This is to certify that the

dissertation entitled

Responses of Pickling Cucumber Plants to Drought Stress During the Reproductive Growth Stage

presented by

Abdul Kader Janoudi

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Horticulture

Irwin E. Widders

Dr. Irvin Widders
Major professor

Date Feb. 6, 1989

RESPONSES OF PICKLING CUCUMBER PLANTS TO DROUGHT STRESS DURING THE REPRODUCTIVE GROWTH STAGE

By

Abdul Kader Janoudi

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Horticulture

1989

ABSTRACT

RESPONSES OF PICKLING CUCUMBER PLANTS TO DROUGHT STRESS DURING THE REPRODUCTIVE GROWTH STAGE

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Cucumber (Cucumis sativus L.) plants have high water requirements for growth and development. Water deficits during the fruiting growth stage reduce fruit yield and quality. This study was conducted to evaluate the tolerance and physiological responses of selected commercial pickling cucumber parental lines and F1-hybrids to drought stress.

Cucumber plants were grown in containers in the greenhouse and subjected to drought stress during the fruiting growth stage. Plants were rewatered, and another water deficit exposure initiated, when plant water potentials had reached -0.5 to -0.8 Mpa. Leaf sap osmolality was measured using a vapor pressure osmometer. Leaf gas exchange parameters were measured using an open gas exchange system with an infrared CO_2-analyzer. In each experiment, individual fruit dimensions and fresh and dry weights were recorded. At the end of certain experiments, leaf area and dry weight and stem and root dry weights were measured.

Carbon-dioxide assimilation rates (A) of drought stressed plants averaged 6.9 $umol.m^{-2}s^{-1}$ as compared to 19.0 for well-watered plants. However, the adverse effects of water deficits on A were reversible. Within 12 hours of

being rewatered, stressed plants attained photosynthetic rates similar to those of well-watered plants. Only 36.5% of the decrease in photosynthetic rate in drought-stressed plants could be attributed to the decrease in C_i associated with stomatal closure.

Under water-limiting conditions, fruiting plants maintained higher photosynthetic rates than non-fruiting plants. Cucumber plants allocated photoassimilates to developing fruits at the expense of vegetative plant parts.

The magnitude of osmotic adjustment in cucumber leaf tissue of stressed cucumbers ranged between 0.06 and 0.1 Mpa. Increases in K^+ concentration in leaf lamina tissue could account for most of the observed decrease in osmotic potential under drought stress conditions. In water stressed plants, leaf osmotic potential increased following rewatering.

Drought stress reduced cucumber vegetative growth and fruit set by 20.8% to 38.8% and 25.5% to 46.4%, respectively. Water deficits reduced fruit growth rates but did not alter the fruit bearing pattern of stressed plants. It was concluded that, under the experimental conditions of this study, the genotypes tested have a low drought tolerance.

To My Family

ACKNOWLEDGEMENTS

I would like to thank a number of people and organizations for their assistance and support. I thank the members of my graduate committee -- Dr. Irvin Widders, advisor; James Flore; Dr. Kenneth Poff; Dr. Hugh Price and Dr. Maurice Vitosh -- for reviewing, editing and critiquing this study. I must express my sincere gratitude and appreciation for the advice, assistance and encouragement provided by my Major professor, Dr. Irvin Widders. His continuous support and concern as an advisor were major factors in helping me to complete my studies.

Thanks also go to the Campbell Institute for Agriculture Research, Napoleon- Ohio, and to Vlasic Foods for their financial support and cooperation which made this study possible. The financial support provided by the Hariri Foundation during the first year of my studies at Michigan State University is also greatly appreciated. The efforts of Mr. Rafic Hariri and the Hariri Foundation in providing aid for Lebanese students can not be given enough appreciation.

Finally, I would like to thank my wife for her continuous support and love, especially during the dark days of the war in Lebanon.

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LIST OF ABBREVIATIONS

A : CO_2 assimilation rate
C : Degree celsius
C_A: Ambient carbon dioxide
C_i : Intercellular CO_2
cc : Cubic centimeter
cm : Centimeter
CO_2 : Carbon dioxide
dm : Decimeter
g : Gram
g_s : Stomatal conductance
HID : High Intensity Discharge
hr : Hour
H_2O : Water
IRGA : Infra-red gas analyzer
K : Potassium
K^+ : Potassium ion
kPa : Kilopascal
l : Liter
LD ratio: Length to diameter ratio
L.S.D : Least significant difference
M : Molar
m : Meter
mg : Milligram
min : Minute
ml : Milliliter
mmolal : Millimolal
MPa : Megapascal
N : Nitrogen
NaOH : Sodium Hydroxide
P : Phosphorus
PAR : Photosynthetically Active Radiation
PPFD : Photosynthetic Photon Flux Density
ppm : Parts per million
s : Second
VPD : Vapor pressure deficit
wt : Weight
WUE : Water Use Efficiency
um : Micrometer
umol : Micromole

Introduction

Cucumbers are fleshy plants which have a high water requirement for growth and development. Machine harvested pickling cucumbers are mainly grown under rainfed conditions. In the mid-western United States, periods of drought, 7 to 10 days in duration, are common during the summer months, June through August, and lead to moderate to severe water deficits in rain-fed cucumber crops. Transient water deficits are also observed frequently in cucumber plants due to high transpirative water loss at mid day. Such water deficits result in temporary leaf wilting and stomatal closure. In many crops, stomatal closure has been found to result in reductions in photosynthetic rates. Decreases in cucumber fruit quality have been associated with the decrease in photoassimilate supply which can be expected under conditions of drought stress. The flowering and fruiting period has been identified as an important stress-sensitive growth stage in plant development as related to crop productivity. It was hypothesized that water deficits, during the reproductive growth stage, limit plant growth and decrease photosynthetic rates and that the combined effects of smaller leaf areas and lower CO2 assimilation rates decrease fruit quality and productivity.

strategy of cucumber plants. Fruiting cucumber plants have higher photosynthetic rates than non-fruiting plants and allocate photoassimilates to fruits at the expense of vegetative plant parts (Pharr et al., 1986). The effects of fruits on gas exchange properties and carbon allocation in drought stressed cucumber plants have not been studied.

Osmotic adjustment has been reported to increase plant tolerance to drought stress by enabling the plant to maintain cell turgor and tissue hydration at lower water potentials . A number of plant species have been shown to undergo osmoregulation in response to water deficits but it has not been demonstrated to occur in cucurbits. Since cucumbers originated in the semi arid regions of Africa and southwest Asia, drought tolerance or avoidance genes would be expected to be found within a diverse population of Cucumis sativus.

Limited research has been conducted on the responses of pickling cucumbers to drought stress. This study was conducted with the following objectives: (1) to identify genotypic differences in responses to drought that might exist among selected cucumber parental lines and cultivars; (2) to study the effects of water deficits on gas exchange characteristics of cucumber leaves; (3) to evaluate the osmotic adjustment capacity of cucumber leaves in response to drought stress and (4) to identify the effects of fruiting on carbon assimilation and allocation in drought stressed cucumber plants.

Literature Review

Water deficits have adverse effects on plant growth and development. Leaf and stem growth is often retarded and reproductive organs frequently abort under drought stress conditions (Kramer, 1976). Plants have evolved several mechanisms to avoid or withstand drought stress. Thicker cuticles, leaf rolling, stomatal closure and development of extensive root systems are some of the water conservation mechanisms utilized by plants (Simpson, 1980; Turner and Kramer, 1980). Plant responses to water stress have been extensively covered in a number of review articles and books (e.g. Hsiao, 1973; Kozlowski, 1966-1980, Kramer,1983; Levitt, 1980; Turner and Kramer, 1980).

Effects on Plant Growth, Development and Yield

Effects on vegetative growth

Water deficits have direct and indirect adverse effects on plant growth. Direct effects include those on cell division and cell enlargement. Cell division and enlargement are equally sensitive to water stress (Meyer and Boyer, 1972; McCree and Davis, 1974). Leaf elongation becomes slower and eventually stops as soil water tension increases (Acevedo et al., 1971). Retardation of leaf

expansion at low water potentials was not due to lack of substrates (Michelena and Boyer, 1982), however, formation of new leaf primordia is more sensitive to a limited supply of assimilates than is leaf expansion (Milthorpe, 1959). Overall plant growth is reduced as a result of water stress. Cucumber vine and leaf growth are reduced by water deficits (Cummins and Kretchman, 1975). Water stressed cucumber plants have fewer nodes and smaller vines (Ortega and Kretchman, 1982). Plant growth is also indirectly affected by drought. Decreases in nutrient uptake, particularly phosphorus, are observed in water stressed plants (Ackerson, 1985). Plant hormone levels are altered in stressed plants. Abscisic acid (ABA) induces stomatal closure resulting in decreases in the production of assimilates needed for growth. ABA levels increase in water stressed plants (Eze et al., 1983; Raschke et al., 1976). The effects of water stress on photosynthesis will be dealt with in more detail in another section.

Effects on fruit set and fruit quality

Economic yield of a pickling cucumber crop is dependent on the number, weight and quality of fruits produced. Drought adversely affects pollen quality. In squash (Cucurbita pepo L.) and Phaseolus vulgaris L., dehydration reduced the pollen germination percentage, resulting in reduced fruit set and number of seeds per fruit (Gay et al., 1987; Shen and Webster, 1986). A decrease in pollen

viability in water stressed cucumbers might account, in part, for yield reductions. Doss et al. (1977) found that pickling cucumber yields were decreased when more than 70% of the available soil moisture was depleted. Subjecting bush bean plants to soil water tensions of 0.75 bars or more reduced yields by 48% (Stansell and Smittle, 1980). Water stress during the flowering stage caused the largest decrease in bush bean yields (Dubetz and Mahalle, 1969).

Cucumber fruit quality is also affected by water deficits. Cucumber fruits developing under conditions of water stress would have a poor quality, mainly due to the increase in the incidence of carpel separation placental hollows, and fruit deformation. Elkner (1982) reported that plants growing at a soil water tension of 0.45 bars produced 57.5% of their fruits with either carpel separation or placental hollows. The decrease in cucumber fruit quality is apparently due to a decrease in photosynthate production. Kanahama and Saito (1985a) found that defoliation and leaf shading of cucumber plants increases the incidence of crooked fruits; fruit curvature increased as the leaf area/fruit decreases. The results of another study by Kanahama and Saito (1985 b) suggest that competition for available assimilates increases the incidence and degree of fruit curvature. Water deficits reduce photo-assimilate production and consequently, would be expected to have a similar effect on fruit shape.

Water Requirements of Cucumbers

Crop water requirements are highly dependent on environmental factors such as air temperature and relative humidity, wind velocity and sunlight intensity and duration. Consequently, estimates of the water requirements for a cucumber crop vary with the conditions under which measurements were made. Reported values vary between 3.5-5.5 mm/day (Loomis and Crandall, 1977) to 8 mm/day (Ritter et al., 1984).

Strategies for Dealing With Water Deficits

Cultural practices

A number of management practices have been employed in an effort to avoid or delay plant exposure to drought stress. Some of these practices are useful only in arid and semi-arid climates while other practices may also be beneficial in temperate climates. Examples of commonly used practices include:

- soil management and irrigation

Fallowing, to increase stored soil water, is frequently utilized in semi-arid locations to delay the onset of water deficits (French, 1978). In some soils, crusting can occur under drought conditions resulting in poor germination and stand establishment. Sowing germinated seeds in a fluid gel is a technique that is useful where soil crusting can occur (Taylor et al., 1982). However, a prolonged period of drought following sowing would be detrimental to the germinated seeds. The use of irrigation is dependent on

economic considerations and, particularly in arid regions, on the availability of an adequate water supply.

- antitranspirants

Antitranspirants, compounds that reduce plant transpiration, have been tested for use in reducing plant water stress, but are not extensively used commercially. Wax emulsions, polyvinyl chloride and kaolinite are examples of antitranspirants that act as physical barriers to transpiration by forming an impermeable film on the leaves. Phenylmercuric acetate and hydoxyquinoline sulfate are antitranspirants that induce stomatal closure, thus reducing transpiration. All antitranspirants reduce CO2 entry into leaves and consequently decreases in photosynthesis and yield are often observed. Bravdo (1972) and Davenport et al.(1974) reported decreases in photosynthesis, plant growth and yield following the application of antitranspirants. In contrast, Rao (1985) obtained significant increases in tomato yields following the use of antitranspirants. However, these yield increases were due to increased fruit water content as more water became available upon reducing transpiration. Abscisic acid, applied as an anti-transpirant has been found to improve seedling survival following transplanting, and to increase plant water potential and fruit yield (Berkowitz and Rabin, 1988).

- early cultivars

Planting cultivars that mature before the onset of severe drought stress is a useful practice in regions where the beginning of the dry season is clearly defined. In Australia, higher grain yields were obtained in early maturing spring wheat cultivars as compared to late maturing cultivars (Fischer and Maurer, 1987; Reitz, 1974).

Plant breeding

Breeding for drought tolerance is a long term approach for dealing with water deficits. Several morphological and physiological traits, such as root depth, stomatal frequency and sensitivity and the capacity for osmotic adjustment, are associated with drought tolerance in a number of plant species. Genotypic differences in these traits can potentially be used to increase drought tolerance in crops.

Varietal differences in root growth patterns have been reported in tomatoes (Gulmon and Turner, 1978), soybeans (Raper and Barber, 1970) and wheat. Rooting depth is a heritable trait that can be selected for by breeding (Hurd,1974). Stomata that are sensitive to changes in soil moisture would allow plants to conserve their water and delay the onset of water deficits. Significant differences in stomatal sensitivity of different sorghum genotypes were reported by Henzell et al.(1976). A decrease in stomatal frequency might decrease transpiration. Miskin et al. (1972) reported that stomatal frequency is a

heritable trait in barley, and that a decrease in number of stomata reduced transpiration but not photosynthesis.

Osmotic adjustment is a drought tolerance mechanism that is potentially advantageous to crops that are exposed to intermittent periods of water deficits. Differences in the osmoregulation capacity of sorghum and wheat genotypes have been reported (Ackerson et al., 1980; Fisher and Sanchez, 1979; Morgan, 1977; Stout and Simpson, 1978). Genotypic differences in drought tolerance of wheat cultivars have been attributed to differences in their capacity to osmotically adjust (Blum et al., 1983; Keim and Kronstad, 1981; Morgan, 1977), and variation in osmoregulation was positively correlated with grain yield (Morgan et al.,1986). Osmoregulation is a heritable trait that is controlled by a single gene (Morgan, 1984). Morgan et al.(1986) suggested using this characteristic in screening for drought tolerant wheat lines. However, differences in drought tolerance may not reflect differences in osmoregulation. Jones and Turner (1978) did not find significant differences in osmoregulation between two sorghum cultivars that differed in drought tolerance.

Plant Adaptations to Water Deficits:

A number of morphological and physiological traits have been associated with drought tolerance in plants. The most common adaptations include the following:

Stomatal adaptation

Stomatal closure in response to decreasing soil moisture is a physiological adaptation to drought. Stomatal closure during the time of day when evaporative demand is high would conserve plant moisture and delay the onset of water deficit. Stomata of several species, e.g. apricot and sorghum, have been shown to respond to air relative humidity, closing as relative humidity decreases (Farquhar, 1978; Schulze aand Kuppers,1979). Stomatal opening when humidity is high would allow for photosynthesis to proceed with minimal water loss, thus improving the plant's water use efficiency.

Root growth:

Changes in plant morphology have also been associated with development under drought conditions. One of the most common examples of morphological adaptations is the possession of a deep root system. An extensive, deep root system would allow the plant to extract water from a larger soil volume. Deep rooted plants, such as tomato and alfalfa, are thus able to delay the onset of water stress. Genotypic differences in drought tolerance of some wheat varieties are due to differences in rooting depth (Hurd ,1974). Stressed plants allocate more dry matter to roots at the expense of shoots resulting in a larger root to shoot ratio(Huck et al.,1983); this potentially reduces transpiration and increases water uptake.

Leaf rolling:

Leaf rolling is a mechanism that might have an adaptive value in drought tolerance. A decrease in light interception and consequently, a decrease in leaf temperature would be advantageous under water-limiting conditions. Wudiri and Henderson (1985) reported that the tomato cultivar 'saladette' rolled its leaves in response to water stress and suffered a 40% reduction in fruit set, while another cultivar 'VF 145b-7879' that did not roll its leaves, suffered a 90% reduction in fruit set.

Osmotic adjustment:

Osmotic adjustment is suggested as a process by which plants can become more tolerant of low soil water potentials (Morgan, 1977; Turner and Jones,1980). This response to water stress will be discussed in more detail in the following section.

Osmotic Adjustment in Plants

Role in drought tolerance

Osmotic adjustment is one of the mechanisms that plants have developed to avoid tissue dehydration under water-limiting conditions. Osmotic adjustment may be described as the decrease in cell osmotic potential caused by the active accumulation of solutes in response to water or salt stress. A decrease in osmotic potential resulting from cell dehydration is not considered an osmotic adjustment. Turner and Jones (1980) differentiate between the terms osmotic adjustment and osmoregulation which are frequently

used to refer to the same process. They suggested using the first term when referring to this process in higher plants and the latter for microorganisms. In this review, both terms will be used interchangeably.

A plant's water status may be defined by its water potential, which is equal to the sum of the osmotic (solute), pressure, gravimetric and matric potentials. For cell expansion and many other physiological processes to proceed, the pressure potential has to be positive. The threshold cell turgor pressure for growth to occur varies with species, environmental and other factors. While osmotic and water potentials always have negative values, the possibility of a negative pressure potential occurring in cells was disputed by Tyree (1976) who attributed the reported negative values to errors in measuring osmotic potential.

Osmotic adjustment has a role in plant tolerance to water stress through maintaining positive cell turgor. This is achieved via a decrease in osmotic potential in response to water deficit (Morgan,1977; Turner and kramer,1980). Such a process would allow for continued root growth and maintenance of stomatal opening (Graecen and Oh,1972; Van Volkenberg,1985). A number of plant species have been shown to undergo osmotic adjustment in response to water stress; included are tomato, pea, bean, apple, sorghum, sunflower and wheat (Acevedo et al., 1979; Fanjul and Rosher, 1984). Plants that osmotically adjust are capable of maintaining

leaf turgor to lower water potentials than those that do not (Ackerson, 1981; Ackerson and Hebert, 1981). At low water potentials, pressure potentials and water content of adjusted plants are higher than those of non-adjusted plants, reflecting the role of osmotic adjustment in maintaining tissue hydration and thus, survival under stress conditions (Flower and Ludlow, 1986; O'Neill, 1984). However, adjusted and non-adjusted plants reach zero turgor at the same relative water content.

Studies indicate that osmotic adjustment is a rate dependent process. Slow rates of stress imposition were found to allow for more solute accumulation than rapidly developing stress (Flower and ludlow,1986;Thomas,1986). Strawberry plants were subjected to a rapid rate of stress of 1.2 Mpa per day; this rate did not allow for osmotic adjustment to occur while rates of 0.15 and 0.7 Mpa per day allowed for equal levels of adjustment (Jones and Rawson,1979). Osmoregulation in fruits has not been extensively studied. Fruits of stressed cucumber plants were reported to have a higher concentration of solutes than fruits of non-stressed plants (Ortega and Kretchman,1982). However, it was unclear whether the increase was due to an increase in solute content or to dehydration.

Solutes involved in osmoregulation apparently become available for plant metabolism following relief of stress. Consequently, osmotic adjustment is maintained for varying

periods of time following rewatering depending on rate, severity and duration of water stress. Following one stress cycle, the osmotic potential of cotton leaves returned to pre-stress levels within six days of rewatering while plants subjected to several stress cycles maintained low solute potentials for up to 10 days after rewatering (Oosterhuis and Wullschleger, 1987, Shahan et al.,1979). The degree of osmotic adjustment also varies with species. Osmotic potential at full turgor decreased by 0.1 to 0.4 MPa in maize, sorghum and sunflower plants subjected to water stress (Sanchez-Diaz and Kramer,1978).

Solutes in osmotic adjustment:

A number of solutes have been associated with osmoregulation. Sugars, organic acids, potassium and chloride ions, proline and betaine are some of the most commonly reported osmotica.

Glucose is the main solute that accumulated in leaves of stressed cotton plants (Ackerson,1981) while non-reducing sugars were reported to accumulate in stressed sorghum (Acevedo et al.,1979). Tomato cell cultures subjected to low water potentials underwent osmoregulation with reducing sugars accounting for only 20 % of the decrease in osmotic potential; potassium, chloride and amino acids accounted for the remaining 80 percent (Handa et al.,1984). Proline is another solute that has been associated with plant responses to water deficits. The level of proline in leaves acts as an indicator of stress, but its accumulation does

not reflect drought tolerance (Blum and Sullivan, 1974). Betaine levels have also been reported to increase in water stressed plants. Proline and betaine might have a protective role for enzymes in stressed tissues (McCree,1986).

Advantages and limitations:

Turner and Kramer (1980) suggested that osmotic adjustment has the following advantages:

a- maintenance of cell turgor and elongation.

b- maintenance of stomatal opening and photosynthesis.

c- allow for continued root growth.

Osmotic adjustment in roots provides an additional advantage that is the maintenance of water uptake at lower soil water potentials. The benefit from root osmotic adjustment is limited by environmental conditions such as soil type and evapotranspirative conditions. A light soil has a lower water holding capacity than a heavy soil. Consequently, for a plant growing in a light soil, a smaller increase in available water would be expected per unit of root osmoregulation.

Some of the limitations that were cited by Turner and Kramer include the loss of adjustment within a few days of relief of the stress and the limited range of plant water potentials within which turgor can be maintained through osmoregulation. It can be concluded that osmotic adjustment would allow plants to tolerate short term water deficits, as sometimes occurs during the growing season in a

temperate climate.

Effects of Water Deficits on Plant Gas Exchange Characteristics

Stomatal responses

Environmental factors have direct effects on gas exchange characteristics of plants. Stomatal conductance is influenced by soil water potential and air humidity. Stomatal closure in response to decreases in humidity has been attributed to a direct effect of humidity on stomata that is independent of the leaf water status (Schulze and Kuppers,1979;Schulze and Hall,1982,). Stomatal responses to humidity ,not involving changes in leaf water status, are controlled by turgor of the epidermis and are referred to as feed-forward control (Farquhar,1978). Changes in stomatal conductance in response to changes in leaf water status occur through feedback control (Cowan,1977, Farquhar,1978).

Several studies have indicated that a relationship exists between leaf water status and stomatal conductance. Stomatal closure was reported to occur at a threshold value of leaf water potential that varied with several factors including species, leaf age and stress history (Ackerson, 1980; Sionit and Kramer, 1976). More recent studies have demonstrated that stomatal responses to mild soil water deficits were independent of leaf water potential and

turgor pressure. Blackman and Davies (1985) divided the roots of maize seedlings between two pots such that one was watered and the other was allowed to dry. This resulted in partial stomatal closure although leaf water potential, turgor potential and abscisic acid levels were unaffected. In a different approach, Gollan et al. (1986) maintained leaf turgor in stressed plants by placing the root system in a pressure chamber; the stomata still closed irrespective of leaf water status. It can be concluded that stomatal conductance is directly affected by soil water status, independent of leaf turgor. Gollan et al.(1986) and others (Bates and Hall,1982;Bennett et al.,1987; Blackman and Davies,1985), suggested a role for cytokinins in root to shoot communication with a continuous supply of the hormones from the roots being required for complete stomatal opening.

Osmotic adjustment, leading to turgor maintenance, allows plants to maintain stomatal opening under conditions of water stress. Repeated exposure to water deficits induced osmoregulation in sorghum, cotton and sunflower; this allowed plants to maintain higher stomatal conductances at lower water potentials, as compared to non-adjusted plants (Ackerson, 1980; Jones and Rawson,1979).

Photosynthesis:

Plants generally respond to decreases in available soil moisture by stomatal closure which is thought to be a major cause for the observed decline in photosynthesis

(Raschke and Hedrich, 1985). Other causes of the decline in Pn rate has not been clearly identified, but a number of factors have been suggested as causes of the decline; included are: the accumulation of assimilates (Ackerson,1981), localized low water potentials at evaporation sites in the mesophyll (Sharkey,1984) and reduced photochemical activity (Boyer,1971).

Downton et al.(1988) concluded that stomatal closure leading to decreased intercellular CO_2 levels can fully account for the observed decline in photosynthesis in water stressed plants. A similar conclusion was reached by Raschke and Hedrich (1985). Other studies have indicated that the decrease in photosynthesis in water stressed plants is not solely due to stomatal closure, as mesophyll conductance was also found to decrease; this was suggested to be due to the accumulation of assimilates (Ackerson and Hebert, 1981; Thorne and Koller,1974). Bunce (1982) did not find a correlation between mesophyll conductance and total non-structural carbohydrates content of stressed leaves; the increase in carbohydrate content did not account for the decline in Pn rate. Direct inhibition of photosynthesis by water stress has been attributed to a decrease in choloroplast volume leading to increases in concentrations of inhibitory solutes such as K^+ (Kaiser,1986). However, Sharkey and Badger (1982) disputed the possibility of such an effect. Others have reported that stress has direct effects on chloroplasts which lead

to the observed reductions in photosynthesis (Genty et al.,1987). A similar conclusion was reached by Krieg and Hutmacher (1986) who found that assimilation rate was lower at all internal CO_2 levels in water-stressed plants. Berkowitz and Gibbs (1983 a,b) concluded that photosynthesis was inhibited at low osmotic potentials due to stromal acidification which inhibited the activity of the Fructose 1,6-biphosphatase. Later, Pier and Berkowitz(1987) found that K^+ has a protective role involving the exchange of cytoplasmic K^+ for H^+ in stroma, which restored stromal alkalization and photosynthetic activity. Disruption of chloroplast thylakoid membranes has been observed in leaves of stressed plants; this may be a cause for the observed decrease in photosynthesis in stressed plants (Johnson et.al, 1982).

Photosynthesis might acclimate to low water potential, thus allowing for CO_2 fixation to continue under water stress conditions (Matthews and Boyer, 1984). Osmotic adjustment has a protective role for the photosynthetic apparatus (Downton,1983), allowing photosynthesis to continue under stress conditions until turgor is lost (Boyer and Potter,1973). Water deficits also affect overall plant photosynthesis by limiting leaf growth and thus reducing the potential photosynthetic capacity of plants (Acevedo et al., 1971).

Water use efficiency:

Water use efficiency (WUE) may be defined as the ratio of carbon dioxide uptake to water transpired by a plant. The definition may be generalized and expressed as the ratio of dry matter produced to evapo- transpiration of a crop. For a plant growing on a limited supply of soil water, water use efficiency is important in determining the potential of that plant for growth and yield. A high plant WUE reflects more growth per unit of available water, as compared to plants with low WUE.

Water use efficiency is influenced by a number of plant and environmental factors. Vapor pressure deficit, a function of leaf and air temperature and relative humidity, influences stomatal conductance and transpiration and consequently water use efficiency of a plant. In cassava, water use efficiency decreased as vapor pressure deficit increased (Cock et al., 1985), and no difference in WUE between stressed and non-stressed was observed (El-Sharkawy and Cock,1984). Jones (1976) reported that WUE increases as stomatal resistance increases and as boundary layer resistance decreases. Similarly, daily WUE increased when plants avoided the peak transpiration period by closing their stomata in response to increased vapor pressure deficit at mid-day (Ludlow, 1980).

Nobel (1980) developed a theoretical basis for a relationship between cell size and water use efficiency. He attributed the higher WUE values observed in plants that

develop under conditions of water stress, to the smaller size of cells produced under these conditions, as compared to non-stressed conditions. Leaves developing under conditions of high temperature, high irradiance and soil salinity would be expected to have small cells and high WUE values.

Translocation:

Water stress apparently has no direct effect on translocation and phloem loading. The observed decrease in translocation rates in water stressed plants is probably due to a decrease in assimilate production as photosynthesis declines. Sung and Kreig (1979) found that CO_2 assimilation is more sensitive to water deficits than is translocation. Contrary to that, Brevedan and Hodges (1978) reported that translocation is more sensitive to water deficit than photosynthesis.

Effects of Fruiting on Photosynthesis And Assimilate Allocation

Actively growing fruits act as sinks for photo-assimilates. Assimilate demand influences photosynthesis and translocation. Increases in photosynthesis and in carbohydrate export from source leaves is observed when the source to sink ratio is decreased (Thorne and Koller, 1974).

Net photosynthetic rates have been reported to be higher in fruiting than in non-fruiting plants of several species.

Carbon exchange, assimilate export and starch accumulation rates are higher in fruiting than in vegetative cucumbers; the increase in Pn rate was associated with increased sink demand (Pharr et al.1985). Net photosynthetic rate (Pn) is higher in fruiting than in de-blossomed pepper plants (Hall,1977). A similar observation was made on strawberry; however, on a whole plant basis, net photosynthesis was similar in fruiting and non-fruiting plants due to the larger leaf area in non- fruiting plants (Choma et al., 1982). DeJong (1986), concluded that increased photosynthetic rates in fruiting Prunus persica trees were mainly due to increases in leaf rather than mesophyll conductance.

Fruit and flower removal have been associated with decreases in photosynthetic rates. King et al.(1967) observed a 50% decrease in Pn rate of the flag leaf within hours of ear removal in wheat. The photosynthetic rate regained its previous level when other leaves on the plant were darkened, thus precluding them as sources for the young shoots and roots. The cause of the observed decreases in Pn rate upon flower or fruit removal is not clearly identified. Some have attributed the decline in Pn rate to increased stomatal resistance (Gifford and Marshall,1973;Rawson et al.,1976) and to increased leaf and mesophyll resistance (Hall and Milthorpe, 1978). Mesophyll and stomatal conductance of fruiting strawberry plants were 40% higher than those of de-blossomed plants

(Forney and Breen,1985). These results imply that the decrease in Pn rate is due to a limited CO_2 availability. This is in contrast with the findings of Crafts-Brander (1987) who reported that in some maize genotypes, ear removal resulted in a decrease in Pn rate which was not due to limited CO2 availability as the internal CO2 concentration increased upon ear removal.

Accumulation of assimilates in chloroplasts of source leaves has also been suggested as a cause for the decrease in Pn rate upon defruiting (Choma et al.,1982). Leaf starch concentration was negatively correlated with photosynthetic rate in soybean (Nafziger and Koller,1976). Disruption of choloroplast ultra- structure as a result of excessive starch accumulation is a possible cause for the decrease in Pn rate (Schaffer et al.,1986); however, this is difficult to reconcile with the rapid recovery in Pn rate (King et al.,1967). Fruit bearing alters the dry matter partitioning strategy of a plant. Developing fruits represent strong sinks which actively compete for the available assimilates. Fruit growth retards shoot and root growth in cucumber, reflecting the strength of fruits as sinks to which assimilates are preferentially allocated. An estimated 40% of the total amount of photo-assimilates produced by the plant are required for the growth of a single fruit (Pharr et al., 1985). Barrett and Amling (1978) found that within 24 hrs of their production, 80% of assimilates were translocated to the fruit. This might be a

reason for the limited number of fruits that can develop simultaneously on a cucumber vine. In Capsicum annuum, 90% of the assimilates produced are deposited in the fruit. Upon defruiting, partitioning of dry matter among the vegetative parts becomes evenly balanced (Hall,1977). Loomis and Crandall (1977) observed that fruiting cucumber plants had 21% less total leaf area than defruited plants. Similar observations were made on strawberry (Choma et al., 1982; Schaffer et al., 1986). Fruiting strawberry plants had 62% and 44% less dry matter in roots and leaf blades, respectively, than de-blossomed plants (Forney and Breen,1985). The inhibitory effect of fruits on vegetative growth have also been attributed to inhibitors exported by developing fruits (Barrett and Amling, 1978). The final total dry weight of reproductive and vegetative parts are equal in fruiting and deflowered plants (Choma et al., 1982). The higher net photosynthetic rate apparently compensates for the smaller leaf area of fruiting plants and allows for the production of an equal amount of dry matter (Schaffer et al., 1985).

Growing cucumber fruits can also inhibit the growth of other fruits on the same vine (McCollum, 1934). Ells (1983) found that in pickling cucumbers, the inhibitory effect of pre-existing growing fruit did not extend beyond 10 nodes from an existing fruit.

Effects of water deficits and fruiting on carbon assimilation and allocation in pickling cucumber plants

Abstract

Gas exchange measurements were made on leaves of Cucumis sativus L. plants subjected to drought stress. Plant water potentials were allowed to decrease to < -0.7 Mpa, during the flowering and fruiting growth stages. Assimilation rates (A) were measured at saturating PPFDs, for non-stressed plants, 1000 $umol.s^{-1}m^{-2}$ or higher. Leaf temperatures during these measurements ranged from 22C to 32C which were found not to affect A. Drought stressed plants had 63% to 73% lower CO_2 assimilation rates than well watered plants. Stomatal conductances ranged from 0.13 to 0.14 $cm.s^{-1}$, 80% lower than g_s of leaves of control plants. The adverse effects of water deficits on photosynthesis were reversible. Within 12 hours after rewatering, CO_2 assimilation rates of previously stressed plants increased to 11.7 $umol.s^{-1}m^{-2}$, not significantly different from that of irrigated control plants. The decrease in intercellular CO_2 levels accounted for 36.5% of the decrease in A, while the remaining 63.5% of the decrease was attributed to non-stomatal factors. Water use efficiency (WUE) decreased rapidly as leaf-air VPD increased above 2 Kpa. Drought stressed plants tended to have higher WUE than control plants. In drought

stressed and non stressed plants, CO_2 assimilation rates of fruiting plants were higher than those of non-fruiting plants. Under both water regimens, fruiting plants allocated assimilates to developing fruits at the expense of leaves, stems and roots. It is concluded that the effects of water deficits and fruiting on photosynthesis cannot be explained solely by observed changes in stomatal conductance.

Introduction

Cucumbers are fleshy plants which have a high water requirement for growth and development(26,32). In the mid-western United States, periods of drought, 7 to 10 days in duration, are common during the summer months, June through August (34), and lead to moderate to severe water deficits in rain-fed cucumber crops. Transient water deficits are also frequently observed in cucumber plants due to high transpirative water loss at mid day. Such water deficits result in temporary leaf wilting and stomatal closure and ultimately in a reduction in photosynthesis (2,14). Cucumber fruit yield and quality have been reported to decrease under conditions of drought stress (8,10). Decreases in cucumber fruit quality have been associated with the decrease in photoassimilate supply (22) which can be expected under conditions of drought stress. Plant water status and fruit set have been shown to influence photosynthetic activity

(2,14,18,21,24,28). The cause of the decrease in photosynthesis in water stressed plants is still not completely understood. Under water deficit conditions, CO_2 fixation rates are low due to decreased intercellular CO_2 levels (30), accumulation of assimilates (1) and/or localized low water potentials in the mesophyll (38). Fruiting plants have higher photosynthetic rates than defruited or vegetative plants (18,28). Increased photosynthetic rates have been attributed to higher stomatal conductances (7,31) and higher mesophyll conductances (13,18) in fruiting as compared to non-fruiting plants.

Water deficits and fruiting also impact upon dry matter partitioning in plants. Water stressed plants tend to allocate more photoassimilates for root growth at the expense of leaf and stem growth (20,25) which ultimately reduces the photosynthetic leaf area of the plant. In a similar manner, cucumber fruits can limit leaf growth and development by competing with vegetative parts and other fruits for the available photoassimilates (3,11,28) due to their strong sink strength. The combined effects of environmental and plants factors on dry matter production capacity, and consequently potential productivity, and dry matter allocation in cucumber plants have not been studied. An understanding of these factors is needed before a strategy can be developed for improving the crop's performance under water-limiting conditions. This study

was undertaken: (1) to determine the effects of water deficits, light, temperature and vapor pressure deficit on the leaf gas exchange properties in cucumbers, (2) to evaluate the recovery of photosynthetic activity following relief of water stress and (3) to investigate the combined effects of water deficits and fruiting on dry matter production and partitioning in cucumber plants.

Materials and Methods

Plant material: In greenhouse experiments, seeds of the pickling cucumber (Cucumis sativus L.) inbred lines GY14 and M21 were sown in a 1:1 peat (Baccto professional mix) sandy loam soil mixture in 11-liter plastic containers. Plants were fertilized twice weekly using Peter's 20N-8.8P-16.6K soluble fertilizer at a concentration of 0.2 $g.l^{-1}$. Pistillate flowers were hand-pollinated between 10 am and 12 noon on the day the flowers opened. Day/ night temperatures were maintained at about 30 / 20C +~- 5C and no supplemental lighting was provided.

Cucumber plants were also cultured in a field environment during June through August, 1987, by planting seeds into 11-liter plastic containers buried in the soil at the Horticulture Research Center of Michigan State University. Two irrigations during the vegetative stage supplemented natural rainfall. When all plants were bearing fruits, plants were transferred to the greenhouse for additional

measurements.

Water regimen: Water deficit treatments were induced by withholding water from the plants for 3-4 days until the plants were visibly wilted throughout the day and the dawn-plant water potential had reached -0.6 to -0.8 Mpa. Stressed plants used in studying recovery of photosynthetic activity were rewatered 12 hours before gas exchange measurements were made. Control plants were watered daily.

Deflowering. Fruit set and development were prevented by removal of pistillate flowers from the plants on a daily basis throughout the experiment.

Leaf gas exchange measurements. Gas exchange responses to light, temperature and CO_2 concentration of the 4th or 5th attached leaf from the shoot apex were determined using an open gas exchange system previously described by Sams and Flore (37). Each leaf was enclosed in a 20 cm x 10 cm controlled environment chamber. Leaves were allowed to equilibrate with the micro-environment of the chamber for a period of 2 hours before gas exchange measurements were made.

To determine the light response curve, gas exchange measurements were made at several levels of PPFD beginning at a flux density of 1800 $umol.s^{-1}m^{-2}$ and incrementally decreasing to total darkness. Ambient CO_2 temperature were maintained constant at 345 +-5 ppm and temperature of 25 +-0.5C, respectively.

The temperature response curve was determined by raising leaf temperature from an initial temperature of 10-15C up to 40C in increments of 3C to 5C. Vapor pressure deficit was maintained below 1.5 kPa up to a temperature of 30C above which VPD increased rapidly.

The CO_2 responses of leaves of differentially watered plants was determined by exposing the leaves to ambient CO_2 levels of 150 to 350 ppm.

Determinations of net CO_2 assimilation rate (A), photosynthetically active radiation, relative humidity and leaf temperature, under greenhouse and field conditions, were made using a portable open system LCA-2 (Analytical Development Corporation, Hodesdon, England) infrared CO_2 analyzer operated in differential mode, an air supply unit at a flow rate of 600 $cm^3.min^{-1}$, and a Parkinson broadleaf leaf chamber with a window area of 6.25 cm^2. Stomatal conductance (g_s), transpiration rate (E) and vapor pressure deficit (VPD) were calculated using computer programs developed by Moon and Flore (28). All measurements, except for the diurnal measurements, were made under sunlight between 10:30 A.M. and 12:30 P.M. Ambient CO_2 levels were between 325 and 348 ppm. Measurements were made on the fourth and sixth leaf from the shoot apex of each plant. Treatments were replicated 3 times in a randomized complete block design with 2 plants per treatment in a replicate. Measurements of diurnal changes in gas exchange characteristics were made at 10 A.M., 2 P.M. and 6 P.M.,

under a HID low pressure sodium lamp such that the measured PAR at the leaf surface was always greater than a saturating level of 1000 umol.$s^{-1}m^{-2}$. Gas exchange measurements under field conditions were made on July 30th which was a clear, sunny day.

Leaf sugar determinations. Leaf samples were freeze dried for 24 hours then finely ground with a mortar and pastel. Sugars were extracted from tissue subsamples (0.2 g) with 80% ethanol at 70C for 1 hour. The extract was filtered through a No. 1 Whatman filter paper and the ethanol evaporated. The residue was re-dissolved in 25 ml of deionized water an an aliquot of the resultant solution filtered througha 0.45 um Millex-HA filter unit. Sugars and sugar alcohols were assayed using a Dionex Carbopac PA1 anion exchange separation column with a Dionex series 4000i High Performance Ion Chromatography Module and a pulsed amperometric detector with a gold electrode. A 0.1 M NaOH solution was used as the eluant.

Results

Carbon dioxide assimilation rate reached saturation at approximately 900 umol.$m^{-2}s^{-1}$ (Fig. 1). Subsequent measurements of assimilation rates in the field, greenhouse and laboratory were conducted at PPFD levels higher than 1000 umol.$m^{-2}s^{-1}$ to assure light saturating conditions. Maximum carbon dioxide assimilation rates were measured

at stomatal conductances greater than 0.4 $cm.s^{-1}$ while the transpiration rate continued to increase until gs reached 0.6 $cm.s^{-1}$ (Fig 2). Temperature also influenced CO_2 assimilation below 16C and above 34C (Fig 3). Within the range of 16 to 34C, assimilation rates did not fluctuate significantly. High temperature, greater than 34C, resulted in a decline in assimilation rate concomitant with an increase in VPD. Subsequent gas exchange measurements in the field and greenhouse were made at ambient temperatures of 22 to 32C. Water use efficiency decreased rapidly as vapor pressure deficit increased above 1 kPa (Fig 4), but stabilized at a low level of WUE at VPD of 2 kPa or higher.

Drought stressed greenhouse and field plants had 63% and 73% lower CO_2 assimilation rates than well watered plants (Table 1). Stomatal conductances of drought stressed plants averaged 0.13 to 0.14 $cm.s^{-1}$, which is about 80% lower than gs in control plants.

Plant water potentials recovered rapidly and completely within 12 hours after rewatering (Table 2). In drought stressed plants, water potentials increased from -0.77 MPa to a potential not significantly different from non-stressed plants, -0.1 MPa. The osmotic potentials of stressed plants were lower than those of control plants, indicating that leaves of drought stressed plants had undergone osmotic adjustment in response to the stress.

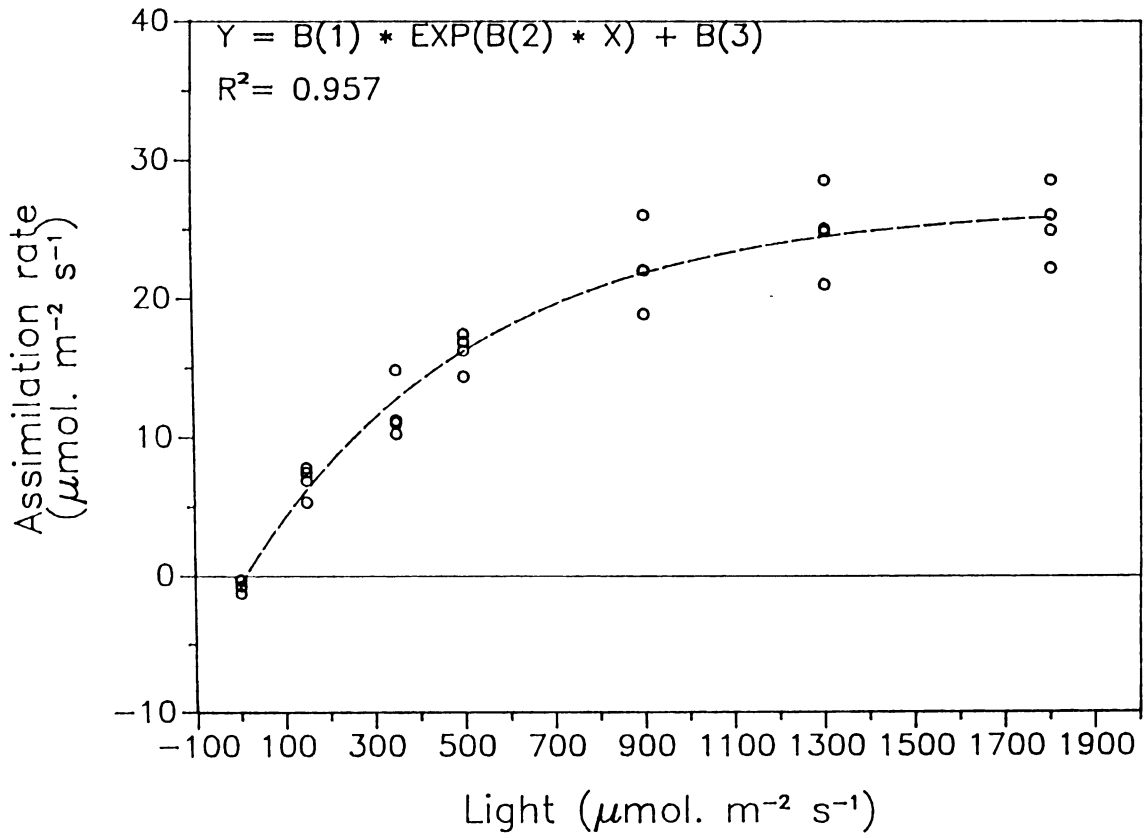

Fig. 1. Effects of increasing PPFD on photosynthetic rate of the 5th leaf from the shoot apex of cucumber plants. Ambient temperature and CO_2 concentration were maintained at 25C and 350 ppm, respectively. Data points represent individual measurements.

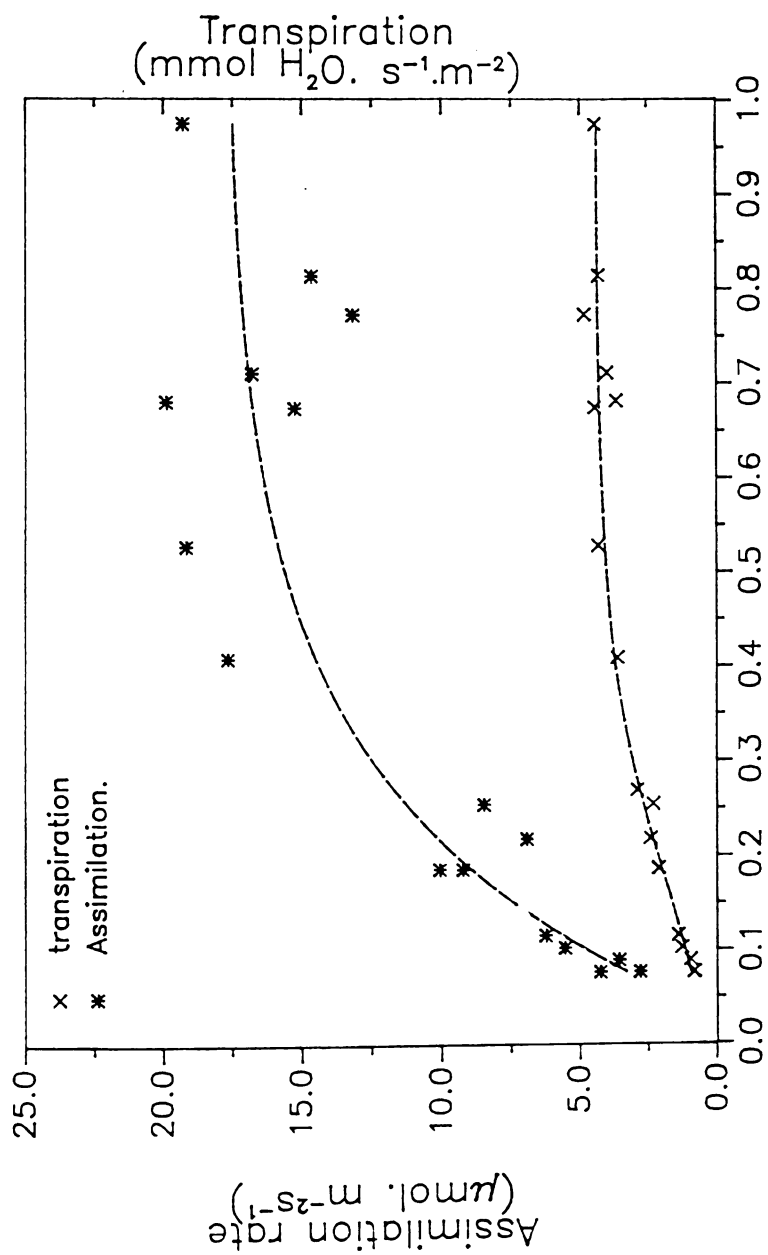

Fig. 2. Correlation between stomatal conductance and leaf gas exchange parameters. Data points represent individual measurements on cucumber leaves at the 5th node from the shoot apex.

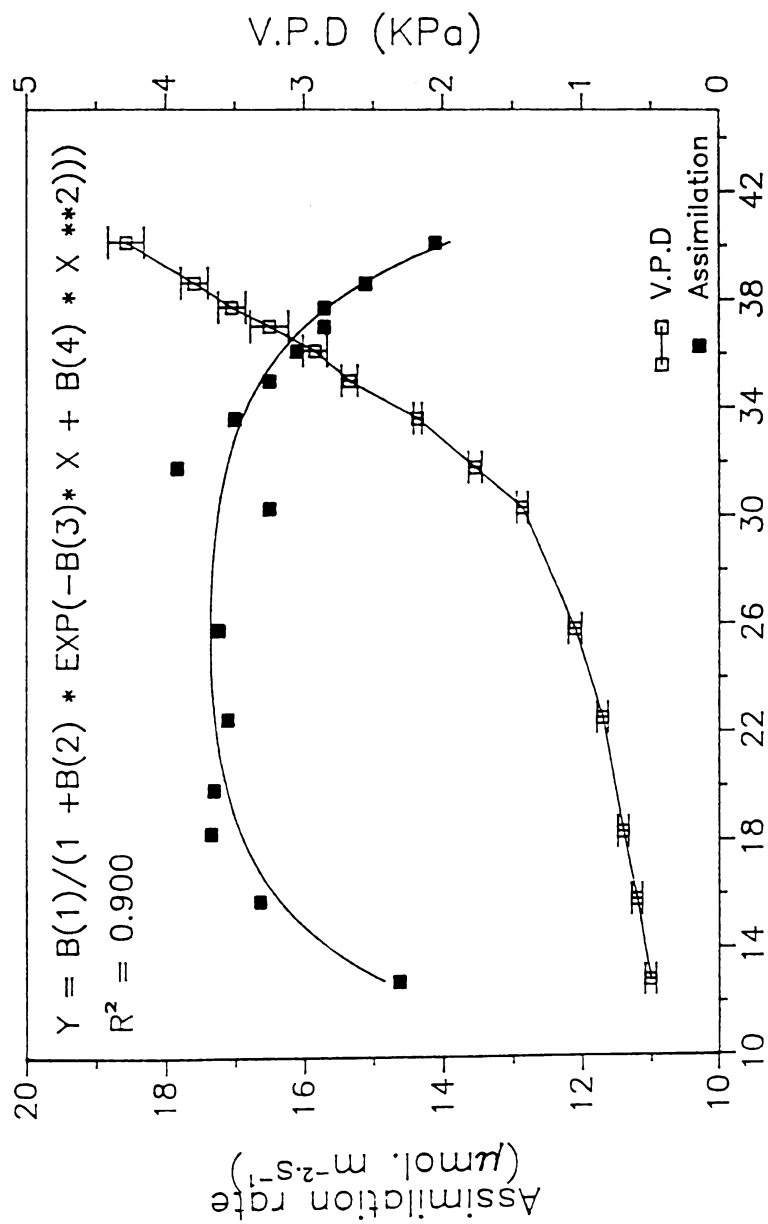

Fig. 3. Temperature response of CO_2 assimilation rate of the 5th leaf on cucumber plants. Values are means of 4 measurements and vertical bars indicate standard error of the mean.

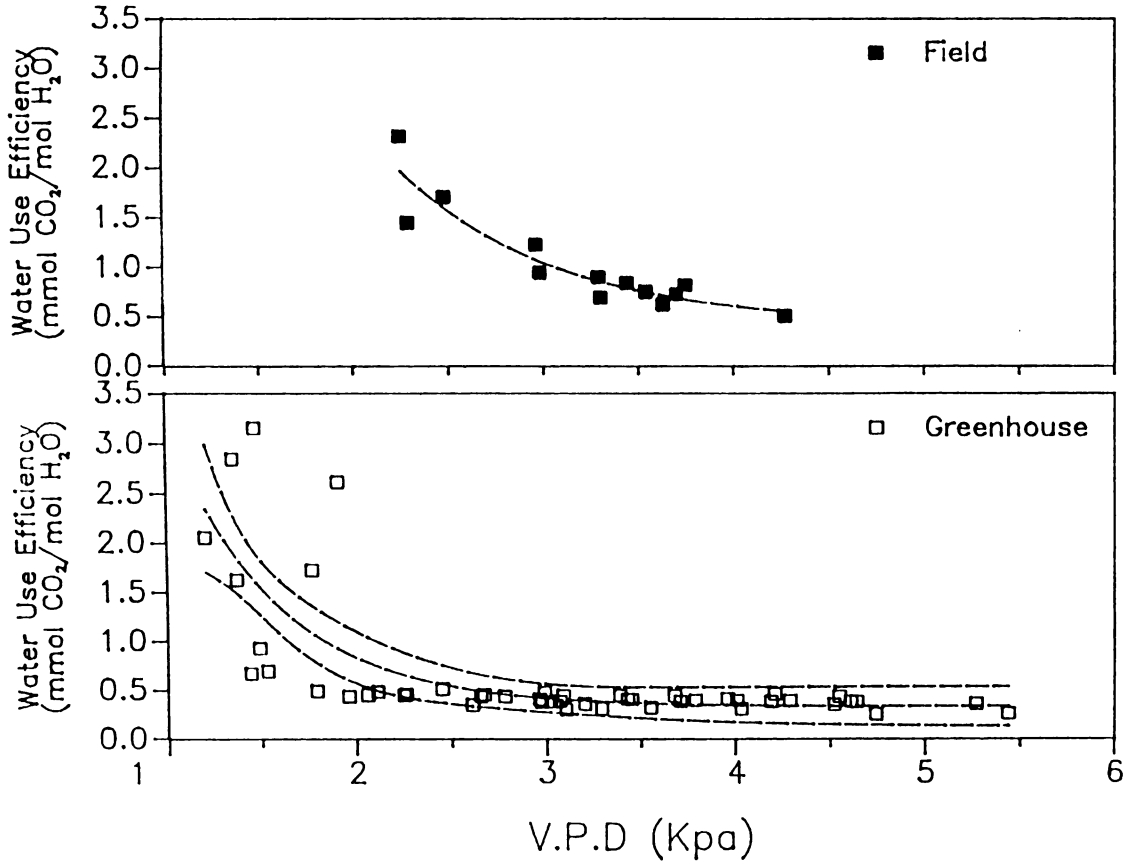

Fig. 4. Influence of vapor pressure deficit on water use efficiency in cucumber leaves. Confidence limits at the 5% level are shown. Data points are from measurements on individual leaves in greenhouse and field plants.

Table 1. Effects of water regimen on gas exchange properties of greenhouse and field grown cucumbers.

Treatment	A (μmol. $m^{-2}.s^{-1}$)		g_s ($cm.s^{-1}$)	
	Field[z]	Greenhouse	Field	Greenhouse
Drought stressed[y]	3.5	6.9	0.14	0.13
Well watered	13.0	19.0	0.65	0.67
L.S.D (0.05)	1.4	4.9	0.01	0.23

z. Plants were grown in plastic containers in the field then transferred to the greenhouse 1 week before measurements were made.

y. Watering was withheld from the plants until plant water potential decreased to 0.5 to 0.8 Mpa.

Table 2. Water use efficiency and water status of greenhouse grown cucumber plants following gas exchange measurements.

Treatment	WUE[z] (mmol CO_2/ mol H_2O)	Potential (MPa)		
		Water	Osmotic	Pressure
Drought stressed	4.3	-0.77	-0.82	0.05
Drought stressed/ rewatered[y]	5.1	-0.10	-0.71	0.61
Non-stressed	4.1	-0.08	-0.63	0.55
L.S.D (0.05)		0.08	0.05	0.06

z. WUE: Water use efficiency.
y. Plants were subjected to water deficit then rewatered 12 hours prior to time of measurement.

Recovery of plants from a water deficit condition following rewatering was rapid for cucumbers. CO_2 assimilation rates increased from 3.5 to 11.7 $umol.s^{-1}m^{-2}$ at 350 ppm CO_2 within only 12 hours after rewatering (Table 3). Increasing ambient CO_2 concentration from 150 ppm to 350 ppm caused significant increases in A and in the estimated intercellular CO_2 (C_i) concentration.

The C_i was calculated according to the model suggested by Downton et al.(1988). Comparison of the CO_2 assimilation rates of stressed and control plants at similar C_i theoretically allows one to evaluate the mode by which water deficits have an inhibitory effect on photosynthesis. In water stressed plants exposed to 350 ppm ambient CO_2, C_i was estimated at 66 $umol.mol^{-1}$ with an A of 3.5 $umol.s^{-1}m^{-2}$. At a similar C_i level (69.7) in a well watered plant (exposed to 150 ppm CO_2), assimilation rate was 9.6 $umol.s^{-1}m^{-2}$ which is approximately 1.75 times higher than the rate (3.5 $umol.m^{-2}.s^{-1}$) measured in plants experiencing water deficit.

Well watered fruiting plants had a 24.4% higher A than that of deflowered plants (Table 4). Under water limiting conditions, A in fruiting plants was 31% higher than A of deflowered plants. Fruiting plants had higher stomatal conductances as compared to deflowered plants. Fruiting drought-stressed plants had the highest WUE (2.17) while deflowered and non-stressed plants had similar WUE that ranged between 1.53 and 1.60 mmol CO_2 per mol H_2O.

Table 3. Effects of water deficits and CO_2 level on photosynthesis in cucumber leaves.

Water regimen	C_a (PPM)	A (umol m^{-2} s^{-1})	z Estimated	y Modelled
Stressed	350	3.5+- 0.8	135.2+-14	66.0
Rewatered	350	11.7+- 1.1	133.0+- 4	123.5 x
Control	350	12.9+- 1.1	178.5+- 9	(178.5)
Stressed	250	2.3+- 0.3	89.0+-14	50.6
Rewatered	250	11.0+- 1.2	92.1+-14	88.5
Control	250	11.2+- 1.2	114.2+- 6	(114.2)
Stressed	150	1.5+- 0.4	75.8+-10	45.7
Rewatered	150	8.0+- 1.2	53.7+- 9	51.5
Control	150	9.6+- 0.7	69.7+- 6	(69.7)

z. Intercellular CO_2 levels were estimated according to Moon and Flore (1986).

y. Intercellular CO_2 level were calculated according to the model: $C_i=[(R-1)r+(C_i,IRGA)]/R$, as suggested by Downton et al. (1988), where C_i is intercellular CO_2, R is the ratio of assimilation rate of control leaves to that of stressed leaves and r is the CO_2 compensation point for photosynthesis. Cucumber leaves were assumed to have a CO_2 compensation point of 40 ppm.

x. Intercellular CO_2 level in control plants is the same as that calculated from IRGA.

Table 4. Effects of water deficit and fruiting on gas exchange parameters of cucumber leaves.

Treatment	Water stress	A[y] ($\mu mol\ m^{-2}.s^{-1}$)	g_s[x] ($mm.s^{-1}$)	W.U.E[z] (mmol CO_2/ mol H_2O)
Fruiting [w]	Yes	8.4	2.7	2.17
Deflowered	Yes	6.4	2.1	1.52
Fruiting	No	15.8	5.8	1.60
Deflowered	No	12.7	4.7	1.53
L.S.D (0.05) Interaction		1.8	0.7	0.37
F- Significance				
Fruiting		***	***	*
Water stress		***	**	NS
Fruiting x Water stress		NS	NS	NS

*, **, *** and NS. Significant at the 5%, 1% and 0.1% levels, and not significant, respectively.

z. Water use efficiency of individual leaves.

y. CO_2 assimilation rate of individual leaves.

x. Leaf stomatal conductance.

w. Plants were deflowered by removing pistillate flowers daily, throughout the experiment.

The highest leaf area per plant was produced on irrigated deflowered plants, 15410 cm^2, which is 47.5% larger than the leaf area produced by non-stressed fruiting plants (Table 5). Under well watered conditions, fruiting plants produced 31.9%, 43.7%, and 38.6% less leaf, stem and root dry matter, respectively, as compared to non-fruiting plants.

Drought stress had a major effect on fruit biomass per plant. Only approximately 20 g dry wt. of fruit was produced per plant under water stress conditions as compared to 66 g dry wt in irrigated plants. Total dry matter produced was similar in stressed fruiting and deflowered plants. Non stressed fruiting plants produced 23.8 g more total dry matter than non-fruiting plants. Specific leaf weight ranged between 317 and 330 $mg.dm^{-2}$ (Data not shown) and no fruiting and drought stress effects were found.

The levels of translocate sugars in cucumber leaves were affected by water deficits and fruiting. The concentrations of sucrose and raffinose in leaves of stressed plants, 0.75 and 0.21 $mg.g^{-1}$ fresh wt., were more than double those detected in leaves of well-watered plants (Table 6). Stachyose concentration in leaves of drought stressed and deflowered plants ranged between 1.03 and 1.13 $mg.g^{-1}$ fresh wt, significantly lower than the 1.65 $mg.g^{-1}$ fresh wt detected in leaves of well-watered fruiting plants.

Table 5. Effects of water deficit and fruiting on dry matter production and partitioning in cucumber plants.

	Water deficit	Leaf area (cm^2)[z]	Dry weight ($g.plant^{-1}$)[y]			
			Leaves	Stems	Roots	Fruits
Fruiting	yes	6250	20.6	23.4	2.8	19.6
Fruiting	no	10445	33.3	25.8	10.7	66.2
Defruited	yes	8575	28.9	31.4	3.8	--
Defruited	no	15410	48.9	45.8	17.5	--
L.S.D (0.05)[x]		1774	5.2	3.3	3.8	14.1
F-Siginificance						
Water		***	***	***	***	**
Fruiting		***	***	***	**	-
Water x fruiting		*	NS	**	*	-

z. Leaf area measured at the end of the experiment, 51 days after planting.

y. Dry weights, except fruit dry wt., were determined at the end of the experiment; fruits were multiple harvested for 3 weeks and dry weights determined upon harvest.

x. L.S.D. for interaction except for leaf and fruit weight means where L.S.D is for main effects.

*, **, *** and NS. Significant at the 5%, 1% and 0.1% probability levels, and not significant, respectively.

Table 6. Soluble sugar levels in the 5th leaf from the shoot apex of drought stressed and non-stressed fruiting and defruited cucumber plants.

Treatment	Concentration ($mg.g^{-1}$ fresh wt.)		
	Reducing sugars	Sucrose	Raffinose
Water regimen[z]			
Drought stressed	0.99	0.75	0.21
Well watered	0.99	0.33	0.10
L.S.D(0.05)	NS	0.31	0.10

Treatment[y]	Stachyose ($mg.g^{-1}$ fresh wt)
Fruiting,stressed	1.15
Fruiting,watered	1.65
Deflowered,stressed	1.13
Deflowered,watered	1.03
L.S.D (0.05)	0.15

z. Values are the averages of concentrations in fruiting and deflowered plants which were not statistically different.

y. Plants were either allowed to set fruit or had all pistillate flowers removed and were either well watered or drought stressed.

Discussion

Light levels needed for CO_2 assimilation rate to approach saturation in greenhouse grown plants were higher than those reported for growth chamber grown cucumber plants (35). Stomatal conductances lower than 0.4 $cm.s^{-1}$ apparently limited CO_2 availability and resulted in lower assimilation rates. As stomatal conductance increased, leaf transpiration rate continued to increase after A had plateaued. Transpiration has been reported to be a function of stomatal conductance and VPD (38). Temperatures in the range of 16 to 35C had no apparent effect on A in cucumber plants. The effects of higher temperatures on leaf photosynthesis could not be elucidated because of the rapid increase in VPD which probably induced stomatal closure and consequently led to the observed decrease in A. In several plant species, stomatal opening is maintained at temperatures of up 36 degrees centigrade (21).

Water use efficiency decreased rapidly as leaf-air vapor pressure deficit increased, which is in agreement with other reports (6). An increase in VPD would induce stomatal closure (38,39) which limits CO2 availability and ultimately reduces photosynthesis (10,32). Concurrently, the increase in VPD leads to an increase in transpiration (43) which reduces water use efficiency. Comparison of the WUE to VPD relationship of greenhouse and field grown

cucumber plants indicates that at VPDs between 1.5 and 3.0 kPa field plants had higher WUE than greenhouse plants. Plants that develop under stress-inducing conditions of high temperature, water deficits or high irradiance, which are characteristic of environmental conditions in the field, have smaller cells (44) and consequently higher WUE (29). The same reasoning can be used to explain the higher WUE observed in drought stressed greenhouse plants as compared to irrigated plants.

The adverse effects of water deficits on photosynthesis were reversible. Recovery of photosynthetic activity following relief from drought stress was rapid. Sunflower plants are reported to have a threshold leaf water potential below which recovery of photosynthetic capacity following rewatering is incomplete (4). Incomplete recovery of photosynthesis has been reported to be due to incomplete stomatal opening (4). A decrease in stomatal conductance leading to a limitation on CO_2 availability and photosynthesis would be a mechanism that is consistent with the rapid recovery of photosynthesis reported in this study and in other studies (10,32). However, we found that at all calculated intercellular CO_2 levels the assimilation rates of leaves of drought stressed plants were lower than those of control plants. Similar findings have been reported by Krieg and Hutmacher (25) in sorghum. Downton et al. (10) claimed that stomatal closure in leaves of drought stressed plants is not uniform and the calculation of intercellular

CO_2 levels based on gas exchange data was inaccurate. They developed a model for calculating C_i in stressed leaves in relation to those of leaves of control plants. Assuming this model to be correct, we found that the decrease in C_i could only account for about 36.5% of the observed decrease in A of drought stressed plants while the remaining 63.5% have to be attributed to non-stomatal factors, e.g. accumulation of photoassimilates. Higher concentrations of sucrose and raffinose were detected in leaves of drought stressed cucumber plants as compared to well irrigated plants. Although gas exchange measurements and sugar determinations were made in different experiments, these observations would be in agreement with others (2,39) who attributed the decrease in photosynthesis in drought stressed plants to the accumulation of photoassimilates in leaves. Stomatal conductance did not recover completely following rewatering, probably due to the presence of ABA, which accumulates in leaves of drought stressed plants (1,12,29), at levels high enough to prevent complete stomatal opening.

Fruiting cucumber plants and other crops have been reported to have higher CO_2 assimilation rates than deflowered plants (5,17,28). These reports are in agreement with our results. A decrease in stomatal conductance has been suggested as the cause of the decrease in photosynthesis following fruit removal (15,31). Although we found that stomatal conductances were higher in fruiting

than in deflowered plants, the difference in gs is unlikely to be the cause of the observed difference in A associated with fruit bearing in cucumber plants. Based on the g_s to A relationship reported in this study, the lower stomatal conductance observed in well-watered defruited plants cannot account for the lower CO_2 assimilation rates of these plants as compared to fruiting plants. On a whole plant basis, fruiting plants, despite having a smaller leaf area as compared to deflowered plants, produced a total amount of plant dry matter that was equal to the amount produced by deflowered plants. This indicates that even under conditions of drought stress, fruiting plants had a higher overall photosynthetic capacity than non-fruiting plants. Under well irrigated conditions, the higher CO_2 assimilation rates of fruiting plants apparently overcompensated for the smaller leaf area resulting in a larger total amount of dry matter being produced as compared to deflowered plants. Choma et al.(5) found that, on whole plant basis, net photosynthesis and total dry matter production were similar in fruiting and deflowered strawberry plants. Fruit bearing altered the dry matter partitioning strategy of the plant. Fruits acted as strong sinks to which photoassmilates were preferentially allocated at the expense of vegetative plant parts. Similar findings for cucumbers have been reported (28). The competitive effect of fruits added to the adverse effects of water deficits in limiting the growth of vegetative

plant parts. The observed reductions in leaf area of drought stressed cucumber plants are in agreement with other studies on field beans (24) and sunflower(44). Drought stressed cucumber plants did not allocate more dry matter to roots as has been reported to occur in other crops (21,26).

Increased sink demand in fruiting cucumber plants has been suggested to induce increases in A and in the synthesis of the translocate sugar stachyose (30). We found that stachyose levels were highest in leaves of fruiting plants, which is in contrast with the findings of Pharr et al. (30) who reported higher rates of stachyose synthesis but lower concentrations of the sugar in leaves of fruiting cucumber plants in comparison with deflowered plants. Our results indicate that when sink demand is limited, e.g. in drought stressed and deflowered plants, stachyose levels in source leaves are lower than those observed in plants in which sink demand is high.

The rapid recovery of photosynthetic activity following a period of drought stress indicates that cucumber plants would be capable of recovering from mild water deficits caused by high transpiration rates under field conditions, without long term adverse effects. Mechanisms through which drought stress could have reversible effects on photosynthesis, such as reduced chloroplast volume, have already been suggested (17,22). The results of this study also indicate that the effects of water deficits and

fruiting on photosynthesis in cucumber plants cannot be explained solely by the observed changes in stomatal conductance. Other factors, such as accumulation of photoassimilates, apparently also impact on CO_2 assimilation in cucumber plants.

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CHAPTER II

Evidence for osmotic adjustment in leaf tissue of pickling cucumbers in response to drought stress

Abstract

Nine pickling cucumber lines including Cucumis sativus L. var. hardwickii were cultured in the greenhouse and subjected to water deficit treatments beginning at the onset of anthesis. Leaf water potentials of stressed plants ranged from -0.71 to -0.77 Mpa. The osmotic potentials of expressed sap of rehydrated leaves were 0.06 to 0.1 Mpa lower in stressed than in non-stressed plants due to solute accumulation within the tissue. No differences in the magnitude of osmoregulation were found among the cucumber genotypes tested. Leaves of cucumber plants did not osmoregulate in response to the first drought exposure. The concentration of potassium in leaf lamina tissue (on a fresh wt. basis) of water stressed plants (82 umol/g) was 2.5 times that of control plants (33.3 umol/g). The increase in leaf potassium could account for all of the observed decrease in leaf sap osmotic potential in water stressed plants. Sucrose concentration was higher while the concentration of stachyose was lower in leaves of drought stressed plants. However, the contribution of sugars to changes in leaf osmotic potential was insignificant. The magnitude of osmotic adjustment in leaves of stressed plants decreased significantly within 48 hrs of rewatering

the plants. Changes in concentration of K^+ and sugars in leaf lamina tissue did not account for the observed decline in solute concentration following rewatering.

Introduction

Osmotic adjustment increases plant tolerance to drought stress by enabling the plant to maintain cell turgor and tissue hydration at lower water potentials (2,3,8,16). A number of plant species have been shown to undergo osmoregulation in response to water deficits (1,6,20) but it has not been demonstrated to occur in cucurbits. In wheat, osmotic adjustment is a heritable trait (13) and is believed to be responsible for differences in the drought tolerance of wheat cultivars (5,11,12). Since cucumbers originated in the semi-arid regions of Africa and southwest Asia (6), drought tolerance or avoidance genes would be expected to be found within a diverse population of Cucumis sativus.

Solutes which accumulate and contribute to osmotic adjustment include potassium, chloride and amino acids (9), betaine (10), reducing sugars (2) and non-reducing sugars (1). Organic solutes are metabolized or assimilated into other compounds following relief of water stress resulting in loss of adjustment. Consequently, the lowered osmotic potential is maintained only for a limited period of time,

six to ten days, after stress is relieved (15,20).

The objectives of this study were to : (1) to evaluate the osmotic adjustment capacity of several pickling cucumber genotypes, (2) to identify solutes involved in osmoregulation in cucumbers and (3) to study the maintenance of osmotic adjustment following relief of drought stress.

Materials and Methods

Plant material: Pickling cucumber (Cucumis sativus L.) plants were cultured during the months of May to August of 1986 and 1988 in the Plant Science Greenhouses at Michigan State University. Genetic lines examined in this study included Gy 14, Monoecious and gynoecious Clinton, M21, Littleleaf, Sumpter and hardwickii, a botanical variety of C. sativus. Seeds were sown in 7 or 11 liter plastic containers filled with a 1:1 peat (Baccto professional mix) to sandy loam soil media depending upon the experiment. Plants were irrigated daily with a drip system and fertilized twice weekly with a 20 - 8.8 - 16.6 (N-P-K) Peter's soluble fertilizer at a concentration of 0.2 g/liter. Day/ night temperatures were 30 / 20C +/- 5C with no supplemental lighting provided. Plants were trained to vertical bamboo stakes and pollination was achieved using bees which were introduced into the greenhouse at anthesis.

Water deficit: Drought stress treatments were initiated at the onset of anthesis by withholding water from the plants for 3 to 4 days until plant water potential decreased to -0.5 to -0.8 Mpa after which stressed plants were rewatered. Stressed plants were subjected to a total of four successive drying cycles. Control plants were watered once or twice daily throughout the experiment.

Fruit set on certain treatment plants was prevented by detaching the pistillate flowers from those plants daily throughout the duration of the experiment.

Water potential determinations: A SoilMoisture Equipment Corp. Model 3000 series pressure chamber was used to measure the water potential of the first fully expanded leaf which usually corresponded to the fourth or fifth leaf from the shoot apex. Measurements were made between 6 and 7 A.M. The inside of the pressure chamber was lined with moistened paper towel to increase relative humidity inside the chamber and thus minimize water loss from the leaf. Following measurement of water potential, the entire leaf was immediately removed from the chamber, folded, sealed in a plastic vial and placed in ice for transfer to the laboratory.

Osmotic potential determinations: Sections of the leaf used in water potential measurement were rehydrated by floating on distilled water for 4 hours at 4C, then blotted dry, placed in plastic vials and stored at -20 C. After thawing the leaf tissue, the leaf was placed in the barrel

of a 3 cc syringe and pressed to express the leaf sap. The osmolality of the expressed sap was measured using a Wescor 5000 vapor pressure osmometer. The pressure potential of the leaf was calculated as the mathematical difference between the estimated water and osmotic potentials of that leaf. When changes in leaf osmotic potential over time were studied, leaf samples were collected at the end of the second drought stress period and at 24 and 48 hours after the plants were rewatered.

Heat girdling: Leaf petioles were heat girdled to block phloem transport by passing hot air, at a temperature of 65C, over a 4 cm region of the petiole for 3-5 minutes. Leaf sections were collected prior to and 24 hours after girdling. All plants were rewatered immediately following girdling. Osmotic potentials of the leaf sections were then determined.

Leaf sugar and potassium determinations: Leaf samples were freeze dried for 24 hours then finely ground with a mortar and pastel. Sugars were extracted from tissue subsamples (0.2 g) with 80% ethanol at 70 C for 1 hour. The extract was filtered through a No. 1 Whatman filter paper and the ethanol evaporated. The residue was redissolved in 25 ml of deionized water and an aliquot of the resultant solution filtered through a 0.45 um Millex-HA filter unit. Sugars and sugar alcohols were separated and were assayed using a Dionex Carbopac PA1 anion exchange separation column with a Dionex series 4000i High Performance Ion

Chromatography Module and a pulsed amperometric detector with a Gold electrode. A 0.1 M NaOH solution was used as the eluant. Potassium concentration in leaf tissue extracts were determined by standard procedures using atomic emission spectrophotometry (Instrumentation Laboratory, Video 12).

Results

Osmotic potentials in leaves from drought stressed plants ranged from -0.71 to -0.77 MPa as compared to -0.64 to -0.68 MPa in leaves of well watered plants (Table 1). These osmotic potential differences are believed to reflect differences in solute accumulation in leaf lamina tissue since the leaves had been rehydrated prior to measurement of leaf osmolality. Osmotic potentials did not vary among the inbred lines tested. Osmotic adjustment, calculated as the mathematical difference between the leaf osmotic potentials of stressed and non-stressed plants, was similar in all genotypes tested.

Plant water potentials at the end of the three water deficit cycles ranged between -0.48 and -0.73 Mpa (Data not shown), which represented a moderate level of stress in the cucumber plants. Differences between leaf osmotic potentials of drought stressed and control plants ranged between 0.03 and 0.09 Mpa and were significant only after the second and third exposures to water deficit (Table 2).

Table 1. Leaf osmotic potentials of eight pickling cucumber genotypes exposed to drought stress or irrigated during fruit development.

Genotype	Osmotic potential (Mpa) [z] Drought stressed	Irrigated	Osmotic potential difference [x]
G. Dwarf 2780	-0.70	-0.64	0.06
Gy14	-0.75	-0.66	0.09
G. Clinton	-0.75	-0.68	0.07
M. Little Leaf	-0.77	-0.67	0.10
M. Clinton	-0.76	-0.68	0.08
M 21	-0.71	-0.65	0.06
C.sativus var hardwickii	-0.74	-0.66	0.08
Sumpter	-0.73	-0.65	0.08
Mean	-0.74	-0.66	
Significance			
Cultivar	NS		NS
Stress	***		—
Cultivar X Stress	NS		—

z. Leaf samples were collected at the end of the second drought exposure.
y. G. and M. indicate a gynoecious or monoecious flowering, respectively.
x. Mathematical difference between the leaf osmotic potentials of stressed and well irrigated plants.
***, NS. Siginficant at the 0.1% probability level and not significant, respectively.

Table 2. Osmotic potentials of cucumber leaves during three exposures to drought stress under greenhouse conditions.

Water regimen	Leaf osmotic potential (MPa)[z] Stress exposure[y] First	Second	Third
Drought stressed	0.73	0.65	0.72
Well-watered	0.70	0.56	0.66
F-Significance	NS	*	*

z. Osmotic potential of the sap of the 4th or 5th leaf from the shoot apex of cucumber plants. Leaves were rehydrated prior to osmotic potential determination.
y. Plants were not watered until leaf water potential had reached about -0.6 Mpa; plants were then rewatered and another stress exposure was initiated.
NS. Not significant at the 5% probability level.

Stressed leaves had an expressed sap osmolality of 306.7 mmolal which was higher than that of non-stressed leaves (Table 3). Reducing sugars, representing the sum of the concentrations of glucose, fructose and galactose, were present at similar levels in leaves of stressed and non-stressed plants. Under both water regimens, reducing sugars accounted for about 2% of the total leaf sap osmolality. Sucrose was present at a concentration of 2.2 umol/g fresh wt. in leaves of drought stressed plants which represented a contribution of 0.73% to the total leaf osmolality. Sucrose concentration in leaves of control plants was less than half the concentration detected in leaves of stressed plants. In well-watered plants, stachyose was detected at a concentration of 2.5 umol/g fresh wt., 0.8 umols higher than the level detected in leaves of stressed plants. Potassium was found at a higher concentration and made a contribution of 26.8% to leaf osmotic potential in leaves of stressed plants, as compared to 12.3% in leaves of control plants.

Continuously well- watered plants maintained solute potentials of -0.63 to -0.65 Mpa throughout the 48 hour period while the solute potentials of stressed plants increased from -0.72 to -0.66 Mpa (Table 4). Forty- eight hours after stressed plants were rewatered, significant osmotic potential differences were still evident in the leaves of these plants. Within 48 hrs of rewatering, leaf osmotic potential in fruiting plants increased from

-0.7 to -0.64 Mpa, while in deflowered plants it increased from -0.67 to -0.65 Mpa during the same period of time.

The concentration of reducing sugars, sucrose and stachyose decreased within the 48 hours following rewatering while no change was observed in the potassium level (Table 5). The cumulative changes observed in solute concentration within 48 hours following rewatering were insignificant in comparison with the observed changes in leaf sap osmolality within the same period. It was observed that changes in assayed solute concentrations following rewatering were similar in fruiting and defruited plants (Data not shown).

Within 24 hours of girdling the leaf petiole, stressed leaf osmotic potential decreased by 43.3 mmolal while the potassium concentration in the same leaves increased from 98.3 to 154.7 umol/g fresh wt., a change of 56.4 umol/g (Table 6) which could account for 100% of the increase in leaf sap osmolality following petiole girdling. Other inorganic solutes imported via the xylem would be expected to have proportional increases in concentration. In non-stressed leaves, the increase in potassium concentration accounted for 52.8% of the increase in leaf sap osmolality following girdling.

Table 3. Leaf osmolality and concentration of selected solutes in cucumber leaf lamina tissue under drought stress and well irrigated conditions.

		Solute concentration (umol/g fresh wt.)			
Treatment	Leaf osmolality (mmolal)	sap sugars[z]	Sucrose	Reducing stachyose	K_+
Stressed	306.7	5.7	2.2	1.7	82.0
Non-stressed	271.3	5.5	1.0	2.5	33.3
F-Significance	***	NS	*	*	**

z. Mathematical sum of concentrations of glucose, fructose and galactose.
NS. Not significant at the 5% probability level.

Table 4. Changes in cucumber leaf osmotic potentials following relief from water stress.

Time after rewatering	Leaf osmotic potential (Mpa)			
	Water regimen[y]		Fruit bearing[z]	
	Stressed	Irrigated	Fruiting	Defruited
0 hrs[w]	-0.72	-0.65	-0.70	-0.67
24 hrs	-0.68	-0.63	-0.65	-0.66
48 hrs	-0.66	-0.63	-0.64	-0.65
F- significance				
Fruiting X Time after rewatering	—		**	
Water regimen X Time after rewatering	**		—	

z. Stressed plants were subjected to 2 drought stress cycles and measurements were made at the end of the second stress cycle.
y. Plants were either defruited by removal of pistillate flowers or allowed to set fruits.
x. The mathematical difference between the leaf osmotic potentials of drought stressed and well watered plants.
w. Leaf lamina tissue samples were collected prior to rewatering of plants.
**.Significant at the 1% probability level.

Table 5. Changes in solute concentrations in leaf lamina tissue of drought stressed cucumbers following rewatering.

Time after rewatering	Solute concentration (mg/g fresh wt.)				
	Reducing sugars	Sucrose	Raffinose	Stachyose	K_+
0 hrs[z]	5.5	2.2	0.35	1.71	65.4
24 hrs	5.5	1.6	0.25	1.73	69.2
48 hrs	3.8	0.3	0.22	1.34	72.3
L.S.D (0.05)	1.3	0.8	NS	0.20	NS

z. Leaf tissue was sampled just before rewatering of plants and rehydrated by floating leaf sections on distilled water for 4 hours at 4C.

NS. Not significant at the 5% probability level.

Table 6. Changes in solute relations in heat girdled leaves of drought stressed and well irrigated cucumber plants following rewatering.

Treatment	Time[z] (hours)	Leaf sap osmolality (mmolal)	Potassium (umol/g fresh wt)
Drought stressed	0	307	98.3
Well irrigated	0	280	46.2
Drought stressed	24	351	154.7
Well irrigated	24	347	81.2
L.S.D (0.05) interaction		20	16.4
F-significance			
Water regimen		*	***
Time after girdling		***	***
Water regimen X Time after girdling		0.09%	0.07%

z. Leaf tissue was sampled prior to and 24 hrs after girdling.

*, and ***. Significant at the 5% and 0.1% probability levels, respectively.

Discussion

Pickling cucumbers undergo osmotic adjustment in response to drought stress based on the observed osmotic potential differences between drought stressed and well watered plants. The magnitude of the adjustment ranged between 0.06 and 0.1 MPa and was reproducible in replicated repeated experiments. In comparison, osmotic adjustments of 0.1 to 0.4 Mpa have been reported for agronomic crops, e.g. maize and sorghum (1,19). Genotypic differences in osmoregulatory capacity have been reported for other crops (7, 11, 12, 21). However, in Cucumis sativus L., the capacity for osmotic adjustment does not appear to vary among the various genotypes tested. The genotypes used in this study were of a relatively narrow genetic base of inbred lines that had been bred for growth under optimal cultural conditions. Because of their limited genetic diversity, these genotypes did not exhibit the variability and the magnitude of the response needed for osmotic adjustment to have a significant impact on the degree of drought tolerance in pickling cucumbers. A more diverse pool of cucumber genotypes should be investigated in order to identify cucumbers with a higher degree of drought tolerance. Cucumber plants did not exhibit changes in osmotic potential in response to the first exposure to drought stress indicating that prior exposure to water deficit might be needed before osmoregulation could occur. The magnitude of osmotic adjustment capacity has been

reported to increase with repeated exposure to water deficits (14,15). Our results indicate that cucumber leaves have a limited capacity for osmoregulation which did not allow for an increase in the magnitude of osmotic adjustment following the second drought stress exposure.

The increase in the concentration of potassium in leaves of stressed plants could account for 100% of the decrease in leaf osmotic potential as a result of drought stress, while the contribution of sugars was insignificant. Handa et al. (1983) found that in tomato cell cultures, potassium contributed 13.8% of the total cell osmotic potential while sugars contributed about 20% of the osmotic potential, much higher than levels observed in our study. Potassium, chloride and amino acids have been reported to account for 80% of the decrease in osmotic potential in stressed leaves, while sugars accounted for the remaining 20% (9). In contrast, reducing sugars (2) and non-reducing sugars (1) were reported as the main solutes that accumulated in stressed leaves of maize and sorghum. However, the levels of sugars we detected in leaf tissue are comparable to those reported for cucumbers (17) which suggests that sugars do not have a major role in osmotic adjustment in cucumbers.

The magnitude of the difference between the osmotic potentials of stressed and non-stressed leaves was found to decrease with time after rewatering, which is in agreement with others (14,15). However, the rate of change

in osmotic potential difference was higher in the current study. Changes in the concentrations of assayed solutes could not account for the observed increase in leaf osmotic potential following rewatering. The increase in leaf sap osmolality following heat girdling of the petiole could be accounted for by the increase in the concentration of inorganic ions.

Fruiting influenced the maintenance of osmotic adjustment in leaves. The more rapid decline in solute concentration in leaves of fruiting plants following rewatering suggests an effect of fruits on leaf solute redistribution. An effect of fruits on osmoregulation was implied by Ackerson (1981) who suggested that solutes accumulated in leaves of stressed plants as a result of a decreased sink capacity. Resumption of fruit growth at a higher rate after rewatering would increase sink strength and the demand for solutes out of leaves. Fruits had no apparent effect on the levels of assayed solutes in stressed leaves following rewatering. The observed effect of fruiting on leaf osmotic potential following rewatering is probably due to effects on other solutes not assayed in this study.

Osmotic adjustments of 0.06 to 0.08 Mpa were apparent in leaves of drought stressed cucumber plants and K^+ appears to be the major ion contributing to osmoregulation. No re-distribution of accumulated K^+ in leaf tissue of drought stressed plants was observed following rewatering. Consequently, the increase in leaf osmotic potential of

drought stressed plants following rewatering must have been due to changes in the concentrations of other solutes.

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CHAPTER III

Water deficit effects on pickling cucumber plant growth, fruit productivity and quality

Abstract

In greenhouse experiments, eleven monoecious and gynoecious pickling cucumber parental lines and F1 hybrids with different vine types were subjected to water deficits during the flowering and fruiting growth stages. In all genotypes tested, drought stress reduced plant productivity. Water stressed plants set 32 to 42.3% fewer fruits and had 25.5 to 46.4% lower total fruit dry weight than non-stressed plants during a three week harvest period. Fruits from stressed plants were significantly shorter and had lower LD ratios than fruits from non-stressed plants. The incidence of incomplete seed set increased in fruits of drought stressed plants. Water deficits had no apparent effect on the incidence of misshapen fruits. Fruit growth rate was reduced by water deficits; the first fruit set on a plant needed about 2 days longer to reach a diameter of 42 mm. It was estimated that 33% of the decrease in fruit growth rate was due to water supply limitation, while assimilate supply limitation accounted for 67% of the total decrease in fruit growth. Water deficits did not alter the fruiting bearing pattern of cucumber plants. The distribution of fruit harvest over the three week harvest period was similar in

stressed and non-stressed plants. Vegetative biomass (on a dry wt. basis) of water stressed plants was 20.8 to 38.8% lower than those of non-stressed plants. It is concluded that, under the experimental conditions of this study, the genotypes tested have a low drought tolerance.

Introduction

Water deficits adversely affect cucumber plant growth (14) which can ultimately result in fruit yield reductions in cucumbers (3). The flowering and fruiting period has been identified as an important stress- sensitive growth stage in plant development as related to crop productivity. Decreases in fruit productivity under conditions of water deficit have been attributed to ovule abortion, and consequently low fruit set, poor seed set and slow expansive growth of fruits (7,17,18).

Machine harvested pickling cucumbers are mainly grown under rainfed conditions. In the midwestern United States, cucumber crops are exposed frequently to temporary droughts of 7 to 10 days during the summer months (16) which reduce potential fruit yield and quality (5,8).

Limited research has been conducted on the responses of pickling cucumbers to drought stress. This study was conducted with the following objectives; to study the effects of water deficits on cucumber plant growth, fruit productivity and quality, and to identify genotypic

differences in responses to drought that might exist among several cucumber parental lines and cultivars.

Materials and Methods

Greenhouse experiments were conducted at Michigan State University during mid summer of 1986 and 1987 and during April and May of 1988.

Plant material:Pickling cucumber (Cucumis sativus L.) seeds were sown in a 1:1 peatmoss to sandy loam soil mixture in 11-liter containers. Plants were fertilized twice weekly with a 20- 8.8- 16.6 (N-P-K) Peter's soluble fertilizer at 0.2 g/l. At anthesis, a beehive was placed in the greenhouse to facilitate pollination. Temperatures were maintained at 30 +-5C during the day and 20 +-5C at night and no supplemental lighting was provided. During the vegetative growth stage, all plants were watered daily.

Water deficit: Drought stress treatments were initiated at the onset of anthesis by withholding water from the plants for a period of 3 to 4 days until plant water potential had decreased to -0.6 to -0.8 Mpa. Plant water potential measurements were made at dawn using a Soilmoisture Equipment Corp. pressure chamber. Control plants were watered daily throughout the experiment.

Fruit length and diameter were measured daily following fruit set. Fruits were harvested when they reached a diameter of 50 +/- 3mm, weighed and internal fruit

characteristics evaluated and measured. Determinations of fruit dry matter content were also made by dehydrating fruit samples in an oven at 65C for 72 hrs.

Genotype evaluation: Seven pickling cucumber genotypes, gynoecious dwarf 2780, Gy14, gynoecious Clinton, M21, M21x Gy14 F1, M21 x Clinton F1 and monoecious Clinton (Campbell Institute for Agricultural Research, Napoleon, Ohio) were included in this experiment. These genotypes are either parental lines of numerous commercial cultivars or F1 hybrids. Plants were subjected to several drought stress cycles during the flowering and fruiting growth stages. Fruits were harvested when they reached 5 +/- 0.3 cm for a three week period. Individual fruit length, diameter and fresh and dry weights as well as total number of fruits harvested per plant were recorded throughout the period. Above ground vegetative plant parts were harvested and dry weights determined after final fruit harvest. Fruit volume was estimated from length and diameter measurements assuming a cylindrical fruit shape. A fruit density factor was calculated by dividing the final fruit dry weight by final fruit volume. Percent dry matter and fruit density have been shown to remain constant during cucumber fruit ontogeny (15) except when placental hollows or carpel separation occur within a fruit. Fruit dry weight used in plotting fruit growth curves were obtained by multiplying density factor by the daily fruit volume. No significant difference in density was found between stressed and non-

stressed fruits (Data not shown). A mean daily fruit growth rate (fresh weight basis) was calculated by dividing the mathematical difference between the final fruit fresh weight and the estimated initial fresh weight by the number of days to harvest. A similar rate was calculated for the increase in fruit dry weight.

Results

Plants grown during the summer of 1986 were characterized by extensive leaf and shoot growth which was probably due to an above average number of cloudy days during the growing period. During the summer of 1987, there were fewer cloudy days and vegetative plant growth was less extensive as compared to 1986.

Drought stress during flower and fruit development adversely affected both vegetative and reproductive growth in pickling cucumber plants during both years of experimentation. The amount of total leaf and stem (shoot) biomass produced by drought stressed plants was 34% to 53% lower than that produced by well-watered plants of the same genotype (Table 1). Reductions in fruit biomass production due to drought stress ranged between 19 and 54% in 1986 (Table 1) and approximately 39% in 1987.

The lower fruit biomass production under drought conditions could largely be attributed to fewer fruits being set on the plants and the slower expansive fruit

growth rates. In 1987, only approximately 3.1 fruits set on each plant during a three week period under drought conditions as compared to 4.9 fruits per plant in irrigated plants (Table 2). Drought induced plant water deficits also delayed fruit maturation, fruits reaching harvestable size (5 cm diameter, 275 ml volume), by 2 days (Figure 1). Expansive fruit growth rates under drought stress conditions, expressed on a volume basis, were significantly lower than the growth rates of fruits from well irrigated plants as evidenced by the lower slopes of the fruit volume X time regression curves (Figure 1).

All the pickling cucumber genotypes evaluated responded similarly to drought stress. Although there was a statistically significant interaction between genotype and water regimen in 1986, the interaction was primarily due to large vegetative growth and fruit productivity differences among the genotypes under well irrigated conditions (Table 1). Gynoecious Clinton and hardwickii, however, produced the highest and lowest fruit biomass (dry weight basis) respectively, under both water regimens.

Table 1. Effects of drought stress on dry matter productivity in selected pickling cucumber genotypes (1986).

Genotype	Dry weight($g.plant^{-1}$)			
	Shoot dry weight[z]		Fruit dry weight[y]	
	Well-watered	Drought-stressed	Well watered	Drought stressed
G. Dwarf	46.0	24.8	52.7	29.3
Gy14	35.0	22.9	45.2	20.7
G. Clinton	38.0	21.7	64.6	30.1
G. Littleleaf	37.1	23.7	50.7	21.7
M. Clinton	60.0	32.1	28.3	23.0
M 21	39.9	26.2	41.1	25.4
M. Littleleaf	51.4	29.0	29.5	15.2
Sumpter	47.4	28.1	41.6	21.7
Hardwickii	72.4	44.8	17.8	8.2
L.S.D(0.05)	4.3		10.4	
Drought stress X Genotype	***		**	

z. Weight of leaves and stems after the final fruit harvest.
y. Fruits were multiple harvested for a period of 3 weeks.
x. G. and M. indicate gynoecious and monoecious flowering, respectively.
*** and **. Significant at the 0.1% and 1% probability levels, respectively.

Table 2. Effects of genotype and water deficits on fruit productivity productivity and quality of greenhouse grown pickling cucumbers (1987).

	Fruit productivity[z]		Percent of fruits[y]	
	number/ plant	total d.wt g/plant	misshapen	Incomplete seed set
Cultivar				
G. Dwarf	4.2	29.4	27.9	29.7
Gy14	4.7	32.8	39.3	22.1
G. Clinton	3.8	28.9	18.8	21.4
M21	4.1	31.6	7.8	28.4
G.Clintonx M21	4.4	34.0	13.6	24.8
Gy14 x M21	4.2	30.0	21.9	22.2
M. Clinton	2.8	24.6	0.0	18.2
x				
L.S.D (0.05)	0.7	NS	10.9	NS
Water regimen				
Drought Stressed	3.1	22.8	17.1	32.2
irrigated	4.9	37.6	15.9	15.3
x				
L.S.D (0.05)	0.4	3.3	NS	6.7

NS. Not significant at the 5% probability level

z. Fruits were harvested for aperiod of 3 weeks.

y. Seed set was evaluated visually for presence of aborted ovules.

x. No genotype X water regimen interaction was found and L.S.D values are for comparison of genotypes and water regimen.

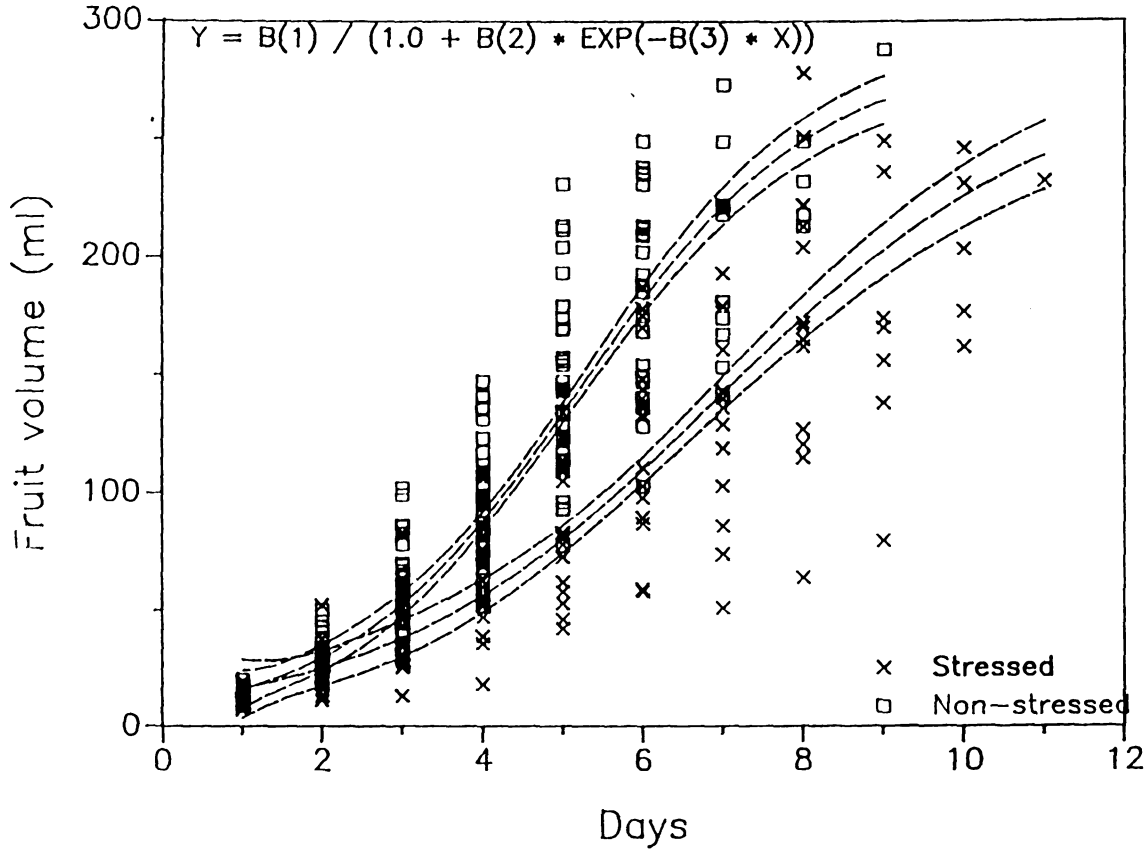

Fig. 1. Effects of water regimen on fruit growth rate. Fruit volume was calculated from daily measurements of fruit diameter and length and assuming a cylindrical fruit shape. Confidence limits at the 5% level are shown.

In the 1987 experiment, the genotypes did not differ in total fruit dry weight per plant (Table 2), and were equally affected by the induced drought stress.

In terms of number and timing of fruit set, genotypic differences were apparent. Monoecious Littleleaf and hardwickii in 1986 (Data not presented) and monoecious Clinton in 1986 (Table 2) set the fewest fruits per plant. Typically, the gynoecious genotypes were the higher yielders when evaluated on a fruit biomass basis especially under irrigated conditions. Gynoecious plants were also observed to set fruit earlier than monoecious plants. Although both flowering habits/ genotypes exhibited cyclical fruit setting patterns, the percentage of total fruit harvested during each of the first two maturation cycles was nearly equal for the gynoeciuos genotypes (e.g. G. Dwarf: Figure 2) under both water regimens. Monoecious lines, in contrast, set only approximately 10% of their fruit production for the three week period during the first cycle.

The incidence of misshapen fruits produced by cucumber plants did not increase in response to water deficits, but were influenced by genotype. No misshapen fruits were produced by monoecious Clinton plants while 39.3% of fruits harvested from Gy14 plants were misshapen (Table 2).

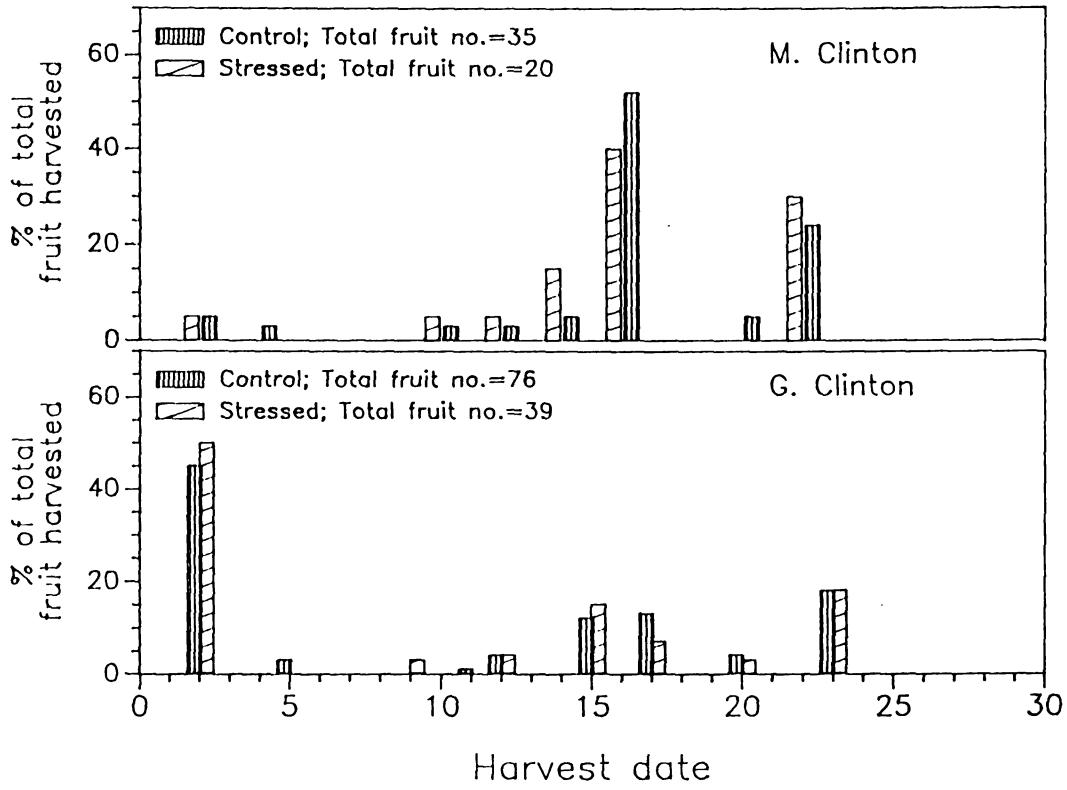

Fig. 2. Distribution of fruit harvest over a three-week harvest period. Fruits were harvested when 50±3mm in diameter. G. and M. refer to gynoecious and monoecious flowering, respectively.

The percentage of misshapen fruits produced by other genotypes in this study ranged between 7.8% and 27.9%. The incidence of fruits with aborted ovules and consequently limited seed set more than doubled in response to drought stress but no differences were found among the genotypes tested.

Fruits of non stressed plants were, on average, 15.8 mm longer and had larger LD ratios than stressed fruits of equivalent diameter. Because fruits were harvested when they reached a diameter of 50 +/- 3 mm, diameters of stressed and non-stressed fruits were not significantly different (Table 3). The seed cavity diameter in drought stressed fruits, expressed as a percentage of the fruit diameter, was 1.9% smaller than that of well-watered fruits.

The rate of fresh weight increase for stressed fruits was 29.9% lower than that of non-stressed fruits (Table 4) but only 19.9% lower when expressed on a dry weight basis. The second fruit set on non-stressed plants grew more slowly than the first fruit set on the plant. In stressed plants, the growth rates of the first and second fruit were similar to that of the second fruit set on watered plants, resulting in an interaction between water regimen and fruit number.

Table 3. Effects of water deficits on cucumber fruit dimensions.

Water regimen	Fruit length (mm)	Fruit diameter (mm)	z LD ratio	Seed cavity (% of diameter)
Drought stressed	115.4	48.0	2.40	47.4
Well-Watered	131.6	49.5	2.66	49.5
F-Significance	***	NS	*	*

z. Ratio of fruit length to fruit diameter.
NS. Not significant at the 5% probability level.

Table 4. Effects of water stress and fruiting sequence on cucumber fruit growth rates.

Water regimen	Fruit number[z]	Growth rate (g/day) Fresh weight basis	Dry weight basis
Watered	1	28.4	1.42
Watered	2	21.9	1.11
Stressed	1	19.9	1.14
Stressed	2	19.9	1.14
L.S.D (0.05)[y]		2.7	0.14
Stress x fruit number		***	**

z. Fruit no. 1 and 2 are the first and second fruits set on the plant.

y. L.S.D for the stress x fruit number interaction. *** and **. Significant at the 0.1% and 1 % probability levels, respectively.

Discussion

Water deficits had adverse effects on cucumber plant growth and productivity. None of the genotypes studied exhibited drought tolerance as they suffered decreases in vegetative and reproductive growth upon exposure to drought stress. Water deficits are known to cause reductions in photosynthetic rates by as stomata close in stressed plants (6). The combined effects of a smaller leaf area and reduced photosynthetic rates would limit a stressed plant's capacity to produce dry matter. This is reflected by the observed decrease in total dry matter produced in water stressed plants. The decrease in fruit dry matter production in drought stressed plants was mostly due to the decrease in the number of fruits set by these plants. Fruits on stressed plants frequently ceased expansive growth at some point following pollination. Pollen viability is known to decrease upon dehydration (9). Pollen used in pollination in the current study, however, was obtained from well watered plants and was viable, as indicated by the successful pollination on non-stressed plants. However, a dehydrated stigma, as was probably the case in stressed flowers, might have retarded pollen germination or slowed down pollen tube elongation which ultimately and lead to a decrease in the percentage of ovules being fertilized. Seed set and development would have been poor under such conditions, which is consistent

with that observed in fruits of drought stressed plants. The genotypes tested did not differ in their capacity to support seed set and development under conditions of drought stress. Although fruit set and the total number of fruits set was decreased by water deficit, drought stress had no apparent effect on the fruit bearing pattern of cucumber plants. Drought stressed cucumber plants were apparently unable to support fruit growth until a certain number of days had elapsed after the first fruit was harvested and consequently no shift toward earlier fruit set was observed.

A high LD ratio is a desirable characteristic in pickling cucumber fruits. Drought stress reduced fruit LD ratios by limiting fruit elongation. The reason for such an effect has not been identified. However, gradients in water potential within the fruit might be expected, with lower water potentials at the blossom end of the fruit which is furthest away from the water source, the peduncle. Fruits on drought stressed plants were frequently observed to develop tapered ends at the blossom end, and in severely stressed plants, shrinkage of fruit tissue also started at the blossom end of the fruit. The observed decrease in seed cavity diameter might be due to poor seed set in stressed fruits which probably led to a decrease in the production of growth promoting hormones needed for placental tissue growth. Limited fruit elongation under conditions of drought stress might also be associated with a reduced

supply of hormones from developing seeds.

The contributions of water limitation and assimilate supply limitation on fruit growth were estimated using data on fruit growth rates. Expressed on a dry weight basis, stressed fruits grew 19.9% slower than non stressed fruits; this probably represents the direct effect of assimilate supply limitation. On a fresh weight basis, growth rate of stressed fruits was 29.9% lower than that of non stressed fruits. The difference between the dry weight and fresh weight basis percentages might reflect the direct contribution of water limitation on cell expansion and the increase in fruit size.

Following the harvest of the first fruit set on a plant, assimilates available for fruit growth apparently become limiting by the time the second fruit is set on a cucumber plant. The first fruit set on the plant probably depleted stored assimilates and limited leaf growth (1,15). The growth rate of the second fruit on well watered plants was similar to that of fruits of stressed plants where photosynthesis is limited by water deficit. Increased competition between fruits and other sinks in the plant probably contributed to the decline in dry weight gain in the second fruit.

It was observed that in stressed plants, small misshapen developing fruits regained normal shape as they increased in size, probably due to rewatering of stressed plants following each stress exposure. Similar observations were

made by Kanahama and Saito (12) in cucumber plants which had been partially defoliated. This might explain the lack of an effect of drought stress on the incidence of misshapen fruits.

Differences in plant morphology and in sex expression had no apparent effect on the degree of drought tolerance in pickling cucumbers. Vegetative shoot growth was extensive under greenhouse conditions and vines were generally larger than typical field grown plants of similar genotypes. However, vine growth characteristics, e.g. gynoecious dwarf 2780 vs Gy 14 which had extensive vine growth, had no apparent effect on the response of cucumber plants to the water deficits. Both, monoecious and gynoecious genotypes were equally susceptible to drought stress. The delayed fruiting habit in monoecious genotypes allowed them to produce a larger leaf area but did not improve their tolerance to drought stress, expressed on the basis of fruit and total biomass productivity.

The genotypes tested in this study had a relatively similar genetic background which might explain the lack of a difference in their response to drought stress. C. sativus var. hardwickii, which was the only non-commercial genotype included in this study did not exhibit drought tolerance. However, characteristics which might confer drought tolerance in hardwickii and other genotypes under field conditions, such as rooting pattern, might have been suppressed under greenhouse growing conditions. The results

of this study also indicated that inbred parental lines used in development of commercial cultivars have been bred for growth under optimal environmental conditions. Consequently, the potential for improvement of drought tolerance in currently available commercial cucumber genotypes is apparently limited. Increasing drought tolerance of pickling cucumbers would probably require the utilization of C. sativus germplasm from arid and semi-arid regions of the world.

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SUMMARY AND CONCLUSIONS

The objectives of this study were to identify genotypic differences in responses to drought stress, that might exist among several pickling cucumber parental lines and cultivars, and to determine the effects of water deficits and fruiting on selected physiological processes in pickling cucumber plants.

In trying to improve the drought tolerance of cucumbers to drought stress, several environmental and plant factors have to be taken into consideration, including:

a- cucumber plant morphology.

b- the high light intensities, high temperatures and low air humidity which frequently accompany drought stress.

c- the intermittent and unpredictable occurence of water deficits.

d- fruit set (pollination, fertilization),under water limiting conditions.

These factors will be discussed in light of the findings of this study.

Cucumber plants are frequently subjected to persistent water deficits during the summer months, 7 to 10 days in duration (98), accompanied by high light intensities, high air temperatures and low air humidity resulting in

wilting. Plant wilting is also frequently observed at mid day in cucumber plants exposed to high light intensities and low air humidity. This is probably accentuated by the prostrate growth pattern of cucumber vines and the horizontal leaf orientation which maximize light interception, increase leaf temperature and transpiration and lead to transient plant water deficits.

The results of this study indicate that cucumber plants require light intensities in excess of 900 $umol.m^{-2}.s^{-1}$ to achieve maximal CO_2 assimilation rate (A). However, exposure to high light levels for extended periods of time could lead to an increase in leaf temperature, excessive transpiration and possibly transient plant water deficits. It was found that temperatures of up to 32C had no apparent adverse effect on A. However, leaf temperatures most probably exceed 32C considering that seasonal maximum daily air temperature commonly approach 35 to 37C. If such temperatures are accompanied by high irradiance levels, low relative humidity and/or low soil moisture such as to create a mid-day temporary leaf water deficit, leaf temperatures may exceed air temperature if transpirational rates are low. Alternatively, if transpiration rates are sufficiently high to maintain leaf temperatures effectively below air temperature, photosynthetic activity might not be affected.

Reducing leaf temperature without an increase in transpiration, under water limiting conditions,

necessitates the dissipation of excess heat energy via conduction, convection and emission of infrared light. The amount of energy lost via convection and IR emission are functions of air turbulance and leaf temperature. Modification of the environment around the plant, which is likely to be uneconomical, would be required in order to influence heat loss through IR and convection. Conductive heat transfer is a function of leaf size which determines the thickness of the insulating air layer around a leaf such that smaller leaves have higher conductive heat exchange with the surrounding air as compared to large leaves. A plant with small leaves is likely to lose a proportionally smaller amount of water via transpiration as more heat energy is dissipated via conduction.

One of the genotypes tested in this study , "Little Leaf" had characteristically smaller leaves than the other genotypes. Although "Little Leaf" did not differ from the other genotypes in its drought tolerance, it should be pointed out that greenhouse grown "Little Leaf" plants produced leaves that were larger than those typical of the genotype under field conditions. Additionally, the low air tubulence inside the greenhouse probably limited conductive heat loss. It was observed that the increase in leaf temperature was often accompanied by an increase in leaf-air VPD and a decrease in water use efficiency. Because of its more efficient heat exchange system, a "Little Leaf"-type plant would probably have a better overall WUE due to

the fact that lower transpirative water loss would be necessary for leaf cooling. Having plants which have a high WUE would be a drought delaying mechanism which might allow the plant to tolerate short periods of low or no rainfall.

Antitranspirants, which reduce plant transpiration, have been found to reduce photosynthesis in treated plants due to a decrease in CO_2 diffusion into leaves (13,21). However, increases in tomato yields due to an increase in fruit water content have also been documented (91). Application of antitranspirants in situations where fruits are approaching harvest size and no alleviation of the drought condition is anticipated, might allow fruits to continue increasing in size as more water becomes available when transpiration rates are lowered by the antitranspirants.

Intermittent and unpredictable water deficits occasionally occur in the mid-western U.S.A during the summer months Drought avoidance through early maturity, as has been suggested for other crops (36,95), would therefore be of limited benefit for cucumbers. Potential mechanisms for avoidance or tolerance of a sudden drought include the following:

a- lowered transpiration rates: application of antitranspirants and stomatal closure during periods of potentially high transpirative demand would reduce transpirative water loss and delay the onset of plant water deficits. Sensitive stomata that close in response to

minimal decreases in soil water potential (51) would also be advatageous in delaying water deficit.

b- increased water uptake capacity: development of deeper and more extensive root systems in response to water deficit might increase plant water uptake capacity. Osmotic adjustment in roots might also allow the plant to continue water uptake at lower soil water potentials.

c- the capacity for maintenance of cell turgor at low soil and plant low water potentials: Plants might be able to recover from a condition of drought stress more rapidly if cell integrity is maintained and minimal damage is sustained during the exposure to the water deficit. Osmotic adjustment might allow maintenance of cell turgor at low plant water potentials.

d- the ability to regain photosynthetic activity following a period of drought stress: Rapid recovery of photosynthetic activity following an exposure to drought stress would be essential if the adverse effects of water deficit on a crop are to be minimal. A delay in the recovery of photosynthesis would be expected to lead to a delay in resumption of plant growth due to the limited assimilate supply.

Osmotic adjustment is a mechanism through which a cucumber plant could respond to sudden water deficits. Osmoregulation might increase the plant's water uptake capacity (116) and allow the plant to rehydrate at night, allow maintenance of cell turgor in drought stressed plants

(80) and provide protection for photosynthetic enzymes (76,89).

Pickling cucumber plants responded to water deficits with osmotic adjustments of 0.06 to 0.1 Mpa but no genotypic differences in the magnitude of osmoregulation was detected. It was estimated from soil water depletion curves that, for a plant growing in a loamy soil, an osmotic adjustment of 0.1 Mpa in the roots of a cucumber plant would increase the amount of water available for plant uptake by 8 to 10 mm/30 cm of soil depth. Based on estimates of water consumption by cucumber plants (70) an additional 8 to 10 mm of water would be sufficient to support plant transpiration for an additional 2 days.

Cucumber fruits have a high expansive growth rate, 28.4 g/day (Fresh wt. basis) 95% of which is water. Growth rates of fruits on stressed plants were about 30% lower than those of fruits of control plants, two thirds of which was attributed to limited assimilate supply and one third accounted for the direct contribution of water limitation on cell expansion. It is evident that for fruit growth to be maintained, a continuous supply of photoassimilates, the major limiting factor in fruit growth, should be available. Osmotic adjustment is reported to allow for continued root growth and maintenance of stomatal opening (44,118) which would in turn allow for continued water uptake and photosynthesis and support fruit growth or prevent fruit abortion in stressed plants.

The magnitude of osmotic adjustment observed in this study was lower than that reported for other crops (100). Increasing the magnitude of osmoregulation in cucumber plants would probably require the utilization of germplasm of C. sativus species that are natives of semi-arid regions. Osmotic adjustment has been reported to be controlled by one gene (80). If a higher degree of osmoregulation could be detected in other C. sativus species native to semi-arid regions, transfer of the osmotic adjustment gene to commercial lines would probably be feasible.

Potassium was the major solute that accumulated in leaves of drought stressed cucumber plants, increasing from 33 to 82 $umol.g^{-1}$, while the contribution of sugars to osmoregulation was insignificant. Drought stressed plants had lower CO_2 assimilation rates as compared to well watered plants, 3.5 to 6.9 $umol.s^{-1}m^{-2}$ and 13 to 19 $umol.s^{-1}m^{-2}$, respectively. Since gas exchange measurements on stressed plants were made at saturating light levels and at ambient temperatures of 24C to 32C, it was concluded that the decrease in photosynthetic rate was probably not due to temperature or light effects.

Comparisons of photosynthetic rates of drought stressed and control plants at similar intercellular CO_2 levels, it was estimated that the decrease in CO_{2i} could only account for about 36% of the observed decrease in photosynthetic rate in stressed plants. The remaining 64% of the decrease

in photosynthetic rate was attributed to non-stomatal factors. Within 24 hrs of being rewatered, drought stressed cucumber plants regained their photosynthetic activity and it was concluded that mild drought stress did not cause an irreversible damage to the photosynthetic system. This is an important characteristic for cucumber plants which frequently experience temporary water deficits during periods of high transpirative water loss.

Fruiting increases the demand for photoassimilates which can be limiting in a drought stressed cucumber plant and might lead to fruit abortion. The effects of fruiting on CO_2 assimilation and carbon partitioning in drought stressed cucumber plants were investigated. It was found that, drought stressed and non-stressed, fruiting plants had higher CO_2 assimilation rates, about 20-25% higher, than non fruiting plants. It was found that under both water regimens, photoassimilates were allocated to developing fruits at the expense of vegetative plant parts. This indicates that cucumber plants might have a survival strategy which gives priority for fruit and seed development during periods of stress. Cucumber leaves maintained appreciable photosynthetic activity as they aged. No differences in CO_2 assimilation rates were detected among leaves on nodes 3, 6, 9 and 12 from the shoot apex (Appendix A, Table 1). This would be an important characteristic if fruit set is delayed by drought conditions such that older leaves could contribute needed

photoassimilates for fruit growth following a period of water deficit. Diurnal changes in CO2 assimilation rate and stomatal conductance of leaves of irrigated cucumber plants were not significant (Appendix B, Figure 1). However, it should be pointed out that air humidity inside the greenhouse was much higher than what would be expected under field conditions and as such transpiration rates were probably not excessive. Both, CO2 assimilation rate and stomatal conductance of leaves of stressed cucumber plants were lower than those of irrigated plants and both gas exchange parameters decreased throughout the day (Appendix B, Figure 2).

The concentration (fresh wt. basis) of the translocated sugar stachyose, whose synthesis is enhanced by high sink demand (88), in leaves of stressed plants, was similar to that in leaves of deflowered plants. The concentration of the stachyose precursors sucrose and raffinose were higher in leaves of stressed plants than in leaves of non-stressed plants. This indicated that a decrease in sink demand contributed to the low stachyose levels in stressed leaves. A decrease in translocation as a result of water deficit might also cause the observed changes in sugar concentrations and the decrease in assimilate supply to fruits. Translocation has been reported to be adversely affected by water deficits (14,112).

None of the 12 cucumber genotypes tested in this study exhibited an appreciable level of drought tolerance.

However, it should be pointed out that these genotypes were of a limited genetic base and were selected because of their importance as parental lines for several commercial cultivars. Moreover, this study was conducted under greenhouse conditions, which resulted in plant morphological development quite different from plants grown under typical field environment. Plants were grown in plastic containers which, although did not limit overall root growth, did not allow plants to exhibit rooting patterns typical of field grown plants. An extensive root system would allow plants to tap a larger soil volume and consequently, delay the onset of drought stress in the plant. Under field conditions, it is possible that genotypic differeces in drought tolerance, associated with morphological differences, might have been observed among the genotypes in this study.

Drought stress had adverse effects on cucumber plant growth and productivity. Although the genotypes tested in this study exhibited differences in vegetative and reproductive growth under well watered conditions, no genotypic differences were found when plants were grown under water-limiting conditions. This suggests that, in the effort to breed for maximal productivity under optimal environmental conditions, plant tolerance to adverse growing conditions might have been reduced substantially. Leaf area was about 40% smaller in drought stressed as compared to control plants. Drought stressed plants

suffered reductions of 36% to 50% and 19% to 57% in total plant dry matter and fruit dry matter production per plant, respectively, as compared to control plants. The number of fruits set on drought stressed plants was 28% to 55% lower as compared to non-stressed plants.

Fruits with a diameter of about 25 mm or more were observed to continue growth following relief of drought stress whereas smaller fruits frequently aborted upon experiencing water deficits. Larger fruits probably have more developed seeds which could supply growth promoting hormones that may increase the sink strength of the fruit. Small fruits in which seed development is limited would have a lower sink strength leading to fruit abortion. This might indicate that strategies which would either delay the onset of drought stress, until fruits have reached a certain size, by lowering , or increase the plant's water uptake capacity at that time might reduce the incidence of fruit abortion caused by water deficits.

In conclusion, improving the capacity of pickling cucumbers to escape or tolerate drought will probably require the incorporation of some or all of the following characteristics into commercial cultivars:

a- a modified root architecture in which more roots grow deeper into the soil or a greater soil volume is explored for water.

b- an appreciable capacity for osmotic adjustment in leaves, to maintain turgidity, and in roots, to increase

the plant's water uptake capacity at lower plant and soil water potentials. For osmotic adjustment to have a tangible effect on the drought tolerance of cucumber plants, the magnitude of this adjustment would probably have be about 0.2 MPa or larger. c- the capacity for rapid recovery of photosynthetic activity and growth following relief from severe drought stress in which plant water potentials decrease to -1.0 MPa or lower. Cucumber plants commonly experience mid-day water deficits when transpirative water loss is excessive even though soil moisture levels are not low. The results of the current study indicate that photosynthesis recovered rapidly following relief from a drought stress which lowered plant water potential to -0.8 MPa.

Prevention of abortion of fruits smaller than 25mm in diameter might be possible if the sink strength of these fruits, for photoassimilates and water, could be increased. Osmotic adjustment in the fruit tissue might increase the fruit's water uptake capacity. Increasing the fruit's strength in competing for photoassimilates might be achieved by application of chloroflurenol, a chemical which is used to enhance fruit set in cucumber plants (29). In situations where drought conditions are expected to persist, application of chlorflurenol to plants might reduce the incidence of fruit abortion in drought stressed cucumber plants by increasing the sink strength of fruits.

APPENDICES

APPENDIX A

Diurnal changes in gas exchange parameters of cucumber leaves

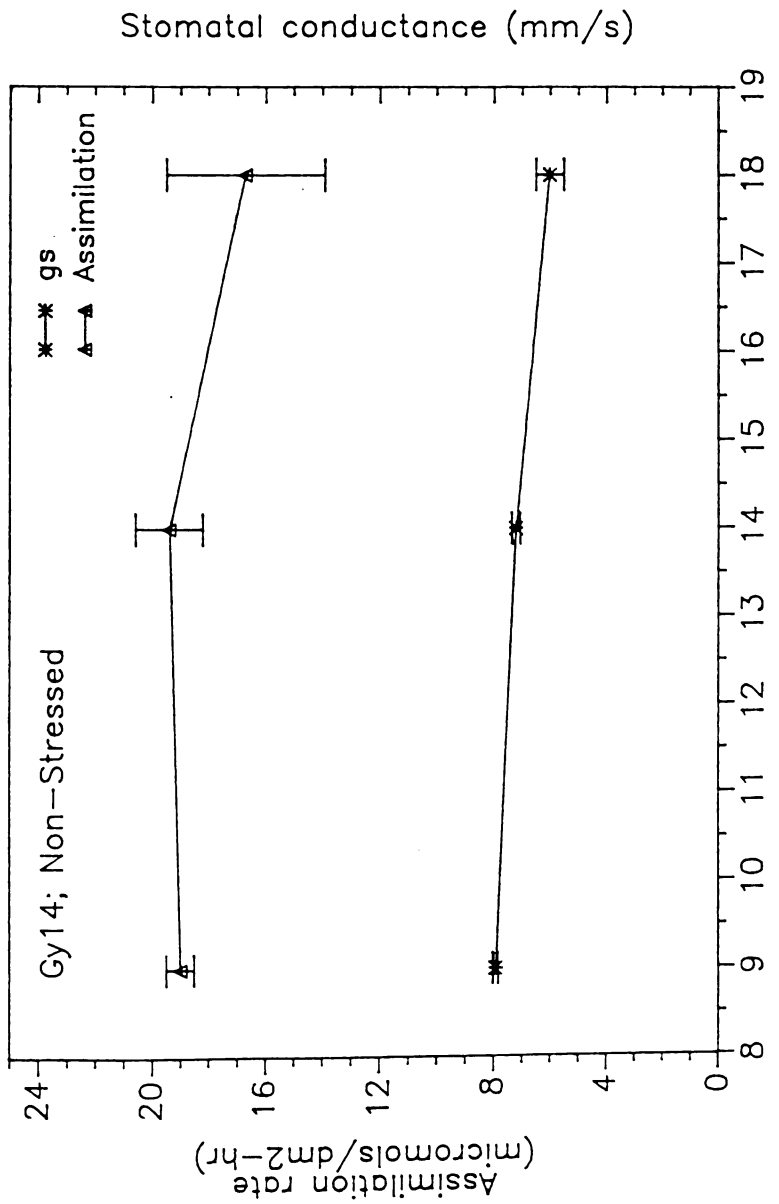

Fig. 1. Diurnal changes in gas exchange parameters of cucumber leaves. Measurements were made on the 4th or 5th leaf from the shoot apex of greenhouse grown cucumber plants. A portable open gas exchange system was used. A HID sodium lamp was used as the light source to provide light levels of >=1000 umol.m2 s-1.

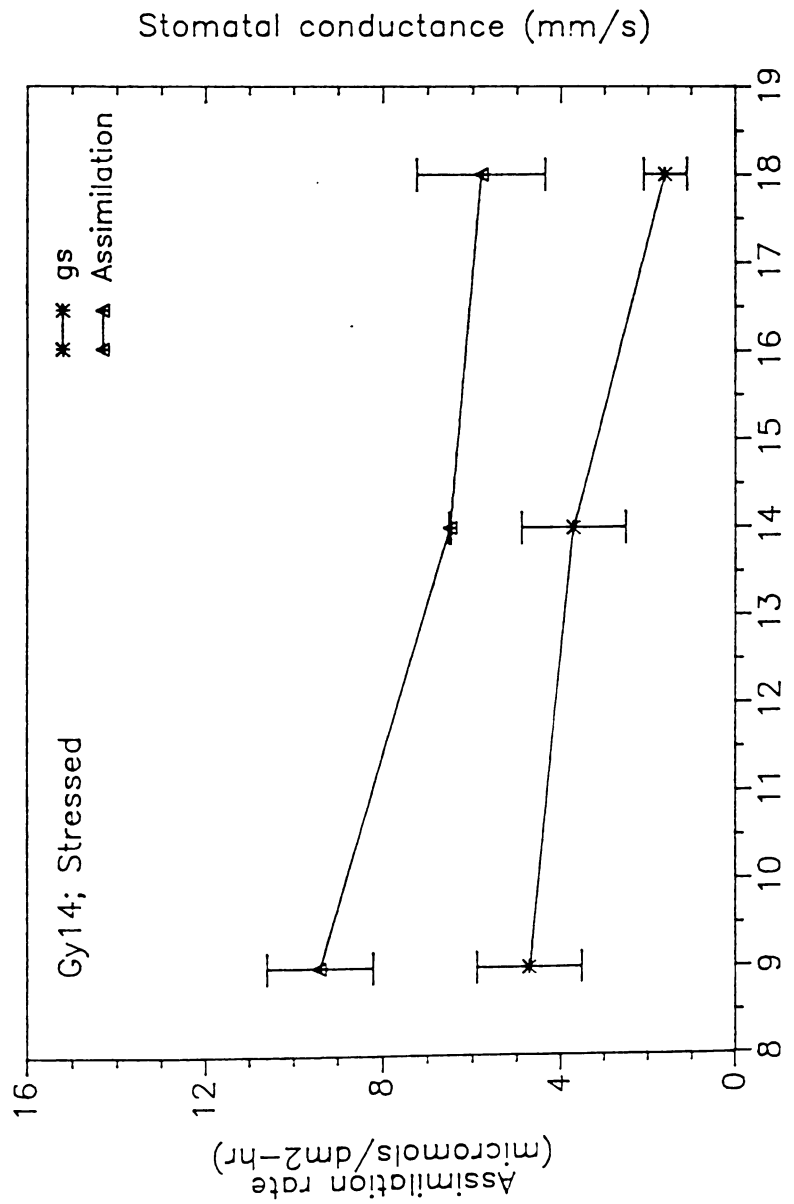

Fig. 2. Diurnal changes in gas exchange parameters of cucumber leaves. Measurements were made on the 4th or 5th leaf from the shoot apex of greenhouse grown cucumber plants. A portable open gas exchange system was used. A HID sodium lamp was used as the light source to provide light levels of >=1000 umol.m2 s-1.

APPENDIX B

Effect of leaf age on photosynthetic rate in cucumber leaves

Effect of leaf age on photosynthetic rate
in cucumber leaves

Table 1. Net photosynthetic rates for leaves at different node positions on pickling cucumber plants.

Leaf position[z]	CO2 assimilation rate (umol CO_2/dm^2-hr)
3	17.2
6	19.1
9	20.9
12	16.5
F-significance	NS

z. Measurements were made on the 3rd, 6th, 9th and 12th leaf from the shoot apex of well watered cucumber plants in the greenhouse under light saturating conditions.
NS.Not significant at the 5% probability level.

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