day before irrigating the wet treatments, when the soil water content in the wet treatment was at its lowest in each irrigation cycle. In the wet treatment, the soil moisture at the top 30 cm depth was sufficiently replenished at each irrigation so that the moisture content before irrigation was almost constant throughout the season except in the last reading. The soil moisture content at 30 cm in dry treatments was higher on day 94 compared to the other occasions because a light irrigation (12 mm) was applied on day 88. There was soil moisture depletion up to 200 cm depth in all treatments. The marked decrease of soil water below 180 cm is the result of sandy layer which occurred at these depths. Dry treatments generally had lower soil moisture content than the wet but this was only marked in the top 60 cm. Between 60 cm and 120 cm soil moisture content in dry treatments was only slightly lower than that of wet treatments. No difference in soil water content occurred between wet and dry treatments below 120 cm. Moisture depletion pattern for the dry profile on 94 DAE indicates that at any one depth, roots could only take up moisture up to a certain minimum value (around 14%)and that this minimum moved deeper with time. In dry treatments, the depletion pattern was generally similar between NIDF and NIF treatments. This was not the case in wet treatments where IDF tended to have lower moisture content than IF.

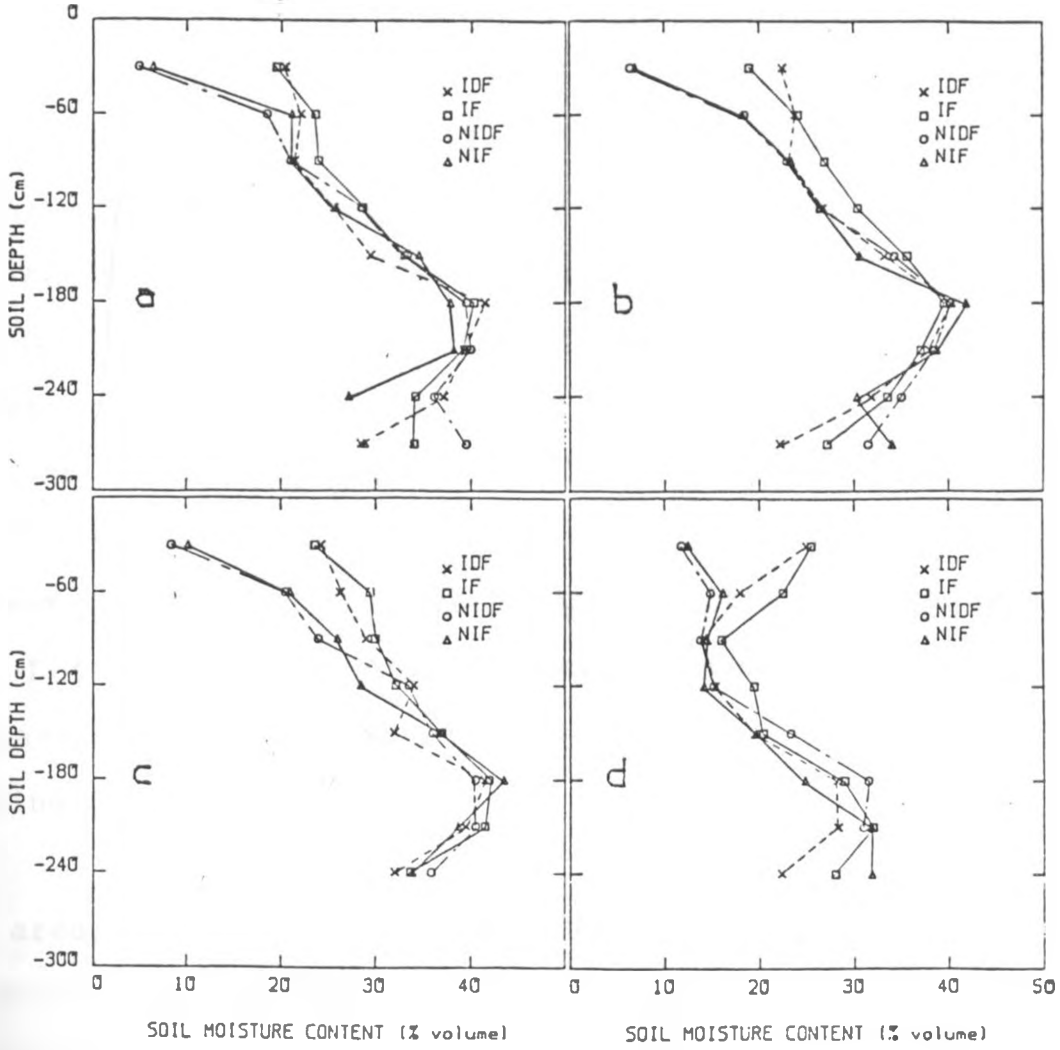

Fig 2. Soil moisture content as a function of depth, in 1983, for the different irrigation and deflowering treatments on 39 DAE (a), 47 DAE (b), 61 DAE (c) and 94 DAE (d). Each point is a mean for 3 replications. Water content values were calculated from neutron probe counts registered in 1/4 of a minute.

Plant water status: Seasonal trend of midday leaf water potential revealed that the dry treatments generally had lower water potential than the wet. This difference was, however, rarely more than 0.1 MPa (Fig. 3a) except late in the season in 1984 (Fig 3b). These late season differences came at a time when the crop was largely mature (for example, full canopy cover was achieved by day 70) and therefore had little effect on crop growth. Fig. 4 presents the midday water potential along irrigation gradient on four occasions during 1984 season. The picture here generally agrees with that presented in Figs. 3a and 3b. There was no difference in water potential along the gradient for much of the season (represented by days 46 and 76). Late in the season, however, there was substantial decrease in water potential associated with decrease in watering level.

Leaf area, solar radiation interception and photosynthesis: The pattern of seasonal leaf area and canopy development (as indicated by percent light interception at midday) are shown in Fig. 5. The only leaf area index (LAI) data, those of 1983, showed that non-irrigated treatments had much lower LAI. Both NIF and NIDF achieved maximum LAI of 0.8 compared to 3.3 in IF. Irrigated deflowered treatment continued to develop more leaves beyond the period included in Fig. 5 and had achieved LAI of 9 by the time the experiment was discontinued at crop harvest (125 DAE).

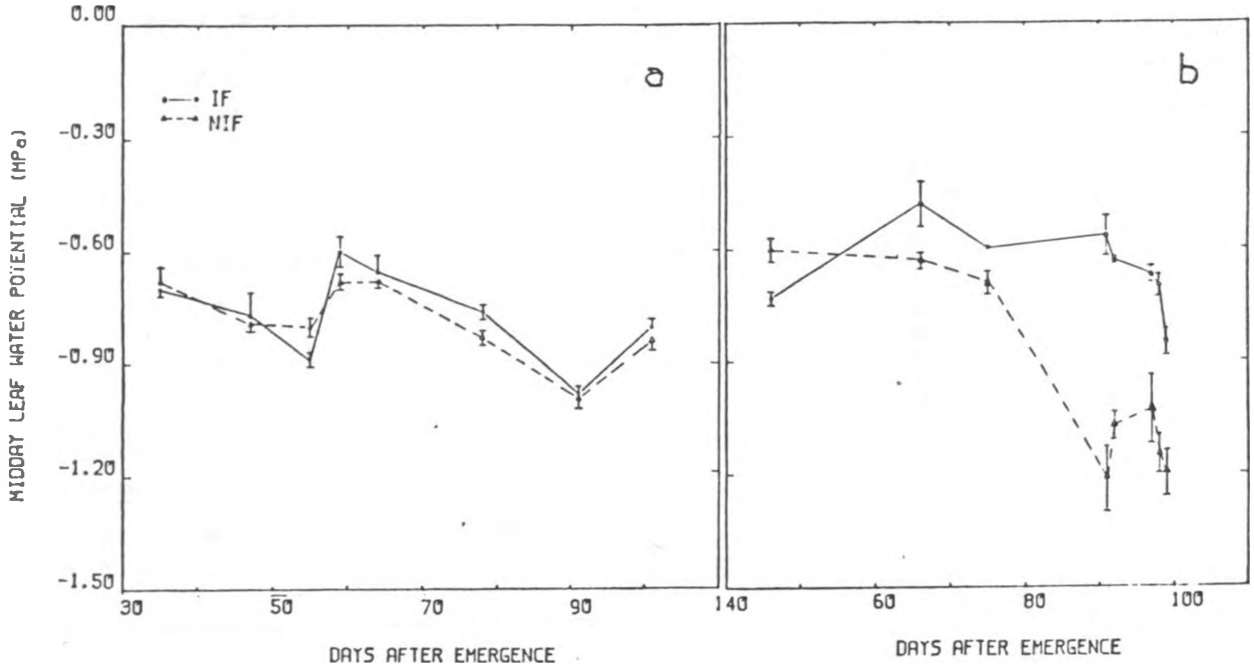

Fig. 3. Trend of midday leaf water potential in irrigated (IF) and non irrigated (NIF) fruit bearing plants in 1983 (a) and 1984 (b). Each point is a mean of 3 replications for 1983 and 2 replications for 1984 data. Four subsamples were taken in each replication. Values are shown ± 1 SE.

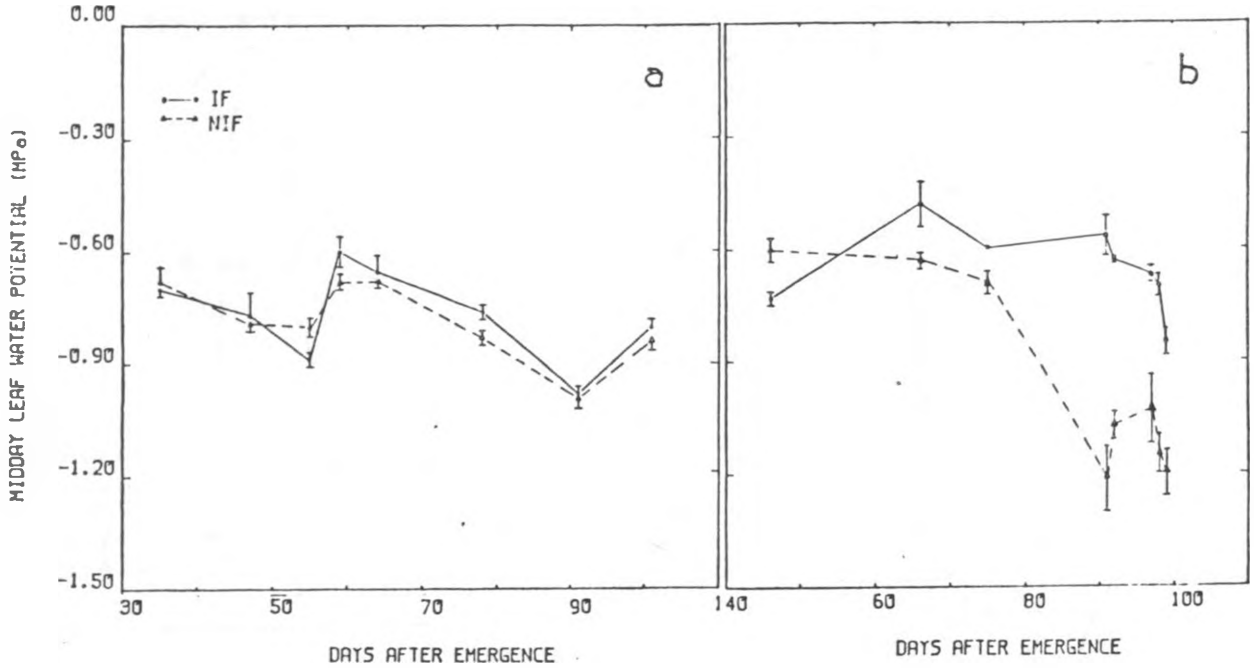

Fig. 3. Trend of midday leaf water potential in irrigated (IF) and non irrigated (NIF) fruit bearing plants in 1983 (a) and 1984 (b). Each point is a mean of 3 replications for 1983 and 2 replications for 1984 data. Four subsamples were taken in each replication. Values are shown ± 1 SE.

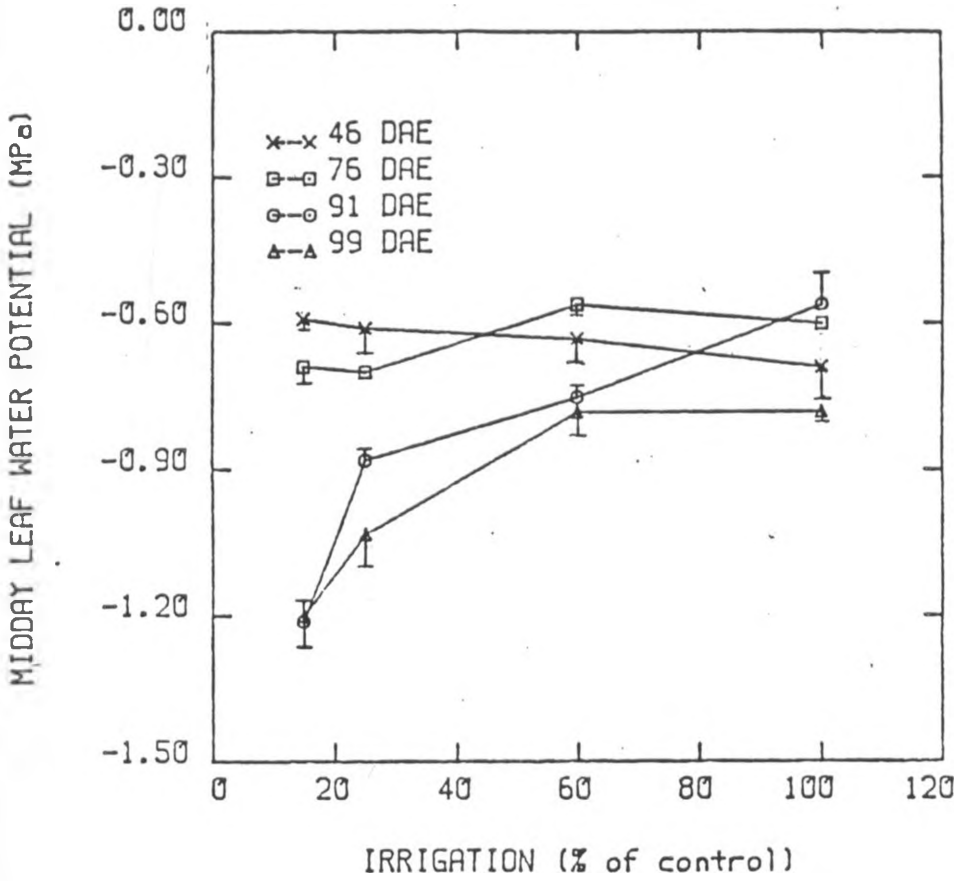

Fig. 4. Response of midday leaf water potential to watering level along irrigation gradient on 4 occasions in 1984. Each value is a mean of 2 replications. Four subsamples were taken in each replication. Values are shown + or - 1 SE.

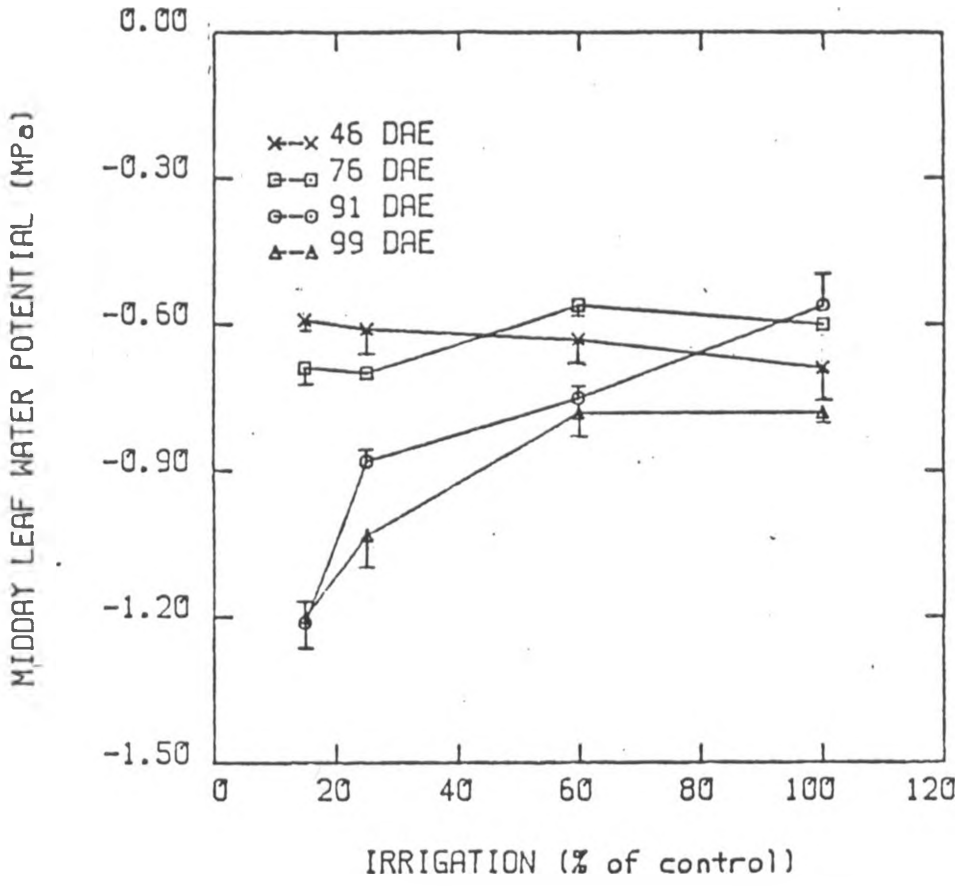

Fig. 4. Response of midday leaf water potential to watering level along irrigation gradient on 4 occasions in 1984. Each value is a mean of 2 replications. Four subsamples were taken in each replication. Values are shown + or - 1 SE.

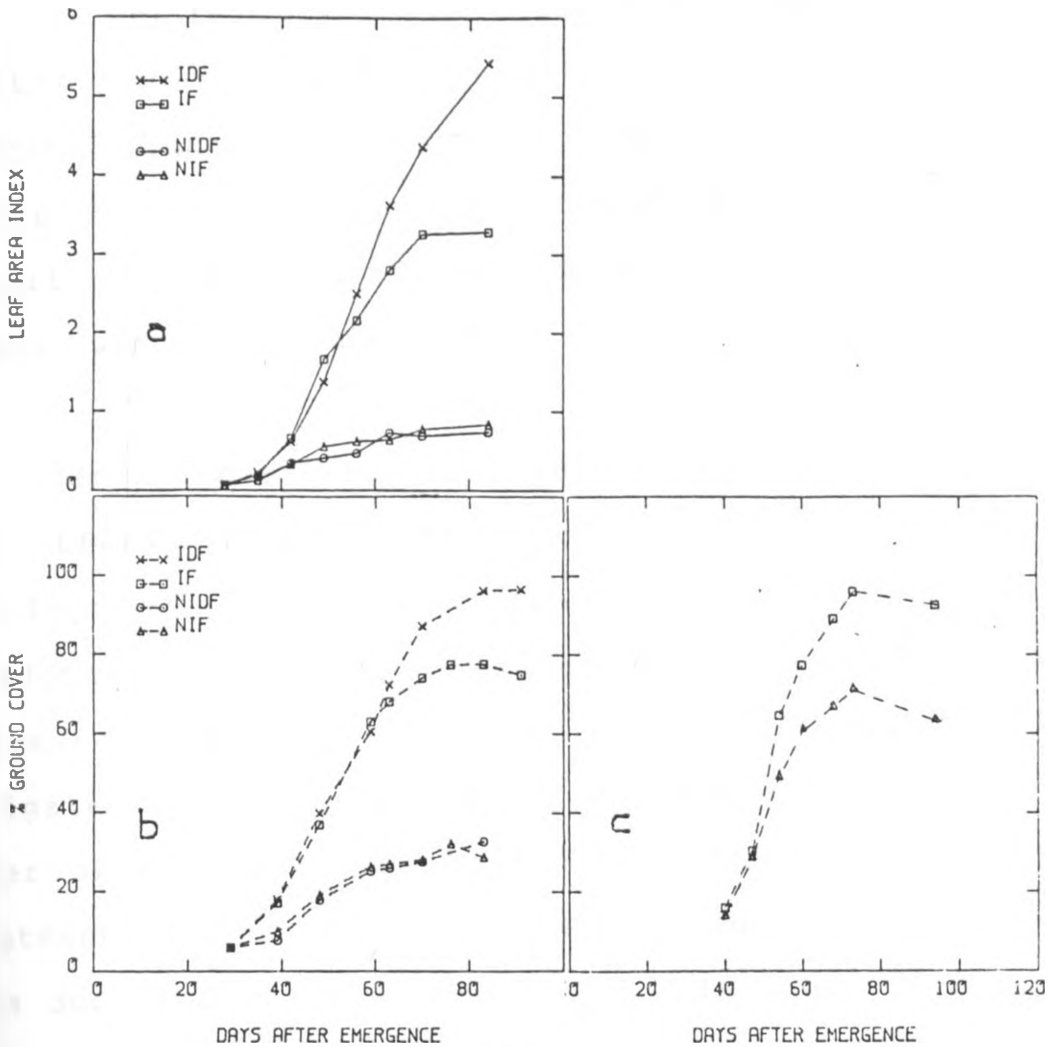

Fig. 5. The seasonal trend of leaf area index in 1983 (a) and canopy ground cover in 1983 and 1984 (b and c, respectively). Each value is a mean of 3 and 2 replications for 1983 and 1984 data respectively.

Flower removal had no effect on LAI of non-irrigated treatment but caused a remarkable increase in LAI of irrigated plants. This effect of deflowering on irrigated plants, however, did not occur until treatment IF started significant fruit growth, around day 50 even though flower removal was started on day 28.

Canopy cover responded in much the same way as LAI. The effect of water stress in retarding leaf area development resulted in great depression of canopy development. The dry treatments (both NIF and NIDF) achieved a peak canopy cover of only 30% compared to irrigated fruit bearing plants which reached peak canopy cover of a little less than 80%. Irrigated deflowered treatment was the only one which achieved full canopy cover. This occurred at LAI of about 5.5. In 1984, IF achieved full ground cover whereas NIF had a maximum ground cover of about 70%. The fact that water stress had less effect on canopy cover in 1984 compared to 1983 may be attributed to the longer crop establishment period in 1984. Pre-treatment irrigation lasted for 28 days in 1983 and 34 days in 1984.

The relationship between ground cover development and LAI is illustrated in Fig. 6 using 1983 data. Percent ground cover increased with leaf area development in a curvelinear pattern composed of a linear initial phase followed by a saturating phase which approached a maximum asymptotic value at full ground cover. Even though only IDF

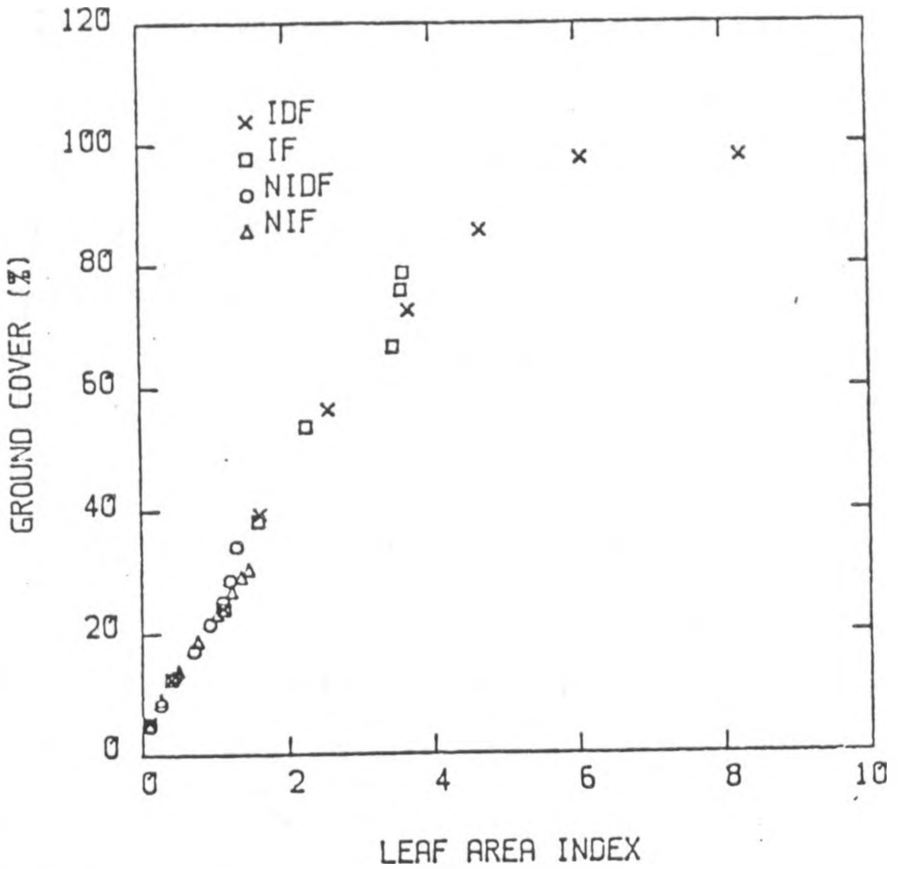

Fig. 6. Solar radiation interception as a function of LAI in 1983. The leaf area index and per cent ground cover data are same as those in Fig. 5a and 5b respectively.

achieved full ground cover, there was no difference among the treatments in terms of change in percent ground cover associated with unit change in leaf area for the range of LAI that was achieved by all or some of the treatments. This indicates that the treatments had no effect on canopy architecture. A positive linear relationship was found between canopy development and irrigation level along the line source irrigation gradient (Fig. 7).

While water stress had a pronounced effect on LAI and canopy cover, its effect on photosynthesis was relatively less dramatic. Midday photosynthetic rate was depressed by 25% - 30% through most of the season (Fig. 8). These values probably mask leaf age effects as discussed below. Effect of water stress *per se* was probably much less. Unpublished results obtained by Jorge Bolanos on the same field showed that water stress had little or no effect on photosynthetic rate of leaves of similar age. Figure 9 shows the leaf photosynthetic rate along the irrigation gradient on three occasions during 1984 season. Water stress generally had little effect on photosynthesis per unit leaf area. Leaf photosynthetic rate, however, decreased remarkably between days 73 and 100, probably due to leaf age effect. Water stress may inhibit leaf (and canopy) photosynthetic rate directly through stomatal and non stomatal factors (Sharkey and Farquhar, 1982). Canopy photosynthetic rate may also be indirectly depressed through

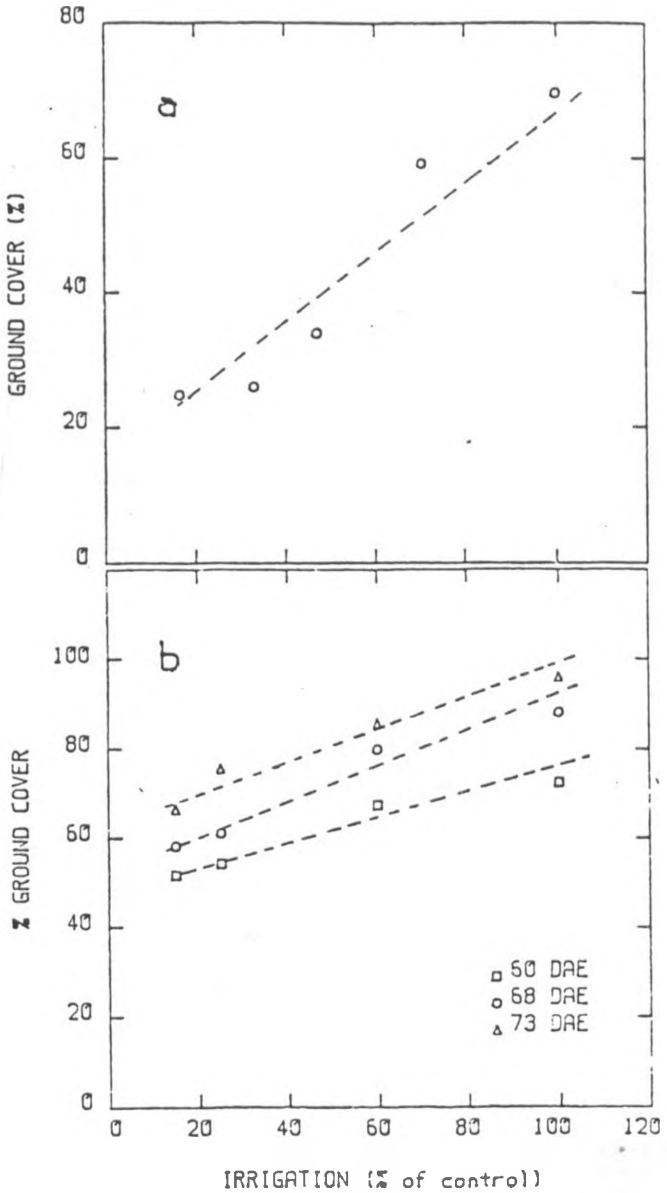

Fig. 7. Percent ground cover as a function of irrigation level on 75 DAE, 1983 (a) and 60, 68 and 73 DAE, 1984 (b). Each value is a mean of two replicates in all cases.

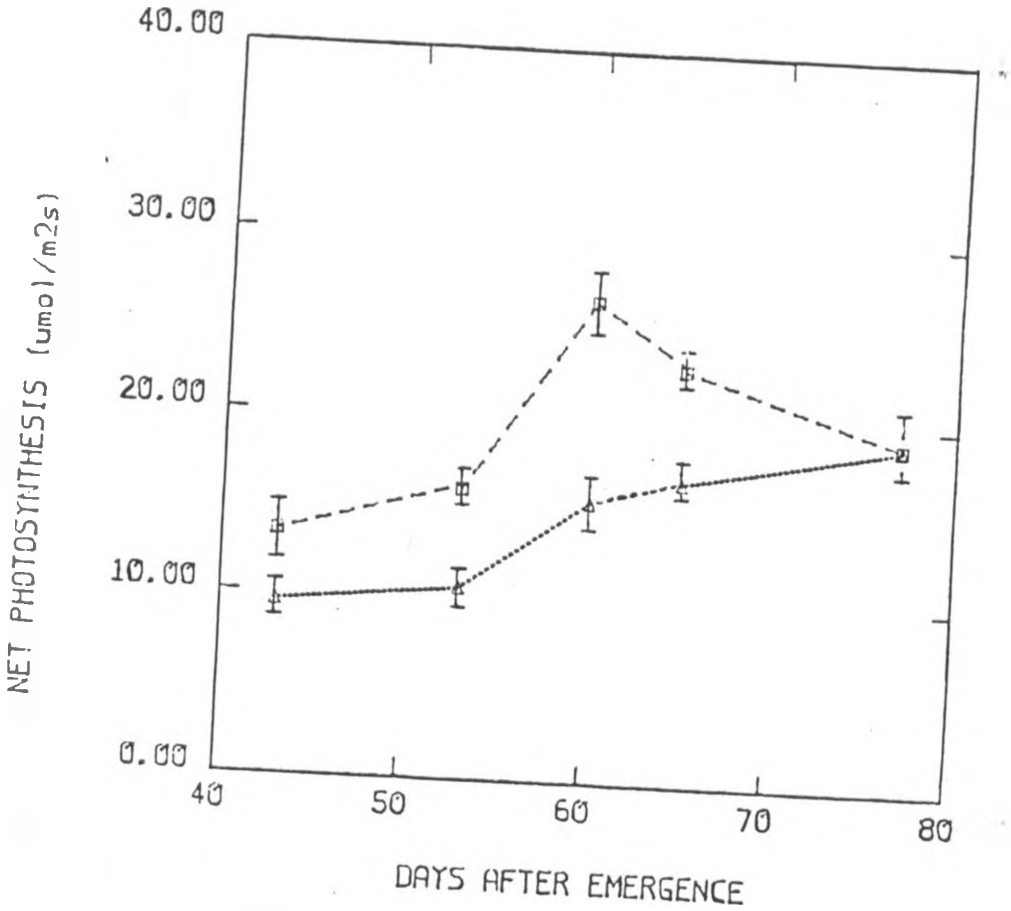

Fig. 8. Seasonal trend of midday net photosynthetic rate in 1983. Each value is a mean for 2 replications. Four subsamples were taken in each replication. □ = irrigated and △ = unirrigated treatments. Values are shown ± 1 SE.

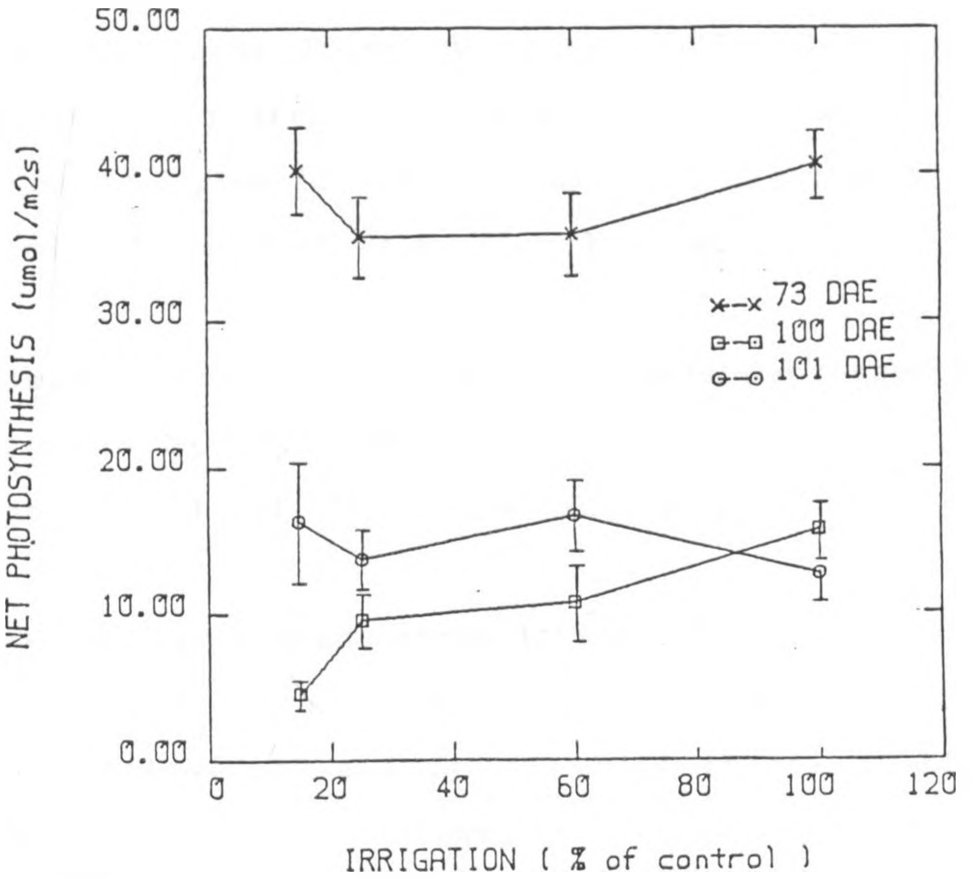

Fig. 9. Net photosynthesis as a function of irrigation level along irrigation gradient in 1984. Each value is a mean for two replications in all cases. Three subsamples were taken in each replication. Values are shown ± 1 SE.

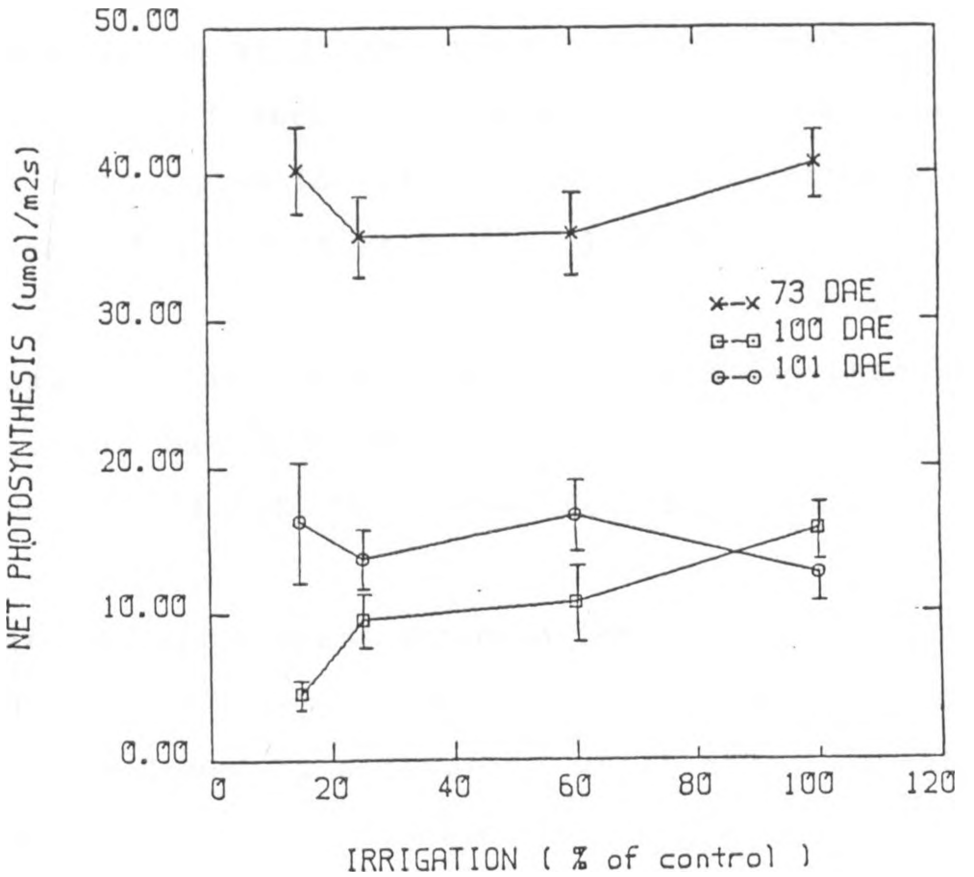

Fig. 9. Net photosynthesis as a function of irrigation level along irrigation gradient in 1984. Each value is a mean for two replications in all cases. Three subsamples were taken in each replication. Values are shown ± 1 SE.

inhibition of new leaf formation and leaf growth so that the canopy consists of a high proportion of older leaves that have low photosynthetic rates. In this study the youngest mature leaf on each plant was sampled for photosynthetic measurement. These leaves were generally older in dry compared to irrigated treatments and so the observed photosynthetic depression was probably a combination of both direct and indirect factors mentioned above.

Biomass accumulation: Water stress depressed peak above-ground biomass to about 30% of well irrigated treatment in 1983 and 50% in 1984 (Fig. 10).

Leaf area and biomass accumulation: There was a linear phase when both canopy size and above ground biomass increased followed by a stage in which there was little canopy development whereas above-ground biomass continued to rise (Fig 11). In treatments NIDF, NIF and IF, the latter phase was initiated when leaf area development ceased and, in consequence, growth of canopy also ceased before full ground cover was achieved. In treatment IDF, however, the second phase did not emerge until it had achieved LAI of about 4 and was only pronounced after full canopy cover. A close look at the linear portion (Figs. 11a and 11b insets) showed that the non-irrigated treatments had higher rates of biomass accumulation associated with unit increase in LAI or canopy cover (slope of the lines) than the wet treatments. Calculated net assimiltion rate (NAR) for the linear portion

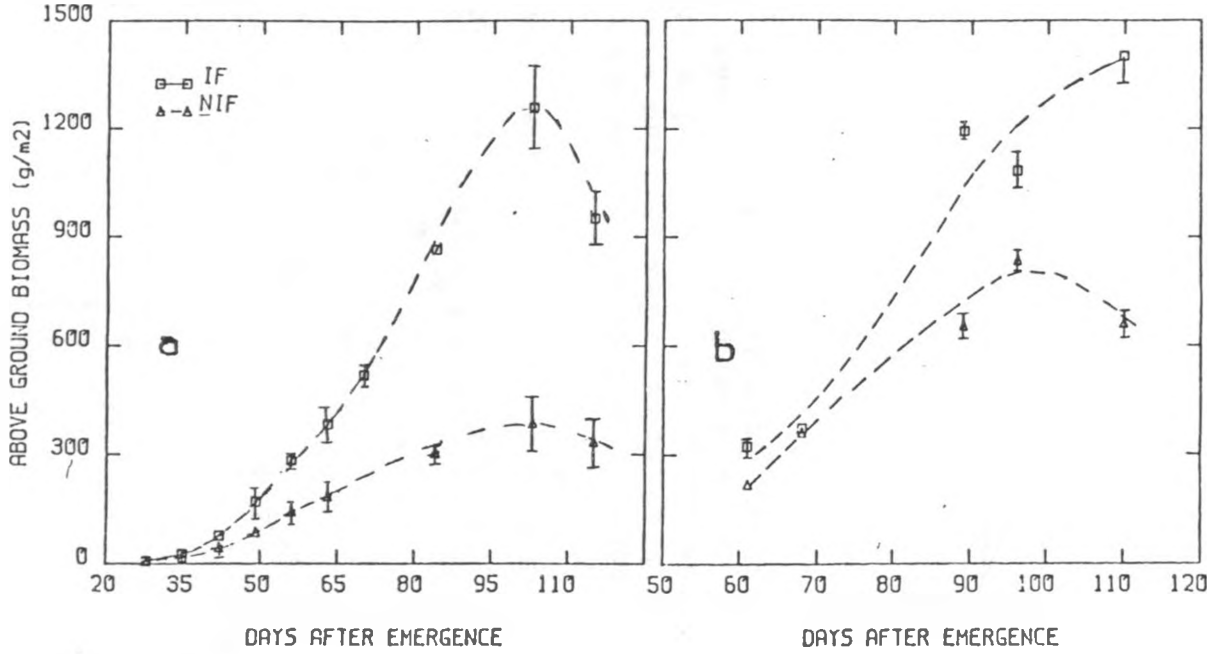

Fig. 10. Seasonal trend of aboveground biomass of irrigated (IF) and non irrigated (NIF) fruit bearing plants in 1983 (a) and 1984 (b). Each point is a mean of 3 replications for 1983 and 2 for 1984 data. Values are shown ± 1 SE.

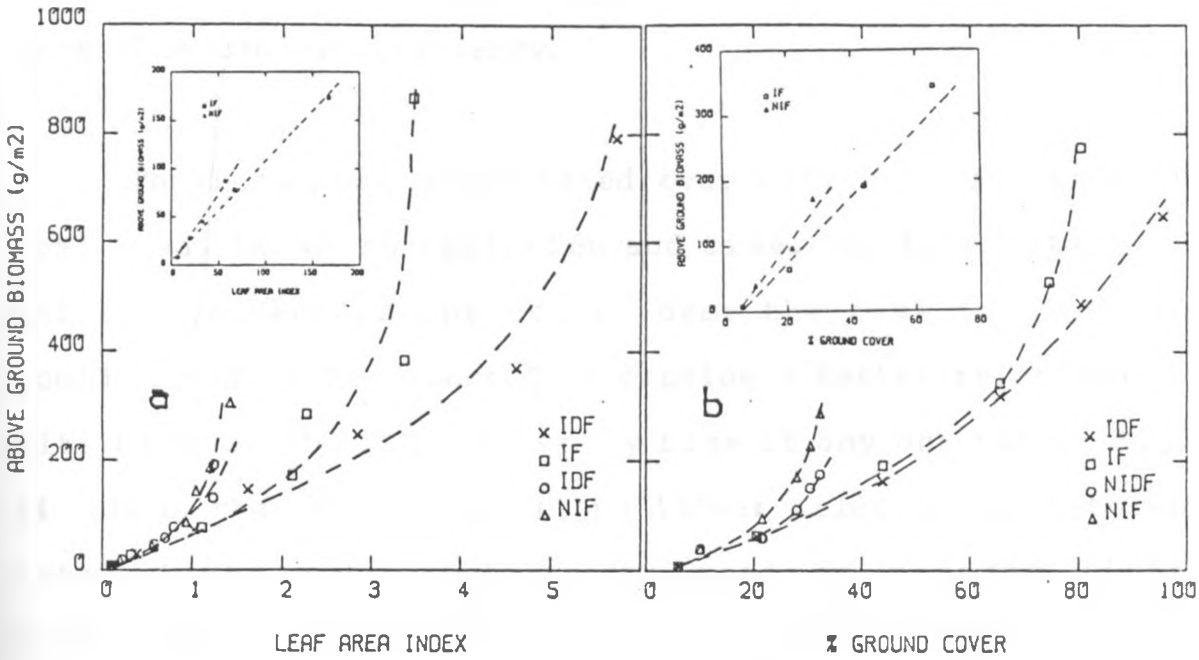

Fig. 11. Seasonal trend of above ground biomass as a function of leaf area index (a) and % ground cover (b) for 1983 season. Leaf area index and per cent ground cover data are same as those in Fig. 5. Aboveground biomass data are same as those in Fig. 10.

(using the equation described by Radford, 1967) (Fig 12) and leaf area ratio (LAR) (Fig 13), for fruit-bearing plants, further indicate that the dry treatments had a greater return on biomass per unit increase in leaf area. This suggests that water stress depressed canopy expansion rate more than canopy efficiency.

Total biomass accumulated over time is a function of leaf area, incoming radiation and time. An integration of LAI and percent canopy cover over the time in question would therefore be expected to provide a better relationship with biomass than LAI or canopy size at any one time. Fig. 14 shows that there was strong linear relationship between total light intercepted (integral of percent light intercepted at midday over time) and above ground biomass. The slope of the integrated light intecepted against biomass expresses canopy efficiency in terms of biomass produced per unit light energy intercepted. The irrigated treatments had about 25% and 10% higher canopy light conversion efficiency than the non-irrigated treatments in 1983 and 1984, respectively. Within the watering regimes, fruited plants had slightly higher canopy light use efficiencies than the deflowered plants but these differences were not significant. The integral of LAI with time has been called leaf area duration (LAD). It takes into account both duration and size of the photosynthetic activity per unit leaf area. Fig. 15 shows that above ground biomass increased with increasing LAD but at a decreasing rate. At

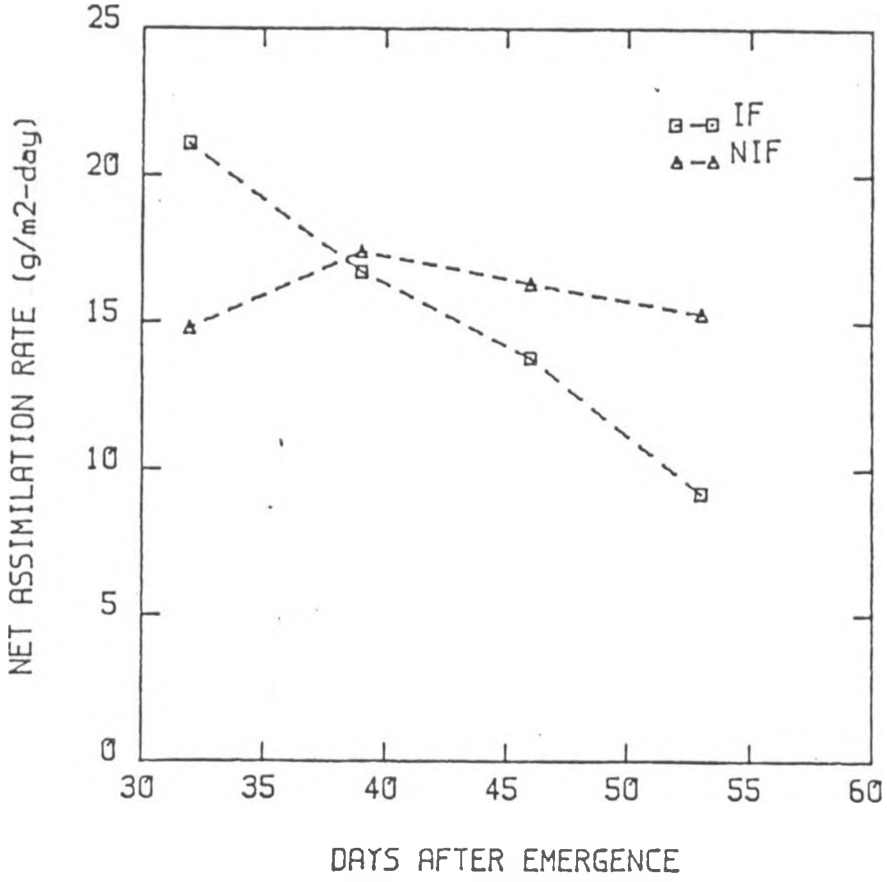

Fig. 12. The seasonal trend of net assimilation rate during the exponential phase of growth in 1983. These values were calculated using sections of aboveground biomass (Fig. 10) and corresponding leaf area data (Fig. 5) using the equation described by Radford (1967).

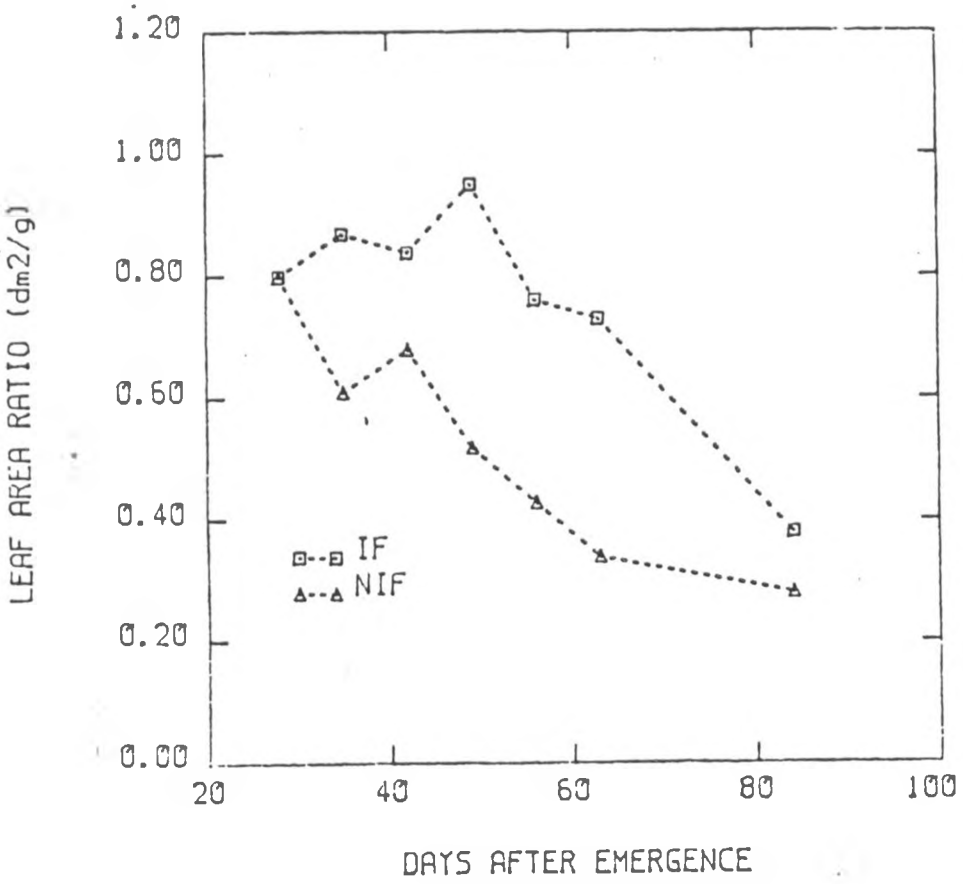

Fig. 13. The seasonal trend of leaf area ratio in 1983. The values were calculated by dividing fresh leaf area by total aboveground biomass for each sample.

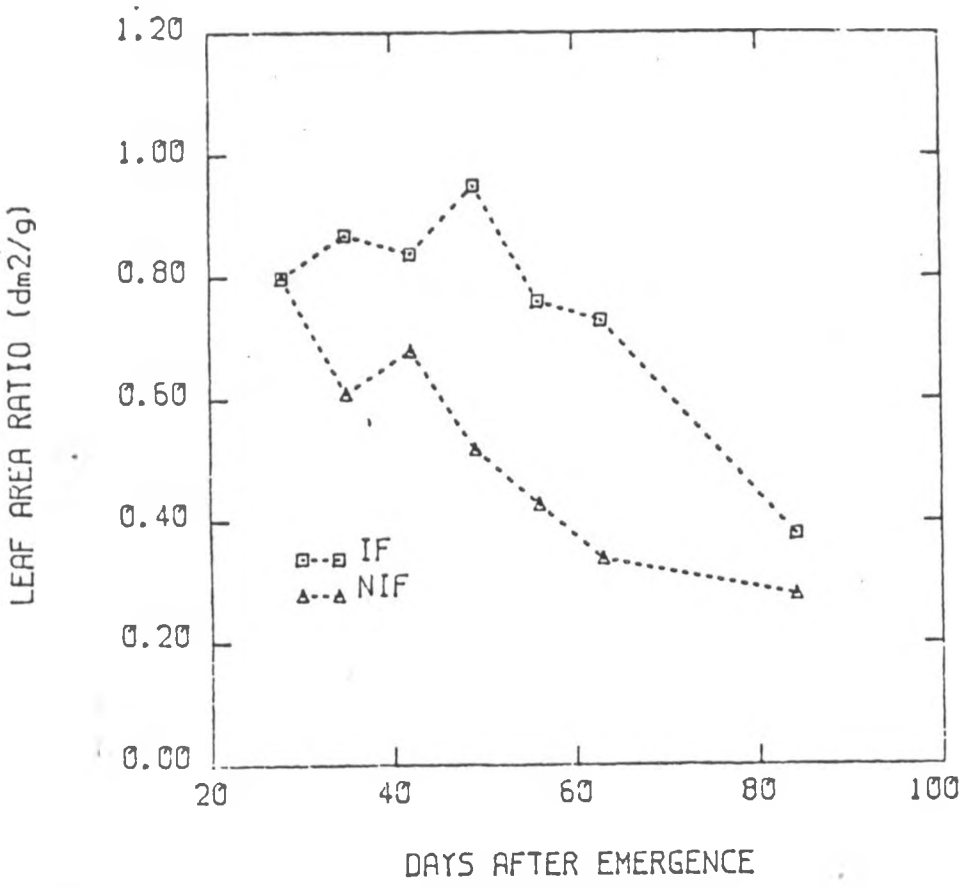

Fig. 13. The seasonal trend of leaf area ratio in 1983. The values were calculated by dividing fresh leaf area by total aboveground biomass for each sample.

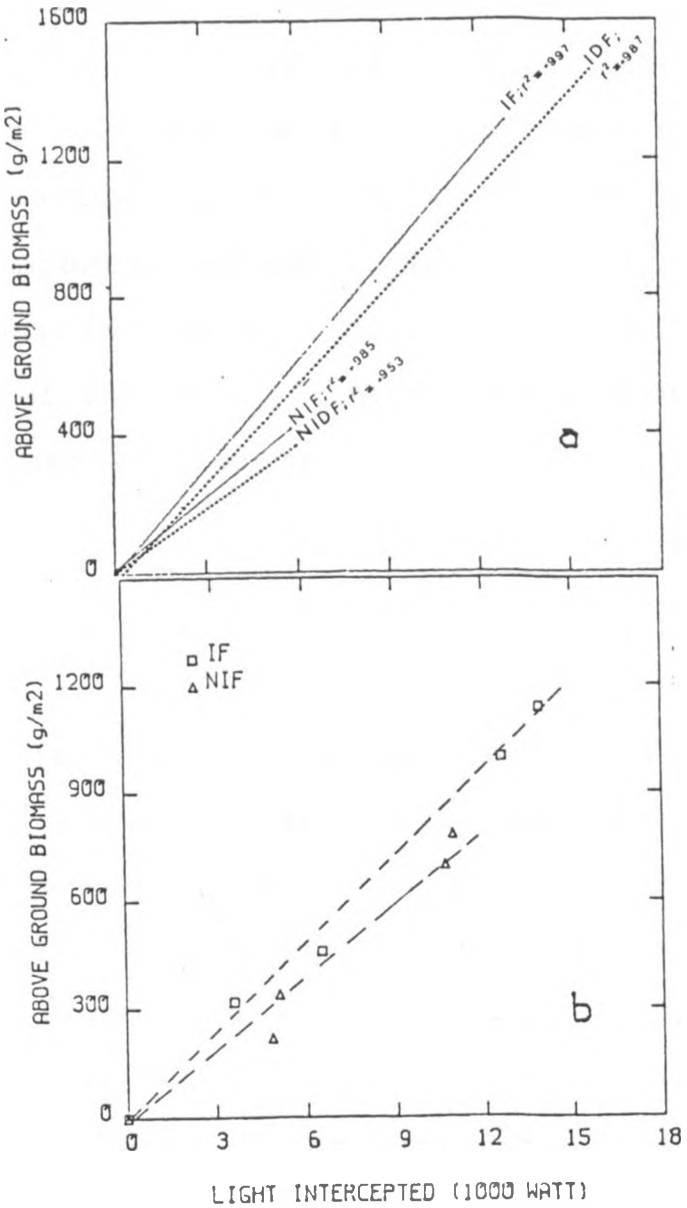

Fig 14. Above ground biomass as a function of cummulative intercepted radiation for 1983 season (a) and 1984 season (b). Cummulative intercepted radiation was calculated by integrating the area under the seasonal per cent ground cover (Fig. 5) for each treatment. Per cent ground cover days so obtained was multiplied by the sum of total radiation for the period in question to obtain cummulated intercepted radiation. Regression analysis showed that effects of water stress were significant at .01 level in 1983 but was not significant even at 0.1 level in 1984. Effects of deflowering were not significant at 0.1 level.

low LAD values all the treatments exhibited similar response in above-ground biomass production but at higher LAD values, the fruited treatments had higher biomass response than deflowered treatments. It should be noted, however, that one of the components of LAD is LAI and that some of these responses partly reflect changes in LAI with time. Furthermore, as the rate of LAI development decreases with time, time component becomes more and more predominant in LAD values.

Discussion

Water stress inhibits canopy growth rate (Bradford and Hsiao, 1982). Expansive growth has been reported as the growth parameter most sensitive to water stress (Hsiao, 1973) so that leaf growth is typically reduced before water stress has any effect on photosynthsis. Hsiao (1982) has observed that much of the growth reduction resulting from water stress can often be accounted for by the effect of water stress on canopy development rather than photosynthesis. In this study, there was little or no difference in plant water potential between irrigated and non-irrigated treatments (Fig. 3) and only a small difference in soil water profiles (Fig. 2). However, non-irrigated treatments had much smaller canopy cover (Fig 5) and aboveground biomass accumulation was highly depressed (Fig.10). During 1983 season, for example, there was 68% depression of peak canopy cover and about equally strong

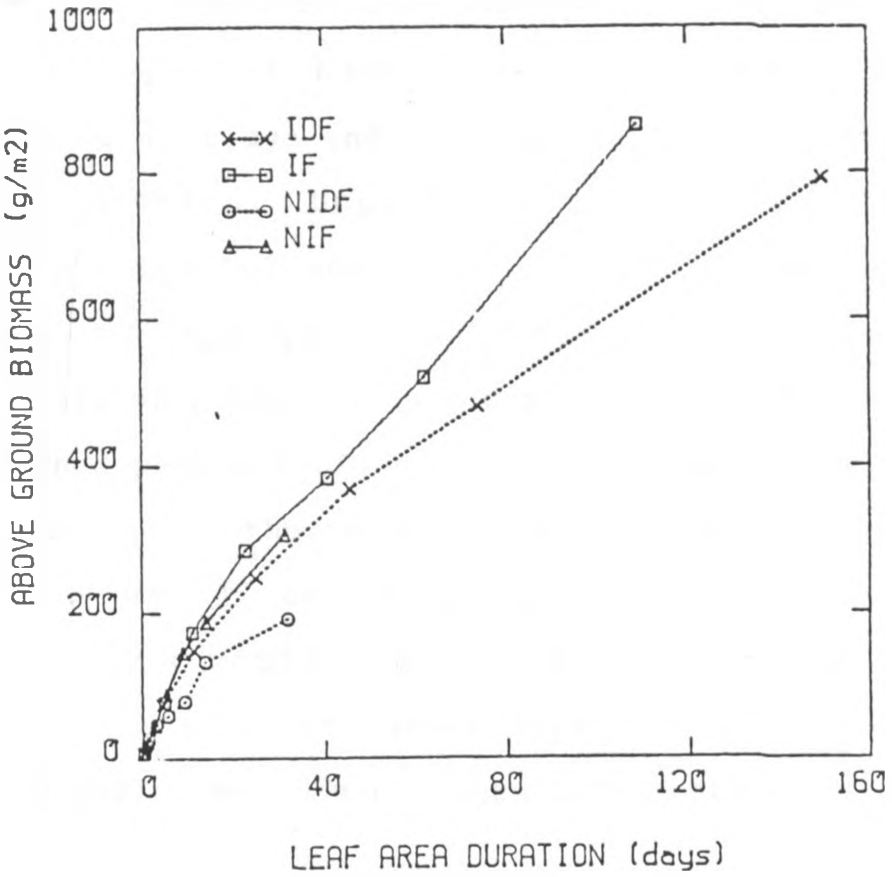

Fig. 15. Seasonal trend of above ground biomass as a function of leaf area duration in 1983. LAD was calculated by integrating the the area under the seasonal leaf area index (Fig. 5) with time.

depression in maximum attained aboveground biomass, yet photosynthesis was generally inhibited by only 25% - 30% (Fig. 8). It should be mentioned that the photosynthetic depression reported here probably resulted from a combination of leaf age and leaf water stress as discussed in results section. Unpublished photosynthetic data obtained by Jorge Bolanos in the same field showed that water stress *per se* had little or no effect on photosynthesis when leaf age was controlled. Water stressed plots attained peak LAI of only 0.8 and canopy cover of 30%. At these low values the relationship between LAI and light interception was linear (Fig 6). Alleviation of soil moisture stress could, therefore, lead to increased production since positive linear relationship also existed between irrigation and canopy light interception (Fig 7).

Deflowering induced faster canopy development in irrigated but not in non-irrigated treatments. It would appear that the influence of deflowering was overridden by drought effects. Since water stress inhibited vegetative shoot growth, deflowered non irrigated plants probably directed their assimilates to root growth as suggested in section V. In the fruit bearing irrigated treatment, the rate of leaf area and canopy developments started to decrease at fruit initiation (around day 50) and by day 70 there was no more canopy growth. Similar reduction in tomato leaf development in fruiting plants has been reported by Murneek (1926), Cooper (1958) and Hurd *et al* (1979) and

is probably associated with preferential partitioning of assimilates into friuts rather than vegetative growth during reproductive phase of tomato growth. The deflowered irrigated treatment had the fastest rate of canopy development and ended with a 20% larger canopy than treatment IF (Fig 5b). However, results reported in section IV show that there was no difference in the rate of above-ground biomass accumulation between treatments IF and IDF. Given that they also had similar efficiencies of canopy light conversion (Fig. 14), and gas exchange rates (section VI), this lack of difference in above-ground biomass accumulation rates could be attributed to possible differences in biomass partitioning to the roots.

Deflowered tomato plants channel relatively larger portion of their assimilates to roots than fruit bearing plants (Hurd et al, 1979). In fact, Hurd et al found that competition by tomato fruit was more serious for roots than vegetative shoot and data in section V obtained on pot grown plants showed that whereas deflowering resulted in a two-fold increase in vegetative shoot weight, root weight was increased 3-fold. Soil moisture content measurements (Fig. 2) shows that IDF tended to have lower moisture content than IF treatments, suggesting a faster rate of soil moisture depletion by a deeper and probably larger root system. If the latter is true then IDF plants could have slightly larger total biomass associated with their larger canopy

size. In any case, the significant difference in canopy size did not occur until late in the season (see Fig. 5) so we could not expect a large difference in biomass.

The sensitivity of canopy development to water stress is well demonstrated in this experiment. Fig. 2 illustrates that no significant differences in soil moisture content occurred between irrigated and non-irrigated treatments below 90 cm. It is interesting that whereas the canopy was reduced to about one third of the well irrigated treatments in 1983, canopy light conversion efficiency (Fig. 14) was only reduced by about 25% and photosynthesis was little affected as discussed earlier. Leaf water potential also remained largely unaffected. Similarly, in 1984, canopy size was reduced by about 30% while canopy light conversion efficiency was reduced by only 10% and there was no consistent difference in photosynthesis per unit leaf area along irrigation gradient (Fig. 9). The relative insensitivity of photosynthesis per unit leaf area to water stress may be partly accounted for by the fact that non-irrigated plants had higher specific leaf weight than irrigated plants (Fig. 16). Gifford and Evans (1981) reported that a positive relationship occurs between specific leaf weight and photosynthesis per unit leaf area. Enhancement in photosynthesis accruing from higher specific leaf weight in non-irrigated plants would tend to counterbalance the depressing effects of water stress. It

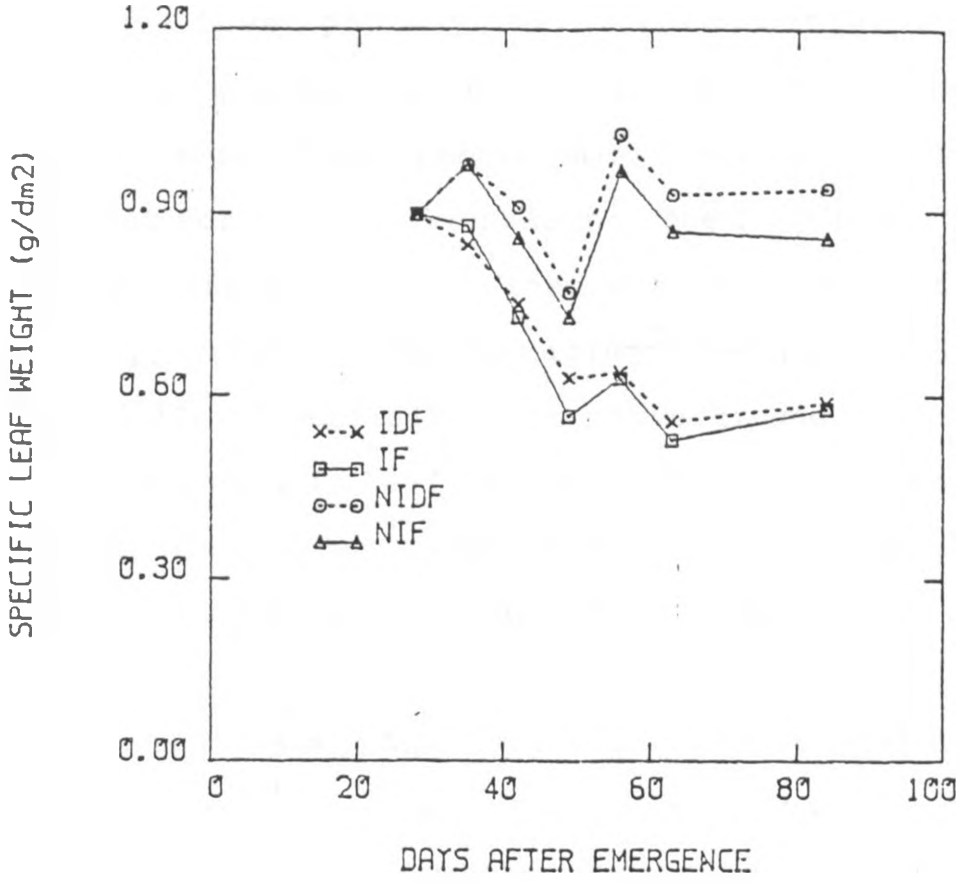

Fig. 16. Effect of water stress and flower removal on seasonal trend of specific leaf weight in 1983. Each point represents a mean of 3 replications.

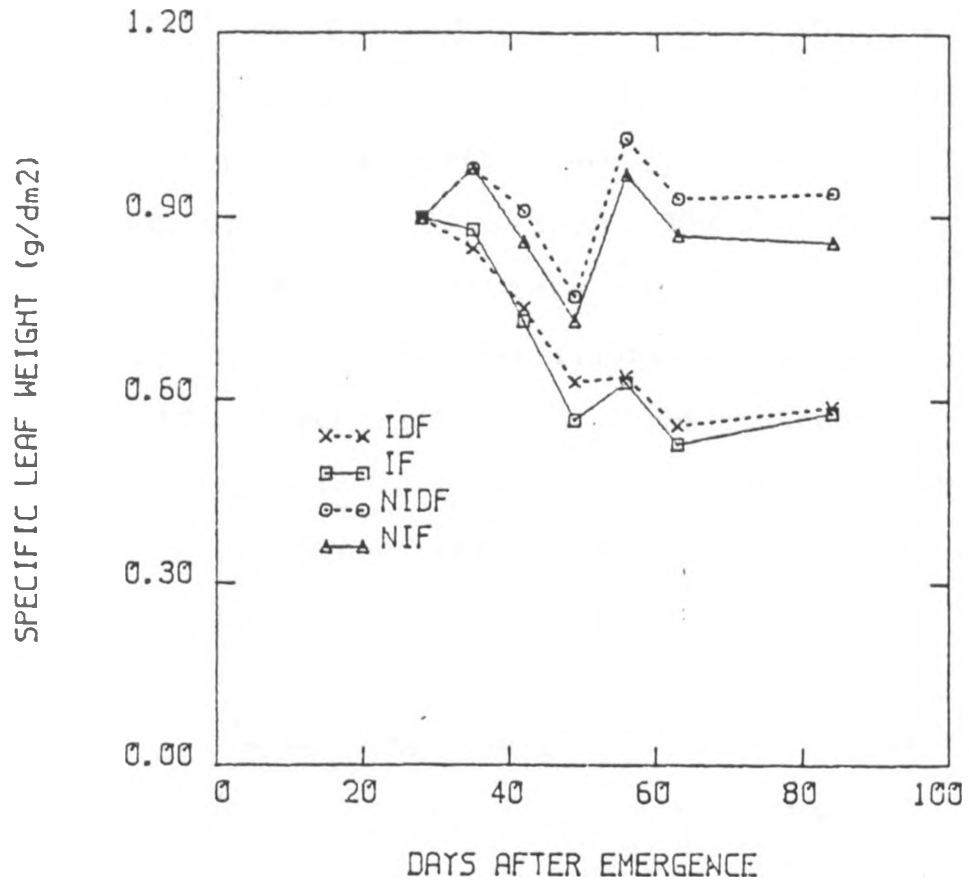

Fig. 16. Effect of water stress and flower removal on seasonal trend of specific leaf weight in 1983. Each point represents a mean of 3 replications.

should be pointed out that the lower light conversion efficiency exhibited by the dry treatment may be partly attributed to higher proportion of light intercepted by fruits which have lower photosynthetic rates compared to leaves. The data reported in section IV showed that dry treatment had a larger fruit partitioning coefficient than the wet treatment for most of the season. The fact that the light conversion efficiency was less sensitive to water stress than canopy growth is further illustrated by Fig. 11, (insets), 11 and 12. Essentially, the above ground biomass gained per unit increase in leaf area was higher in dry than wet treatments because water stress reduced canopy expansion rate more than photosynthesis per unit leaf area.

Apparently the plant adapted to soil moisture deficit by reducing canopy size thus reducing the evaporative surface. The high internal water status was possibly maintained by developing deep roots which penetrate intc wet soil layers. Root data were not collected in the field studies but soil moisture content data (Fig. 2) indicate that water was adequately available in the dry treatment below 90 cm to 120 cm depths. In that case the degree of water stress would probably be a function of the proportion of total root suface area which penetrate the deep soil layers with ample water and the ratio of this to the evaporative leaf surface. This kind of response to soil water deficit has been observed in other plants. Klepper et al (1973) found that increase in height of cotton plants

slowed drastically even when 35% of root system was still in well watered soil. Their results and those of Taylor and Klepper (1974) also illustrated that the pattern of rooting shifted during a drying cycle in such a way that the rooting density increased with depth while the opposite was true for irrigated treatment. The shift resulted from death of older roots in the top dry soil layers and production of new ones in deeper moist soil. Salter (1954) reported a similar shift for tomatoes.

These results suggest that root turnover rate may increase in conditions of water stress and that roots grow faster in high than in low soil moisture potentials. Arnon (1975) noted that roots tend to grow towards water. It would appear, therefore, that the reduction of shoot growth in response to mild water stress is a partitioning phenomenon linked to increase in root turnover rate. Sharp and Davies (1979) found a close connection between reduction in leaf elongation rate and increase in the ratio of root to shoot in maize seedlings as water stress developed. It is however not clear whether the shoot stops growth because of increased demand by the roots or the root growth increases relative to shoot growth because of an increase in assimilate supply following reduction in shoot growth. The observation (e.g. Barlow and Boersma, 1976) that assimilates accumulate in the source leaves of water stressed plants may suggest that shoot growth is not source limited. There is

also the possibility that the total root length penetrating moist soil (effective root length, Klepper et al, 1973) may limit the maximum size attainable by the shoot in the same way that small containers and resulting small root systems limit the size of pot-bound plants.

Since leaf water potential was little affected in these experiments and tomato plants do not adjust osmotically (Jorge Bolanos, personal communication; Cerda et al, 1979) the reduction in expansive growth can not be explained in terms of turgor potential. There is, however, the possibility that water stress could affect cell wall extensibility as observed by Van Volkenburgh and Boyer (1985).

None of the mechanisms suggested above necessitate immediate and corresponding reductions in leaf water potential and may therefore be plausible explanations for the present results. The influence of effective root length on canopy growth may be challenged by the results of work by Tan et al (1981) which indicated that the application of water to only 25% of root systems did not reduce leaf surface area of tomato plants. However, a critical evaluation of their data reveals that the water stress treatment did not affect any of the vegetative growth parameters in a consistent manner and that the decrease in shoot to root ratio was directly related to a fall in fruit yield. It is apparent that their experiment was conducted

late in the season when vegetative growth had largely stopped. Moreover, the fact that their zero irrigation treatment showed signs of wilting after only 8 days suggests that they had a relatively small container to root area ratio and therefore their results may not be applicable to field situations involving deep soils.

In conclusion, this work has shown, using biomass and photosynthetic data, that canopy size is more sensitive to water stress than canopy photosynthetic efficiency. It has also been shown that the effects of deflowering in enhancing canopy size can be largely overridden by water stress. Deflowering enhanced canopy size development in well irrigated plants but since it also influences assimilate partitioning as discussed earlier, we may not expect a corresponding increase in above ground-biomass.

SECTION IV

Effect of Water Stress on Biomass Partitioning BetweenVegetative and Reproductive Growth of Field Grown Tomatoes

Introduction

Much work in crop-water relationships has been geared towards irrigation management for maximum economic yield. The common approach has been to study the effects of withholding water at different stages of crop growth on the final yield and the results typically suggest that vegetative stage is the least sensitive to water stress whereas early reproductive (flowering and fruit set) is the most sensitive stage (Martin et al, 1966; Salter, 1954; Salter and Goode, 1967). Little work has been done, however, to study the specific effects of water stress on each phenological stage in order to understand how they interact to affect yield. In fact, the little evidence available suggests that reproductive processes are relatively insensitive to water stress compared to vegetative growth.

In tomato plants, both fruit set (Cannell and Asbell, 1974; Haghighi, 1980; Wudiri, 1980) and individual fruit growth (Salter, 1958) have been found to be insensitive to mild water stress. Aljibury and May (1970) and Martin et al

(1966) also found that water stress during tomato fruit growth hastened fruit maturation even though there was a highly significant reduction in tomato fruit yield. These studies, however, did not provide a direct comparison of the response of vegetative and reproductive growth processes to water stress. In a general note on effects of water stress on crops, Hsiao (1982) suggested that leaf growth is very sensitive to water stress followed by number of flowers per plant, fruit abortion and pollination and fruit set in that order of decreasing sensitivity.

Crop yield is a function of total biomass accumulated and the partitioning of biomass into organs of agricultural importance. The proportion of biomass partitioned to economic yield at harvest is known as harvest index (HI). The rate of biomass accumulation is a function of source size and source activity. Water stress is known to reduce source size through its effects in inhibiting the rate of canopy development (Bradford and Hsiao, 1982; Radulovich, 1984). Photosysnthesis per unit canopy cover may also be depressed by water stress through both stomatal and non-stomatal mechanisms (see Farquhar and Sharkey, 1982; Pearcy, 1983). Biomass production per unit land area will thus decrease in conditions of drought. Effect of water stress on harvest index is not so well established. The observation, mentioned earlier, that differences do occur in the sensitivity of various plant organs to water stress

is evidence that water stress may influence biomass partitioning in the plant. Where water stress favors partitioning into organs that constitute economic yield, the higher harvest index may offset at least part of the yield reduction arising from lower accumulated biomass.

Water stress may also affect partitioning by shortening the duration that a crop takes to mature. Many semi-arid areas have short rainfall seasons which are also unpredictable. A good crop for such areas should not only be capable of fast growth during the rainy season but also be able to accomplish much of crop maturity during the drying period at the end of the rains. An even better crop should hasten carbon partitioning into the organs that compose yield as water stress develops so that it can achieve maturity before exhausting the soil moisture reserves. Withholding water has been reported to hasten crop maturity in tomatoes (Aljibury and May, 1970; Martin et al, 1966). In cotton mild water stress around the time of flowering has been observed to favour reproductive growth such that no further vegetative growth occurs (Radulovich, 1984). It should be realised that such water stress-induced earliness can make a difference between a small profit and total crop loss. The study of carbon partitioning under conditions of water stress, therefore, needs further attention in order to better understand the mechanisms involved and incorporate these in crop improvement for dryland areas.

In this study, the effect of water stress on biomass partitioning between vegetative and reproductive parts was examined in processing tomatoes under field conditions.

Materials and methods

Tomato cultivar UC 82B was subjected to two different levels of water stress as part of a larger study which also included flower removal treatments as described in section III. The experiments were conducted in the summer season of 1983 and 1984. Field design and plant culture have also been described in section III. The treatments were started at the beginning of flowering stage. Irrigation was done using line-source sprinklers which also provided a zone of irrigation gradient between between wet and dry treatments. Watering levels consisted of a control treatment (I) which received 40-50 mm of water at weekly intervals and a dry treatment (NI) which depended solely on stored water in the soil after the beginning of the treatments. Each treatment was replicated 3 times in 1983 and 2 times in 1984. The irrigation gradient zone was further divided into 4 watering levels during 1983 corresponding to 70 (I1), 47 (I2), 33 (I3) and 16 (I4) percent of I. There were only three watering levels on the gradient zone during the 1984 season and these corresponded to 60 (Ia), 25 (Ib) and 15 (Ic) percent of I. In both seasons the watering levels were determined using catch cans placed at intervals along the watering gradient.

Deflowering was performed only during 1983 season and involved treatments I and NI only. No deflowering was done in the irrigation gradient plots. The idea was to compare the sensitivity of vegetative and reproductive growth processes to water stress by examining the biomass accumulation rate of deflowered vegetative plants and that of fruit bearing plants under conditions of similar soil moisture content. There were two treatments: the fruit bearing (or non-deflowered) plants (F) and deflowered (DF) plants. All open flowers of DF plants were removed weekly so that fruit formation was prevented.

Biomass samples were taken periodically and dried as described in section III.

A flower retention study was conducted during 1984 season. Flowers were tagged on day 47 after emergence (47 DAE) and on 60 DAE in treatments I and NI. Ten randomly chosen flowers were tagged per plant and a total of 5 plants were used per replicate. This operation was replicated 2 times so that there were 100 flowers tagged per treatment on each of the two occasions. Two weeks after each tagging episode, the number of flowers that had set fruit and were retained was recorded. Typically such flowers shed their petals while retaining a healthy green calyx while flowers which were not bound to set fruits shed both calyx and

petals.

Fruit ripeness was judged visually. Yellow and red fruits were considered ripe. Percent ripe fruit (ripe fruit/total fruit %) was determined on dry weight basis.

Results

Biomass accumulation in fruits: Water stress depressed fruit biomass at harvest to about a third of well irrigated treatment during 1983 and a half in 1984 (Fig. 1). In both years, however, the irrigated treatment did not have significantly higher fruit weight until after about 30 days into the fruiting period. In 1983 irrigated plants had higher fruit biomass for most of the season but this was not significant until after fruit growth in non-irrigated plants had stopped (around day 70). During the 1984 season, non-irrigated treatments actually had higher fruit biomass early in the fruiting period (61 DAE and 68 DAE). Irrigated treatment once again did not achieve significantly higher biomass until fruit growth in non-irrigated treatment started levelling off. It would appear that water stress had little effect on fruit biomass development (also see Fig. 6) and that the depression in fruit biomass later in the season can be largely attributed to the effect of water stress in shortening the duration of fruit formation.

Fruit partition coefficient: Water stressed plants

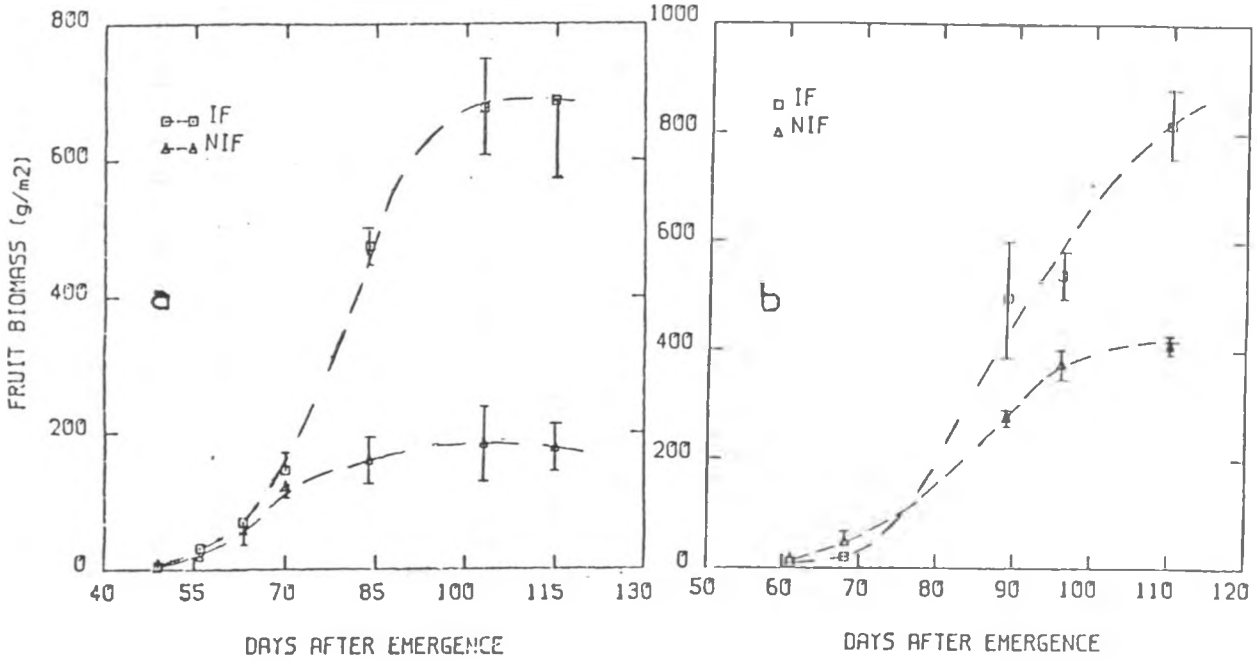

Fig. 1. Seasonal trend of fruit biomass for irrigated (IF) and non-irrigated (NIF) plants in 1983 (a) and 1984 (b). Each point is a mean of 3 replications for 1983 and 2 for 1984 data. Values are shown ± 1 SE.

had a higher proportion of total aboveground biomass allocated to fruits (fruit partition coefficient) than well irrigated plants for most of the 1983 season (Fig. 2). Actually, the non-irrigated treatment maintained a higher fruit partition coefficient (FPC) for as long as fruit growth continued in these plants. After fruit growth had stopped in the dry treatment (around day 70, see Fig. 1), however, the irrigated treatment caught up so that there was no significant difference in FPC at the end of the season.

The seasonal trend of the ratio of FPC between treatments NI and I for 1983 is shown in Fig. 3. The difference in FPC between NI and I was relatively large early in the season but decreased as the season progressed so that by harvest time, it was more or less the same. Hence, water stress had no significant effect on harvest index (FPC at harvest time). Both treatments achieved harvest index of about 50%.

The relationship between irrigation and biomass partitioning was further studied along the irrigation gradient. In 1983, samples were taken on only one occasion (75 DAE) when the crop was almost mature (50% ripe fruit by visual assessment). There was no further increase in fruit biomass in the dry treatment at this time while fruit growth continued in the wet treatment. The fruit partition coefficient remained nearly constant along the irrigation gradient, at approximately 50%. This is consistent with the

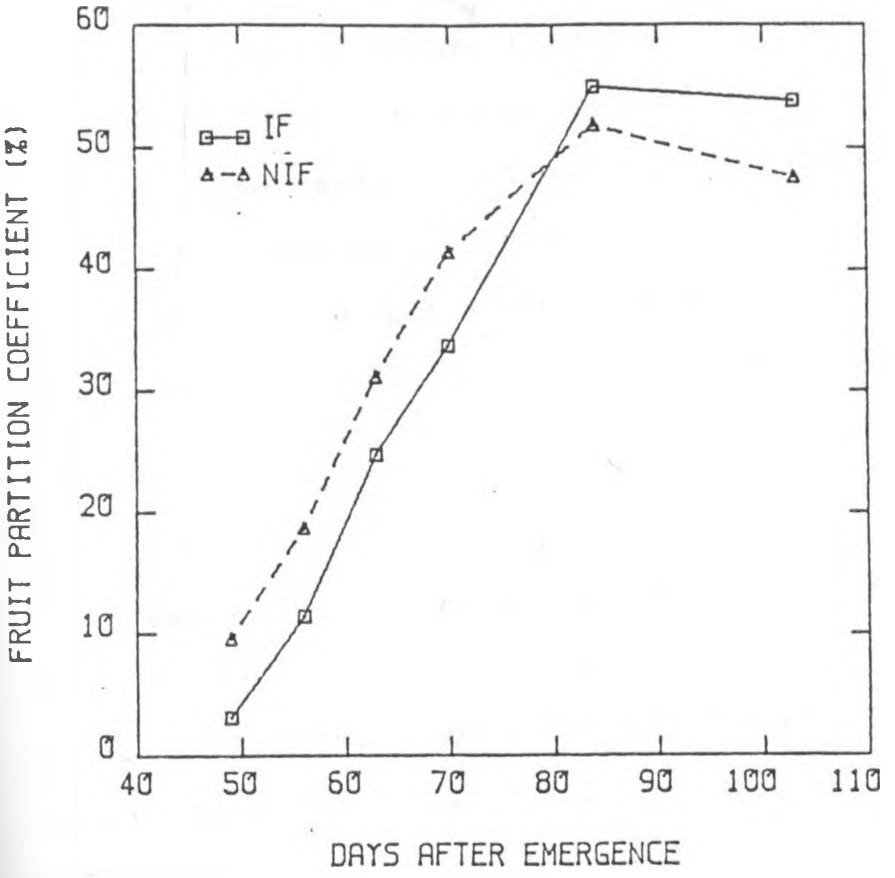

Fig. 2. Seasonal trend of fruit partition coeffficient (FPC) of irrigated (IF) and non-irrigated (NIF) treatments in 1983. FPC was calculated as the percent of fruit biomass (Fig. 1) in the total aboveground biomass (section III). Each value is a mean of 3 replicates.

data presented in Fig. 3. In 1984 measurements were taken at four different stages of fruit growth. Fig. 4b shows that FPC values were generally higher at low than high irrigation levels for much of the season but levelled out towards the end of the season. The highest FPC occurred at 25% I. The FPC at 15% I was usually lower than that at 25% I but it was still higher than FPC at 100% I. On a relative scale the effect of water stress in increasing FPC was higher during early fruit growth than late in the season. For example, FPC was 3 times higher at 25% I than 100% I on day 61 but only 1.3 times higher on day 89. This is consistent with 1983 results for I and NI treatments (Fig. 3.)

Water stress could enhance FPC by increasing fruit development rate or inhibiting aboveground vegetative growth. Results along the irrigation gradient in 1984 showed that, during early fruit growth, actual fruit biomass tended to increase with decreasing irrigation (Fig. 5). Although a peak fruit biomass was reached at 25% I, fruit biomass at 0% I was still higher than at 100% I, significantly so on 68 DAE. This trend was reversed later in the season (96 DAE). The relationship between irrigation level and fruit biomass was very similar to that between irrigation and FPC, suggesting that water stress enhanced FPC, at least partly, by stimulating fruit development. For example, both FPC and fruit biomass reached their peak at

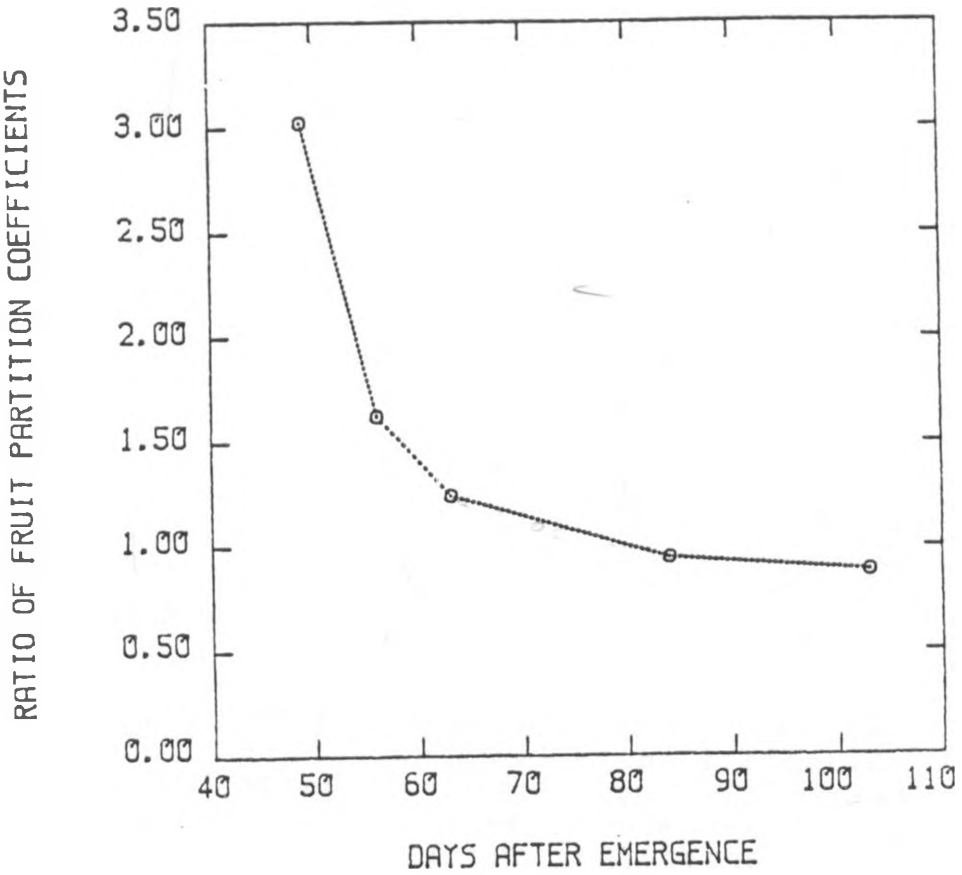

Fig. 3. Seasonal trend of ratio of fruit partition coefficent of non-irrigated treatment (NI) to that of irrigated treatment (I) for 1983.

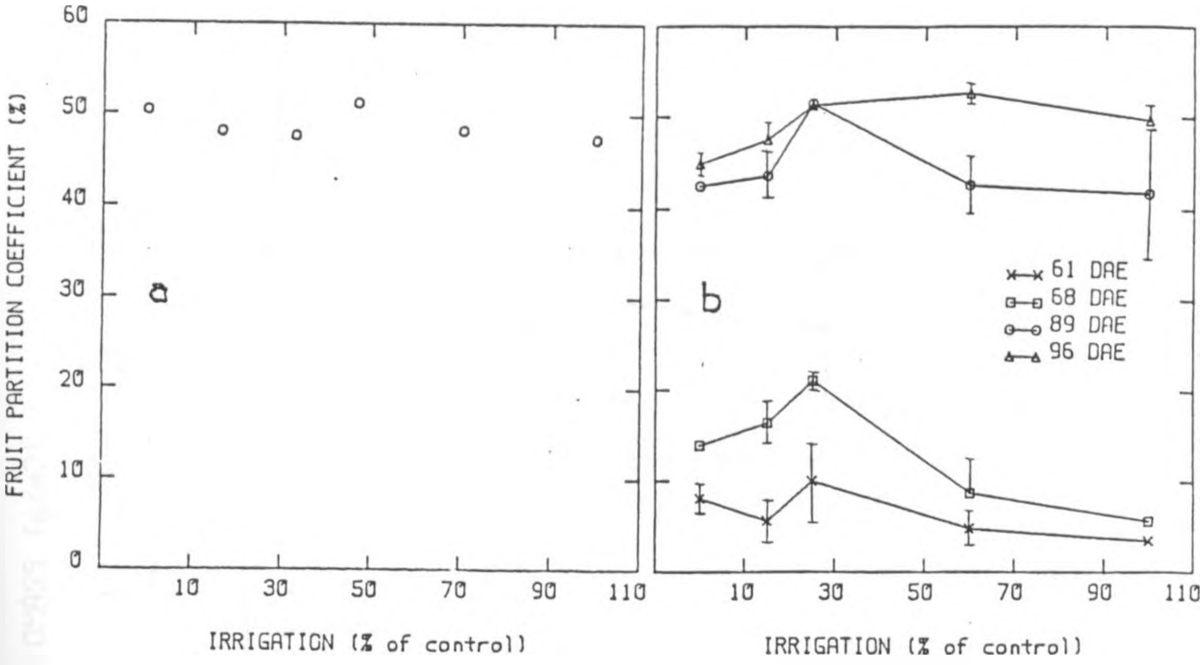

Fig. 4. Relationship between fruit partition coefficient and irrigation level along irrigation gradient on day 75 after emergence in 1983 (a) and on days 61, 68, 89 and 96 after emergence in 1984 (b). Each value is a mean of two replicates and is shown ± 1 SE.

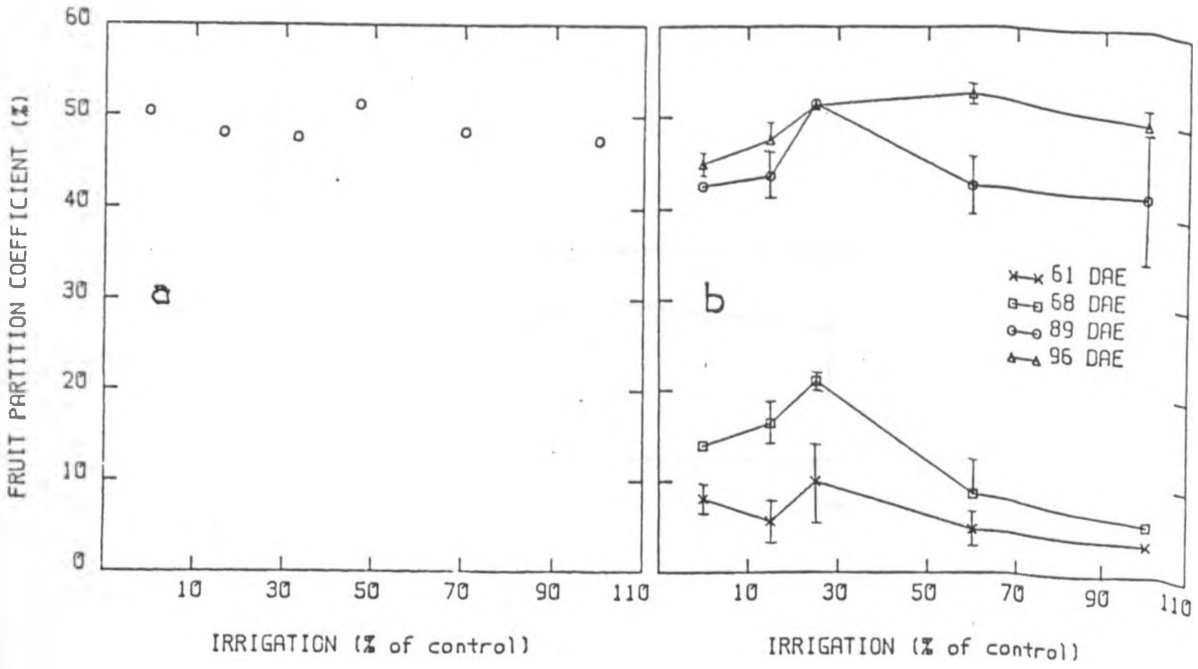

Fig. 4. Relationship between fruit partition coefficient and irrigation level along irrigation gradient on day 75 after emergence in 1983 (a) and on days 61, 68, 89 and 96 after emergence in 1984 (b). Each value is a mean of two replicates and is shown ± 1 SE.

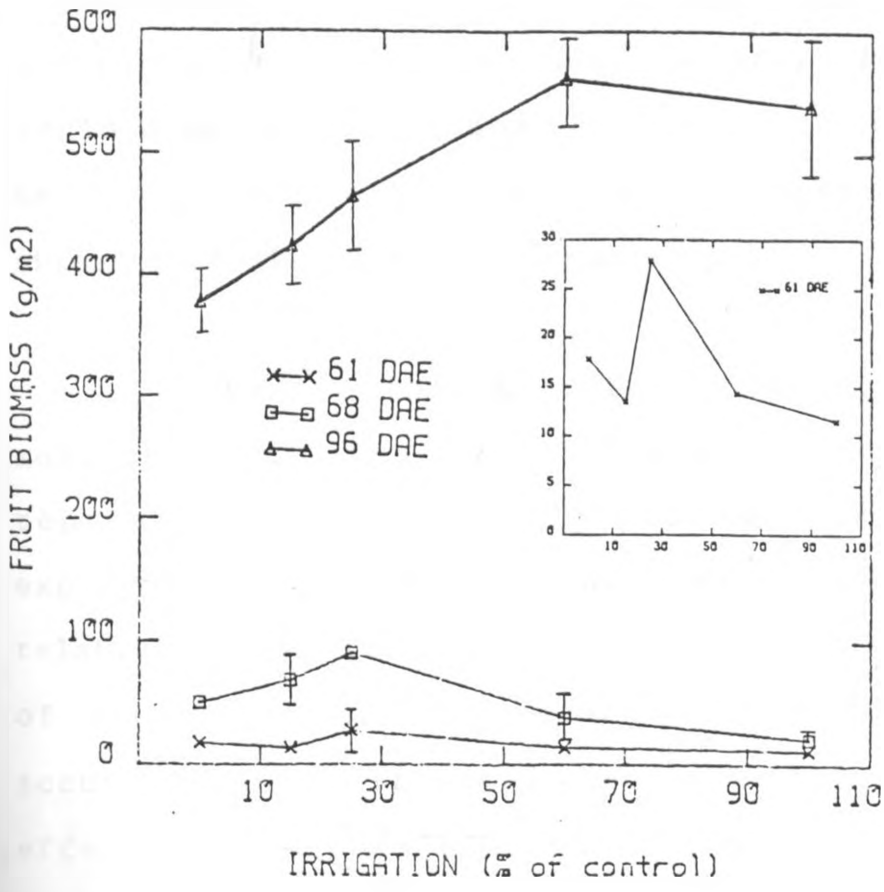

Fig 5. Relationship between fruit biomass and irrigation level along an irrigation gradient on days 61, 68 and 96 after emergence in 1984. Each value is a mean of two replicates. The inset represents day 61 DAE data on an expanded ordinate.

25% I on days 61 and 68. This raises the question of whether the enhancement in partitioning into fruit biomass was associated with inhibition in aboveground vegetative development.

The sensitivity of vegetative and reproductive growth processes to water stress was compared by analysing the exponential phase of each growth process. Effects of deflowering on biomass accumulation were also evaluated. It was postulated that, under water stress, deflowered plants would show lower biomass accumulation compared to fruit bearing plants if fruit growth is less sensitive to water stress than aboveground vegetative parts.

In Fig. 6, the logarithm of biomass was plotted against time. The initial linear portions of the curve represent the relative growth rate (RGR) during the exponential phase of growth. Water stress depressed relative growth rate of vegetative shoot but enhanced that of fruit. Flower removal had no effect on biomass accumulation in irrigated treatments but had a depressing effect in the non-irrigated treatments (Fig. 7). This depression did not occur until after the beginning of fruiting, around day 50. These results suggest that aboveground vegetative growth is more sensitive to water stress than reproductive growth. Hence the enhancement in FPC discussed earlier can be attributed to both stimulation of fruit growth and depression of aboveground vegetative

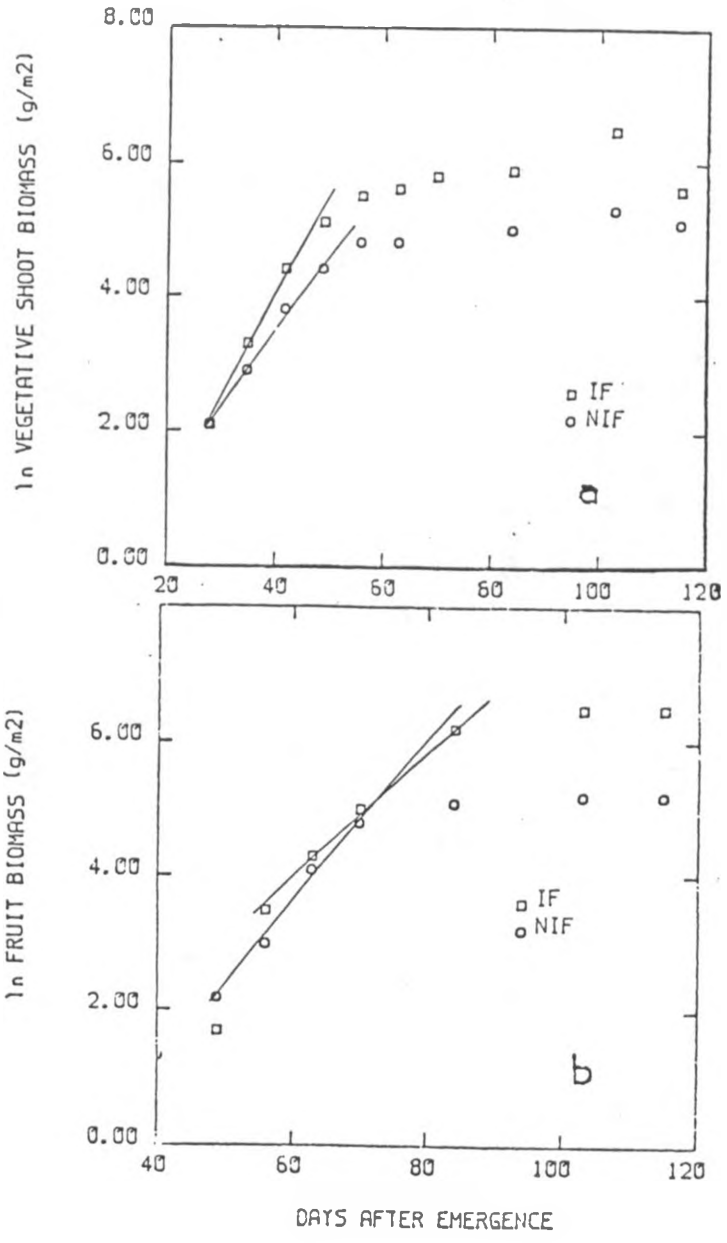

Fig. 6. Seasonal trend of the logarithm of vegetative (a) and fruit (b) biomass in 1983. The lines join points which fall in the exponential phases of vegetative and fruit growth and the slope of each line represents relative growth rate during exponential phase of growth. Regression analysis showed that water stress significantly (0.1 level) depressed RGR of vegetative biomass. The RGR of fruit biomass was significantly (.05 level) increased. The first data point for IF (Fig. b) was not included in the regression calculation.

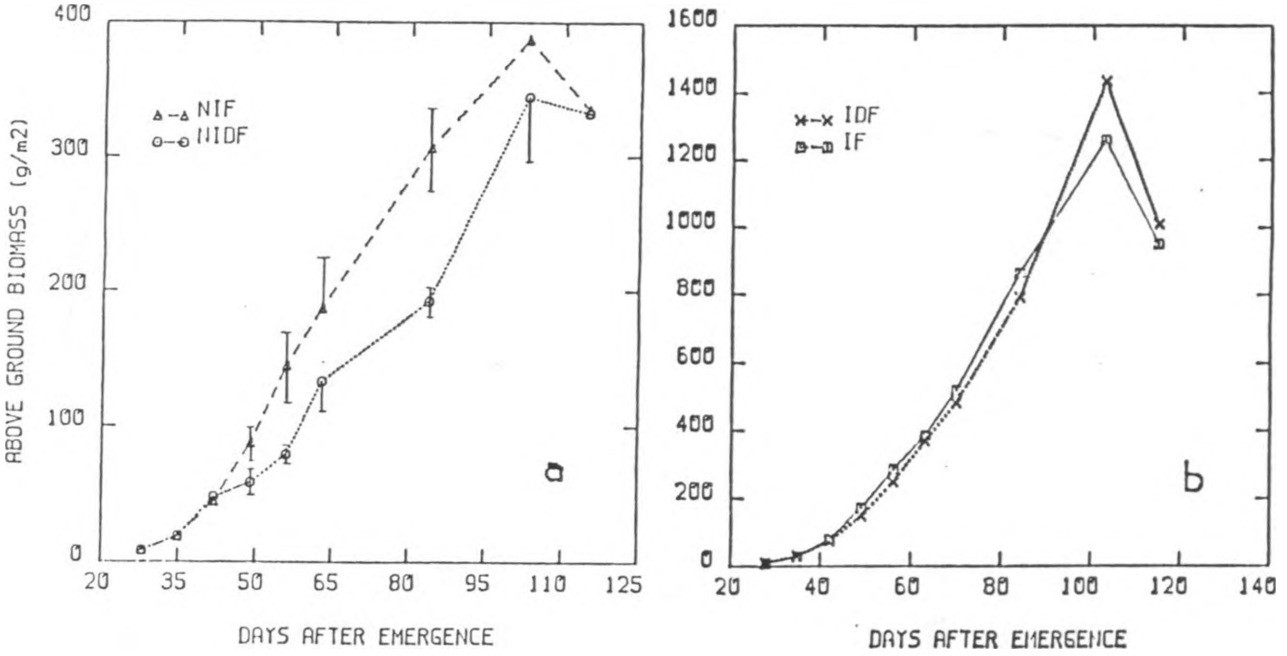

Fig. 7. Effect of flower removal on the seasonal trend of above ground biomass in non-irrigated (a) and irrigated (b) treatments during 1983 season. Each value is a mean of three replicates. Values for non-irrigated treatment are shown ± 1 SE except where the SE value is less than 5.

growth.

Flower retention: The enhanced biomass accumulation in fruits in the non-irrigated treatment may arise from a larger number of fruits resulting from better flower retention or higher growth rate of individual fruits. Results of flower tagging (Fig. 8) showed that non-irrigated plants retained close to 80% of the flowers in the first two to three flower trusses (at 47 DAE) compared to 35% retained by irrigated plants. Later on (at 60 DAE) there was no difference in flower retention between wet and dry treatments. Essentially, the dry treatements had almost constant flower retention between the two occasions as shown in Fig. 8. Irrigated plants showed marked increase in flower retention between the two occasions.

Duration to crop maturity: The percent biomass of ripe fruits in the total fruit biomass was taken as indicator of crop maturity. Water stressed plants matured earlier than well irrigated plants (Fig 9). The high percent retention of early flowers by the non-irrigated treatement was, at least, partly responsible for this earliness. It is also important to note that fruit growth stopped about 30 days earlier in the dry compared to the wet treatments (Fig. 1). This means that, at any one time, the fruit load of non-irrigated treatment consisted of relatively larger proportion of early fruits. The observed early maturity could, therefore, be partly attributed to the

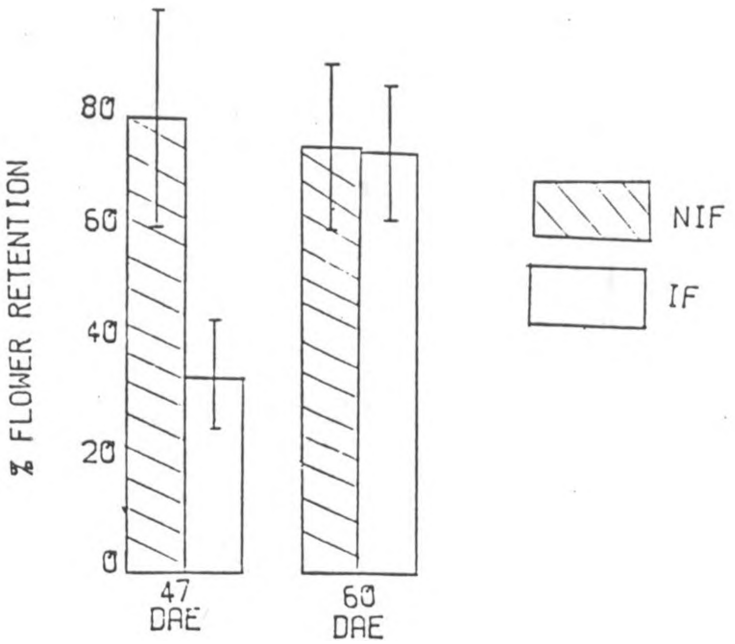

Fig. 8. Effect of irrigation treatments on flower retention in 1984. Each value is a mean of 2 replications and 5 subsamples were taken in each replication. The points are plotted ± 1 SE.

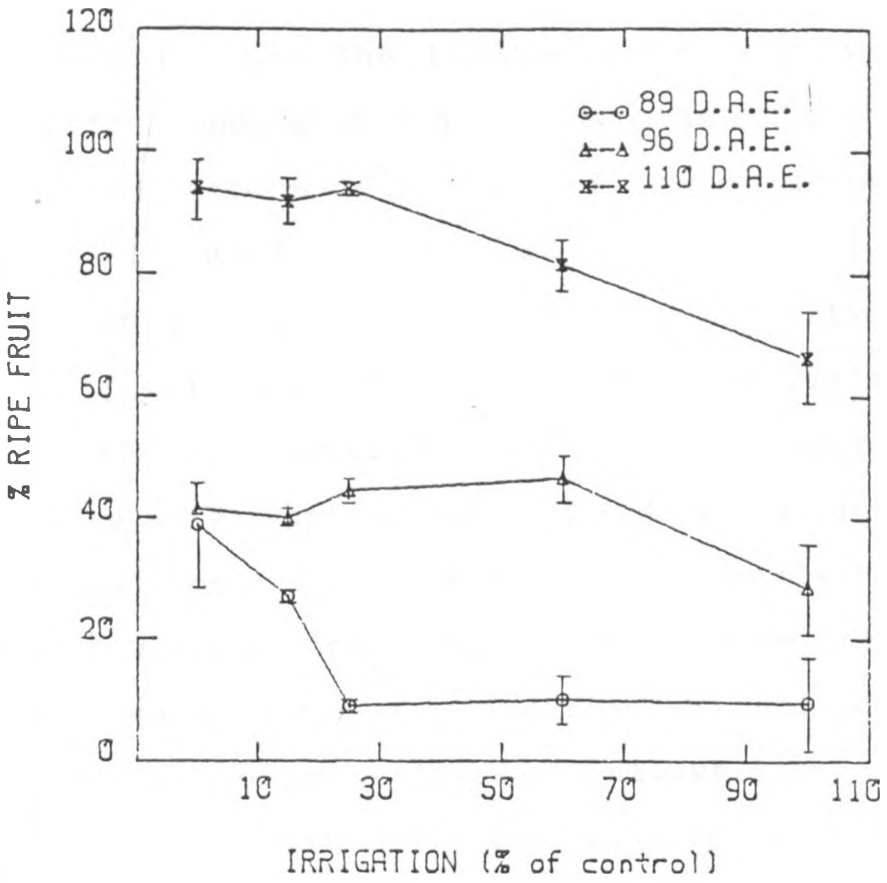

Fig. 9. Biomass of ripe fruit percent of total fruit biomass as a function of watering level as along an irrigation gradient on three occasions in 1984. Each point represents a mean for two replicates. Each value is shown ± 1 SE.

effect of water stress in shortening the duration of reproductive growth.

Discussion

Due to both the limited water supply and cost of irrigation, much work has been done in attempts to improve irrigation efficiency in terms of crop yield per unit water supplied. Most of this work has been based on the hypothesis that moisture availability at certain phenological stages is critical for crop yield (Salter and Goode, 1967). Identification of such stages would allow selective water application thus reducing irrigation without much sacrifice on crop yield. Studies involving withholding water at different phenological stages have provided results which suggest that vegetative stage is the least sensitive whereas early reproductive stage (flowering and early fruit growth) is the most sensitive stage to water stress. Some of the shortcomings of such studies have been discussed by Salter (1958). A common limitation of the approach is that care is rarely taken to ensure that the plants are subjected to comparable stress intensity and duration in each of the phenological stages under study. In addition, these studies usually do not consider the progressive effects of water stress leading to yield reduction but instead concentrate on analysis of yield components at harvest time. For example, it is frequently reported in literature that the number of fruits per plant is a major component limiting crop yield

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under conditions of water stress yet work is rarely done to evaluate the extent to which this response can be ascribed to low flower set or increased fruit abortion.

In this study there was little difference in water potential between irrigated and non irrigated treatments for most of the season (see section III). In 1984, significant decrease in water potential occurred late in the season but this coincided with the maturity stage when there was little growth. The experiments therefore provided a good opportunity to compare vegetative and reproductive growth under conditions of mild and more or less similar stress. Furthermore, the flower removal experiment was used to study vegetative and reproductive growth in plants growing side by side under conditions of similar soil moisture content.

Vegetative growth was found to be more sensitive to water stress than reproductive growth. Actually, water stress had a depressing effect on vegetative growth but had no effect on or slightly stimulated reproductive growth. The vegetative phase of non-irrigated plants had lower exponential phase RGR than irrigated plants while the exponential phase RGR for fruit growth was higher in non irrigated than irrigated plants (Fig. 6). It was also found that deflowered, vegetative plants had lower biomass accumulation rate than fruit bearing plants under conditions of water stress even though no such differences occurred in

irrigated plants (Fig. 7). Biomass accumulation in fruits was either unaffected or slightly stimulated by water stress (Fig. 1) as long as fruit growth continued in non-irrigated plants. The depression of fruit yield by water stress was attributed mainly to hastened maturity and hence shorter duration of fruit growth. Water stress inhibited growth of vegetative shoot apices thus precluding further formation of new flower nodes and shortening the duration of reproductive growth.

The fact that fruit growth was favored by water stress may be attributed to differential partitioning in favor of fruit growth as shown in Figs. 2 to 4. The physiological basis of this phenomenon is not clear. Tomato fruits are protected from rapid evaporative water loss by thick cuticle covering the pericarp. Consequently the water content would undergo little change during water stress. Furthermore, as a storage organ and a major sink during reproductive growth, fruits would have high concentration of solutes that might be used for osmotic adjustment in the same way as wheat apices reported by Barlow et al 1980. Fruit cells may thus maintain turgor and continue to grow and serve as active sinks long after vegetative growth has stopped. Unpublished results of Jorge Bolanos obtained from the same field as this study showed that water stress had little effect on photosynthesis per unit leaf area even though shoot growth was markedly depressed (see section III). It is thus conceivable that leaves of water stressed

plants had surplus of assimilates.

During the reproductive stage, fruit growth formed a major sink which was also less sensitive to water stress as mentioned earlier. Although the difference in growth between leaf and fruit in response to stress is not understood, it is conceivable that developing fruit benefits from surplus assimilates that accumulate following depression of leaf growth. Johnson and Moss (1976) reported that the proportion of assimilates translocated to the grain was increased following water stress in wheat. This would explain the higher fruit partition coefficient exhibited by water stressed plants and the increase in absolute fruit biomass relative to the irrigated treatment observed early in fruit in 1984. Apparently, therefore, water stress stimulated fruit growth by inhibiting vegetative growth. Under well watered conditions vegetative growth continued over a longer period and probably provided a strong competition to fruit growth. This could be responsible for the poor fruit set in early flower trusses (Fig. 8) and lower fruit partition coefficient (Figs. 2 to 4). As fruit formation and growth increased, however, they probably formed a strong sink which suppressed vegetative growth and this led to a rapid increase in partition to fruits late in the season so that there was no difference in harvest index between wet and dry treatments at harvest time. This study shows that the higher tomato yield observed in well

irrigated treatments resulted mostly from larger canopy size and accompanying higher number of flower nodes and a longer period of reproductive growth. During the 1983 season, fruit growth levelled out around 80 DAE in the dry treatment but continued for another 30 days in well irrigated plants (Fig. 1). Partitioning into fruit was favoured by water stress. Probably the mildly water stressed plants could have had a higher yield if only they could develop more flower nodes.

The response of reproductive growth to water stress has been reported by other workers. Hsiao et al (1976) noted that reduced vegetative growth resulting from water stress would lessen competition for assimilates and thus help fruit growth. Hsiao (1982) further suggested that pollination and fruit set are generally insensitive to water stress. Wudiri (1980) found that water stress had little effect on pollen viability. Turk et al (1980) reported that cowpeas subjected to water stress in the field are probably sink limited so that they produced fewer but larger seeds than well irrigated plants. Stockton et al (1961) and Hearn (1975) observed that when cotton plants were liberally supplied with water there was increased shedding of young bolls probably due to internal competition between vegetative and reproductive growth (Hearn, 1980). Hearn (1975) found that mild water stress during reproductive growth led to an increase in the number of fruits set on early flowers. The results of this study showed that mild

water stress actually enhanced flower retention and fruit partitioning coefficient and stimulated early maturity. These results are to a large extent similar to those observed in cotton (see Hearn, 1980). In other studies with tomatoes, Cannell and Asbell (1974) and Haghighi (1980) found that water stress had no effect on fruit set under field conditions. It should be noted, however, that these workers did not perform detailed studies of fruit set at different stages of flowering. Their results, therefore, represent average fruit set and thus potentially masked the possibility that water stressed plants had higher fruit set on early flower trusses. Aljibury and May (1970) and Martin et al (1966) found that water stress during reproductive growth hastened maturity but did not study fruit set. In this study, water stress promoted early fruit set (Fig. 8) and short fruiting period (Fig. 1). Stressed plants could, therefore, tend to show an early maturity simply because their fruit load coonsists of relatively high proportion of early fruits. In view of these findings, the results of Aljibury and May (1970) and of Martin et al (1966) could be attributed, at least partly, to early termination of fruit formation in water stressed plants.

In summary, the results of this study and those of the other workers discussed above have shown that mild water stress during reproductive phase favors assimilate partitioning into reproductive rather than vegetative

growth. Thus, in plants such as tomatoes whose flowering spread over a long period of time, yield reduction results from fewer flower nodes rather than flower abscission and retarded fruit growth. Mauney (see Jordan, 1982) made a similar observation for cotton.

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SECTION V

Effects of Flower Removal on Plant Water Status Under Conditions of Water Stress

Introduction

Flower removal has been reported to stimulate vegetative shoot growth (Hurd, 1979; Murneek, 1929; Lenz, 1978; Lenz and Williams, 1973) and root growth (Hurd *et al*, 1979). Hurd *et al* (1979) observed an increase in root biomass which was relatively higher than that in shoot biomass in deflowered tomato plants. Similarly, Lenz and Williams (1973) found approximately four-fold increase in root biomass following deflowering of soybean compared to only two-fold increase in above-ground vegetative biomass. It is apparent, therefore, that flower removal not only increases root growth but also root-shoot ratio. All these findings were obtained under conditions of favourable plant water status and effect of flower removal on root growth under conditions of water stress is not known.

Increase in root growth that accompanies flower removal would increase the soil moisture available to a plant (Kramer, 1983) and thus improve plant water status under conditions of limited soil moisture. Loewing (1940) and Salter and Drew (1965) observed that root growth is depressed at the onset of reproductive growth. They

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postulated that this phenomenon could be responsible for the high sensitivity of crops to water stress during early reproductive growth (see Salter and Goode, 1967). More research is needed to study the interaction between root growth and reproductive growth and how these affect plant water status particularly in situations of soil water deficits.

This experiment was conducted to examine the influence of flower removal on plant water status under conditions of water stress.

Materials and methods

Tomato cultivar UC 82B was subjected to different levels of water stress and deflowering during 1983 and 1984 summer seasons. There were two levels of irrigation: irrigated (I) and non-irrigated (NI) and two levels of deflowering; deflowered (DF) and non-deflowered or fruit bearing (F). The treatments were arranged in a 2 x 2 factorial structure so that we had: Irrigated deflowered (IDF), irrigated fruit bearing (IF), non-irrigated deflowered (NIDF), and non-irrigated fruit bearing (NIF). The field design, plant culture, irrigation and deflowering procedures have been discussed in section III. Deflowering involved removal of all flowers at weekly intervals so that fruit formation was prevented. Leaf water potential was measured using a pressure chamber as discussed in section

III.

During the 1983 season, leaf water potential was measured on several occasions during the growth period. In 1984, however, these measurements were not done until late in the season when the fruit bearing plants were already getting into the maturity stage.

Results

The effects of deflowering on leaf water potential under field conditions is shown in Figs. 1-3. During the 1983 season, there was no difference in leaf water potential between deflowered and fruit bearing non-irrigated plants early in the season, up to around 70 days after emergence (70 DAE). Subsequently, however, the deflowered plants had a consistently higher water potential (0.1 to 0.2 MPa) than the fruit bearing plants (Fig. 1a). In the irrigated teatments, deflowering had no efffect on leaf water potential throughout the season (Fig. 1 b).

Leaf water potential was measured only in the late part of the season in 1984. Fig. 2 illustrates midday leaf water potential on several occasions. Once again it is demonstrated that deflowering had no effects on the leaf water status of irrigated plants but improved that of non-irrigated plants. Diurnal trend of leaf water potential was followed on two occasions (Fig. 3) and the results are

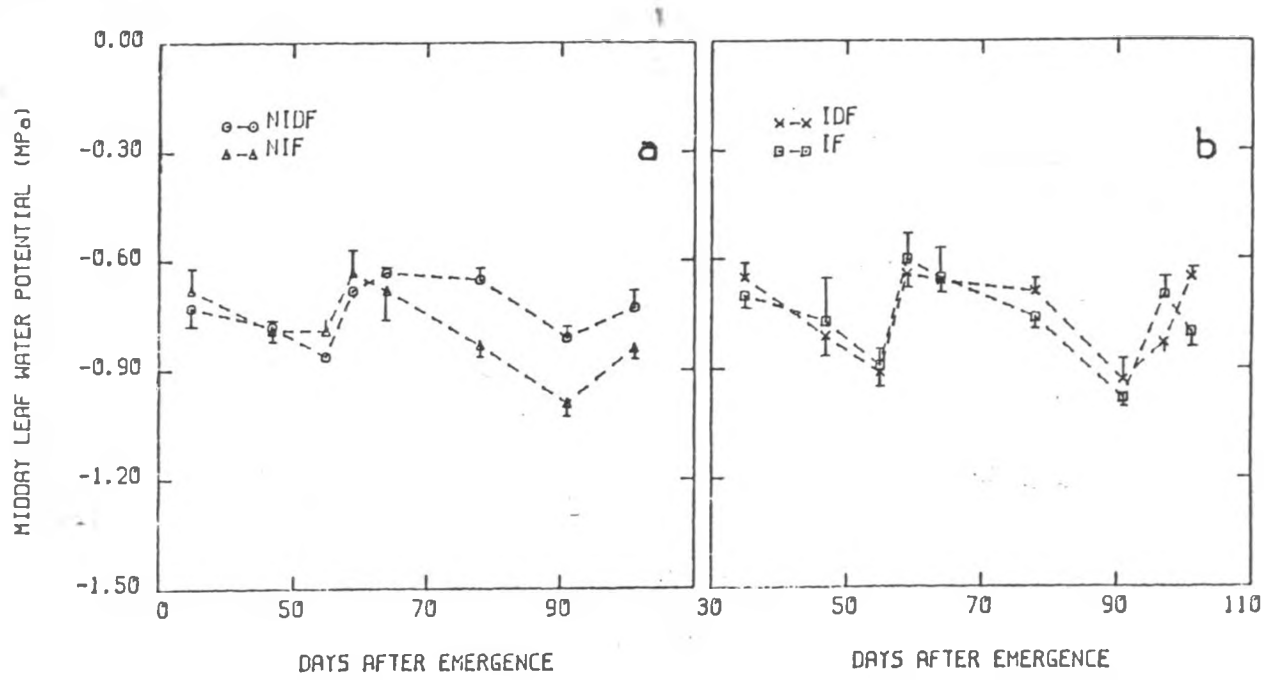


Fig. 1. Effect of flower removal on seasonal trend of midday leaf water potential in non-irrigated (a) and irrigated treatments (b) in 1983. Each point is a mean of 3 replicates. Three leaves were sampled in each replicate. Each value is shown + or - 1 SE.

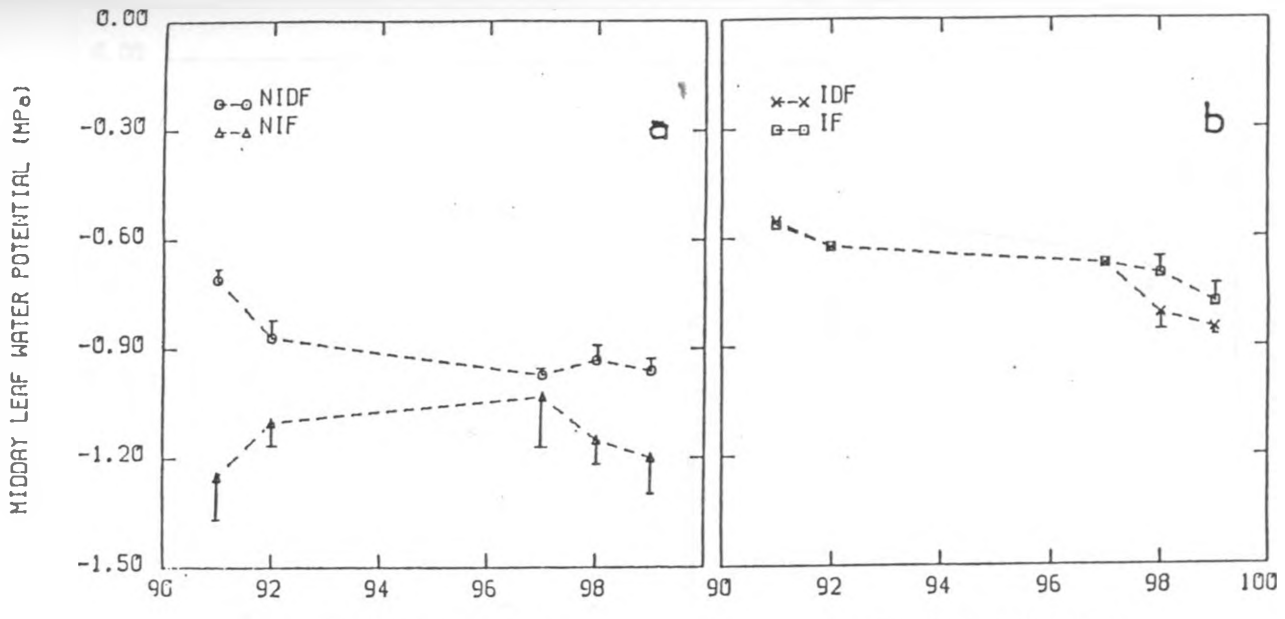
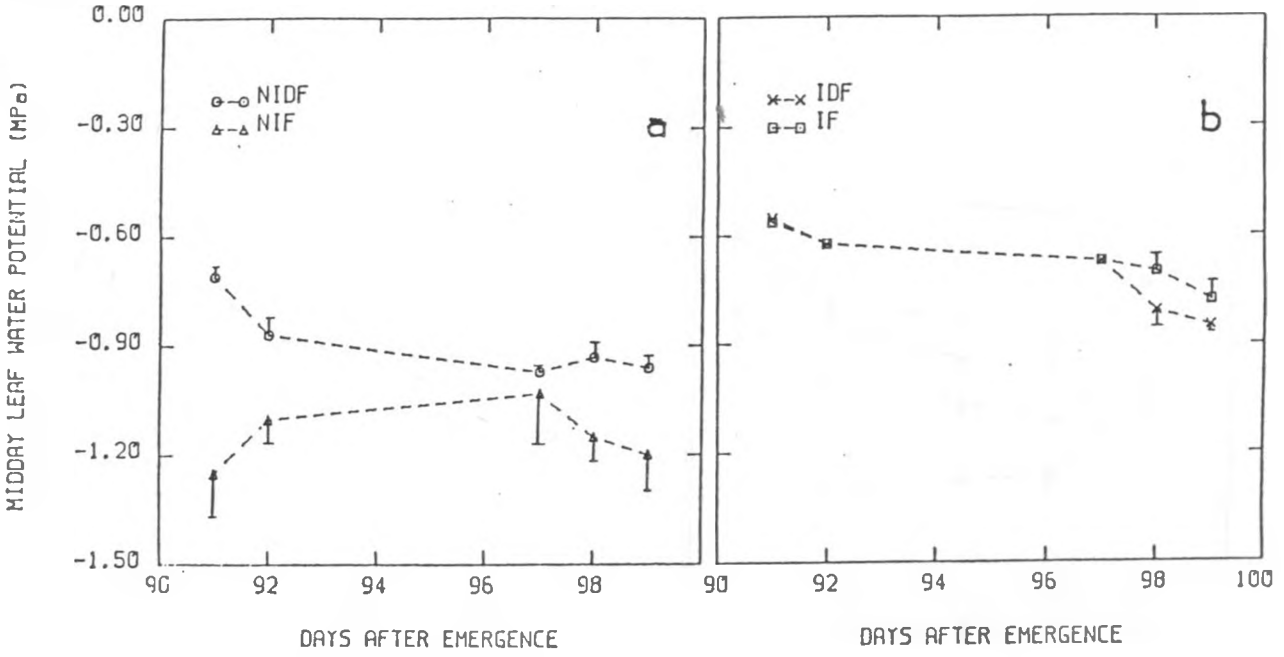


Fig. 2. Effect of flower removal on midday leaf water potential in non-irrigated (a) and irrigated (b) treatments late in the 1984 season. Each point represents a mean of 2 replicates. Three subsamples were taken for each replicate. Each value is shown + or - 1 SE.



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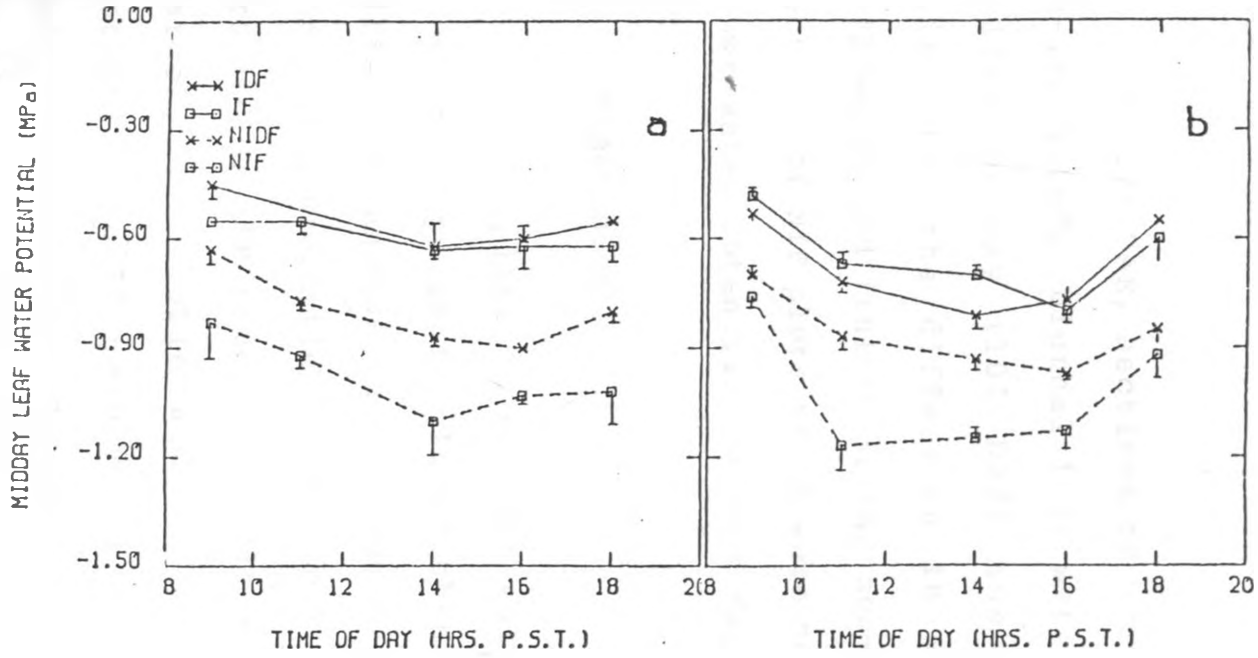

Fig. 3. The effect of flower removal on diurnal trend of leaf water potential of irrigated (IDF and IF) and non-irrigated (NIDF and NIF) treatments late in 1984 season; days 92 (a) and 98 (b). Each point represents a mean of 2 replications. Two leaves were sampled in each replication. Each value is shown + or - 1 SE.

consistent with the midday trend shown in Fig. 2. Throughout the day, deflowered plants had higher leaf water potential than fruit bearing plants under conditions of water stress.

On 100 DAE, sections of both NIDF and NIF plots were re-irrigated. Diurnal leaf water potential taken on the following day (101 DAE) showed that re-irrigation eliminated the difference in water potential between deflowered and fruit-bearing, non-irrigated plants (Fig. 4). Sections of NIF plots which were not re-irrigated maintained lower water potentials on that day.

Discussion

For a plant to extract water from the soil it must have water potential lower then that of the soil. This difference depends on the evaporative demand and the water conducting properties of the soil and the plant. For plants growing in the same field, the evaporative demand would be largely comparable and any differences in leaf water potential would mainly arise from differences in soil moisture potential and resistance to water flow in the soil (R_s) and plant (R_p.)

In this study deflowering improved the leaf water status of non-irrigated plants while having no effect on irrigated plants (Figs 1-3). In the 1983 season it was shown

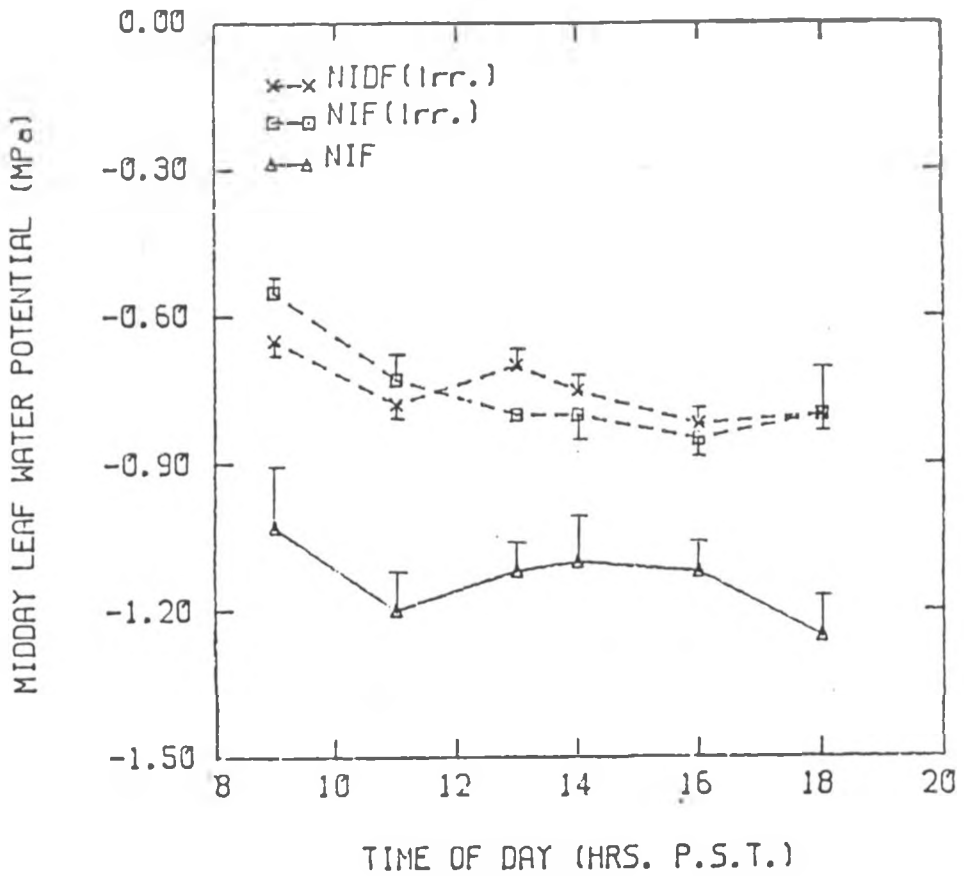

Fig. 4. The effect of re-irrigation on the diurnal leaf water potential of deflowered and fruit bearing non-irrigated plants late in 1984 season (day 101 after emergence). Each point represents a mean of 2 replications. Two leaves were sampled in each replication. Each value is shown + or - 1 SE. NIDF (irr) and NIF (irr) represent the re-irrigated sections.

that non-irrigated treatments (NIF and NIDF) had similar soil moisture content through much of the season (see section III) and, hence can be assumed to have had comparable soil moisture potential. It can also be assumed that the evaporative demand was similar in the two treatments since it is mainly determined by atmospheric conditions. Furthermore the two treatments had similar canopy size (see Section III) and hence similar potential for evapotranspiration water loss. The differences in leaf water potential could, therefore,be explained mainly by possible differences in soil and plant resistances.

The dependence of R_s on root geometry and soil hydraulic conductivity (K) has been discussed by a number of workers (e.g. Greacen, 1977; Hsiao et al, 1976; Jordan and Miller, 1980; Passioura, 1982 and Taylor, 1980). The root geometry term is usually dominated by the root length density (L_v) expressed in cm root per cm^3 soil. An increase in L_v or K reduces R_s. In wet soil K is very high and R_s is almost negligible. As soil water potential falls in a drying cycle, soil hydraulic conductivity declines rapidly and a high root length density would be desirable as it reduces the distance water has to travel to reach the root surface. In this study it was found that re-irrigation eliminated the difference in leaf water potential between treatments NIF and NIDF (Fig 4). This result suggests that differences in R_p were proportionally very small or negligible. Hence the increase in leaf water potential

effected by deflowering under dry conditions can mostly be attributed to difference in R_s. Since the soil moisture content between the two treatments were similar as reported in section III, K is not likely to have been important in determining these differences. It may, therefore, be concluded that the differences in leaf water potential were probably due to differences in L_v. It should, however, be pointed out that NIDF plants could also reduce R_s by growing deeper roots which penetrate into soil layers with ample water content.

Deflowering has been shown to stimulate root growth in tomato (Hurd, 1979) and soybean (Lenz and Williams, 1973). If similar increase in root growth relative to shoot growth occur under conditions of drought it should contribute importantly to improving plant water status. The ecological significance of this response is obvious. Plants often shed their flowers and developing fruits when exposed to high water stress. Increase in root growth which may follow such flower shedding would be useful in plant acquisition of water from soil and thus impart drought resistance. This subject deserves more research since it could be important in crop management. Apparently, forfeiting some fruit yield may impart drought resistance.

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SECTION VI

Photosynthetic Response of Tomatoes to Fruit Removal, Stem Girdling, and Deflowering.

Introduction

Assimilate sink strength is thought to influence CO_2 exchange rate of source leaves. Literature on sink-source relations studies indicate that reduction in the sink/source ratio can lead to depression in photosynthetic rate (Azcon-Bieto, 1983; Guinn and Mauney, 1980; Neales and Incoll, 1968, Setter et al., 1980a and 1980b) but the mechanisms involved are not well understood.

Neales and Incoll (1968) reviewed work on this subject which in general suggests that sink/source ratio controls photosynthesis through its influence on assimilate export from source leaves. A low sink/source ratio is postulated to favor assimilate accumulation in leaves and this inhibits photosynthesis through biochemical feedback inhibition. Recently, a number of workers (e.g. Azcon-Bieto, 1983; Koller and Thorne, 1978; Setter et al, 1980a; 1980b) have reported depression in leaf conductance following sink reduction. Setter et al (1980a) reported a reduction in leaf conductance following soybean pod removal which could account for observed photosynthetic inhibition. The work of Azcon-Bieto (1983), however, revealed that reduction in

stomatal conductance following sink reduction was unlikely to be the cause of photosynthetic inhibition since it had no effect on internal CO_2 concentration (C_i). His work suggested that sink limitation on photosynthesis operates mainly through non-stomatal mechanisms.

Much of the literature on this subject is based on short term studies using abrupt and drastic reduction in sink/source ratio. Consequently little attention has been given to the development of alternative sinks and their influence on photosynthesis following initial reduction in sink/source ratio. This study reports the effect of sudden fruit removal and continuous deflowering on tomato photosynthetic rates in the field. Effects of fruit removal and source leaf girdling on photosynthesis was also examined in growth chamber plants and gas exchange characteristics were analysed on the basis of relative contribution of stomatal and non-stomatal CO_2 exchange parameters.

Materials and methods

Field experiment: Tomatoes, cultivar U.C. 82B, were grown in the field during the summer of 1983. Plant culture, deflowering procedure and biomass sampling and drying methods have been described in section III. Deflowering involved weekly removal of all flowers so that fruit development was prevented. On two occasions, 76 days

after emergence (76 DAE) and 86 DAE, all fruits were removed from a section of 40 plants in the well irrigated treatment. Neighboring fruit-bearing plants served as controls. Two different plots were used, one for each occasion. This operation was timed to coincide with the stage when fruit growth constituted more than 85 per cent of total above ground biomass growth (Fig. 1). Phenologically it coincided with the yellowing stage of early fruits.

Leaf net photosynthetic rate was measured on randomly chosen uppermost, mature and fully exposed leaves using a portable infra-red gas analyser as described in section III. Epidermal conductance of abaxial side of a leaf was also determined on the uppermost, mature and fully exposed leaves using a steady state diffusion porometer. Air flowing through the leaf cup (covering an area of 1.7 cm^2) was maintained at a constant relative humidity near that of the canopy by passing dry air through the cup at a rate that compensated for increases in humidity resulting from leaf transpiration. Whenever leaf epidermal conductance and photosynthetic measurements were taken together, two different leaflets (on for each measurement) were used for each sampled compound leaf.

Growth chamber experiment: Well watered plants were grown in 5-liter pots filled with potting mix in a controlled environment growth chamber (Controlled

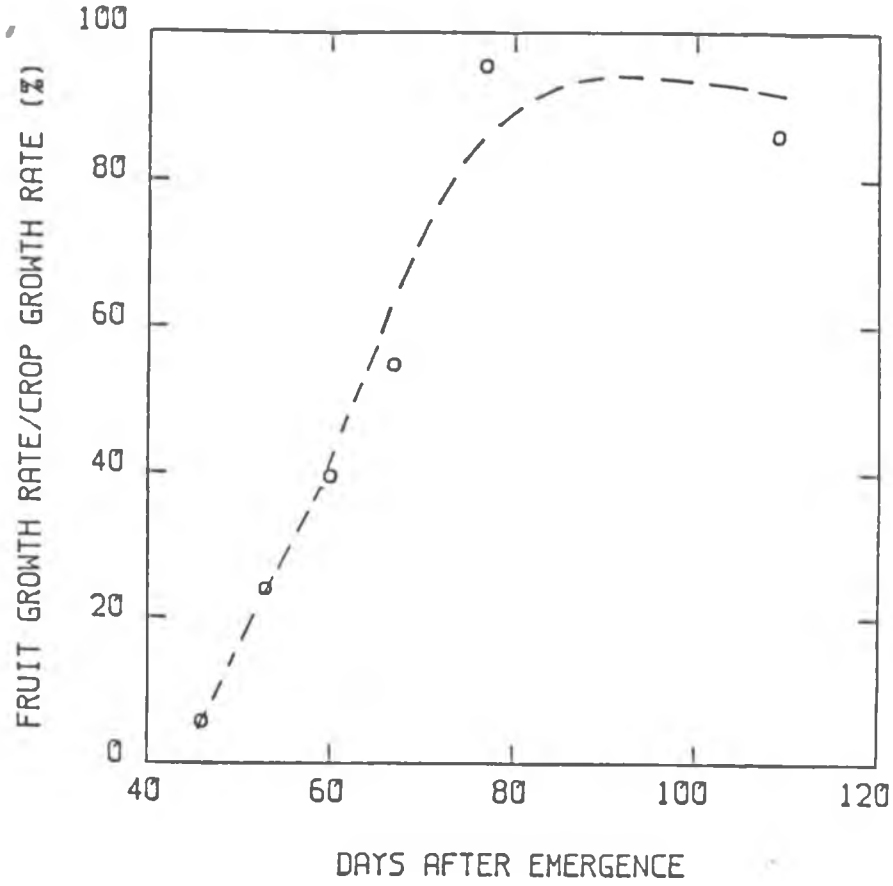

Fig. 1. Seasonal pattern of ratio of fruit growth rate to crop growth rate in irrigated plots during 1983 season. Crop growth rate = dry matter accumulation rate of total above ground plant material in g m^{-2} of land area day^{-1}. Fruit growth rate = Friut biomass accumulation rate in g m^{-2} of land area day^{-1}. These values were calculated from seasonal aboveground biomass and fruit biomass data for irrigated treatments shown in sections III and IV respectively.

Environments Ltd. Winnipeg, Canada). The temperature was programmed to simulate a typical diurnal summer regime in Davis, California. Light was maintained at 1000 uE m^{-2} s^{-1} in a 14 hour day period. Humidity was not controlled.

Seeds were planted in shallow trays filled with commercial potting mix (Supersoil). At the third leaf stage, twelve seedlings were selected for uniformity and transplanted into 5 liter pots (one plant per pot). Nutrients were supplied in form of full strength modified Hoagland solution (Johnson et al, 1957) applied twice a week. The pots were kept well watered.

At flowering time the plants were divided in groups of four for deflowering and defruiting treatments and control. Source leaf girdling was done on the same group of plants as defruiting. The deflowering procedure involved weekly removal of all flowers so that fruit formation was prevented. On one occasion, when the fruit bearing plants were in the yellow fruit stage, the photosynthetic rate of fully exposed mature leaves of both deflowered and control fruit bearing plants was determined in a laboratory infra-red gas exchange system at ambient CO_2 concentration and 1000 uE m^{-2} s^{-1}. The leaves had been tagged earlier and were known to be of similar age.

Generally the growth chamber plants had lower fruit

load than field plants and preliminary experiments showed that leaves selected at random in the canopy had no consistent response to overall defruiting. Defruiting treatments were, therefore, restricted to units consisting of a stem subtending a single leaf and a truss of fruits. The gas exchange characteristics of such a leaf were measured before and after fruit removal in the infra-red gas exchange apparatus.

To isolate a source leaf from its sinks and effect assimilate accumulation, the stem of a determinate branch subtending a single mature leaf or a leaf and a fruit truss was girdled. A ring of bark tissue (including the phloem) was cut out just below the leaf axil. Caution was taken not to cut out the xylem wood and no signs of water stress were observed in the leaves. Gas exchange parameters of such a leaf were also monitored in the gas exchange system.

The laboratory gas exchange equipment has been described by Wolfe (1984). Air of known CO_2 and water vapour concentration was passed over a leaf in a chamber measuring 20.8 x 11.3 cm in size with a glass top. The chamber interior was stirred vigorously with two miniature fans (Micronel, Fallbrook, California) to minimize boundary layer resistance. The fan block occupied close to half of the leaf chamber so that the chamber available for leaf was only 9.3 x 8.8 cm. Water vapour concentration of the inlet air was controlled by passing the air over warm water then

condensing out excess moisture in a copper coil maintained at a known temperature. Leaf temperature was controlled by four peltier modules fastened to aluminium bottom of the chamber which bore aluminium fins extending within the chamber itself. The difference in CO_2 concentration between incoming and outgoing air was monitored with an infrared gas analyser (Horiba, Model VIA 500, Kyoto, Japan). Vapour pressure was monitored with a dewpoint hygrometer (EG and G Environmental Equipment, Model 880, Walttham, Mass.). Rate of air flow was controlled with a mass-flow controllers. Photosynthetic measurements were done with the leaf temperature maintained at 27°-28° C, and vapour pressure deficits at 1.2-1.5 KPa. Epidermal conductance was calculated from transpiration, vapour pressure and leaf temperature measurements.

Results

Effect of defruiting and girdling: Sudden removal of all fruits caused a reduction in leaf photosynthetic rate in field plants (Figs. 2). One day after defruiting photosynthetic rate was already depressed by as much as 50% at certain times of the day (Figs. 2). Decline in photosynthetic rate was realized as early as 6 h after fruit removal and persisted even after 4 days (Fig. 3). Fruit removal also appeared to depress leaf epidermal conductance (Fig 4b) but the response here was not as marked as that of photosynthesis (Fig. 4a).

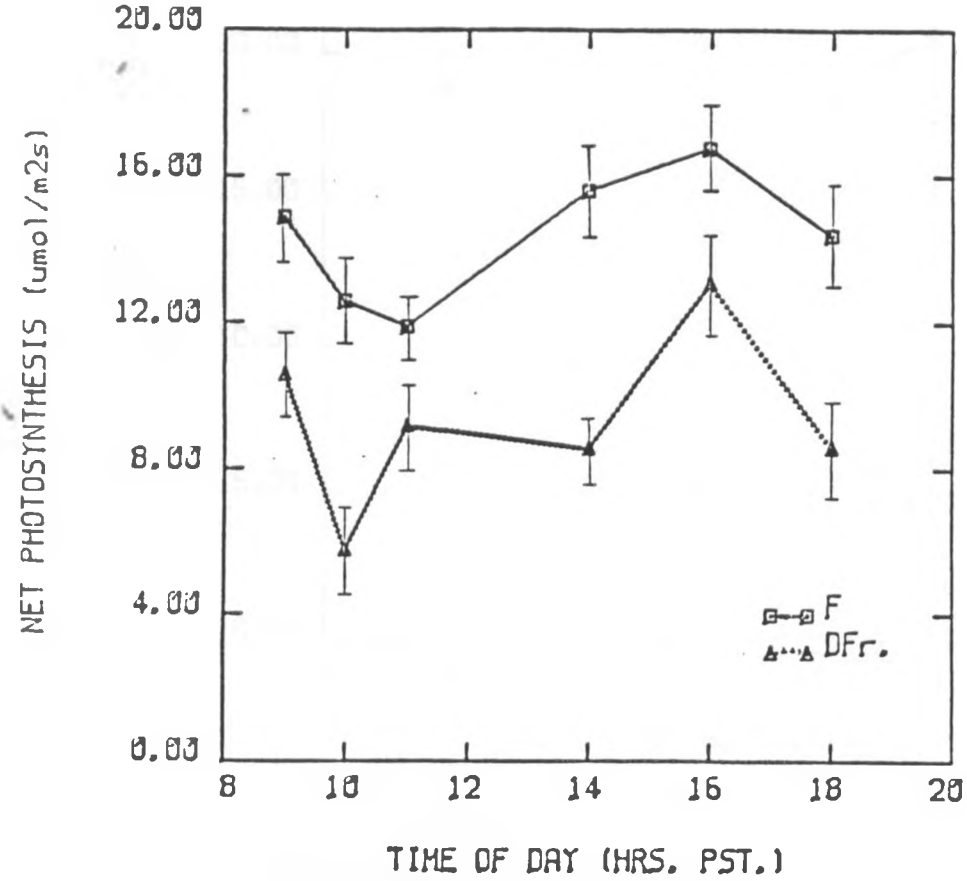

Fig. 2. Response of diurnal photosynthetic trend to fruit removal in irrigated field plants in 1983 . F = control plants and DFr = Defruited plants. Fruits were removed 75 DAE emergence and photosynthetic measurements were taken 1 day later. Each point is a mean for 6 leaves, each from a different plant. The values are shown ± 1 SE.

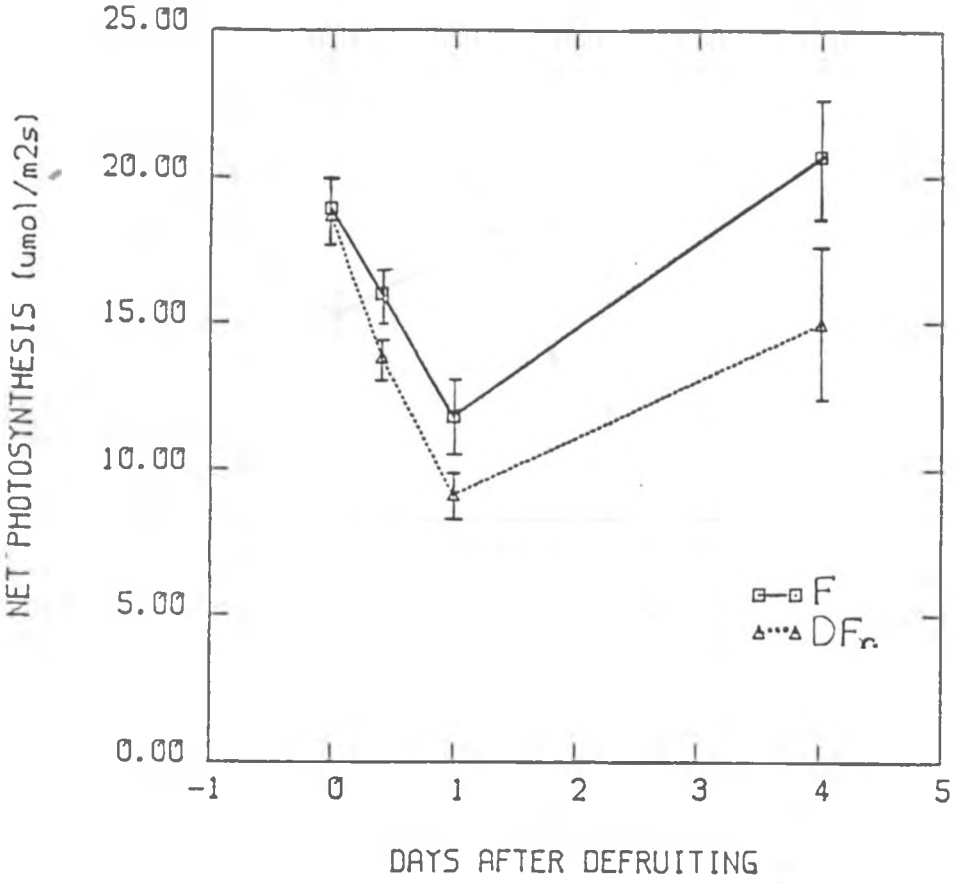

Fig. 3. Response of photosynthesis to fruit removal showing the persistence of photosynthetic inhibition. Day zero indicates measurements taken just before fruit removal. Fruits were removed at 10 a.m., and the first measurements taken at 4 p.m. 75 DAE, 1983. The other two measurements were taken at midday on the respective days. F = control plants and DFr = Defruited plants. Each point is a mean for 6 leaves each from a different plant. Each value is shown $\pm$ 1 SE.

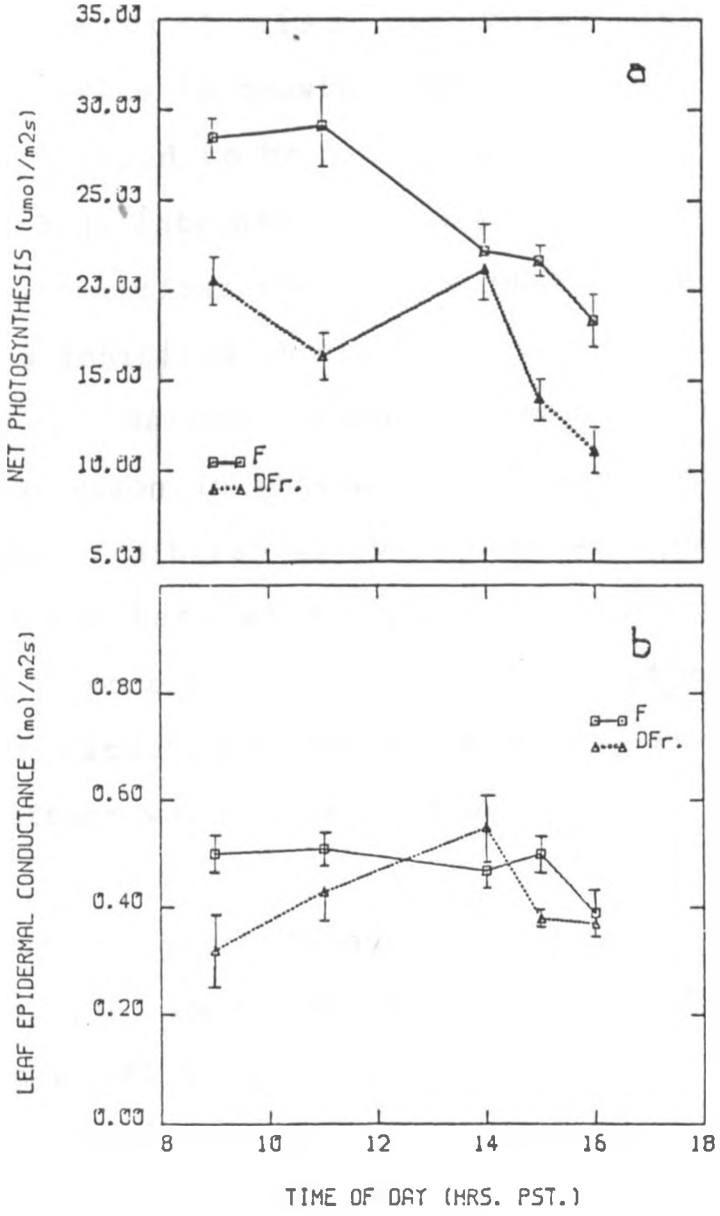

Fig. 4. Diurnal photosynthesis (a) and leaf epidermal conductance (b) in response to fruit removal 86 DAE in 1983. The measurements were taken one day after fruit removal. Notations are the same as in Fig 2. Each point is a mean for 6 leaves from different plants and is shown $\pm$ 1 SE. Photosynthetic and conductance measurements were done on different leaflets for each leaf.

Fruit removal also can cause depression in photosynthetic rate in growth chamber plants. The relative depression appeared to be larger at high light intensity (Fig. 5) and high internal CO_2 concentrations (Fig. 6). Stem girdling caused similar response in photosynthetic rate (Fig 7). Girdling inhibited photosynthesis more than defruiting (Figs. 5 and 6). However, whereas stem girdling always caused a depression in photosynthetic rate, the effect of growth chamber fruit removal procedure were often variable. Results reported here were typical of fruit trusses which had 3 or more fruits each having a diameter of 2.5 cm or more. In situations where the fruits were smaller or fewer, the effect was less marked or absent.

Analysis of gas exchange characteristics at ambient CO_2 concentration (about 340 ppm) and 1000 uE $m^{-2}s^{-1}$ light (similar to conditions in growth chamber), showed that defruiting and girdling had depressing effect on net photosynthetic rate, leaf epidemal conductance (g_e) and, to a much less extent, internal CO_2 concentration (C_i) (Fig. 8). The inhibition of photosynthesis associated with stomatal closure and fall in C_i, however accounted for a relatively small proportion of the total photosynthetic depression. This is shown by a re-examination of the data of Fig. 7 (see Fig. 9). The reduction in photosynthesis attributable to the reduction in C_i is small. Most of the reduction appears to be due to effects not related to C_i.

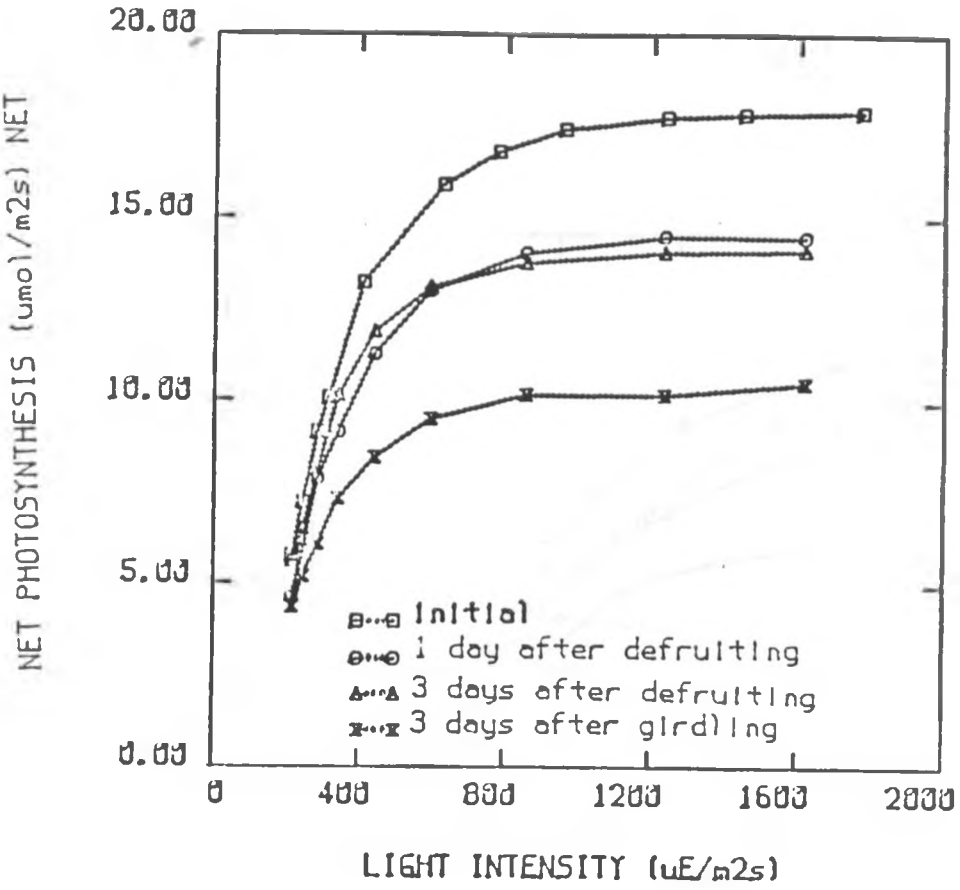

Fig. 5. The pattern of photosynthetic light curves at ambient CO_2 concentration following fruit removal and girdling of stem subtending the source leaf. Measurements were first taken before (initial) and at one and three days after fruit removal. Then the stem subtending the same leaf was girdled (4 days after fruit removal) and another measurement taken three days later.

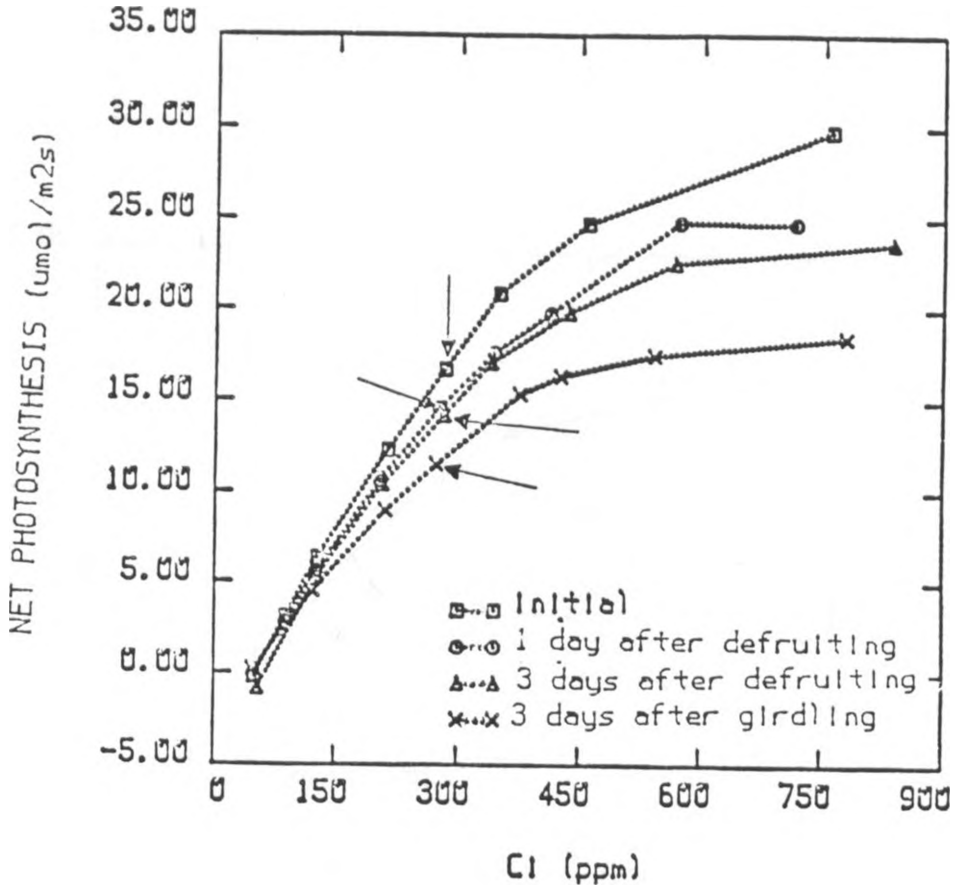

Fig. 6. The pattern of photosynthetic CO_2 curves following fruit removal and girdling of stem subtending the source leaf. Measurements were taken at 1000 uE m^{-2} s^{-1} on the same leaf and same occasions as the light curve (Fig. 5). The arrows point to the photosynthetic rate at C_i corresponding to ambient CO_2 for each curve.

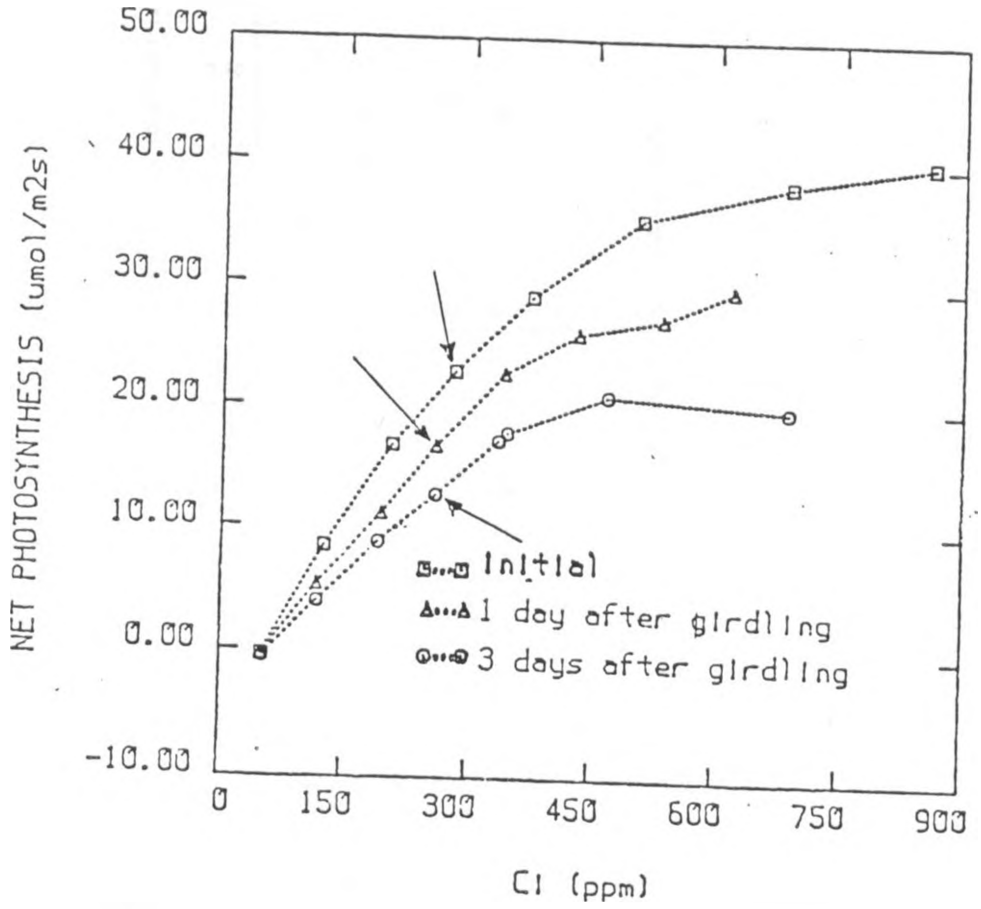

Fig. 7. The pattern of photosynthetic CO_2 curves following girdling of stem subtending source leaf. The arrows point to photosynthetic rate at C_i corresponding to ambient CO_2. Measurements were taken at 1000 uE m^{-2} s^{-1}.

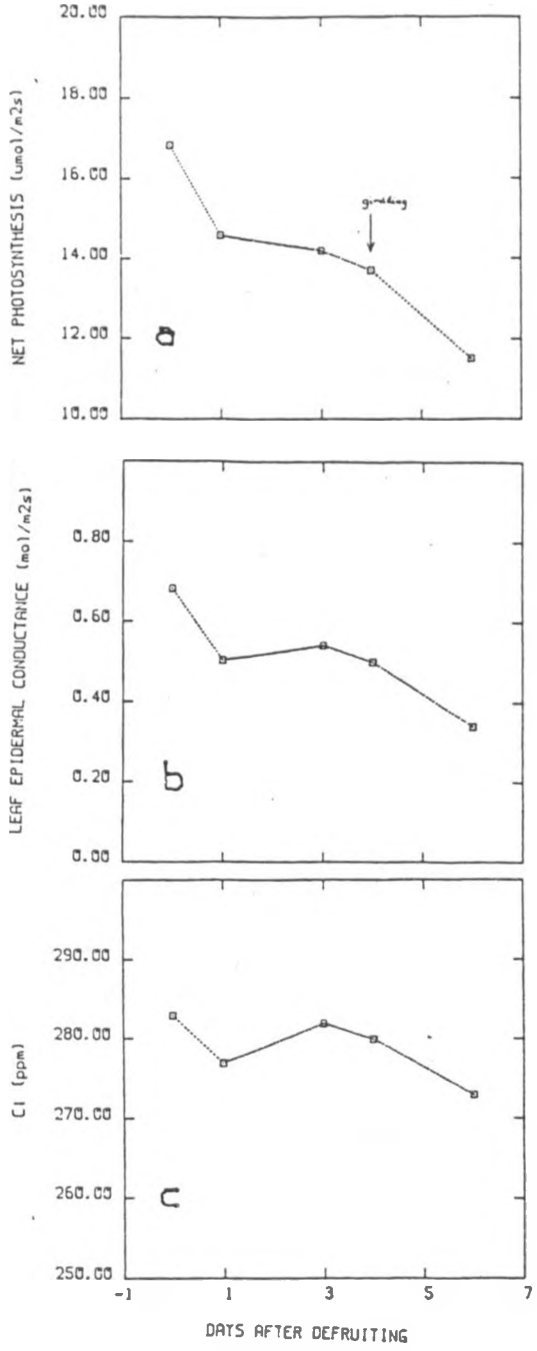

Fig. 8. Influence of fruit removal and girdling of stem subtending source leaf on photosynthesis (a), leaf epidermal conductance (b), and internal CO_2 concentration (C_i) at ambient CO_2 concentration and 1000 uE m^{-2} s^{-1} light intensity. Values were obtained from the experiment depicted in Fig. 6. One more value was taken on the girdling day.

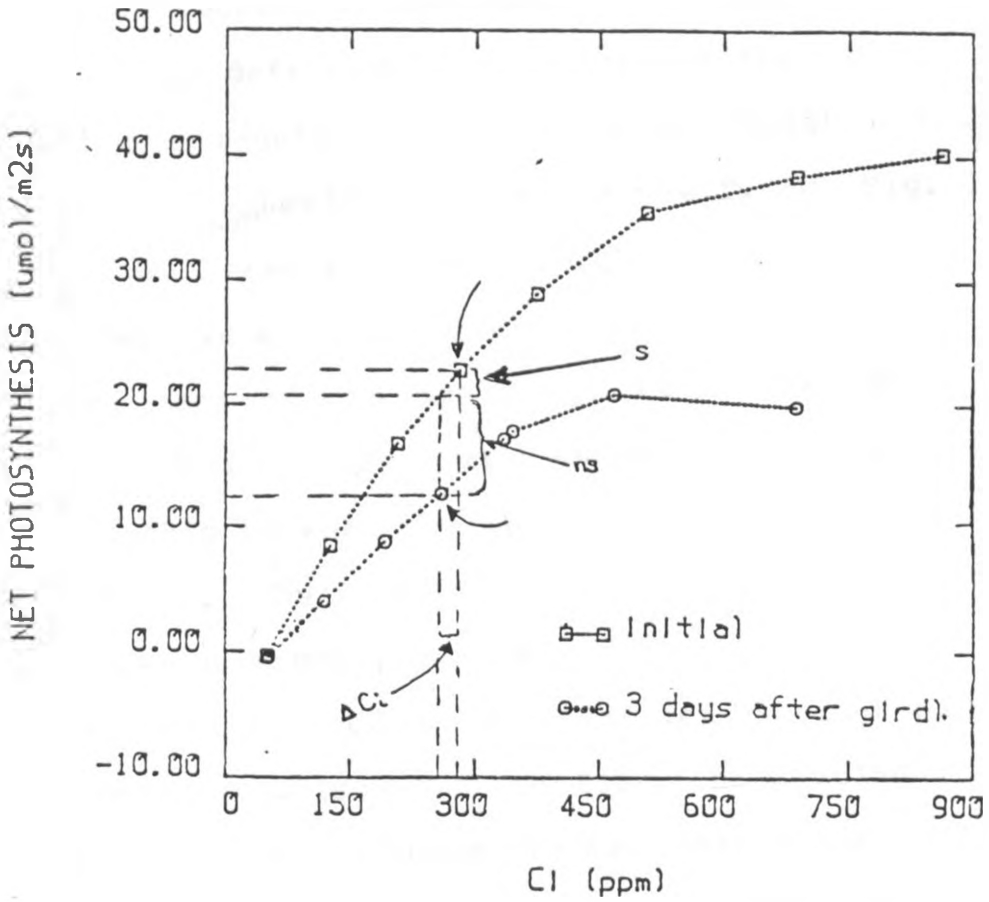

Fig. 9. Analysis of stomatal and non-stomatal components of photosynthetic depression at ambient external CO_2 concentration arising from stem girdling. This analysis is based on the data shown in Fig. 7. ΔC_i = depression in C_i following girdling. The total photosynthetic depression consisted of the stomatal (s) and non-stomatal (ns) components.

This observation suggests that depression of photosynthesis arising from fruit removal or source leaf girdling can be attributed largely to non-stomatal rather than stomatal factors.

Effect of continuous deflowering: In contrast to the effect of one-time defruiting, prevention of fruit formation by deflowering at regular intervals had no consistent effect on midday photosynthesis measured in the field (Fig. 10). However, the measurements taken throughout the day on 86 DAE showed that deflowered plants had higher photosynthetic rate in the later part of the day (Fig. 11). They also had higher leaf epidermal conductance all day but there was no close relationship between the trend of conductance and that of photosynthesis. The field measurements were performed on randomly chosen uppermost, mature and fully exposed leaves. Because leaf growth continued in deflowered plants throughout the season (see section III), the sampled leaves were generally younger in these plants. This difference was particularly marked late in the season and could explain why deflowered plants had higher photosynthesis at the last determination. Deflowering also appeared to delay leaf senescence so that towards the end of the season fruit-bearing plants had yellowish, aging canopy while the deflowered plants showed no signs of senescence. Laboratory measurements in which leaf age was controlled showed that there was no significant difference in gas exchange parameters between continuously deflowered and fruit bearing

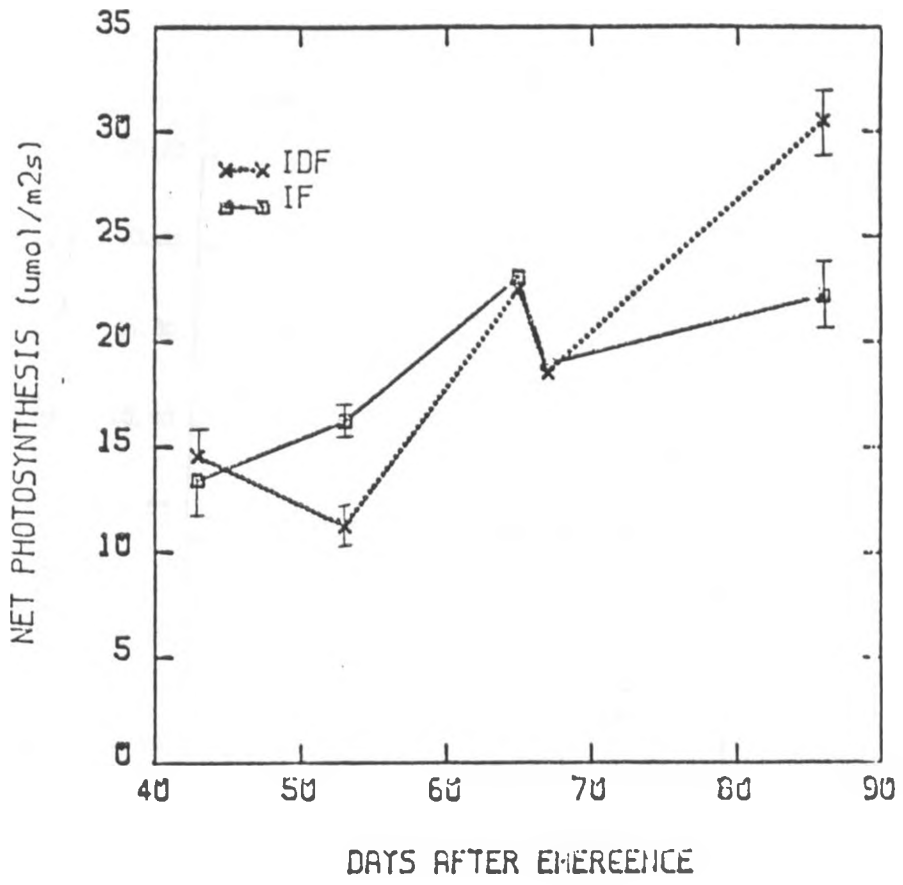

Fig. 10. Effect of continuous flower removal on seasonal trend of midday photosynthesis of youngest mature and fully exposed leaves in the field. IDF = Deflowered plants and IF = Fruit bearing control. Each point is a mean for 8 leaves from different plants and is shown ± 1 SE.

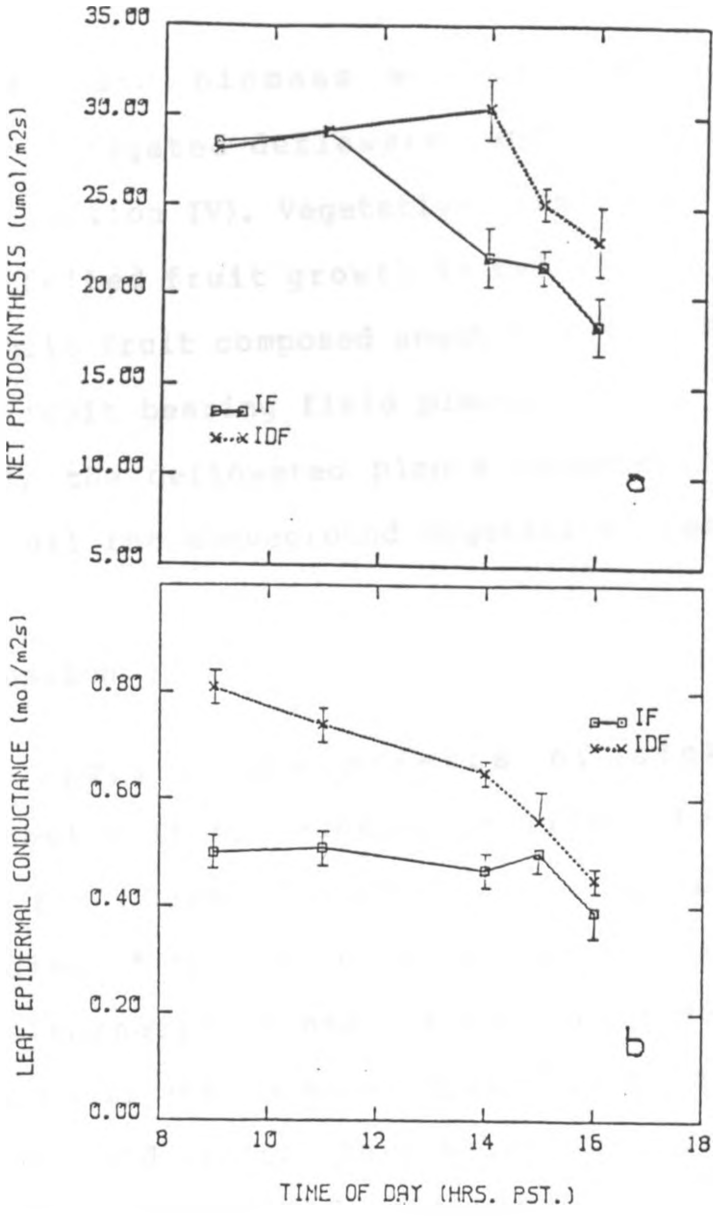

Fig. 11. Effect of continuous flower removal on diurnal trend of photosynthesis (a) and leaf epidermal conductance (b) in the field at 86 DAE. Each point is mean for 6 leaves from different plants and is shown ± 1 SE. For each leaf, photosynthetic and conductance measurements were taken on separate leaflets. The notations are the same as in Fig. 10.

control (Table 1).

Aboveground biomass was very similar between continuously irrigated deflowered and fruit-bearing field plants (see section IV). Vegetative growth fully compensated for the forfeited fruit growth in deflowered plants. For example, while fruit composed about 50% of total aboveground biomass in fruit bearing field plants at crop maturity (see section IV), the deflowered plants compensated by doubling biomass of all the aboveground vegetative organs (Fig. 12).

Discussion

In studying the effects of sink demand on photosynthesis, it is necessary to identify the dominant sinks for the source leaves in question and to have an understanding of the availability or ease of formation of possible alternative sinks. Plants in vegetative growth phase have their active sinks spread in growing points all over the root and shoot. This makes it difficult to induce effective sink reduction by manipulation of one or a few of the sinks except in studies that involve petiole girdling of source leaf. During peak fruiting, on the other hand, plants often deposit a large proportion of the current assimilates into fruits (Fig. 1) which, therefore, form easily identifiable dominant sink. Little vegetative growth usually occurs at that time so that availability of strong alternative sinks or their rapid formation is precluded.

Table 1. Net photosynthesis leaf epidermal conductance and internal CO_2 concentration of continuously deflowered and fruit bearing plants. Each value is a mean for 3 plants. Two leaves were sampled per plant. All leaves were of similar age (about 3 weeks old) and plants were in the yellow fruit stage. The measurement conditions were same as in growth chamber (1000 uE m^{-2} s^{-1} light and ambient CO_2).

	Net Photosynthesis (umol m^{-2} s^{-1})	Leaf Epidermal Conductance (mol m^{-2} s^{-1})	Internal CO_2 Concentration (ppm)
Deflowered	27.25	.76	263.3
Fruit-bearing	26.50	.74	262.6

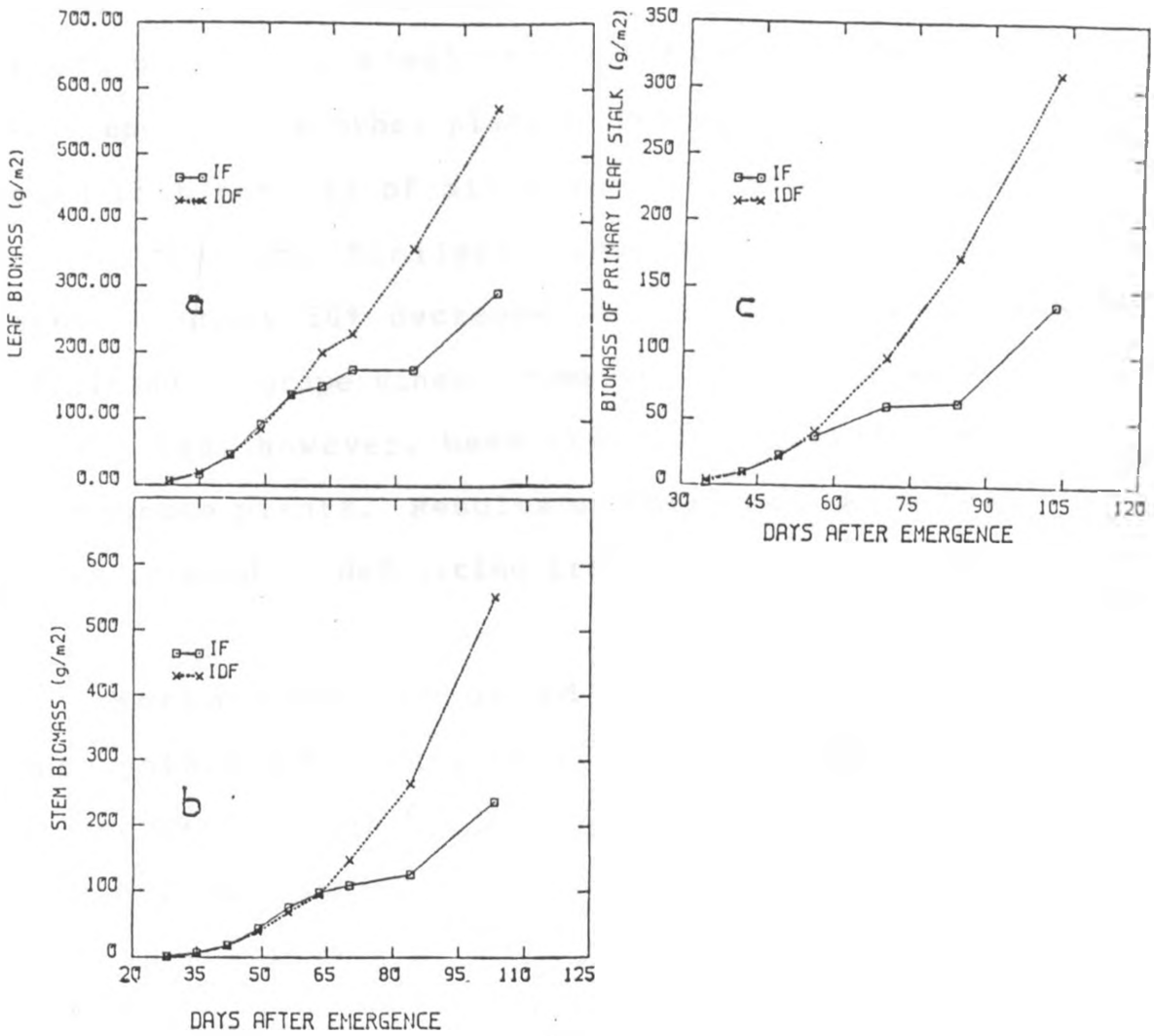

Fig. 12. Response of vegetative biomass accumulation in the field to continuous flower removal in irrigated treatments of 1983. Each point is a mean for 3 replications. Notations are the same as in Fig. 10.

The results of this study show that tomato fruit removal and disruption of assimilate export from leaves through stem girdling depressed photosynthetic rate. The effect of fruit removal in inhibiting photosynthesis has been reported for other plants. Setter et al (1980a; 1980b) found that removal of all pods depressed carbon exchange rate in soybean. Similarly, Loveys and Kriedemann (1974) reported about 50% decrease in photosynthesis following defruiting of grape vines. Most of the earlier work on this subject has, however, been limited to growth chamber and glass-house plants. Results of this study show that field plants respond to defruiting treatment in much the same way.

Mechanisms involved in the inhibition of photosynthesis by fruit removal are not well understood. The end product inhibition hypothesis (Guinn and Mauney, 1980; Herold, 1980; Neales and Incoll, 1968) has dominated literature for over a century (Neales and Incoll, 1968). Basically the hypothesis states that any process that enhances assimilate accumulation in source leaves would lead to inhibition in photosynthesis. Azcon-Bieto (1983) found a positive relationship between concentration of carbohydrates and depression of assimilation. Thus it would be assumed that a process which favors accumulation of more assimilates should lead to a larger depression of assimilation. Present results show that stem girdling produced a larger photosynthetic depression than fruit removal (Figs. 5 and 6). Defruiting may remove a major assimilate sink but as

long as the leaf maintains phloem contact with the rest of the plant it will continue to export some assimilates. Girdling, however, severs this phloem contact so that the leaf is likely to build up assimilates more rapidly.

Although a number of workers (e.g. Azcon-Bieto, 1983; Kriedemann et al, 1976; Loveys and Kriedemann, 1974; Setter et al, 1980b) have reported increase in carbohydrate concentration in leaves following defruiting and petiole girdling, the biochemical sequence of events that would lead to assimilate-induced negative feedback effect on photosynthesis has not been well established (Geiger and Giaquinta, 1982; Herold, 1980). The hypothesis thus remains equivocal and workers are in constant search for alternative hypotheses.

Since the review of Neales and Incoll (1968), a number of workers have shown that sink-limited plants often have lower leaf epidermal conductance (g_e) (Azcon-Bieto, 1983; Koller and Thorne, 1978; Kriedemann, 1976; Lenz, 1978; Setter et al, 1980a; 1980b). Field results of this study showed that leaves of defruited plants tended to have lower g_e (Fig. 4b) and laboratory results indicated a clear decrease (Fig. 8) following defruiting and stem girdling. Setter et al (1980a) reported that the reduction in photosynthetic rate following soybean pod removal and leaf girdling could be attributed to the decrease in g_e. Results presented in

Figs. 6 and 7 show that although fruit removal and stem girdling produced a fall in g_e, the accompanying decrease in C_i was small and accounted for only a small proportion of total photosynthetic depression (see Fig. 9). These results agree with those reported by Azcon-Bieto (1983) following heat girdling of wheat leaves and may account for the fact that g_e differences were not only less marked, but also bore no close relationship with differences in photosynthesis on day 86 (Fig. 4).

Results of this study suggest that non-stomatal factors are principally important in photosynthetic depression in conditions of sink limitation. It should be mentioned that Setter et al (1980a) did not measure C_i. Their findings, therefore, do not necessarily contradict results of this study or those of Azcon-Bieto. Direct product regulated feedback and hormone mediated control (Guinn and Mauney, 1980; Herold, 1980) are the non-stomatal mechanisms commonly mentioned with respect to sink-limited photosynthesis. Geiger and Giaquinta (1982) discussed hormonal control as possible and probably more viable alternative to direct product regulated feedback hypothesis. Evidence supporting this hypothesis, however, does not appear to be any better established. Abscissic acid (ABA) accumulation in leaves has been observed following fruit removal or girdling (Kriedemann et al, 1976; Setter et al, 1980a; 1980b). Its influence has, however, only been linked to reduction in g_e (Setter et al, 1980b). Hence in the

absence of significant stomatal effect as discussed earlier, the role of ABA remains questionable. The possibility of involvement of other hormones has been considered but no direct link has been established between their production in sink, translocation to source and subsequent response of source (see Herold, 1980).

The effect of flower removal on photosynthesis has also been studied under the general topic of sink-source relationships and their influence on source activity. In that context deflowering has been reported to depress photosynthetic rate (Lenz, 1974; 1978; Lenz and Williams, 1973) presumably through feedback inhibition. Results of this study, however, showed that continuous flower removal which prevented fruit formation had no consistent effects on leaf photosynthesis (Fig. 10) with the exception of the data for day 86 (Fig. 11). These measurements were done on randomly selected uppermost, mature and fully exposed leaves. Such leaves were generally younger in the deflowered plants particularly late in the season (see Results) and this could explain the results of day 86. In growth chamber plants where leaf age was controlled, there was no significant difference in gas exchange parameters between deflowered and fruit bearing plants (Table 1).

The sink demand hypothesis described earlier is based on the principle that source leaves that have the capacity

to supply a certain sink size accumulate excess assimilates upon removal or exclusion of such sinks. These surplus assimilates inhibit photosynthesis through some not well established mechanism. It is easy to visualise that such assimilate accumulation can occur following source leaf girdling or fruit removal. Assimilate accumulation when continuous deflowering prevented fruit formation is more difficult to conceive. In the work of Lenz (1974; 1978) and Lenz and Williams (1973), plants from which flowers had been removed developed vegetative growth that fully compensated for the forfeited fruit load. There was no difference in total biomass suggesting that total sink was probably comparable to that of control plants. However, they also reported some puzzling results: the non-fruiting plants had lower assimilation rates and higher assimilate accumulation in their leaves, suggesting sink limitation. It should be pointed out that their observations were mainly based on biomass data and whole plant CO_2 exchange rates and therefore represent average assimilation per unit leaf area. Leaf area was usually higher in deflowered plants but, in the absence of information regarding canopy cover, it is difficult to tell whether or not there were any differences in terms of effective source size between the treatments.

Compensatory vegetative growth similar to that reported by Lenz and coworkers was observed in this study. There was no difference in total aboveground biomass (see section IV). At harvest, fruits constituted approximately

50% of the aboveground biomass in the fruit bearing plants (see section IV) and this was compensated by doubling in vegetative parts in deflowered plants (Fig. 12). It would appear that there was no sink limitation in the deflowered plants. Vegetative growth apparently compensated at least partly for the loss of fruit formation potential as an alternative sink. The deflowered plants had about twice the leaf area of fruit bearing plants so that they had a lower sink to source ratio. This wide difference in leaf area, however, produced only 20% increase in canopy size (see section III). The difference in canopy size presumably represents the difference in effective photosynthetic surface area. Actually deflowered irrigated plants showed a slightly faster rate of soil moisture depletion (see section III) thus suggesting a deeper and possibly larger root size. Since deflowered plants tend to have larger root/shoot ratio (Hurd, et al, 1979), it is conceivable that this difference in canopy size caused little or no difference in aboveground biomass because differences in root growth accounted for the use of the extra assimilates.

Results of this study suggest that while sudden and drastic reduction in sink/source ratio such as caused by defruiting and stem girdling lead to depression of photosynthesis, continuous flower removal allowed the plants to develop vegetative alternative sinks. There was thus no sink limitation in deflowered plants and no photosynthetic

inhibition. It is also suggested that sink limitation on photosynthesis may be attributed largely to non-stomatal factors. In sections III and IV it was suggested that since water stress depressed canopy growth before having any effect on photosynthesis, the plants were probably limited by vegetative sinks. Such a limitation could lead to assimilate accumulation in the source leaves (Barlow and Boersma, 1979) and, consequently to photosynthetic inhibition by negative feedback in the same way as fruit removal and girdling discussed in this section. Indeed, recent workers (e.g. Farquhar and Sharkey, 1982 and Pearcy, 1983) have indicated that water stress inhibits photosynthesis largely through non-stomatal mechanisms similar to the ones potrayed in Fig. 9. This apparent similarity in mechanism, however, does not establish cause-effect relationship and more research is needed to explore the possibility that water stress may depress photosynthesis through vegetative sink limitation.

SECTION VII

General Discussion

Crop yield is a function of biomass production and partitioning of assimilates into plant parts that constitute economic yield. In this study attention has been given to the effects of water stress on biomass accumulation (section III) and partitioning (sections IV and V). Section VI deals with sink limitation on photosynthesis. Detailed discussion of the results for each topic has been given in the relevant sections. An effort is made in this section to provide an overall synthesis of the data by examining how the different plant responses to water stress considered in the previous sections interact to affect crop yield.

As already discussed in section III, the large depression in aboveground biomass under conditions of water stress can be attributed mainly to reduced light interception per unit land area resulting from incomplete ground cover. Unpublished results obtained by Jorge Bolanos on the same field showed that there was little or no difference in single leaf photosynthesis between irrigated and non-irrigated treatments. His results, however, showed that leaf age had significant influence on photosynthetic rate. After full leaf expansion, photosynthetic rate decreased with leaf age. Since water stress depressed leaf area development, as shown in section III, it is likely that canopy of water stressed plants had higher proportion of

older and photosynthetically less efficient leaves. Apparently lower canopy light conversion efficiency of the unirrigated treatment (Fig 12, section III) may thus be a result of older canopy rather than a direct effect of water stress through stomatal or non-stomatal mechanisms. The author's photosynthetic data (Fig. 7a, section III), showed that the unirrigated plants generally had 25%-30% lower photosynthetic rates than well watered plants. However these data were derived from randomly selected uppermost leaves without control of leaf age and it is likely that the leaves from water stressed plots were older on the average as discussed earlier.

The effect of water stress in depressing vegetative growth was not associated with significant difference in leaf water potential. For example, during 1983 season, there was no difference in leaf water potential between irrigated and dry treatments througout the season (see Fig 3a, section III). Furthermore, tomatoes show very little osmotical adjustment under drought (J. Bolanos. personal communication; Cerda et al, 1979). It is, therefore unlikely that there were any differences in turgor potential between the irrigation treatments. However, the leaf water potential measurements were taken on mature leaves and it is not known whether or not growing leaves (or portions of leaves) behaved in a similar way. Differences in solute accumulation and turgor maintanance have been reported

between growing and mature leaves (e.g. Michelena and Boyer 1982). Water stress may also reduce leaf growth, and hence canopy development, by reducing cell wall extensibility (see relationship between leaf growth and turgor potential, Lockhart 1965). For example Van Volkenburgh and Boyer (1985) reported that water stress may depress cell wall extensibility by inhibiting proton extrusion into the apoplast. With increasing amount of evidence showing that mild water stress often has little effect on turgor potential (Michelena and Boyer, 1982; Van Volkenburgh and Boyer, 1985), studies of water stress effects on cell wall extensibility and threshold turgor should be given more attention.

While water stress depressed vegetative shoot growth as discussed above, reproductive growth was relatively less affected. Plants of the unirrigated treatment had slightly higher fruit relative growth rate and higher fruit partition coefficient through most of the season. Retention of early flowers and absolute weight of early fruits were also higher in dry plots. The duration of biomass accumulation in fruits was, however, longer in irrigated than in the dry treatments. These results have been discussed in more detail in section IV. The fact that fruit growth was less affected by water stress may be attributed to differential partitioning in favour of fruit growth as shown in Figs. 2, 3 and 4a of section IV. The physiological explanation of this phenomenon is not clear. Tomato fruits are protected

from rapid evaporative water loss by thick cuticle covering the pericarp. Consequently fruit transpiration is low and water potential and water content would be high relative to leaves. Moreover, as a storage organ and a major sink during reproductive growth, fruits are likely to have higher concentrations of solutes that can be used for osmotic adjustment in a manner similar to that reported by Barlow et al (1980) for wheat shoot apices. Fruits may thus be able to minimize internal water stress and continue to grow and serve as active sinks even after vegetative growth has stopped. Results reported in section III showed that water stress remarkably depressed canopy growth. Reference has also been made earlier to unpublished data of Jorge Bolanos which showed that water stress had little effect on photosynthesis in the same field. It is thus conceivable that water stressed plants were limited by vegetative sinks and had surplus of assimilates in their leaves. Such assimilate accumulation in conditions of inhibited leaf growth has been reported by Barlow and Boersma (1976). Since fruit growth continued after vegetative growth had stopped (see setions III and IV), they probably formed active sinks which utilized the excess assimilates. This explanation would be supported by the work of Johnson and Moss (1976) which showed that water stress enhanced assimilate translocation to reproductive growth in wheat. Apparently, therefore, water stress had a relative stimulation on fruit growth by inhibiting vegetative growth.

The response of reproductive growth to water stress has been studied by other workers (see Fischer and Turner, 1978 and Salter and Goode, 1967) and seems to be complicated depending on the stress intensity and crop history. Mild water stress tends to enhance or have no effect on reproductive growth (Fischer and Turner, 1978). Hsiao et al (1976) noted that reduced vegetative growth resulting from water stress would lessen competition for assimilates and thus help fruit growth. This suggestion seems to be supported by the observation (e.g. Stockton et al, 1961; Hearn, 1975) that a liberal supply of water during flowering can increase shedding of young bolls in cotton. Hsiao (1982) further suggested that pollination and fruit set are generally insensitive to water stress and Hearn (1975) found that water stress induced early fruit set in cotton. Wudiri (1980) reported that mild water stress stimulated fruit set in early flower trusses in some tomato cultivars but not others. The results of this study seems to be in general agreement with these earlier studies. Water stressed processing tomato plants seemed to be limited by vegetative sink so that more assimilates were available for reproductive growth. Yield reductions, therefore, resulted mainly from fewer flower nodes rather than flower abscission or retarded fruit growth.

Since mild water stress depresses vegetative growth more than photosynthesis so that the plant may be limited by

vegetative sink and accumulate assimilates in source leaves, a relationship may be drawn between depression of photosynthesis and inhibition of canopy development under conditions of mild water stress. The mechanism of photosynthetic depression in situations of water stress is not clearly understood. Earlier workers (see Hsiao, 1973) tended to suggest that water stress inhibits photosynthesis through its effects in reducing stomatal conductance. Recently, however, with the use of sophisticated gas exchange equipments, workers have increasingly questioned the contribution of stomatal closure in water stress induced photosynthetic depression. This school of thought has been highlighted by the work of Farquhar and Sharkey (1982). Essentially their analysis shows that photosynthetic inhibition arising from water stress is caused largely by non-stomatal factors.

In this study it is speculated that water stress which depresses canopy growth markedly with minor effects on photosynthesis would cause assimilate accumulation in leaves. Barlow and Boersma (1976) found that decrease in leaf elongation increased assimilate build up in source leaves and this was accompanied by depression in photosynthesis. The fruit removal and stem girdling treatments of this study depressed photosynthesis presumably through sink limitation which causes assimilate build up in leaves (Setter *et al*, 1980b). Gas exchange analysis data

(see section VI) revealed that photosynthetic depression resulting from both defruiting and stem girdling could be accounted for largely by non-stomatal factors. Similar results have been reported by Azcon-Bieto (1983) for heat girdled wheat leaves. A hypothesis is here suggested that water stress may inhibit photosynthesis indirectly by inhibiting canopy growth and thus enhancing assimilate build up in leaves. Assimilates build up is thought to inhibit photosynthesis through negative feedback (see Neales and Incoll, 1968).

Data emanating from this study certainly do not provide enough proof for this hypothesis but it has been shown that some similarities probably occur in the mechanisms of sink limitation and water stress limitation on photosynthesis. In order to establish cause-effect relationship, it has to be unaquivocally established that build up of assimilates does indeed cause photsynthetic depression. Biochemical evidence for the this requirement has proved elusive (see Herold, 1980).

LITERATURE CITED

Aljibury, F.K. and D. May. 1970. Irrigation schedules and production of tomatoes on the San Joaquin Westside. Calif. Agr. 24: 10-11.

Angus, J.F. and Moncur, M.W. 1977. Water stress and phenology in wheat. Aust. J. Agric. Res. 28: 177-178.

Arnon, I. 1975. Physiological principles of dryland crop production. In. U.S. Gupta (ed).Physiological aspects of dryland farming. Oxford and IBH. Publishing Co. New Delhi. pp.3-145

Azcon-Bieto, J. 1983. Inhibition of photosynthesis by carbohydrates in wheat leaves. Plant Physiol. 73: 681-686.

Barlow, E.W.R. and L. Boersma. 1976. Interaction between leaf elongation , photosynthesis and carbohydrate levels of water-stressed corn seedlings. Agron. J. 68: 923-926.

Barlow, E.W.R., R.E. Munns, and C.J. Brady. (1980) Drought responses of apical meristems. In. N.C. Turner and P.J. Kramer (eds.). Drought responses of plants to water and high temperature stress. pp. 191-205.

Begg, J.E. 1980. Morphological adaptations of leaves to water stress. In. N.C. Turner and P.J. Kramer (eds). Adaptation of Plants to Water and High Temperature Stress. Wiley Interscience, New York. pp 33-42.

Begg, J.E. and Turner, N.C. 1976. Crop water deficits. Adv. Agron. 28:16-207.

Boyer, J.S. 1968. Relationship of water potential to growth of leaves. Plant Physiol. 43: 1056-62.

Boyer, J.S. 1974. Water transport in plants:mechanism of apparent changes in resistance during absorption. Plantal17: 187-207.

Boyer, J.S. 1976. Photosynthesis at low water potentials. Philos. Trans. R. Soc. Londoon Ser. B. 273: 501-512.

Bradford, K.J. and T.C. Hsiao. 1982. Physiological responses to moderate water stress. In. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Zeigler (eds). Encyclopedia of Plant Physiology, New Series, Vol 12B. Springer-Verlag, New York. pp 263-324.

Bunce, J.A. 1977. Leaf elongation in relation to leaf

water potential in soybean. J. Exp. Bot. 28: 156-161.

Cannell, G.H. and C.W. Asbell. 1974. Irrigation of field tomatoes and measurement of soil water changes by neutron moderation methods. J. Amer. Soc. Hort. Sci. 99: 305-308.

Cary, J.W. and J.L. Wright. 1971. Response of plant water potential to the irrigated environment of southern Idaho. Agron. J. 63: 691-695.

Catsky, J., I. Ticha and J. Solarova. 1976. Ontogenetic changes in the internal limitations to bean-leaf photosynthesis. 1. Carbon dioxide exchange and conductances for carbon dioxide transfer. Photosynthetica. 10: 394-402.

Cerda, A., F.T. Bingham, G.J. Hoffman and C.K. Huszar. 1979. Leaf water potential and gaseous exchange of wheat and tomato as affected by NaCl and P levels in root medium. Agron. J. 71: 27-31.

Chalmers, D.J., R.L. Canterfore, P.H. Jerie, T.R.Jones and T.D. Ugalde. 1975. Photosynthesis in relation to growth and distribution of fruits in peach trees. Aust. J. plant Physiol. 2: 635-645.

Clarkson, N.M. and J.S. Russel. 1976. Effect of water stress on phasic development of annual Medicago spp. Aust. J. Agric. Res. 27: 227-234.

Constable, G.A. and A.B. Hearn. 1978. Agronomic and physiological responses of soybean and sorghum crops to water deficits. I. Growth, development and yield. Aust. J. Plant Phsiol. 5:

Davis, C.H. 1942. Response of Cyperus rotundus L. to 5 moisture levels. Plant Physiol. 17: 311-316.

Doss, B.D., D.A. Shley and O.L. Bennet. 1960. Effect of soil moisture on root distribution of warm season forage species. Agron. J. 52: 569-572.

Ehleringer, 1980. Leaf morphology and reflectance in relation to water and temperature stress. In. N.C. Turner and P.J. Kramer (eds). Adaptation of Plants to Water and High Temperature Stress. Wiley Interscience, New York. pp 295-308.

Ehleringer, J. 1983. Ecolphysiology of Amaranthus palmeri, a Sonoran desert summer annual. Oecologia. 57: 107-112.

El Nadi, A.H. 1974. Growth, yield and quality of cotton

under three watering regimes in the Sudan. Expl. Agric. 10:313-318.

El Nadi, A.H. 1969. Water relations of beans. II. Effects of differential irrigation on yield and seed size of broad beans. Expl. Agric. 6: 107-111.

Farquhar, G.D. and T.D. Sharkey. 1982. Stomatal conductance and photosynthesis. Annu. Rev. Plant Physiol. 33:317-345.

Fischer, R.A. 1980. Influence of water stress on crop yield in semi-arid regions. In. N.C. Turner and P.J. Kramer (eds). Adaptation of Plants to Water and High Temperature Stress. Wiley Intersciences, New York. pp 323-339.

Fischer, R.A. and N.C. Turner. 1978. Plant productivity in the arid and semi-arid zones. Annu. Rev. Plant Physiol. 29: 277- 317.

Flinn, A.M. 1974. Regulation of leaflet photosynthesis by developing fruit in the pea. Physiol. Plant. 31:275-278.

Gardener,W.R. 1960. Water availability to plants. Soil Sci. 89: 63-73.

Gardener, W.R. and R.H. Nieman. 1964. Lower limit of water availability to plants. Science. 143: 1460-1462.

Geiger, D.R. 1979. Control of partitioning and export of cabon in leaves of higher plants. Bot. Gaz. 140: 241-248.

Geiger, D.R. and R.T. Giaquinta. 1982. Translocation of photosynthate. In. Govindjee (ed). Photosynthesis, Vol II. Academic Press, New York. pp 345-386.

Gifford, R.M. and C.L.D. Jenkins. 1982. Prospect of applying knowledge of photosynthesis toward improving crop production. In. Govindjee (ed). Photosynthesis, Vol II. Academic Press, New York. pp 419-157.

Greacen, E.L. 1977. Mechanism and models of water transfer. In. J.S. Russels and E.L. Greacen (eds). Soil Factors in Crop Production in Semi-arid environment. Univ. Queensland Press. pp 333-338.

Green, P.B., R.O. Erickson and J. Buggy. 1971. Metabolic and physical control of cell elongation rate. Plant Physiol. 47: 423-430.

Guinn, G. and J. Mauney. 1980. Analysis of CO2 exchange assumptions: Feedback control. In. J.D. Hesketh and J.W. Jones (eds). Predicting Photosynthesis for Ecosystem Models, Vol II. CRC Press, Boca Raton, Florida. pp 1-16.

Haghighi, A.A.K. 1980. Effects of variable water supply on growth parameters, partitioning of assimulates and water production functions of processing tomatoes. Ph.D. dissertation. Univ. California, Davis.

Hall, A.E., K.W. Forster and A.G. Waines. 1979. Crop adaptation to semi-arid environments. In. A.E. Hall, G.H. Cannell and H.W. Lawton (eds). Ecological Studies, Vol 34. Springer- Verlag, New York. pp 148-179.

Harris, F.S. 1914. Effect of siol moisture, plant food and age on the ratio of tops to roots in plants. J. Amer. Soc. Agron. 6:65-75

Hawker, J.S. 1967. Inhibition of sucrose phosphatase by sucrose. Biochem. J. 102:401-406.

Hearn, A.B. 1975. response of cotton to water and nitrogen in a tropical environment. I. Frequency of watering and method of application of nitrogen. J. Agric. Sci. 84: 407-417.

Hearn, A.B. 1980. Water relationships in cotton. Outlook Agric. 10:159-166.

Herold, A. 1980. Regulation of photosynthesis by sink activity. New Phytol. 86:131-144.

Herold, A., D.H. Lewis, and D.A. Walker. 1976. Sequestration of cytoplasmic orthophosphate by mannose and its differential effect on photosynthetic starch synthesis in C3 and C4 species. New Phytol. 76:397-407.

Herold, A., E.E. McGee and D.M. Lewis. 1980. The effect of orthophosphate concentration and exogenously applied sugars on the distribution of newly fixed carbon in sugar beet leaf discs. New Phytol. 85:1-13.

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

Hsiao, T.C. 1982. The soil-plant-air-atmosphere continuum in relation to drought and crop productivity. In: Drought Resistance in Crops, with Emphasis on Rice. IRRI, Los Banos, Philippines. pp. 39-52.

Hsiao, T.C. and E. Acevedo. 1974. Plant responses to water deficits, water use efficiency and drought resistance. Agric. Meteorol. 14: 39-56.

Hsiao, T.C. and K.J. Bradford. 1983. Physiological consequences of cell water deficits. In. H.M. Taylor, W.R. Jordan and T.R. Sinclair (eds) Limitations to efficient water use in crop production. American Society of Agronomy, Madison, WI. pp.227-265.

Hsiao, T.C., E. Fereres, E. Acevedo and D.W. Handerson. 1976. Water stress and dynamics of growth and yield of crop plants. In: O.L. Lange, L. Kappen and E.-D. Schulze (eds). Ecological Studies, Vol. 19. Springer-Verlag, New York. pp 281- 305.

Hsiao, T.C., E. Acevedo, E. Fereres, and D.W. Henderson. 1976a. Water stress, growth and osmotic adjustment. Philos. Trans. R. Soc. London, Ser. B. 273: 479-500.

Hudson, J.P. and P.J. Salter. 1953. Effects of different watering regimes on the growth of tomatoes under glass. Nature. 171:480-481.

Hurd, E.A. 1968. Growth of roots of seven varieties of spring wheat at high and low water levels. Agron. J. 60:201-205.

Hurd, E.A. 1974. Phenotype and drought tolerance in wheat. Agric. Meteorol. 14:39-56.

Hurd, R.G., A.P. Gay and A.C. Mountifield. 1979. The effect of partial flower removal on the relation between root, shoot and fruit growth in the indeterminate tomato. Ann. Appl. Biol. 93:77-89.

Johnson, C.M., P.R. Stout, T.C. Broyer and A.B. Carlton. 1957. Comparative chlorine requirements of different plant species. Plant and Soil 8:337-353.

Johnson, R.R. and D.N. Moss. 1976.Effect of water stress on ^{14}C fixation and translocation in wheat during grain filling. Crop Sci. 16:697-701.

Jordan, W.R. (1982). Cotton. In. I.D. Teare and M.M. Peet (eds.). Crop-Water Relations. John Wiley and sons, New York. pp. 213-254.

Jordan, W.R. and F.R. Miller. 1980. Genetic variability in sorghum root systems: Implications for drought tolerance. In: N.C. Turner and P.J. Kramer (eds). Adaptations of Plants to Water and High Temperature Stress. Wiley Interscience, New York. pp 383-399.

King, R.W. and L.T. Evans. 1967. Photosynthesis in artificial communities of wheat, lucerne and subterranean clover plants. Aust. J. Biol. Sci. 20:307-310.

King, R.W., I.F. Wardlaw and L.T. Evans. 1967. Effect of assimilate utilization on photosynthetic rate in wheat. Planta. 77:261-276

Klepper,B., H.M. Taylor, M.G. Huck and E.L. Fiscus. 1973. Water realtions and growth of cotton in drying soil. Agron. J. 65:307- 310.

Koller, H.R. and J.H. Thorne. 1978. Soybean pod removal alters leaf diffusion resistance and leaflet orientation. Crop Science. 18:305-308.

Kramer, P.J. 1937. The relation between rate of transpiration and rate of absorption of water in plants. Amer. J. Bot. 24: 10-15.

Kramer, P.J. 1983. Water relationships of plants. Academic Press.

Kriedemann, P.E., B.R. Loveys, J.V. Possingham and M. Satoh. 1976. Sink effects on stomatal physiology and photosynthesis. In: I.F. Wardlaw and J.R. Passioura (eds). Transport and Transfer Processes in Plants. Academic Press, New York. pp 401-414.

Lenz, F. 1974. Fruit effects on formation and distribution of photosynthetic assimilates. Proceedings of XIXth International Horticultural Congress, Warsaw. pp. 155-166

Lenz, F. 1978. fruit effects on photosynthesis light and dark respiration. In: R. Marcelle, H. Cljisters and M.Van Poucke (eds). Photosynthesis and Plant Development. Dr. W. Junk bv Publisher, London. pp 271-281.

Lenz, F. and C.N. Williams. 1973. Effect of fruit removal on net assimilation and gaseos diffusive resistance of soybean leaves. Angew Bot. 47:57-63.

Lockhart, J.A. 1965. An analysis of irreversible plant cell elongation. J. Theor. Biol. 8: 264-276.

Loewing, W.F. (1940). Mineral nutrients in relation to flower development. Science. 92: 517-520

Loveys, B.R.and P.E. Kriedemann. 1974. Internal control of stomatal physiology and photosynthesis. I. Stomatal regulation and associated changes in endogenous

levels of abscissic acid and phaseic acid. Aust. J. Plant Physiol. 1:467-415.

Maranville, J.W. and Paulsen, G.M. 1970. Alteration of carbohydrate composition of corn seedlings during moisture stress. Agron. J. 62: 605-608.

Marc, J., and J.H. Palmer. 1976. Relationship between water potential and leaf and inflorescence initiation in Helianthus anuus. Physiol. Plant. 36: 101-104.

Martin, E.V. 1940. Effect of soil moisture on growth and transpiration in Helianthus anuus L. Plant Physiol. 15: 449-466.

Martin, P.E., J.C. Lingle, R.M. Hagan and W.J. Flocker. 1966. Irrigation of tomatoes in a single harvest program. Calif. Agric. 20(6):12-14.

McCree, K.J. and J.H. Troughton. 1966. Prediction of growth rate at diferent light levels from measured photosynthesis and respiration rates. Plant Physiol. 41:559-566.

McWilliam, R.F. and P.J. Kramer. 1968. The nature of perennial response in mediterranean grasses. I. Water relation and summer survival in Phalaris. Aust. J. Agric. Res. 19: 381-395.

Michelena, V.A. and J.S. Boyer. 1982. Complete turgor maintenance at low water potentials in the elongating region of maize leaves. Plant physiol. 69: 1145-1149.

Mott, J.J. and A.J. McComb. 1975. Effects of moisture stress on the growth and reproduction of three annual species from an arid region in Western Australia. J. Ecol. 63: 825-834.

Molz, F.J. and J.S. Boyer. 1978. Growth induced water potentials in plant cells and tissues. Plant Physiol. 62:423- 429.

Monteith, J.L. 1977. Climate and the efficiency of crop production in Britain. Philos. Trans. R. Soc. London. Ser. B. 281:277-294.

Mooney, H.A., J. Ehleringer and O. Bjorkman. 1977. The energy balance of leaves of the evergreen desert shrub Atriplex hymenelytra. Oecologia. 29:301-310.

Moore, K.G., A. Illsley and P.H. Lovell. 1973. Effects of sucrose on petiolar carbohydrate accumulation and photosynthesis in excised Sinapsis cotyledons. J. Exp. Bot. 25: 887-898.

Murneek, A.E. 1926. effects of correlation between vegetative and reproductive functions in the tomato (Lycopersicon esculentum Mill). Plant Physiol. 1:1-12.

Neales, T.F. and L.D. Incoll. 1968. The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: A review of the hypothesis. Bot. Rev. 34:107-124.

Newman, E.I. 1969. Water movement through root systems. J. applied Ecol. 6:1-12.

Passioura, J.B. 1982. Water in the plant-soil-atmosphere continuum. In. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Zeigler (eds). Encyclopedia of Plant Physiology. New Series, vol 12B. Springer-Verlag New York. pp. 5-33.

Passioura, J.B. 1976. Physiology of wheat growing on stored water. Aust. J. Plant Physiol. 3: 559-565.

Pearcy, R.W. 1983. Non stomatal inhibition of photosynthesis by water stress. In. H.M.Taylor, W.R. Jordan and T.R. Sinclair (eds.). Limitations to efficient water use in crop production. American Society of Agronomy Madison, WI. pp. 277-287.

Portas, C.A.M. and H.M. Taylor. 1976. Growth and survival of young plant roots in dry soil. Soil Sci. 121:170-175

Radford, P.J. 1967. Growth analysis formulae. Their use and abuse. Crop Sci. 7:171-175.

Radulovich, R.A. 1984. Reproductive behavior and water relations of cotton. Ph.D. dissertation. Univ. California, Davis.

Rayle, D.L. and R.E. Cleland 1977. Control of plant cell enlargement by hydrogen ions. In. A.A. Moscona and A. Monroy (eds.). Current topics in developmental biology. Vol. 11. pp. 187-214.

Rudich, J., D. Kalmar, C. Geizenberg and S. Havel. 1977. Low water tensions in designed growth stages of processing tomato plants and their effects on yield and quality. J. Hort. Sci. 52: 391-399.

Rudich, J., E. Rendon-Poblete, M.A. Stevens and A. Ambri. 1981. Use of leaf water potential to determine water stress in field-grown tomato plants. J. Amer. Soc. Hort. Sci. 106: 732-736.

Murneek, A.E. 1926. effects of correlation between vegetative and reproductive functions in the tomato (Lycopersicon esculentum Mill). Plant Physiol. 1:1-12.

Neales, T.F. and L.D. Incoll. 1968. The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: A review of the hypothesis. Bot. Rev. 34:107-124.

Newman, E.I. 1969. Water movement through root systems. J. applied Ecol. 6:1-12.

Passioura, J.B. 1982. Water in the plant-soil-atmosphere continuum. In. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Zeigler (eds). Encyclopedia of Plant Physiology. New Series, vol 12B. Springer-Verlag New York. pp. 5-33.

Passioura, J.B. 1976. Physiology of wheat growing on stored water. Aust. J. Plant Physiol. 3: 559-565.

Pearcy, R.W. 1983. Non stomatal inhibition of photosynthesis by water stress. In. H.M.Taylor, W.R. Jordan and T.R. Sinclair (eds.). Limitations to efficient water use in crop production. American Society of Agronomy Madison, WI. pp. 277-287.

Portas, C.A.M. and H.M. Taylor. 1976. Growth and survival of young plant roots in dry soil. Soil Sci. 121:170-175

Radford, P.J. 1967. Growth analysis formulae. Their use and abuse. Crop Sci. 7:171-175.

Radulovich, R.A. 1984. Reproductive behavior and water relations of cotton. Ph.D. dissertation. Univ. California, Davis.

Rayle, D.L. and R.E. Cleland 1977. Control of plant cell enlargement by hydrogen ions. In. A.A. Moscona and A. Monroy (eds.). Current topics in developmental biology. Vol. 11. pp. 187-214.

Rudich, J., D. Kalmar, C. Geizenberg and S. Havel. 1977. Low water tensions in designed growth stages of processing tomato plants and their effects on yield and quality. J. Hort. Sci. 52: 391-399.

Rudich, J., E. Rendon-Poblete, M.A. Stevens and A. Ambri. 1981. Use of leaf water potential to determine water stress in field-grown tomato plants. J. Amer. Soc. Hort. Sci. 106: 732-736.

Salter, P.J. 1954. The effects of different water regimes on the growth of plants under glass. I. Experiments with tomatoes (Lycopersicum esculentum Mill.). J. Hort. Sci. 29:258-268.

Salter, P.J. 1957. The effects of different water regimes on the growth of plants under glass. III. Further experiments with tomatoes (Lycopersicum esculentum Mill.). J. Hort. Sci. 32:214-226.

Salter, P.J. 1958. The effects of different water regimes on the growth of plants under glass. IV. Vegetative growth and fruit development in tomato. J. Hort. Sci. 33:1-12.

Salter, P.J. and D.M. Drew. 1965. Root growth as a factor in response of Pisum sativum L. to irrigation. Nature. 206: 1063-1064.

Salter, P.J. and J.E. Goode. 1967. Crop responses to water at different stages of growth. Commonwealth Bur. Hort. Plant Crops Res. Rev. No. 2.

Setter, T.L., W.A. Brun and M.L. Brenner. 1980a. Stomatal closure and photosynthetic inhibition in soybean leaves induced by petiole girdling and pod removal. Plant Physiol. 65: 884-887.

Setter, T.L., W.A. Brun and M.L. Brenner 1980b. Effect of obstructed translocated on leaf abscisic acid and associated stomatal closure and photosynthesis decline. Plant Physiol. 65: 1111-1115.

Sharp, R.E. and W.J. Davies. 1979. Solute regulation and growth by roots and shoots of water stressed maize plants. Planta. 147: 43-49.

Shibles, R.M., and C.R. Weber. 1966. Leaf area, solar radiation interception and dry matter production by soybean. Crop Sci. 6:55-59.

Slatyer, R.O. 1967. Plant water relationships. Academic Press, New York.

Slatyer, R.O. 1973. The effect of internal water status on plant growth, development and yield In. O.T. Denmead (ed). Plant responses to climatic factors. Proc. Uppsala Symp. 1970, pp. 177-191. Unesco, Paris.

Stockton, J.R., L.D. Doneen and V.T. Walhood. 1961. Boll shedding and growth of the cotton plant in relation to irrigation frequency. Agron. J. 53: 272-275.

Taylor, H.M. 1980. Modifying root systems of cotton and

soybean to increase water absorption. In. N.C. Turner and P.J. Kramer (eds). Adaptation of plants to water and high temperature stress. Wiley Interscience, New York. pp. 75-84.

Taylor, H.M. and B. Klepper. 1974. Water relations of cotton. I. Root growth and water use as related to top growth and soil water content. Agron. J. 66:584-588.

Taylor, H.M. and B. Klepper. 1975. Water uptake by cotton roots: An examination of assumptions in single root model. Soil Sci. 120:57-67.

Taylor, H.M. and B. Klepper. 1978. The role of rooting characteristics in the supply of water to plants. Adv. Agron. 30:99-128.

Terry, N. and A. Ulrich. 1973. Effects of phosphorus deficiency on the photosynthesis and respiration of leaves of sugar beet. Plant Physiol. 51:43-47.

Tinker, P.B. 1976. Transport of water to plant roots in soil. Philos. Trans. R. Soc., London. Ser. B. 273:445-461.

Turk, K.J., A.E. Hall and C.W. Asbell. 1980. Drought adaptation of cowpea. I. Influence of drought on seed yield. Agron. J. 72:413-420.

Turner, N.C. 1981. Designing better crops for dryland Australia: Can the desert help us? J. Aust. Inst. Agric. Sci. 46:29-34.

Turner, N.C. and Begg, J.E. 1977. Response of pasture plants to water deficits. In J.R. Wilson (ed). Plant relations in pastures. Melbourne CSIRO. pp. 50-66.

Turner, N.C. and J.E. Begg. 1981. Plant water relations and adaptation to stress. Plant and Soil 58: 97-131.

Turner, N.C. and G.J. Burch. 1981. The role of water in plants. In. I.D. Teare and M.M. Peet (eds.). Crop water relations. Wiley Interscience, New York. pp. 73-126.

Tyree, M.T. and H.T. Hammel. 1972. The measurement of turgor pressure and the water relations of plants by the pressure bomb technique. J. Exp. Bot. 20: 341-349.

Van Volkenburgh, E. and J.S. Boyer. 1985. Inhibitory effects of water deficits on maize elongation. Plant Physiol. 77: 190-194.

Wardlaw, I.F. 1968. The control and pattern of movement of carbohydrates in plants. Bot. Rev. 34: 79-105.

Wenkert, W., E.R. Lemon and T.R. Sinclair. 1978. Leaf elongation and turgor pressure in field-grown soybean. Agron. J. 70: 761-764.

Williams, W.A., R.S. Loomis and C.R. Lepley. 1965. Vegetative growth of corn as affected by population density. I. Productivity in relation to interception of solar radiaton. Crop Sci. 5:211-215.

Wolfe, D.W. 1984. Water and nitrogen effects on leaf senescence in maize. Ph.D. dissertation. Univ. California,Davis.

Wudiri, B.B. 1980. Effects of water stress on flowering, pollination and fruit set in processing tomatoes. Ph.D. dissertation. Univ. California, Davis.