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WATER RELATIONS OF
CUCUMBER, TOMATO, AND
SWEET PEPPER

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M. H. BEHBOUDIAN

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**WATER RELATIONS OF CUCUMBER,
TOMATO, AND SWEET PEPPER**

Dit proefschrift met stellingen van

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B. Sc. in Agriculture, M.Sc. in Horticulture, American University of Beirut, geboren te Hamadan (Iran) op 29 juni 1943, is goedgekeurd door de promotor, Dr. Ir. J. F. Bierhuizen, hoogleraar in de Tuinbouwplantenteelt.

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M. H. BEHBOUDIAN

WATER RELATIONS OF CUCUMBER, TOMATO, AND SWEET PEPPER

Proefschrift

TER VERKRIJGING VAN DE GRAAD
VAN DOCTOR IN DE LANDBOUWWETENSCHAPPEN,
OP GEZAG VAN DE RECTOR MAGNIFICUS,
DR. IR. J. P. H. VAN DER WANT,
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THEOREMS (STELLINGEN)

I

Completion of a Ph.D. thesis should not officially be allowed to exceed five years.

II

A need exists for definition and characterization of drought resistance in plants.

This thesis

III

In the world of scientific communication, people are more impressed by the status of the person conveying an idea than the idea itself.

IV

Visits of foreign experts are of less benefit to a developing country than the sending out of students to be educated abroad.

V

If scholarships are meant to enhance the scientific prospects of the recipient countries or individuals, preference should be given to degree courses such as B.Sc., M.Sc., and Ph.D. as compared to short term training courses.

VI

Inclusion of humanities (sociology, psychology, philosophy, etc..) to technical degree courses (such as agriculture and engineering) improves the quality of education.

VII

Research personnel should work by job and not by hour.

VIII

In admitting students to a university, the element of chance should be eliminated.

IX

In communications aiming abroad, the titles 'Ir.', 'Ing.', 'drs.', and 'mr.' should be officially banned.

M. H. BEHBOUDIAN

B. Sc. (Agriculture) and M. Sc. (Horticulture),
American University of Beirut

**WATER RELATIONS OF
CUCUMBER, TOMATO, AND
SWEET PEPPER**

**THESIS
IN PARTIAL FULFILMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF AGRICULTURAL SCIENCES
AT THE AGRICULTURAL UNIVERSITY,
WAGENINGEN, THE NETHERLANDS
ON WEDNESDAY, 11 MAY 1977 AT 16 O'CLOCK**

FOREWORD

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1. GENERAL INTRODUCTION

The subject of plant water relations has gained increasing importance in the last 15 years. This is partly due to a new appreciation of water as a limiting factor in crop production, a factor which may become critical if drought occurs. As a limiting factor in food production, the availability of water has also had a great impact on ancient civilizations. For example, the elaborate network of irrigation canals built some 2000 years ago in Khuzestan, a province in Southwestern Iran, bears witness to the efforts which had to be expended to combat the chronic water shortages, especially in arid and semi-arid regions. The sophisticated irrigation technology of today shows to what extent our society depends on a secure supply of water for food production.

Another important factor contributing to the increased popularity of studies on water relations is the adoption of a standardized set of terminology dealing with the status of water in the soil-plant-atmosphere continuum (KRAMER, 1974). Improvement of methodology, such as the construction of diffusion porometers and pressure chambers, as covered by SLAVIK (1974), has also been an important breakthrough in advancing the research possibilities in this field.

The major part of research on water relations reported in the literature has been devoted to field crops. This is understandable in view of the importance those crops have for human livelihood. A good deal of attention has been paid to cotton, corn, wheat, and sorghum. Horticultural crops, especially vegetables, have received relatively less attention, probably because vegetable production has always been associated with an abundance of water. However, when water is considered as a critical resource, its scarcity can greatly affect vegetable production both in open and in protected cultivation. Information on water relations of vegetables therefore could be of help in both types of cultivation.

The series of investigations presented here deal with some aspects of water relations in cucumber, tomato, and sweet pepper. Cucumber and tomato were chosen because they are important horticultural crops in both The Netherlands and Iran, my home country. Sweet pepper is gaining popularity in The Netherlands and has always been popular in Iran. In the present research, emphasis has been placed on reactions of these species to drought. Variations in some plant parameters as affected by drought, and assessment of methods for their measurements, are presented in Chapter 2. Physical aspects of internal water relations, with an attempt to characterize the drought resistance of the three species, are given in Chapter 3. It was of interest to study simultaneously the effects of drought on transpiration and photosynthesis, and these studies are reported in Chapter 4. Research on diurnal changes of various parameters are scarce for vegetables. Aspects of this phenomenon are reported in Chapter 5. The introduction of each chapter includes a review of relevant literature. The presentation is accompanied by English and Dutch summaries.

2. EFFECTS OF DROUGHT ON SOME PLANT PARAMETERS MEASURED AT VARIOUS LEVELS OF IRRADIANCE AND TEMPERATURE

2.1. INTRODUCTION

The measurement of plant water status is indispensable in water relations studies. Any method which accurately indicates the water status of plants could also be used as a basis for timing of irrigation, provided the method is easy to carry out. The indicative criteria for scheduling irrigation could come from the plant environment or from the plant itself. The plant indicators deserve more attention because of their direct relation to yield and the fact that they are a reflection of soil water conditions and of the evaporative demand of the atmosphere. The plant indicators as described by HAISE and HAGAN (1967) include visual indicators, growth indicators, leaf reflectance and temperature, and plant water measurements. The plant water measurements cover the parameters of relative water content (RWC), transpiration and stomatal aperture, osmotic potential, and water potential. HAISE and HAGAN (1967) stated that relative water content should be a useful indicator for timing of irrigation because sampling and measurements are relatively simple, and a good correlation is generally obtained with plant water potentials. The authors indicated that measurements of stomatal aperture (by microscopy and infiltration) is practical and easy, although the results are dependent on the age of the leaves, and their exposure to light and wind in the canopy. It was probably for this reason that the authors believed that measurements of transpiration are not useful for scheduling irrigation although these measurements are carried out in ecophysiological studies. The authors asserted that there was need for development of simple but reliable methods for measuring the stomatal aperture. HALEVY (1960) evaluated some physiological indicators as a basis of irrigation timing for gladiolus. He measured the transpiration, leaf water content, stomatal aperture, water saturation deficit (100-RWC), osmotic values and leaf elongation with increasing soil water stress. He concluded that plants vary in their reactions to decreasing soil moisture, and that none of the parameters could be used as a universal indicator for irrigation. Although he showed that the water saturation deficit was the most sensitive index, he felt that the stomatal aperture index was the most suitable, since it was only slightly less sensitive, and was easier to measure (using the infiltration method). According to HALEVY (1960), each species must be studied individually to determine which of the parameters is most sensitive to drought.

The use of plant water potential (ψ_{plant}) as a criterion for irrigation timing appears to be sound if a suitable method can be found for its measurement. Various methods of measurements are described and evaluated by SLAVIK (1974, pp. 12-75). The pressure chamber method is deemed as an easy, reli-

able, and accurate method, although it cannot be used for some plant types due to their unsuitable anatomy (e.g. lettuce). Plant water potential of some horticultural crops has been measured by this method successfully. Some examples are measurements of water potentials in orange, pear, apricot, and grapes (KLEPPER and CECCATO, 1969), and of root water potentials of sweet pepper (GEE et al., 1974). However, the applicability of this method seems to be species dependent. HOPMANS (1974) showed that the method could be satisfactorily applied for carnation, chrysanthemum, pepper, and spinach, while in French beans it very much overestimated the plant water potentials, and in roses underestimated the potentials.

Reactions of plants to water stress depend on their prevailing environmental conditions. JORDAN and RITCHIE (1971) observed that for glasshouse grown cotton plants placed in a growth chamber, stomata closed when leaf water potential decreased to -16 bars. However, at a plant water potential of -27 bars in the field, the stomata were still open. They suggested that the field grown plants had either lost the ability to close their stomata in response to water stress, or that the threshold deficit required for closure was extended due to internal changes caused by prolonged exposure to severe water deficits. They also reported that at leaf water potentials of -15 bars, wilting did not occur in field-grown plants but did in the upper leaves of the glasshouse-grown plants. WATTS (1975) indicated that the relationship between stomatal resistance and plant water potential obtained in field conditions is often different from that in controlled conditions. He attributed this difference to the lower osmotic potential in the field, caused by higher irradiances relative to controlled conditions, and suggested that critical water potentials for stomatal closure in the field may be several bars lower than for the same species in a controlled environment.

In water relations studies, stomata receive much attention because they are the regulators of water transport in the soil-plant-atmosphere continuum. The basic stomatal mechanisms are covered in the recent reviews of LEVITT (1974) and RASCHKE (1975). The following brief account partly deals with reactions of stomata to environmental factors while plants are under water stress.

Stomata of water stressed plants sometimes show an opening reaction to increasing levels of irradiance, although the closing effect of drought could override the opening effect of light. HANSEN (1971) reported that in *Beta vulgaris* the stomatal diffusive resistance (r_s) did not decrease at light intensities higher than 60 W m^{-2} for three levels of water stress. At all levels of irradiance, r_s was lower for the treatment having a leaf RWC of 85%, as compared to that at 57%. The treatment having an RWC of 75% was intermediate in the stomatal opening. However, by decreasing the osmotic potentials of the root medium for sweet pepper, JANES (1970) found that the stomatal resistances in the low light treatments were generally lower than those of the higher light treatment. For stressed plants of snap beans in KANEMASU and TANNER's (1969) study, stomatal opening depended on exposure. The east side of the field had the highest opening in the morning and the west side the highest opening in the

afternoon, for abaxial stomata. For adaxial stomata, the top of the north-south row had the highest opening.

The effects of temperature on stomatal opening is controversial (HOPMANS, 1971) and for plants under water stress only the report of SCHULZE et al. (1973) seems to be available. MEIDNER and MANSFIELD (1968, pp. 87-91) maintained that the contradictory temperature effects on stomatal opening could be interpreted through the common basis of intercellular CO₂ levels. Species (e.g. onion) in which higher temperatures enhance the CO₂ compensation point close their stomata when the temperature is raised. Plants exhibiting less sensitivity of intercellular CO₂ levels to higher temperatures (e.g. alfalfa), would show an opposite response. This point was further confirmed by results of SHARPE (1973) with cotton plants. He showed that with a rise in temperature from 20 to 30°C, stomatal opening was enhanced due to higher photosynthesis, causing a depletion of intercellular CO₂ levels.

Stomata of well watered and stressed plants seem to be sensitive to the air humidity. Higher air humidity enhances opening. HALL and KAUFMANN (1975) reported that in *Sesamum indicum* the leaf resistance increased when the vapour pressure gradient between leaf and air was increased. SCHULZE et al. (1972) showed that plants of *Prunus armeniaca*, *Hammada scoparia* and *Zygo-phyllum dumosum* closed their stomata in dry air and opened them in humid air. The stomata opened at high air humidity in spite of a decrease in leaf water content. This excluded a reaction via the water potential in the leaf tissue and showed that the leaf resistance was directly linked to air humidity. In the three species, this response was maintained over a period of many hours, including when the soil was dry. The response was greater in plants with a poor water supply than in well watered plants. CONDE and KRAMER (1975) reported that the diurnal variations in stomatal diffusion resistance of *Opuntia compressa* paralleled the vapour pressure deficit (vpd). Lower vpd resulted in lower r_s in light and in dark periods. For Engelmann spruce, KAUFMANN (1976) reported substantial stomatal opening at high humidity even under high water stress and low light. Stomatal responses were not correlated with air or soil temperature, and no sensitivity was observed to decreasing xylem pressure potentials in sun or shade. In a UNESCO (1970) report, it is evident that the stomata of young, adult, and old leaves of maize showed a closing pattern with the increasing vpd.

The main objectives of the experiments presented in this chapter were: (1) to evaluate different plant parameters for expression of water status and for suitability as a basis of irrigation timing in tomato, cucumber, and pepper; and (2) to study the effects of drought on some plant parameters at two levels of temperature and three light intensities. Variations in the air humidity were not planned, but occurred in some experiments. Effects of this factor are presented and discussed where applicable.

2.2. MATERIALS AND METHODS

Seeds of *Cucumis sativus* L. cv. Fertila, *Lycopersicon esculentum* Mill. cv. Money maker, and *Capsicum annuum* L. cv. California Wonder were purchased from the Royal Sluis Seed Company at Enkhuizen. They were sown in sand using wooden boxes. Seedlings were transplanted into plastic pots (top diameter 10, bottom diameter 7.5, and depth 7.5 cm) containing a mixture of garden peat and loamy soil. The pF of the mixture was determined. The plants were cultivated in a glasshouse in which supplementary light during autumn and winter was given by five 400-watt HPLR lamps suspended 50 cm apart at a distance of 150 cm above the bench. In these cases, total irradiance ranged from 31 to 36 Wm^{-2} over the bench at the pot height. Before the water stress experiments began, the plants were transferred to appropriate climate rooms of the phytotron described by DOORENBOS (1964).

Various experiments were performed under three light intensities (designated as high, intermediate, and low) and two temperatures (21 and 25°C) for each species. The environmental conditions in the climate rooms, descriptions of the experiments, and plant ages at the beginning of each experiment are presented in Table 1.

The irradiance in the climate rooms was obtained from Philips TL 57 fluorescent tubes during a 16 hr photoperiod. The plants were put on trolleys which could be raised or lowered to obtain higher or lower irradiance values. Lower light levels in pepper experiments were obtained by canvas shading. The irradiance data are presented in Table 1. Drought was induced by suspension of watering. The pots were covered with fine gravel or Tempex to reduce soil evaporation.

Transpiration was measured regularly throughout the drying cycles by pot weighing at the beginning and end of each photoperiod. After rewatering, the plants were harvested and their leaf area was measured for use in calculation of transpiration rates. The calculated stomatal resistance (r_s) values were obtained by applying the transpiration formula cited by SLATYER (1967, p. 248). The general form of this formula is given in Chapter 4. Air boundary layer resistances (r_a) were calculated according to the formulae cited by KUIPER (1961, p. 12) and were subtracted from the total resistance pathway to obtain r_s . For other measurements, plants parallel to those designated for transpiration were used. The following measurements were taken at the first four hours of the photoperiods. The r_s of the fourth leaf from the base was measured by a diffusion porometer built as described by KANEMASU et al. (1969) and calibrated according to STIGTER et al. (1973). Only the resistance of abaxial stomata was measured, except in cucumber, for which the resistances of both abaxial and adaxial stomata were determined for the high and low light intensity experiments. Temperature of the 4th leaf was measured by a Heimann infrared thermometer type kt 24. The leaf water potential of the fourth leaf was determined with the pressure chamber described by SCHOLANDER et al. (1965). Relative water content of the third leaf was estimated by the

TABLE 1. Environmental conditions in the climate rooms, description of experiments, and plant ages at the beginning of each experiment.

Description of experiments	Plant	Period of drying cycle	Temp. (°C) ± S.D.	Vapour pressure deficit range (m bar)	Wind speed (cm sec ⁻¹)	Irradiance (Wm ⁻²)	Plant age (week)	
Drying cycle: intermediate irradiance	Tomato	25°C	25°C	25°C	25°C	25°C	25°C	
		14.12.74-21.12.74	08.03.75-19.03.75	25.0 ± 0.6 20.6 ± 0.6	7.2-12.5 3.9-5.3	16 30	29.3 29.3	21°C 25°C 21°C 25°C 21°C 25°C
Drying cycle: intermediate irradiance	Cucumber	02.01.75-09.01.75	24.9 ± 1.1 21.1 ± 0.4	13.0-15.8 8.4-9.8	16	29.3	6	
		01.12.75-11.12.75	25.3 ± 0.2 21.6 ± 0.3	6.4-8.0 1.3-5.2	16	87	29.3	8
Drying cycle: high irradiance	Tomato	03.01.75-10.01.75	24.7 ± 1.2 21.1 ± 0.4	11.5-14.5 8.8-9.9	11	35.7	6	
		24.02.75-11.03.75	24.7 ± 0.6 20.7 ± 0.7	5.0-12.2 2.0-5.6	11	35.7	35.7	5
Drying cycle: high irradiance	Pepper	16.04.75-03.05.75	25.4 ± 0.5 21.6 ± 0.4	5.2-7.1 3.5-5.7	16	35.7	8	
		03.01.75-10.01.75	24.7 ± 1.2 21.1 ± 0.4	11.5-14.5 8.8-9.9	41	10	22.3	6
Drying cycle: low irradiance	Cucumber	24.02.75-11.03.75	24.7 ± 0.6 20.7 ± 0.7	5.0-12.1 2.0-5.6	41	10	22.3	5
		16.04.75-05.05.75	25.5 ± 0.4 21.6 ± 0.4	7.6-8.9 3.7-5.8	16	30	18.7	8

method of BARRS and WEATHERLEY (1962). Further recommendations of BARRS (1968) were applied in the measurements. Soil samples were taken from the pots for gravimetric determination of moisture content. Leaf area was estimated by an optical planimeter (Technical Physical Service of Agricultural University at Wageningen 66-2014). The plants were rewatered as wilting symptoms became apparent. One day after rewatering, the above parameters were measured to observe the pattern of possible recoveries. Three plants were sampled for the measurements described above.

2.3. RESULTS

Changes in transpiration rates and stomatal diffusive resistances to water vapour of tomato, cucumber, and pepper, in relation to decreasing soil water potentials at 25 and 21 °C climate rooms for high, low, and intermediate levels of irradiance are shown in Figure 1. Since the equations for linear regressions of r_s on soil water potential could not be accommodated in the figure, they are presented in Table 2. The results for each species are described separately, followed by a discussion covering the three species.

2.3.1. *Tomato*

The effect of light on transpiration was in general almost negligible in the range of light intensities used, whereas a clear distinction between temperatures could be demonstrated. Transpiration rates were higher in 25 °C as compared to those in 21 °C for all levels of soil water potentials. AL-ANI and BIERHUIZEN (1971) performed drying cycle experiments on tomato, cucumber, and beans under similar conditions. The maximum transpiration rate of tomato measured in their experiment was comparable with that of the present investigation (0.57 vs 0.53 gH₂O dm⁻² hr⁻¹).

Stomatal diffusive resistance (both measured and calculated) increased almost linearly with decreasing soil water potentials at both temperatures. In most cases a decline occurred in the measured r_s values at the lowest levels of soil water potentials. This could be due to the effect of drying which reduces the epidermal pressure on the guard cells and causes a hydropassive stomatal opening (RASCHKE, 1975). The slope of measured r_s line was higher than that of the calculated one at 25 °C. The discrepancy between measured and calculated r_s values in this and other experiments could be due to different sampling techniques. For measured r_s values, single leaves were used at only one point in the photoperiod, whereas for the calculated r_s values whole plant transpiration rates were used over the entire 16-hr photoperiods. The calculated and measured r_s values of tomato at 21 °C were almost the same, both being lower than the corresponding values at 25 °C.

2.3.2. *Cucumber*

At the beginning of the drying cycles, transpiration rates at 25 °C were higher

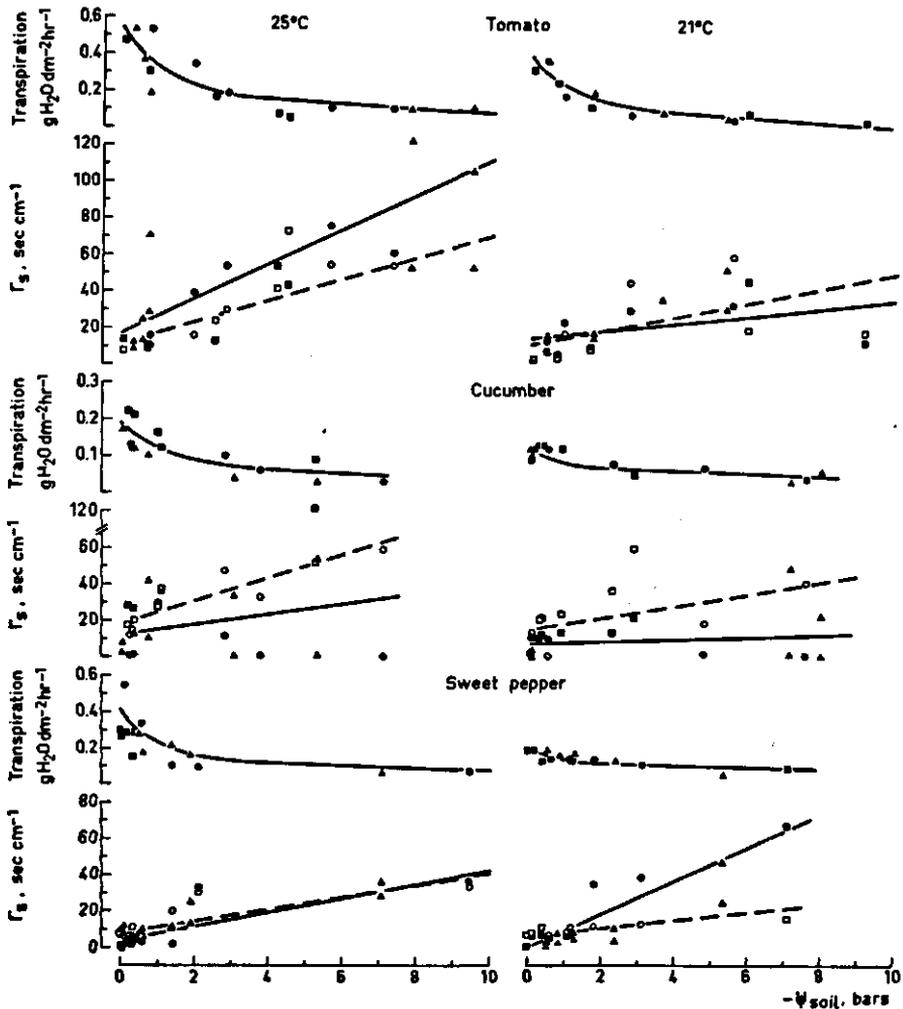


FIG. 1. Changes in transpiration rate and stomatal diffusive resistance (r_s) of tomato, cucumber, and pepper in relation to decreasing soil water potential (ψ_{soil}) at 25 and 21°C for high (●), intermediate (■), and low (▲) levels of irradiance. Calculated r_s values (dotted lines) are also shown for high (○), intermediate (□), and low (△) levels of irradiance. The linear regression equations of r_s on ψ_{soil} are indicated in Table 2.

for intermediate irradiance, due to the higher vapour pressure deficits of the atmosphere (Table 1). The decline in transpiration rates with increasing drought was less pronounced than in the case of tomato. The humidity control of the climate rooms failed during the experiments and high humidities occurred. Therefore it is meaningful to compare transpiration rates of tomato and cucumber only at the intermediate levels of irradiance (for which the humidity control had not failed). For this treatment (Figure 1) the lower rates of transpiration in cucumber are accounted for by generally higher values of

TABLE 2. Linear regression equations of calculated and measured stomatal diffusive resistance (y) on soil water potential (x) for tomato, cucumber, and pepper at 25 and 21°C. The corresponding regression lines are shown in Figure 1.

Treatment and plant	Equation	Level of significance of \bar{r}
a. 25°C		
Tomato	calculated $y = 11.67 - 5.85 x$, $n = 15$, $r = 0.85$	0.1%
	measured $y = 14.27 - 9.72 x$, $n = 16$, $r = 0.84$	0.1%
Cucumber	calculated $y = 17.99 - 6.36 x$, $n = 15$, $r = 0.86$	0.1%
	measured $y = 12.32 - 2.74 x$, $n = 15$, $r = 0.20$	not significant
Pepper	calculated $y = 8.62 - 3.22 x$, $n = 16$, $r = 0.86$	0.1%
	measured $y = 4.24 - 3.80 x$, $n = 16$, $r = 0.82$	0.1%
b. 21°C		
Tomato	calculated $y = 11.26 - 3.78 x$, $n = 13$, $r = 0.54$	5%
	measured $y = 13.78 - 2.29 x$, $n = 13$, $r = 0.51$	5%
Cucumber	calculated $y = 15.56 - 3.29 x$, $n = 15$, $r = 0.59$	5%
	measured $y = 8.09 - 0.62 x$, $n = 13$, $r = 0.26$	not significant
Pepper	calculated $y = 6.60 - 2.00 x$, $n = 15$, $r = 0.81$	0.1%
	measured $y = 0.21 - 9.15 x$, $n = 15$, $r = 0.91$	0.1%

r_s (both measured and calculated). Transpiration rates observed here are lower than those reported by AL-ANI and BIERHUIZEN (1971) for cucumber. Higher vpd in their experiment and/or cultivar differences could have played a role. For the high and low levels of irradiance, measured r_s values were very low in both climate rooms. This was clearly due to the direct effect of high humidity on the stomates. Such a phenomenon is reported for sesame (HALL and KAUFMAN, 1975), *Opuntia compressa* (CONDE and KRAMER, 1975), and Engelmann spruce (KAUFMANN, 1976). The low vpd apparently overrode the enhanced stomatal openings and led to diminished rates of transpiration. The calculated whole plant r_s values increased over the drying cycles. These values are averages over 16 hr photoperiods. Declines of transpiration over the photoperiod in constant environmental conditions are shown for cucumber, tomato, and pepper in Chapter 5. Therefore, the calculated r_s values would not be expected to show similarly low values as of those measured. Figure 1 and Table 2 show that the calculated regression line of r_s on soil water potentials has a smaller slope at 21°C compared to that at 25°C. The difference was significant at 5% level.

2.3.3. Pepper

Transpiration rate at 25°C was highest for high irradiance only at lower levels of soil moisture stress. The rates were lower than those of tomato in both

climate rooms, but the r_s values in pepper were not accordingly higher. The lower vpd in pepper experiments (Table 1) could account for the transpiration difference. For the same cultivar of pepper at similar ranges of irradiance, JANES (1970) reported slightly higher transpiration rates. His plants were grown in nutrient solution and therefore the magnitude of resistances in the transport of water in the substrate-plant-atmosphere continuum is expected to have been different. Figure 1 shows that the calculated values of r_s at 25°C were higher than those at 21°C. The differences were significant at 5% level.

2.3.4. *Interrelationships of RWC, ψ_{plant} , and ψ_{soil}*

Figure 2 shows the relationships of RWC and leaf water potential with soil water potential for tomato, cucumber, and pepper. The highest correlation between leaf and soil water potential was obtained with the relation: $\psi_{\text{leaf}} = a + b \sqrt{|\psi_{\text{soil}}|}$. The correlation coefficients were significant at 0.1%. An essential feature of this equation is that with a slight drop in soil water potential at the beginning of the drying cycle, a relatively large drop in leaf water potential occurs, a common observation for these species. Similar relationships between soil and leaf water potentials were reported for sugarbeet by BISCOE (1972) and for wheat by HANSEN (1974). The highest correlation between RWC and soil water potential was obtained with a linear relationship. The correlation coefficients were significant at 0.1%. Among the three species, relative water content in cucumber seemed to decline significantly less with decreasing soil water potentials. Tomato maintained significantly higher RWC than that of pepper over the drying cycles. These observations can perhaps be explained by similar trends in changes of leaf water potentials over the drying cycles. Cucumber shows a significantly smaller decline in leaf water potential compared to tomato and pepper. Leaf water potential in tomato in turn declined significantly less than in pepper. To evaluate the effect of temperature on the nature of the relationships discussed above, separate regressions were tried for 21 and 25°C data. Since the relationships were not significantly different for the two temperature regimes, the data were combined for analysis as described above and were presented in Figure 2.

2.3.5. *Patterns of post stress recovery in some plant parameters*

In each drying cycle experiment, the stressed plants were rewatered and all the parameters described above were measured one day after rewatering. This treatment is hereafter designated as recovery. Table 3 shows values of leaf water potential, transpiration rate, and relative water content for recovery treatments as compared to those of plants just exposed to water stress. The plants designated as control in Table 3 are those not receiving water for 24 hours only. For each temperature, the data in Table 3 are averages of experiments performed at the three light intensities. Leaf water potentials did not recover fully one day after rewatering, but they were close to the initial values. The greatest difference of 1.9 bars occurred for cucumber at 21°C. For other treatments, the differences were less than 0.9 bars. Values of relative water

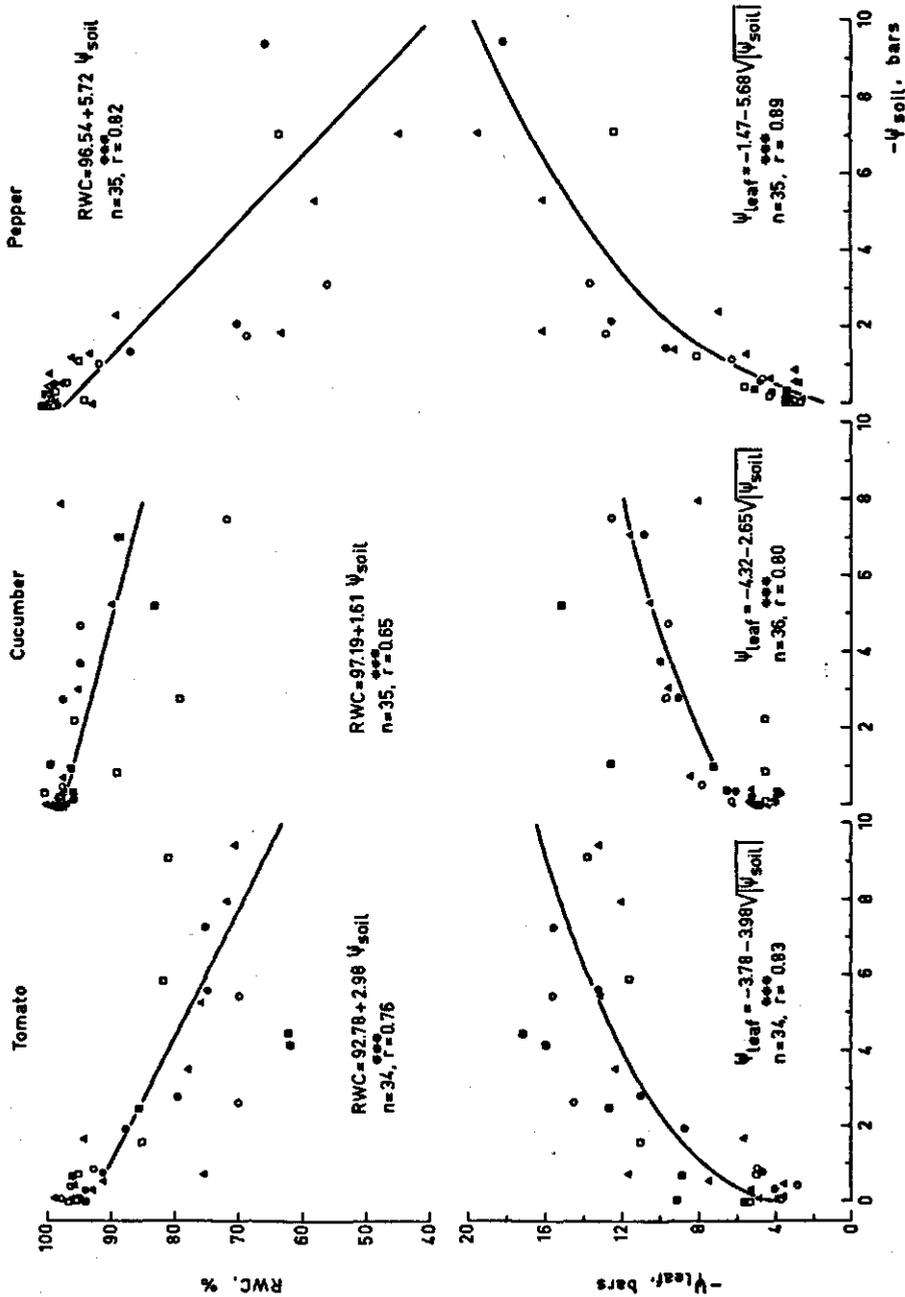


FIG. 2. Regressions of relative water content (RWC) and leaf water potential (ψ_{leaf}) on soil water potential (ψ_{soil}) for tomato, cucumber, and pepper in 25 (closed symbols) and 21°C (open symbols) at high (circles), intermediate (squares), and low (triangles) levels of irradiance. All the correlation coefficients are significant at 0.1% level.

TABLE 3. A comparison of leaf water potentials, transpiration rates, and relative water content of control (C) and recovery (R) treatments in tomato, cucumber, and sweet pepper in climate rooms 25 and 21 °C. Recovery figures relate to measurements taken one day after rewatering the severely stressed plants. For each climate room, the figures are averages of high, medium, and low light intensities.

	Leaf water potential (bars)				Transpiration (g dm ⁻² hr ⁻¹)				Relative water content (%)			
	25°C		21°C		25°C		21°C		25°C		21°C	
	C	R	C	R	C	R	C	R	C	R	C	R
Tomato	-4.4	-4.9	-4.6	-4.8	0.51	0.24	0.34	0.15	94.63	95.72	97.70	89.80
Cucumber	-4.4	-5.2	-4.7	-6.6	0.17	0.11	0.12	0.07	97.21	95.89	97.14	94.10
Sweet pepper	-3.1	-3.9	-2.8	-3.7	0.37	0.23	0.19	0.15	98.17	97.86	96.12	97.62

content during recovery were also close to those of the unstressed plants, except for tomato at 21 °C, for which recovery values lagged behind the prestressed levels by 7.9%. For the three species in both temperatures, transpiration did not recover to the prestressed value one day after rewatering. This could not be due to a persisting water stress because plants with the same leaf water potential over the drying cycles had much higher rates of transpiration. Therefore an aftereffect of stress on stomata is evident for the three species.

2.4. DISCUSSION

Figure 1 shows that transpiration rates at 25 °C were higher than those at 21 °C for the three species. The differences could be explained by the higher vapour pressure deficits at 25 °C (Table 1). The effect of vapour pressure deficits in enhancing transpiration rates is even more pronounced if we consider the phenomenon that calculated r_s values were higher at 25 °C for the three species. The higher r_s values over the drying cycles at 25 °C as compared to 21 °C could be explained on the basis of internal CO₂ levels (MEIDNER and MANSFIELD, 1968, pp. 87–91). It is proposed that drought could have increased the CO₂ compensation point (HEATH, 1969, p. 180) of the three species, resulting in higher internal CO₂ levels. Such phenomenon would have been more pronounced at 25 °C than 21 °C, leading to more stomatal closure in the former because of a higher respiration rate. Higher r_s values at 25 °C could also be due to the higher vapour pressure deficits. SCHULZE et al. (1973) studied stomatal responses to increased temperatures of four Negev Desert species and that of *Prunus armeniaca* for well watered and stressed plants. In well watered plants, stomata opened with higher temperatures, due to increases in potassium ion concentration in guard cells. For stressed plants, stomata closed upon gradual increases in air temperature. They explained that with decreasing

plant water potentials, intercellular CO₂ concentrations increased, causing stomatal closure.

For the experiments reported in this chapter, differences in irradiance in general did not have pronounced effects on measured plant parameters. For example, higher transpiration rates at the high irradiance level occurred for tomato and pepper only at 25°C at the beginning of drying cycles. The irradiance difference between high and low levels were only 13 Wm⁻² for tomato and cucumber and 17 Wm⁻² for sweet pepper (Table 1). These differences were presumably not large enough to invoke appreciable plant responses, considering also the variations in wind speed and humidity occurring for the various treatments. Higher irradiance levels could not be obtained in the climate rooms. To further examine the effects of irradiance on some plant parameters during drying cycles, other series of experiments with higher irradiances were performed and are reported in Chapter 4. Figure 1 shows that for all species the transpiration rates at low levels of soil water potentials became almost similar regardless of different light and temperature treatments. Similarly, KUIPER and BIERHUIZEN (1958) reported that the difference in transpiration rate of rye plants under various light intensities and temperatures decreased as soil moisture declined. It seems that the effect of drought through stomatal closure overrides those of irradiance and temperature on transpiration.

Variations in the air humidity for cucumber experiments made it difficult to visualize the effects of irradiance and temperature on measured r_s values during the drying cycles. Stomata of this species reacted to humidity variations more than to drought, temperature, or irradiance. Their response to humidity was independent of the soil water potential levels. Therefore, those reactions were not mediated through variations in leaf water status; rather, the guard cells seem to have responded directly to the air humidity through peristomatal transpiration. Examples of such a phenomenon were given in section 2.1. Some pepper experiments had similarly low vpd ranges as those of cucumber (Table 1). However, the effect of low vpd on measured r_s values of pepper was far less pronounced. It seems that stomata of the two species show different degrees of sensitivity towards humidity. SCHULZE et al. (1972) maintained that although air humidity-controlled stomatal response seems to be of wide spread occurrence among plants, not all species react in the same way.

The appropriate curves and equations of Figure 2 show that for a soil water potential approaching a zero value, the leaf water potentials of tomato, cucumber, and pepper are expected to be respectively -3.87, -4.32, and -1.47 bars. This order of magnitudes has been repeatedly observed in individual experiments. Since the measurements have always been carried out at the early hours of photoperiods, it seems that leaf water potentials in these species do not equilibrate with soil water potentials in well watered plants. According to KLEPPER et al. (1973) this lack of equilibration could be due to nocturnal transpiration, high resistance to water transport through plants, and utilization of water in cellular expansion instead of transferring energy directly to an

increase in water potential. The latter mechanism could explain the lower leaf water potential in cucumber as compared with pepper (for well watered plants), since cucumber is a faster growing species with presumably higher rates of cellular expansion. Nocturnal transpiration has been reported for tomato (KUIPER, 1961), therefore an equilibration of plant and soil water potentials after nyctoperiods would not be expected even if the other mechanisms cited by KLEPPER et al. (1973) could be disregarded. As the soil dried, the drop in leaf water potential was most pronounced for pepper, intermediate for tomato, and the least for cucumber. For cucumber, lower transpiration rates (Figure 1) could account for maintaining higher plant water potentials. Differences in rates of transpiration between pepper and tomato cannot account for the faster decline of leaf water potential in pepper. There could be a higher plant resistance developing in pepper at the onset of stress, leading to its faster reduction in leaf water potential.

To obtain evidence on differences in plant resistance to water flow among the three species, the generalized equation of VAN DEN HONERT (1948) was used for the resistance of water flux through the soil-plant system:

$$R_s + R_p = \frac{\psi_s - \psi_l}{T} \quad (1)$$

where R_s and R_p are resistances to water flow in the soil and plant respectively, ψ_s and ψ_l are soil and leaf water potentials respectively, and T is the transpiration or water flux rate through the system. In the experiments described in this chapter ψ_s and ψ_l have been expressed in bars and transpiration in $\text{g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$. The total resistance ($R_s + R_p$) calculated from the above mentioned parameters is then expressed in bars sec cm^{-1} . The soil resistance R_s can be written as b/k (FEDDES, 1971, p. 64) where b is a constant reflecting the length and geometry of the root system, and k is the hydraulic conductivity of the soil. The hydraulic conductivity of unsaturated soil was determined as described by KLUTE (1972) and its reciprocal value in sec cm^{-1} was plotted against $R_s + R_p$ as shown in Figure 3.

At the initial stages of the drying cycles, the total resistance in cucumber was higher than that in tomato and pepper. This partly accounts for the lower leaf water potential in cucumber, as compared with tomato and pepper, in favourable moisture conditions. As the soil dried, however, the increase in total resistance for tomato and pepper was more pronounced than that in cucumber, especially at higher stress levels. This can also at least partly account for the slower reduction of plant water potential in cucumber as compared to the other two species (Figure 2). A comparison of $R_s + R_p$ values for tomato and pepper in Figure 3 does not account for the faster reduction in leaf water potentials for pepper in Figure 2. The soil volume was the same for the three species and relatively small. It can be assumed that the roots had entirely occupied the soil volume, and the b factor could perhaps be the same for the three species. The differences in the values of $R_s + R_p$ for the three species, as mentioned above, could then be a reflection of differences in their internal plant resis-

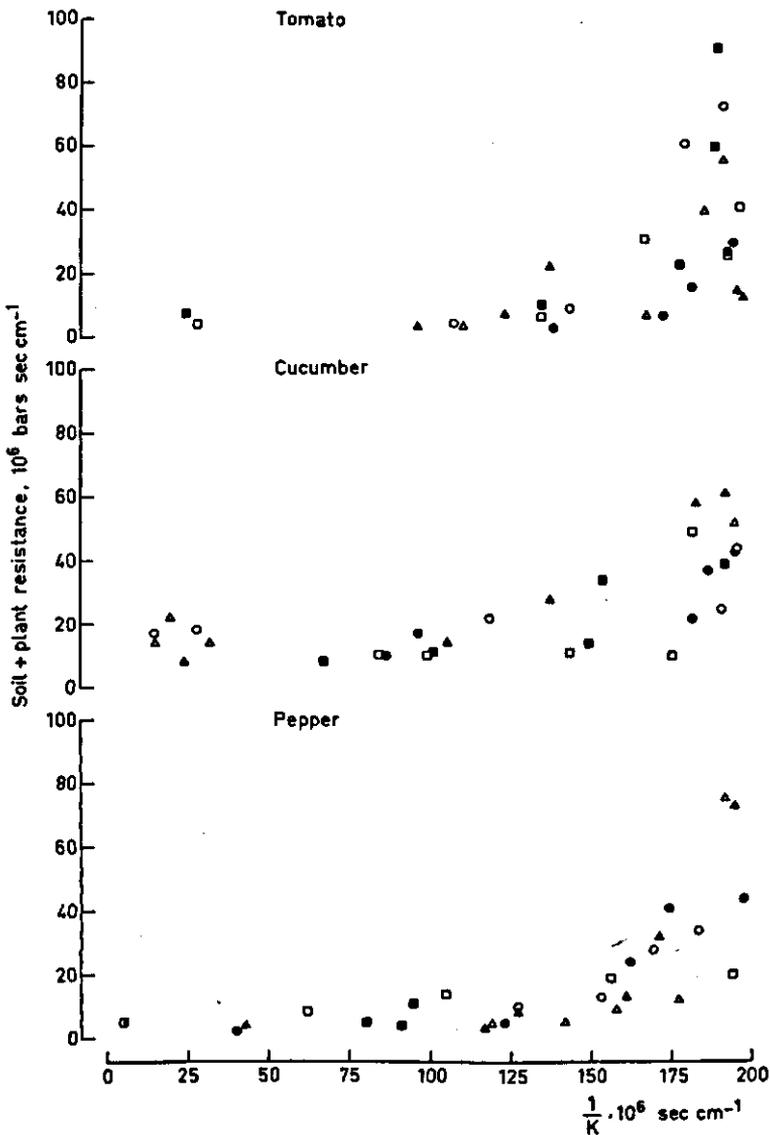


FIG. 3. The relationship between the sum of soil and plant resistances and the reciprocal of the soil hydraulic conductivity ($1/k$) for tomato, cucumber, and pepper in 25 (closed symbols) and 21 °C (open symbols) at high (circles), intermediate (squares), and low (triangles) levels of irradiance.

tance to water transport. If this assumption is justified, then the plant resistance to water flow in cucumber is the highest among the three species at low moisture deficits, but the plant resistance in tomato and pepper increases faster as the soil dries. In the earlier literature (e.g. GARDNER, 1960) the in-

crease in the total resistance ($R_s + R_p$) by drought was attributed mainly to the increase in R_s because of the large decrease in soil hydraulic conductivity as drying occurs. NEWMANN (1969) however, made a critical review of the earlier literature reports and concluded that only in very dry soil would there be a soil resistance high enough to impede the flow. He therefore concluded that the plant resistance is the more important one. Recent investigations have confirmed the phenomenon of increasing plant resistances to water transport in the liquid phase as drought occurs. For example, this phenomenon has been shown for pepper (JANES, 1970) in a nutrient culture and for sugarbeet (LAWLOR and MILFORD, 1975) in a soil culture. SLAVIK (1975) stated that the development of leaf water deficits is primarily due to the plant resistances when water moves from the soil to atmosphere. The same viewpoint was expressed by MEIDNER and SHERIFF (1976, p. 53). As suggested by HANSEN (1974), this increase in R_p under stress conditions could be due to: (1) increased cavitation in the water pathway within the plant, (2) shrinking of xylem vessels, (3) the influence on root-soil interface by a collapsing of the cortex during the stress, and (4) decrease in root permeability due to increase in cytoplasmic viscosity. Dying of the root hairs and suberization of the roots under drought could also contribute to increases in plant resistance in stress conditions. Although for the present investigation the b factor was not evaluated, based on the literature cited above, it can be assumed that most of the resistance was contributed by the plants.

As explained in section 2.3., the incomplete recovery of transpiration after rewatering the stressed plants was not due to persisting water stress, but was more likely due to an aftereffect of stress on stomata. HSIAO (1973) has reviewed the literature on this phenomenon. He cited studies showing that the aftereffect was not due to persisting water deficiency but could be ascribed to an accumulation of inhibitors, most probably abscisic acid (ABA). RASCHKE (1975) stated that ABA could accumulate in pools remote from guard cells and be responsible for aftereffect on stomata if the pools leak some ABA into the transpiration stream. HSIAO (1973) mentioned studies in which changes in internal CO_2 concentration as a major factor in stomatal aftereffect were ruled out. BOUSSIBA and RICHMOND (1976) reaffirmed an earlier hypothesis that the aftereffects of several stresses, and not only water stress, are caused by modification of the hormonal balance of plants. They provided evidence that in tobacco ABA played a role in aftereffects of stresses caused by mineral deprivation or salination of the root medium. In both cases the stress-induced ABA accumulation adversely affected the stomatal opening, although water content of the plants had not been affected.

One objective of the present experiments was to assess relative water content, stomatal opening, and plant water potential measurements as indicators of stress and as a possible method for scheduling irrigation. Results of RWC measurements presented in this chapter did not give a good indication of the plant water status in individual drying cycles. At relatively high plant water potentials in early stages of a drying cycle, the RWC values were either stable,

decreasing, or even increasing. However, only after the lowest water potentials had been reached the RWC values showed a decline. This is in agreement with the conclusions of AL-ANI and BIERHUIZEN (1971) for cucumber, tomato, and beans. Although some reports indicate a sensitivity of RWC in an imminent stress situation (e.g. HALEVY, 1960), it is generally maintained that this parameter is not a sensitive indicator of water status when stress is not severe (HSIAO, 1973). The applicability of this method probably depends on the environment. When evaporative demand is high, such as in arid or semi-arid conditions, RWC might give better indications of plant water status compared to the situation in which evaporative demand is low such as in glasshouses in The Netherlands or conditions employed for the present investigation. In spite of its limitations, if RWC could be calibrated against leaf water potential, it will be a useful indicator of the latter parameter (BOYER, 1969). Although for single drying cycles the values of RWC were not good indicators of plant water status in the present investigation, highly significant correlations were found between this parameter, leaf water potentials (Chapter 3), and soil water potentials (Figure 2).

Regression of measured r_s on soil water potentials was in some cases better than that of RWC on soil water potentials (pepper experiments and tomato at 25°C, Table 2). For other cases (cucumber experiments and tomato at 21°C, Table 2) lower correlation coefficients were obtained between r_s and soil water potentials. Although for research purposes they are indispensable, r_s measurements may not be quite satisfactory as guidelines for irrigation timing. This is due to: (1) rapid and transitory nature of stomatal movements in response to changing environmental conditions, giving a poor basis for judgement of irrigation timing, (2) sampling problems caused by the fact that stomata of different leaves on the same plant might be affected to different extents by outside factors, such as water stress, as exemplified by the results of JORDAN et al. (1975) with cotton, and (3) requirement of relatively sophisticated equipment (diffusion porometer) for measuring stomatal diffusive resistances. The maintenance and continued use of reliable diffusion porometers require a degree of technical sophistication which is not ubiquitous. Moreover, the r_s values cannot be measured when leaves are wet in the field. Field measurements of r_s values have not always correlated with plant water potentials, as exemplified by the results of KAUFMANN (1976) with Engelmann spruce. WATTS (1975) advocated the use of modelling for prediction of stomatal movements as preferred to their measurements.

Based on the results of the present investigation, leaf water potentials measured with a pressure chamber offered the best possibility for assessing plant water status. It had the highest overall correlation coefficient with soil water potential and was the most simple method. The use of pressure chamber is also possible when only limited technical sophistication is available. For pepper and tomato, good agreements have been found between this method and other more accurate methods such as thermocouple psychrometry and hygrometry. GEE et al. (1974) reported that measurements of pepper leaf water

potentials with pressure chamber were in excellent agreement with those of thermocouple psychrometer. Similar results were obtained for tomato by DUNIWAY (1971). BAUGHN and TANNER (1976) compared pressure chamber measurements with those of in-situ hygrometer for five species, including sweet pepper cv. California Wonder. Pressure chamber and hygrometer measurements agreed within 1.0 to 1.5 bars. They concluded that pressure chamber is a reliable method for estimating leaf water potential if post excision evaporative losses are minimized. For cucumber, leaf water potential measurements by pressure chamber offer some difficulty, as also noticed by HOPMANS (1974). Cucumber gives a bubbling from the xylem vessels before the pressure is raised to the potential of the tissue. This is due to the air passing through the vessels and blowing the contents of the xylem out. When pressure is increased to that of the tissue potential, the fluid ejects more copiously and does not contain many bubbles. To distinguish between false and real readings some experience is required. This is easily obtained, since the bubbling occurs at lower pressures and stops when pressures are increased to the proper levels, especially in stressed plants. In Chapter 5, methods are suggested as to the application of plant water potentials for scheduling irrigation.

3. SOME PHYSICAL ASPECTS OF INTERNAL WATER RELATIONS

3.1. INTRODUCTION

Water potential of plant cells consists of pressure, matric, and osmotic potentials (SLATYER, 1967, p. 145). The magnitude of each component will change when plants are subjected to drought. HSIAO (1973) stated that unless the tissue is severely dehydrated, a change in the matric potential component can be neglected. He maintained that at the onset of stress, the decline in pressure potential is more pronounced than that of the osmotic potential, the latter playing a dominant role after water potentials as low as -12 to -16 bars are reached. In spite of its slower change at the earlier stages of drying, osmotic potential has been used as an indicator of water status. An evaluation of this method has been done by BARRS (1968, p. 313). If osmotic potential is to be used as a criterion for timing of irrigation, methods requiring simple equipment and easy handling are necessary for its measurements. It is envisaged that electrical conductivity measurements of cell sap could be useful in practice. Such measurements are evaluated in this chapter.

The ability of plants to maintain a high relative water content at decreasing plant water potentials is an indication of their drought resistance. WEATHERLEY and SLATYER (1957) obtained relationships between water potential and relative water content for tomato and privet leaves. They attributed the divergence of the curves to differences in cell water relations between the two species and indicated that this difference could be of ecological significance. SLATYER (1962) used the same method for assessing the drought resistance of *Acacia aneura*. Mature and young plants grown either under irrigation or natural rain were sampled. Compared to privet and tomato, the desorption curve attributed a greater drought resistance to *A. aneura* as might be expected otherwise. JARVIS and JARVIS (1963) presented evidence that the relationship between relative water content and water potential in the leaves may be similar for plants grown under different conditions. However, they asserted that environmental conditions causing appreciable changes in osmotic and hydration properties of tissues may lead to a shift in the relation. They conceived a hypothetical situation in which the relationship between relative water content and leaf water potential was linear. They assumed that species having higher relative water content at the same level of plant water potential are more drought resistant. However, they suggested that the growth of more resistant plants is reduced to a greater extent by a moderate water stress because loss of a given amount of water will result in higher reduction of leaf water potentials in them. LEVITT (1972) reasoned that the ability of plants to grow at moderate water stress is limited by vacuole and cell wall properties while prevention of injury depends mainly on protoplasmic properties and therefore the two

phenomena are independent.

Based on the relationship between RWC and water potential in the phylodes of brigalow and mulga, CONNOR and TUNSTALL (1968) found that brigalow was more resistant to desiccation than mulga which by then was considered an extreme in drought resistance among Australian species. SANCHEZ-DIAZ and KRAMER (1971) observed a greater water saturation deficit for the same leaf water potential in corn than sorghum which reaffirmed the latter's greater resistance to drought.

In the present chapter, an attempt is made to clarify some physical aspects of internal water relations of cucumber, tomato, and pepper. Variations in osmotic and matric potentials in relation to total plant water potentials are presented and discussed. Evaluation is made of electrical conductivity as an indicator of osmotic potential. The relative drought resistance of the three species is evaluated.

3.2. MATERIALS AND METHODS

Seeds of cucumber cv. Fertila, tomato cv. Moneymaker, and pepper cv. California Wonder were sown in early January 1976 and the plants were raised in a glasshouse. Drying cycle experiments were performed when the plants were 6, 8, and 9 weeks old respectively for cucumber, tomato, and pepper. Since the growth rate of cucumber was the highest and that of pepper the lowest, different age groups were chosen to obtain plants of similar sizes as much as possible. At different stages of the drying cycles, leaf collections were made for determination of their water potential, sap osmotic potential, and electrical conductivity. After measuring in a Scholander pressure chamber, the leaves were put in plastic bags and placed in a -25°C deep freeze. The measurements were made on the third leaf of the cucumber and the fifth leaf of the tomato and pepper plants, counted from the base.

For measurements of sap osmotic potential and electrical conductivity, five leaves were taken out of the deep freeze (seven in the case of pepper), thawed, and pressed for sap extraction. Osmotic potentials were determined using a dew point hygrometer. A Wescor HR-33 Dew Point Microvoltmeter was employed in conjunction with the Wescor C-52 sample chamber. The hygrometer was calibrated with solutions of NaCl having known osmotic potentials. The electrical conductivity of sap from the same samples was measured with a direct reading conductivity meter. Measurements of osmotic potentials and electrical conductivity were carried out in a 20°C controlled temperature room.

The measured osmotic potentials were thought to be rather high and became higher than water potentials in the early stages of drying cycles. This would mean that negative pressure potentials were already developed at unrealistically high water potential levels. Therefore, it was suspected that the matric potential is not negligible, as is generally assumed in the literature. To clarify this phenomenon, some frozen leaf samples were thawed to room tem-

perature and the collapsed samples were teased into a loose condition to completely eliminate the pressure potential. The samples were then placed in the dew point hygrometer and the sum of their osmotic and matric potentials was determined. From the latter values, osmotic and water potentials were subtracted to obtain the values of matric and pressure potentials respectively. Duplicate samples were used for this purpose except with pepper leaves at water potential of -11.4 bars, for which three replicates were used.

3.3. RESULTS

Figure 4 shows the change in sap osmotic potential and electrical conductivity in relation to that in leaf water potential for cucumber, tomato, and pepper. For each species the linear regressions of osmotic potential and electrical conductivity on plant water potential were highly significant. For cucumber and pepper, inclusion of a quadratic term in the equations significantly improved the regression model. The latter tests of significance were carried out by the extra sum of square principle as described by DRAPER and SMITH (1966, pp. 67-69). Values of water potential components for cucumber, tomato, and pepper are presented in Table 4. At a higher leaf water potential, values of matric potential were 29, 43, and 29% of the leaf water potential for cucumber, tomato, and pepper respectively. Matric potentials decreased in the medium stress range and increased again under the severe stress conditions. However, the values for the latter treatments remained lower than those of the controls. In cucumber and tomato, pressure potentials increased for the medium stress conditions followed by a decline when severe stress set in. For pepper, a decline in pressure potential to even negative values was observed with a decrease in water potential. Figure 5 shows that the regressions of sap osmotic potentials on sap electrical conductivity for the three species were linear. The correlation coefficients were highly significant.

Figure 6 shows the regression lines of relative water content on leaf water potential for cucumber, tomato, and pepper. Although highly significant, the correlation coefficient in cucumber was smaller than those of tomato and pepper. This could be due to the difficulty in the measurements of the cucumber leaf water potential with the pressure chamber as was already discussed in Chapter 2. Slopes of regression lines were significantly different among the three species, with cucumber having the smallest and pepper the largest slope. Therefore, the divergence of regression lines in Figure 6 is real. Within the range of water potentials measured, the relation of RWC and leaf water potential for tomato in Figure 6 is similar to that cited by SLATYER (1967, p. 147). For pepper cv. California Wonder, JANES (1970) reported higher RWC values for the same water potential range of Figure 6. The plants in his experiments were grown in Hoagland nutrient solution, and for the same leaf water potential the osmotic potential could have been lower. Assuming that the matric potential was the same in this experiment as that of JANES' (1970),

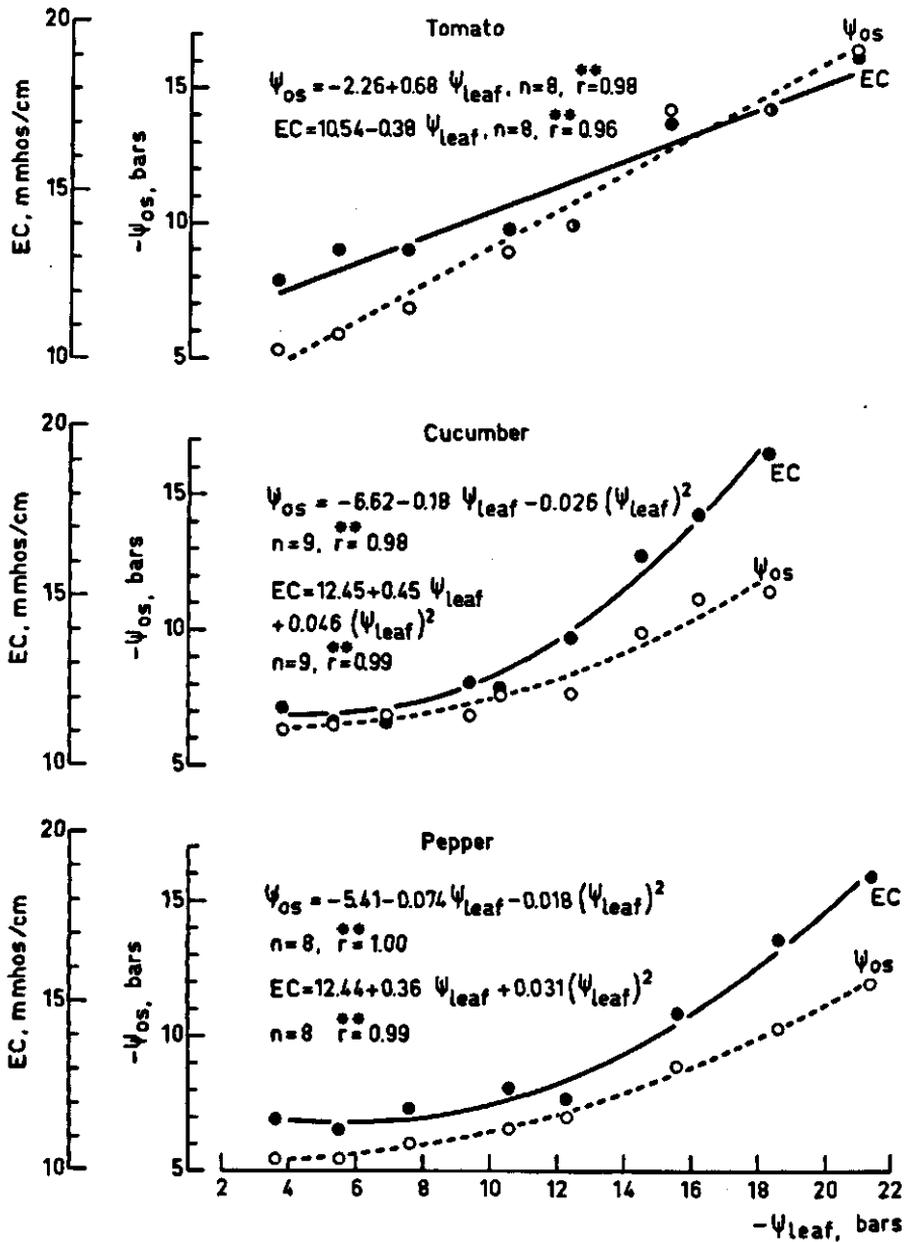


FIG. 4. Regressions of sap osmotic potential (ψ_{os}) and sap electrical conductivity (EC) on leaf water potential (ψ_{leaf}) for tomato, cucumber, and pepper. All the correlation coefficients are significant at 1% level.

TABLE 4. Components of leaf water potential (in bars) for cucumber, tomato, and pepper.

Plant	Water potential	Osmotic potential	Matric potential	Pressure potential
Cucumber	- 5.5	- 7.67	-1.59	3.76
	-11.2	-11.13	-4.64	4.57
	-18.5	-15.43	-3.53	0.46
Tomato	- 4.3	- 6.42	-1.94	4.06
	-12.0	-13.35	-4.71	6.06
	-18.4	-16.67	-3.33	1.60
Pepper	- 3.9	- 6.63	-1.11	3.83
	-11.4	- 8.78	-5.26	2.64
	-20.1	-13.07	-4.02	-3.01

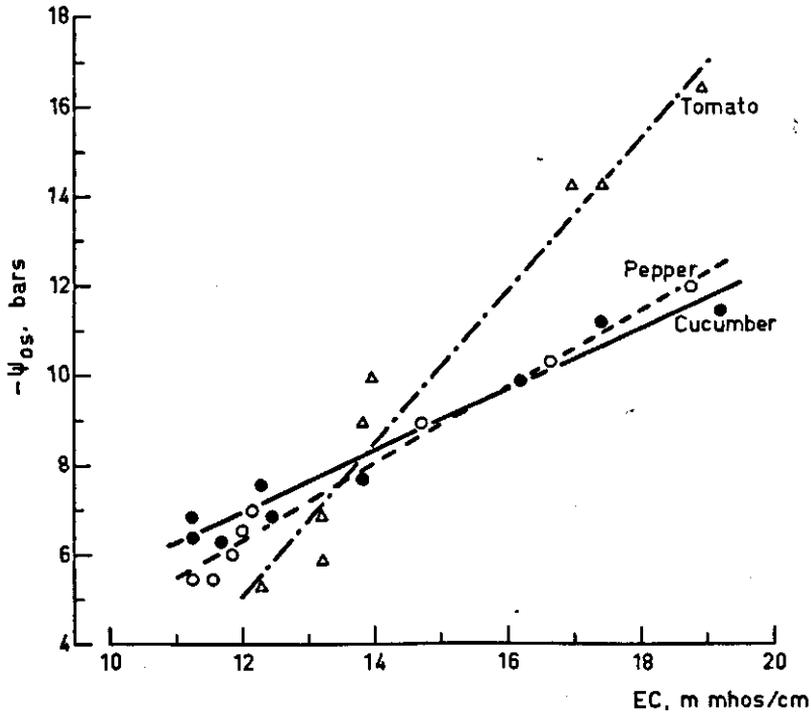


FIG. 5. Linear regressions of sap osmotic potential (ψ_{os}) on sap electrical conductivity (EC) for tomato, cucumber, and pepper.

Tomato : $\psi_{os} = 15.45 - 1.71 \text{ EC}$, $n = 8$, $r = 0.98$

Cucumber: $\psi_{os} = 1.21 - 0.68 \text{ EC}$, $n = 9$, $r = 0.98$

Pepper : $\psi_{os} = 4.02 - 0.86 \text{ EC}$, $n = 8$, $r = 0.99$

All the correlation coefficients are significant at 0.1% level.

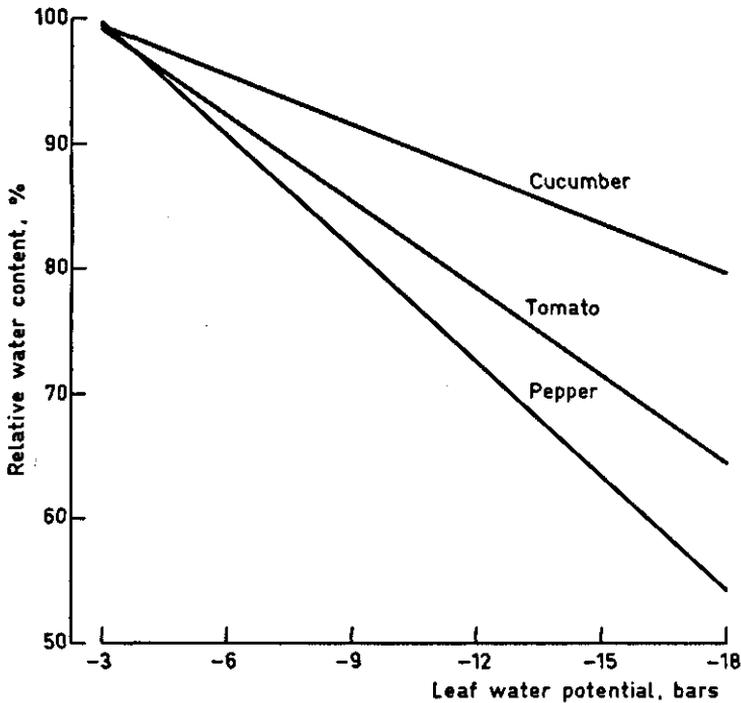


FIG. 6. Regressions of relative water content (RWC) on leaf water potential (ψ_{leaf}) for cucumber, tomato, and pepper.

Cucumber: $RWC = 103.46 + 1.32 \psi_{leaf}$, $n = 35$, $r = 0.64$

Tomato : $RWC = 106.26 + 2.32 \psi_{leaf}$, $n = 34$, $r = 0.92$

Pepper : $RWC = 108.66 + 3.02 \psi_{leaf}$, $n = 35$, $r = 0.95$

All the correlation coefficients are significant at 0.1% level.

higher pressure potentials would then exist in his plants, which could lead to higher RWC values compared to those of Figure 6. For cucumber, no report relating RWC to leaf water potential was found for comparison.

3.4. DISCUSSION

For water stressed plants, the decline in osmotic potential is due to a decrease in leaf water content. Also the addition of solutes to the leaves either by translocation or by retention of assimilates is important (BISCOE, 1972). The latter mechanism could cause the species differences observed among plants as far as the relationship between osmotic and plant water potential is concerned. A parabolic relationship similar to that of cucumber and pepper in Figure 4 has been reported by GARDNER and EHLIG (1965) for cotton, sunflower, birdsfoot trefoil, and pepper. Linear relationships such as that of tomato in Figure 4 were reported for apple (GOODE and HIGGS, 1973) and

sugarbeet (BISCOE, 1972). At a similar plant water potential, the osmotic potential of pepper in Figure 4 was higher than that reported by GARDNER and EHLIG (1965). With tomato, the osmotic potential was higher than that reported by SLATYER (1960). The osmotic potential of plants could be affected by weather, soil moisture status, amount of crop, and nutritional conditions (GOODE and HIGGS, 1973). For example, the osmotic potential in the field is lower than that in controlled conditions (WATTS, 1975). The higher osmotic potential observed for pepper and tomato could be due to the lower irradiance level in the present experiment as compared to the experimental conditions of GARDNER and EHLIG (1965) and SLATYER (1960).

Figure 4 can serve as a guideline for comparing the osmotic adjustments of the three species. In cucumber and pepper the osmotic potential initially remained relatively constant as drought set in. The decline in the osmotic potentials was sharper for tomato compared to cucumber and pepper. If osmotic adjustment was the only factor in maintaining turgor, the pressure potential could be maintained at a more favourable level in tomato, followed by cucumber and pepper. The significant correlation between osmotic and water potentials suggests that the latter could be estimated from the former if the necessary equipment is not available. Calibrations should be done for varying environmental conditions. However, as discussed in Chapter 2, the suitability of the pressure chamber for measurements of water potential of these three species will obviate such indirect measurements. The use of such regressions will be of value for plants whose anatomy does not allow for application of pressure chamber, as exemplified by lettuce. For the latter species, a highly significant correlation between osmotic and plant water potentials (measured with a dew point hygrometer) was also obtained in this laboratory (unpublished data).

The results cited in Table 4 show that the matric potential contributes appreciably to the water potential and its variation, along with that of the osmotic potential, helps to maintain turgor. Matric potential has been neglected by a majority of research workers in calculating the pressure potential. This could have resulted in erroneous conclusions regarding the magnitude of the pressure potential. SHEPHERD (1975) showed that for wheat leaves ignoring matric potential resulted in an underestimation of the pressure potential by 64%. For the present investigation, erroneous conclusions would be drawn if the magnitude of the pressure potential was to be calculated from Figure 4 without considering the matric potential mentioned in Table 4. Based on Figure 4, osmotic potentials became equal to leaf water potentials at values of -6.8, -7.1, and -5.7 bars for cucumber, tomato, and pepper, respectively. Below these values, osmotic potentials were higher than leaf water potentials, implying negative pressure potentials if matric potentials are ignored. However, the appreciable contribution of the matric potential helped to maintain a positive pressure potential at the relatively low water potential mentioned in Table 4.

For cucumber and tomato, pressure potentials at the highest water potential

values were less than those occurring at water potentials of -11.2 and -12.0 bars, respectively (Table 4). These could have occurred due to osmotic and matric adjustments of the two species. SIMMELSGAARD (1976) reported an increasing pattern of pressure potentials in wheat as the substrate water potential declined. The above mentioned increase in pressure potential for cucumber and tomato could also be an artifact. In the measurements of sap osmotic potential, there could be some contribution of matric components (WARREN WILSON, 1967). As shown in Table 4, values of matric potentials in stressed plants were lower than those in well watered plants. Similar results were reported by SHEPHERD (1975) for wheat leaves.

If turgor is maintained at medium stress levels as suggested by the results in Table 4, turgor dependent processes such as stomatal opening might be kept at normal levels. However, at this level of water potential stomatal closure is observed for the three species (Chapters 2 and 4). Stomatal movements depend on the turgor of subsidiary and guard cells while the pressure potentials indicated in Table 4 belong to the bulk leaf. For wheat plants, SIMMELSGAARD (1976) reported increasing values of pressure potentials concomitant with stomatal closure. He attributed the discrepancy to the disparity of guard cell pressure potentials and those of the bulk leaf. Data of both Figure 4 and Table 4 indicate that tomato had better osmotic and matric adjustments and consequently a better ability to maintain its turgor compared to cucumber and pepper. Cucumber in turn rated better than pepper in this respect.

The most important components acting osmotically in plant cells are inorganic salts followed by sugars, while organic acids and their salts are of third importance (SLAVIK, 1959). To be able to measure it readily in the field, SHIMSHI and LIVNE (1967) assumed that osmotic potentials are the combined result of electrolytes and metabolites. For 17 plant species, they measured the former component by conductivity meter and the latter by a hand refractometer. Addition of the two components gave a good approximation of plant osmotic potential. Their conductivity and refractometry results were correlated with their cryoscopy results by the present author. It was calculated that the conductivity as well as the refractometry values correlated significantly with the total osmotic potential ($r = 0.79$ and 0.74 respectively). In general, however, the contribution of the electrolyte component to osmotic potential was more than that of the metabolite component. Therefore, the contention of SLAVIK (1959) that inorganic salts are the most important contributors to osmotic potential was reaffirmed. Figure 5 also corroborates the importance of electrolyte contribution to osmotic potential in cucumber, tomato, and pepper. In tomato, the contribution of electrolytes to the osmotic potential seems to be less than that in cucumber and pepper at lower osmotic potentials. This relationship was found to be species dependent in the results of SHIMSHI and LIVNE (1967) too. SLAVIK (1959) showed that during the ontogeny of plants, changes occur in the proportion of metabolites and electrolytes. This is further shown in Figure 4. At the lower values of plant water potentials, electrical conductivities increased sharply in cucumber and pepper, implying a larger

contribution of inorganic salts to osmotic potentials. The highly significant regressions of electrical conductivities on leaf water potentials for the three species make it possible to determine values of the latter from those of the former. Regressions such as those in Figure 5 could also be used to determine osmotic potentials by the simple determination of electrical conductivity. In methods of osmotic potential measurements described by SLAVIK (1974, pp. 75-109), this procedure was not included. In view of satisfactory results with tomato, cucumber, and pepper as well as lettuce (unpublished data), this method seems to deserve consideration.

Maintenance of more water at decreasing plant water potential will favourably affect physiological functions, presumably because of maintaining higher turgor (HSIAO and ACEVEDO, 1974). In this respect, according to Figure 6, cucumber can function better at conditions of water stress as compared to tomato and pepper. According to the literature reviewed in section 3.1., the decreasing order of drought resistance in the three species would be for cucumber, tomato, and pepper. KRAMER (1969, p. 374) stated that drought resistance in plants is due to their protoplasm being able to endure dehydration without permanent injury, or because they possess structural or physiological characteristics to avoid or postpone lethal levels of desiccation. It is doubtful that the ability to endure desiccation will contribute much to the success of crop plants because yields would reduce below a profitable level before severe desiccation sets in (KRAMER, 1974). LEVITT (1972) also asserted that for economically important higher plants, drought avoidance is more important than drought tolerance. SULLIVAN and EASTIN (1974) stated that in drought resistant crops either stomata close at low levels of water stress or if they do remain open, water loss will be low. An examination of Figure 1 (Chapter 2) shows that at 25°C the slope of regression line for calculated r_s values on soil water potentials is highest for cucumber, followed by tomato and pepper. Although at 21°C the corresponding slope for cucumber is lower than that of tomato (both being higher than pepper), the lower transpiration rate of cucumber would probably give it an advantage in drought avoidance. The ability to close the stomates faster could bestow to cucumber and tomato a better drought avoidance mechanism as compared to pepper. Another criterion for assessment of drought resistance is the extent photosynthesis will be affected by drought (HURD, 1974; DEDIO et al., 1976). Although photosynthesis experiments reported in Chapter 4 were carried out for different cultivars, pretreatments, and time of the day, and will not be quite suitable for comparison in this context, the following deductions could be made for almost comparable conditions. Figure 9 shows that the photosynthesis rate for cucumber is generally higher for the same duration of stress, as compared to pepper. The percentage decline in photosynthesis was higher in cucumber only for two days of measurements, but percentage decline in transpiration was always higher for cucumber. A comparison of Figures 16 and 17 reveals that for the same drop in leaf water potential, photosynthesis of tomato decreases less than that of cucumber. Therefore photosynthesis of tomato was affected least by drought,

followed by cucumber and pepper. Since the accumulation of photosynthates affects the metabolite levels in the cell sap and leads to lower osmotic potentials (DEDIO et al., 1976), the above deductions are in accordance with conclusions drawn from Figures 4 and 5. The photosynthesis experiments just compared, as well as measurements of Figure 4, were carried out at higher levels of irradiance, while measurements shown in Figures 1 and 6 are for phytotron measurements. Therefore, the discrepancy as to the relative position of cucumber and tomato in drought avoidance should not be surprising. JARVIS and JARVIS (1963) stressed that shifts could occur in the relationships of RWC and water potentials according to environment.

Although the foregoing discussion does not fully account for better drought resistance property of cucumber as compared to tomato, it can justify the conclusion that pepper is inferior in its drought resistance compared to the other two species. HSIAO and ACEVEDO (1974) asserted that plants have evolved a variety of strategies in dealing with water stress and therefore the basis of drought resistance can differ from one species to another. They warned against focusing attention narrowly on one or two aspects when considering yield, water use efficiency or drought resistance. The differing ideas on drought resistance in papers edited by STONE (1975) illustrate the present limited knowledge in this subject. KRAMER (1974) stressed that in applied fields, there is need to learn more about the causes of differences in ability to resist drought among plants of various kind.

4. GAS EXCHANGE PROPERTIES AS AFFECTED BY DROUGHT

4.1. INTRODUCTION

In studying the effects of water stress on transpiration and photosynthesis, it is of interest to compare the relative sensitivities of the two processes. In this connection it is of relevance to determine if photosynthetic reduction is brought about entirely by reduced availability of CO₂ through stomatal closure or whether a direct effect of water stress on the photosynthetic system is an accompanying mechanism.

To allow for such an evaluation, diffusion patterns of CO₂ and water vapour in photosynthesis and transpiration are cited as described by GAASTRA (1959) and based on Fick's law of diffusion. As a diffusion process, photosynthesis is proportional to the CO₂ gradient between the bulk air and the chloroplasts and inversely proportional to the overall resistance encountered in the CO₂ pathway. This could be written as:

$$P = \frac{C_a - C_i}{r'_a + r'_i + r'_m} \quad (2)$$

in which P is the rate of photosynthesis, C_a and C_i are CO₂ concentrations in the bulk air and chloroplasts respectively, r'_a and r'_i are resistances to CO₂ diffusion in the air boundary layer and leaf respectively. The resistance r'_m which has been popularly called mesophyll resistance after GAASTRA (1959), denotes physical and biochemical resistances to CO₂ assimilation within the leaf. It could be conceived as a solubility resistance at the cell walls, resistance to transport in solution, resistance associated to cell membrane, and the activity of enzymes associated with transport or carboxylation (TROUGHTON and SLATYER, 1969). Any direct effect of water stress on the photosynthetic mechanism is reflected in a rise of r'_m value (TROUGHTON and SLATYER, 1969). For transpiration (T) the relationship would be:

$$T = \frac{\Delta e}{r_a + r_l} \quad (3)$$

in which Δe is the difference between maximal water vapour pressure at the leaf surface and actual vapour pressure of the ambient air, r_a and r_l are resistances of the air boundary layer and the leaf in the gaseous pathway of water vapour. The leaf resistance r_l consists of a stomatal resistance r_s in parallel with a cuticular resistance r_c for which the following relationship exists:

$$\frac{1}{r_l} = \frac{1}{r_s} + \frac{1}{r_c} \quad (4)$$

With completely open stomata, r_s can be in the order of 1 sec cm^{-1} whereas quoted values of r_c are in the order of 100 sec cm^{-1} . The calculated value of r_l in this case is 0.99 sec cm^{-1} . When r_s is 10 sec cm^{-1} , r_l would be 9.09 sec cm^{-1} . In the literature the cuticular resistances to both water vapour and CO_2 diffusion are often neglected because the leaf resistance will almost be the same with that of the stomatal diffusive resistance. Such an assumption has been made for the analysis of data in this chapter. Since the diffusion coefficients of water vapour and CO_2 in the air are taken to be 0.24 and $0.14 \text{ cm}^2 \text{ sec}^{-1}$ respectively, then it follows that $r'_a = 1.71r_a$, and $r'_l = 1.71r_l$.

It is generally maintained that r_a and r'_a depend on windspeed, wind direction, and leaf size. A survey of environmental factors affecting r_s has been done by KETELLAPPER (1963). Effects of water stress on stomatal movements were elaborated by HSIAO (1973). It should be mentioned that photosynthesis and transpiration of stressed plants subjected to increasing levels of light are governed, at least partially, by the persistent alteration between light controlled opening and drought controlled closure of stomata. WILLIS and BALASUBRAMANIAM (1968) reported that in pelargonium plants with moderate water deficits, stomatal opening on illumination was delayed. For severely stressed plants, opening was both delayed and limited and was soon followed by a closure, resulting in much reduced rates of photosynthesis and transpiration.

In view of the above relationships (equations 2 and 3), factors causing an increase in stomatal and air boundary layer resistances would be expected to reduce transpiration to a greater extent than photosynthesis (BIERHUIZEN and SLATYER, 1964). This is due to the presence of the mesophyll resistance in the CO_2 diffusion pathway in addition to other resistances in common with the vapour diffusion pathway. Since stomatal resistance accounts for a smaller portion of the total resistance in the CO_2 pathway as compared to the water vapour pathway, moisture stress will then be expected to reduce transpiration to a greater extent than photosynthesis. This effect would be even more pronounced when photosynthesis is more controlled by r'_m than r'_s due to the higher values of the former. Based on this assumption, SLATYER and BIERHUIZEN (1964) attempted to increase the water use efficiency of cotton leaves using transpiration suppressants. However, not all research results have confirmed the theoretical expectations in this context and there are examples of increasing transpiration coefficients (the ratio transpiration/photosynthesis) at the onset of stress (BIERHUIZEN et al., 1969). In some species, this has been shown to occur as a result of an increased mesophyll resistance (REDSHAW and MEIDNER, 1972). Therefore, species showing an increase in mesophyll resistance will not have a higher water use efficiency when moisture deficiencies occur (HSIAO and ACEVEDO, 1974).

When experimental results are interpreted on the basis of variations in r'_m , attention should be paid to the way this parameter is calculated. In case C_i (equation 2) is considered to be zero or constant, a stronger decrease in photosynthesis upon drought than could be accounted for by an increase in $r'_a + r'_s$ will be attributed to a rise in the calculated value of r'_m . It is possible that the

reduction of photosynthesis had been brought about by a rise in C_i and a reduced CO_2 gradient. In such a case, r'_m could have remained constant at least for the early stages of water stress, as shown by SLATYER (1973). The increase in C_i could be ascribed to an increase in photorespiration and/or a reduced efficiency in CO_2 conversion by the photosynthetic mechanism, as discussed later.

Changes in energy balance parameters as a result of drought could be partially responsible for differences in sensitivities of photosynthesis and transpiration to drought. When stomatal closure reduces transpiration, the resulting decline in the latent heat should be compensated for by an increase in the sensible heat transfer which results in an increase in leaf temperature. This change in leaf temperature will in turn increase the vapour gradient, with a tendency to enhance transpiration. Elevated leaf temperature may reduce the net exchange of CO_2 through increased rates of respiration. The actual change in leaf temperature depends to a large extent on the prevailing windspeed and irradiance. Therefore, it should be realized that a comparison of $r'_a + r'_s$ with that of r'_m as the main factors causing differences in transpiration and photosynthesis is an oversimplification. Direct measurements of C_i (equation 2) would add an important dimension to those comparisons, but this measurement is rather difficult to carry out.

Photosynthesis is brought about through three general processes, one of which (the diffusion of CO_2 to fixation sites) was described above. The other two processes are activation of light energy and the so called 'dark' chemical processes (which also proceed in light) associated with the chemical reduction of CO_2 . External conditions affect these processes differently according to the concept of limiting factors. For example, photosynthesis responds to light through different mechanisms, depending on the level of irradiance. GAASTRA (1962) stated that for normal CO_2 concentrations, photosynthetic rate is limited by diffusional and photochemical processes at lower levels of irradiance and by diffusion at the light saturated phase. Thus, when effects of some external factors (such as water stress) on photosynthesis are studied, distinction should be made as to which mechanism is involved. If the effects of water stress through diffusional processes are to be studied, light saturated and CO_2 limited conditions should be employed (SLATYER, 1973). These conditions were applied in some of the experiments presented in this chapter.

Water stress affects both diffusional and photochemical aspects of photosynthesis but not to the same extent. PIETERS and ZIMA (1975) showed that in desiccating poplar leaves photosynthesis at high light was decreased due to reduced diffusion of CO_2 . They proposed that the stress-induced reduction of photosynthesis at low light was caused by reduced activity of enzymatic system. For sunflower and pea, BOYER and BOWEN (1970) reported that water stress decreased the rate of photosynthesis due to diffusional limitations at high light and changes in the chloroplasts at low light. They observed that in light limiting conditions the photosynthetic rates of desiccated leaves were lower than those of well watered controls. They suggested that some part of

the photosynthetic electron transport is affected by exposure of chloroplasts to low water potentials within the leaves. They cited a literature example reporting low levels of NADPH occurring in desiccated tissue.

The reduction of photosynthesis of water stressed plants at saturated light is mainly caused by stomatal closure as documented by HSIAO (1973), and according to the same author, nonstomatal mechanisms could also be involved even at mild or moderate water stress in some species. WESSELIUS and BROUWER (1972) increased the ambient CO₂ partial pressure for stressed leaves to compensate the already increased diffusion resistances by an increase in the CO₂ gradient. They did not observe any increase in the rate of photosynthesis and concluded that a reduction of biochemical activities had occurred under stress. For sunflower and pea, BOYER and BOWEN (1970) stated that moderately low leaf water potentials affect the photosynthesis in at least two ways: inhibition of oxygen evolution by chloroplasts and closure of stomata in intact leaves. However, SLATYER (1973) provided evidence that for *Atriplex spongiosa*, *A. hastata*, bulrush millet, cotton, wheat, and maize the direct effect of water stress on photosynthetic system was not discernible until after permanent wilting had been reached. Even then, a direct effect was observed for the two relatively drought sensitive species, cotton and maize. Based on their results with sorghum, SULLIVAN and EASTIN (1974) stated that the reduction in photosynthesis of intact plants depends on the stage of development and previous treatment. They asserted that the assignment of a threshold water potential for reduction of photosynthesis should be treated with caution. They further noted that previous investigators reporting on an impairment of the Hill reaction by droughting had usually obtained their results with potted plants or desiccated excised leaves. In those cases desiccation had been occurring rather rapidly.

In spite of the earlier conflicting reports on the effects of water stress on dark respiration, it is generally maintained that dark respiration decreases with the onset of stress (HSIAO, 1973). However, as has been demonstrated by the results of BRIX (1962) for tomato and loblolly pine, a pattern of species differences at different stages of stress cannot be ruled out.

In practice, drought may occasionally occur, thus reducing the growth of plants temporarily. It has been often observed that the rate of growth after drought is higher as compared with a well watered control. It is often assumed that cell elongation is more sensitive to drought than is photosynthesis, resulting in an accumulation of photosynthates in stress conditions. Upon irrigation, this surplus may give an enhanced rate of growth. It is of general importance in this respect to observe if recovery of plant parameters takes place rapidly after a period of stress. The recovery depends on the degree of stress (BIELORAI and HOPMANS, 1975), the plant species (SLAVIK, 1975), the sensitivity of the parameter involved (WESSELIUS and BROUWER, 1972), the method by which stress develops in plants (BRIX, 1962), and the mechanism by which stress affects the plant processes (LUDLOW, 1975).

Since data on the effect of water stress on gas exchange properties of tomato,

and especially cucumber and pepper, are scarce, experiments were performed in which the effects of drought on those properties were studied in saturated and limited light. Since there was a time limitation on the use of the gas exchange assembly situated at the Centre for Agrobiological Research, the three species could not be given equal attention. The least emphasis was put on tomato because for this species there are some relevant data in the literature (e.g. BRIX, 1962; DUNIWAY and SLATYER, 1971). Twenty four hours after the severely droughted plants were rewatered, gas exchange properties of cucumber and pepper were studied to observe the extent of recovery from drought.

4.2. MATERIALS AND METHODS

The different gas exchange experiments presented in this chapter were performed on plants cultivated and treated under various circumstances. For better clarification, then, the materials and methods for each set of experiment are described separately.

4.2.1. *Effects of drought on gas exchange properties of cucumber and pepper in saturating light and in darkness*

Plants of cucumber cv. Fertila, and pepper cv. California Wonder were grown in a standard soil mixture during the summer months of 1975 in a glasshouse. Experimental treatments were imposed when the plants were 5 and 8 weeks old respectively for cucumber and pepper. The stress treatments were applied on different groups of plants by suspending watering a few days before the gas exchange measurements were carried out. This method provided plants of different stress levels for appropriate measurements on the same day.

For gas exchange measurements, attached leaves were set up in leaf chambers (inner dimensions of $12 \times 12 \times 5$ cm) the environment of which was controlled at desired gas concentrations, air transfer rates, air and leaf temperature, and irradiance. The chambers were equipped with a small fan, heating elements, and a thermostat designed to keep a constant temperature throughout the whole range of light intensities. The wind speed in the leaf chambers was approximately 100 cm sec^{-1} . A detailed account of the gas exchange assembly has been given by LOUWERSE and VAN OORSCHOT (1969). The brief account given here is based on their paper and additional personal communication with the senior author.

Measurements were carried out simultaneously with four leaf chambers. Respiration was first measured during a dark period. Thereafter, net photosynthesis and transpiration were measured in light saturation of 300 W m^{-2} ($\lambda < 700 \text{ nm}$) which was supplied by four 400 W Philips HPLR lamps. A layer of 5 cm deep running water between the light source and the chamber reduced the percentage of infrared radiation ($\lambda > 700 \text{ nm}$) from 50% to 9%. The irradiance inside each leaf chamber was determined by four silicon photoelectric cells (0.1 cm^2 area each). The room temperature was kept at 21°C and

that inside the leaf chamber at 25°C. Air temperature in the chambers was measured continuously with copper-constantan thermocouples. Transpiration was determined by measuring the vapour pressure of in- and outgoing air of the chambers with wet thermocouple psychrometers which were immersed in a temperature-controlled water bath. Carbon dioxide exchange was measured with two infrared gas analyzers (Beckman Model 15A and Model 215) which were continuously calibrated with a 200 ppm CO₂ in-flux. The CO₂ concentration of the in-going air to the leaf chamber was kept at 300 ppm by means of artificial gas mixtures which were prepared by mixing CO₂-free air from a cylinder by a system of flow meters. In this way the variability of the CO₂ content of the outside air was avoided.

Two 16 point Honeywell Electronic 15 recorders were used for data collection for various parameters in the four leaf chambers. These parameters included CO₂ content of in- and outgoing air, CO₂ content of calibration air, wet bulb temperature of in- and outgoing air, irradiance, and air temperature. The data were computer analyzed and it was possible to calculate the total diffusive resistances to CO₂ and water vapour as well as the diffusive resistance to CO₂ in the mesophyll (r'_m).

Immediately after the termination of the gas exchange measurements, the leaf water potential was measured in a Scholander pressure chamber. The leaf area was then measured by a Hyashi Denke planimeter type AAM-5. For each stress level, four plants were sampled for gas exchange and water potential measurements. The 3rd and 5th leaves (counted from the base, disregarding the cotyledonous leaves) were used respectively for cucumber and pepper. To determine the air boundary layer resistance in the leaf chambers, pieces of moist filter paper were used as artificial leaves.

4.2.2. *Effects of drought and irradiance on gas exchange properties of cucumber, tomato, and pepper*

Seeds of cucumber cv. Fertila and Sweet pepper cv. Agronomico 8 from Brazil (pepper seeds kindly provided by Prof. E. Pochard of I.N.R.A. at Avignon, France) were sown respectively on 8 September and 8 August 1975 and the plants were raised in a glasshouse. Before the gas exchange measurements were started, the plants were transferred to a climate room for imposition of water stress. The environmental conditions in the climate room were: day/night temperatures of 28/25°C, irradiance of 58 Wm⁻² (obtained from 400 Watt HPLR lamps), relative humidity range of 55–70%, and wind speed range of 40–50 cm sec⁻¹. A 16-hour photoperiod was employed from 0600 to 2200 hr. The tomato plants (cv. Moneymaker) were raised with the cucumber and pepper plants of section 4.2.1. Their gas exchange measurements were also carried out along with the latter plants. However, the tomato experiments are described in this section since their photosynthesis-light responses were studied for both control and stressed plants. At the time of gas exchange measurements, the plants were 4, 8, and 6 weeks old respectively for cucumber, pepper, and tomato.

The gas exchange assembly employed was the same as that described in section 4.2.1. After placing the leaves in the chambers, different levels of irradiance were given stepwise from 0 up to 300 Wm^{-2} for cucumber and pepper, and down from 300 to 0 Wm^{-2} for tomato. The latter procedure for tomato offered technical difficulties, and it was therefore abandoned for ensuing cucumber and pepper experiments. The irradiance level was changed by inserting metal screens between the lamps and the leaf chambers. The measurements were carried out on the third leaf for cucumber and the fifth for tomato and pepper (counting from the base excluding the cotyledonous leaves). For cucumber and pepper, the experimental treatments consisted of controls, medium stress, severe stress, and recovery. The recovery treatment applies to rewatering of the severely stressed plants and measuring their gas exchange rates 24 hours after rewatering. Medium and severe stress treatments did not receive water respectively for 2 and 3 days in cucumber, and 3 and 5 days in pepper. For tomato, the treatments included control and severe stress (5 days without irrigation). The designation of terms 'medium' and 'severe' stress in this paper is purely arbitrary and is not meant to relate or bear similarity to any other stress treatment encountered in the literature. The leaf water potential was measured using a Scholander pressure chamber. In these experiments, four replicates were used for each treatment except in tomato, for which two replicates were employed. Each leaf chamber is considered as one replicate. Other details in the techniques and equipment used are described in section 4.2.1.

For gas exchange experiments reported in this paper, the methods used in the calculation of transpiration rate, net photosynthesis rate, resistances in the diffusion pathway of water and CO_2 , and mesophyll resistance are described by LOUWERSE and VAN OORSCHOT (1969). Since the leaf temperature could not be measured directly, it was calculated according to the following formula:

$$T_l = T_a + \frac{(Li - EHL) R_{ah}}{H_c} \text{ in which} \quad (5)$$

T_l is the leaf temperature in $^{\circ}\text{C}$

T_a is air temperature in $^{\circ}\text{C}$ measured with a thermocouple

Li is absorbed radiation by the leaf in $\text{J m}^{-2} \text{ sec}^{-1}$ (assumed to be 70% of the measured total radiation)

EHL is the latent heat loss in $\text{J m}^{-2} \text{ sec}^{-1}$ (known from the transpiration rate)

R_{ah} is resistance to transfer of heat in the laminar air layer in sec m^{-1} ($= 1.07 r_a$)

H_c is the heat capacity of air ($= 1250 \text{ J m}^{-3} \text{ }^{\circ}\text{C}^{-1}$).

4.3. RESULTS

For the ease of reference, the results are presented in three sections.

4.3.1. Gas exchange properties of cucumber, tomato, and pepper as affected by radiation in favourable moisture conditions

Gas exchange properties of well watered cucumber, tomato, and pepper for different light intensities are presented in Figures 7 and 8. Figure 7 shows the variation of transpiration, leaf temperature, and stomatal diffusive resistance to water vapour as a function of irradiance for the three species.

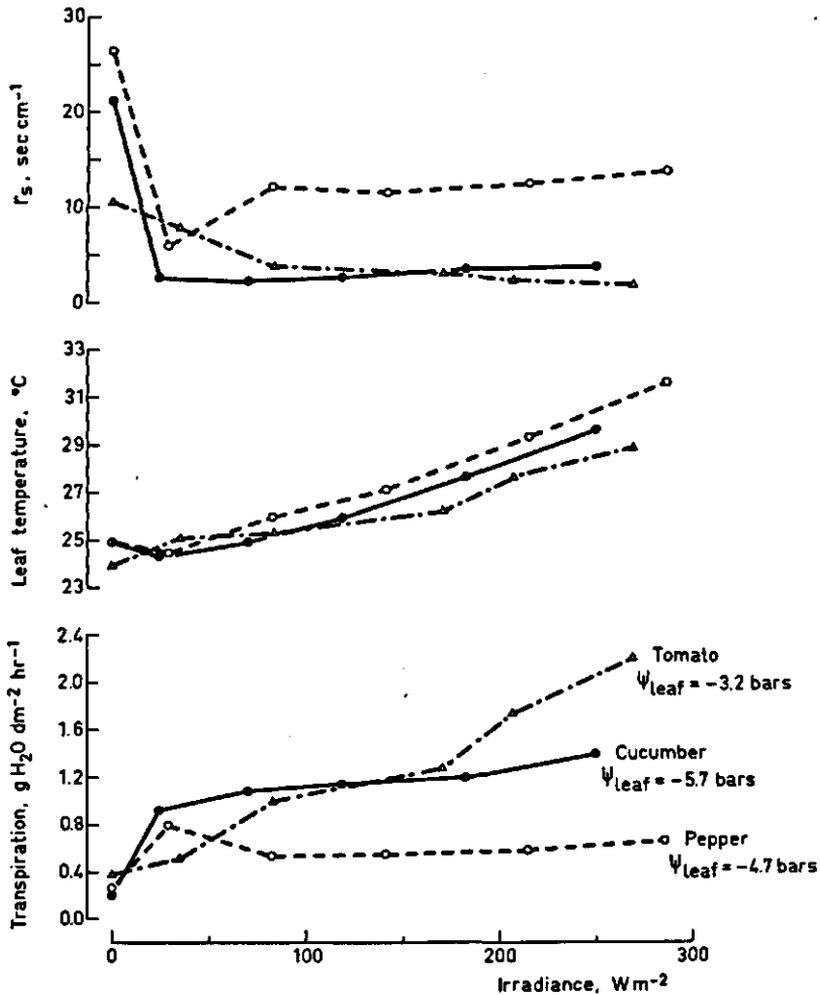


FIG. 7. Values of transpiration, leaf temperature, and stomatal diffusive resistance to water vapour (r_s) as a function of irradiance for well watered tomato, cucumber, and pepper.

Transpiration rates for cucumber and sweet pepper increased rapidly with an increase in irradiance up to 29 Wm^{-2} . Transpiration of pepper showed a small decline (due to the contribution of the afternoon samples because of a diurnal decreasing rhythm discussed in Chapter 5) and then an increasing trend up to a value of $0.66 \text{ g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$. Transpiration of cucumber showed a slowly increasing pattern up to a maximum of $1.39 \text{ g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$ at the highest measured irradiance. Transpiration of tomato increased continuously upon increasing radiation and achieved the highest rate ($2.21 \text{ g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$) among the three species at the highest irradiance. The calculated leaf temperatures showed an increasing pattern for the three species. At the highest light intensities, the leaf-air temperature difference was the highest for pepper (6.8°C), followed by tomato (5.0°C) and cucumber (4.8°C). The stomatal diffusive resistance of tomato decreased with increasing levels of irradiance whereas with cucumber and pepper r_s values declined initially until an irradiance of 29 Wm^{-2} and gradually increased afterwards.

Figure 8 shows the CO_2 exchange rates and mesophyll resistances for well

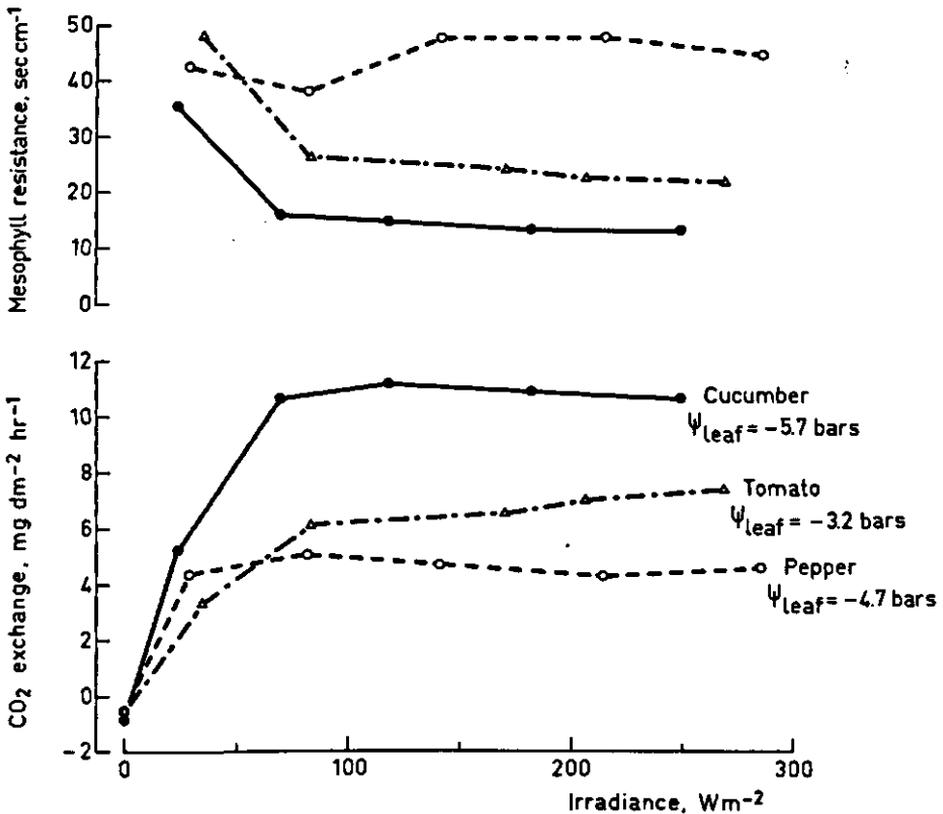


FIG. 8. Carbon dioxide exchange rate and mesophyll resistance of well watered cucumber, tomato, and pepper in relation to irradiance.

watered plants of cucumber, tomato, and pepper. Light saturated photosynthesis for cucumber and pepper occurred at irradiance of 70 and 29 Wm^{-2} respectively. For both species, complete light saturation is thought to have been realized in the neighbourhood of 100 Wm^{-2} (see Discussion). For tomato, a light saturation point could not clearly be defined but occurred approximately at 83 Wm^{-2} . At the highest level of irradiance, the rates of photosynthesis for cucumber, tomato, and pepper were 10.80, 7.51, and 4.69 $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, respectively. Mesophyll resistance decreased with the onset of light in the three species, and then increased in pepper, declined in tomato, and remained constant in cucumber. The values of r'_m were generally the highest for pepper and the lowest for cucumber. The lowest r'_m values for cucumber, tomato, and pepper were respectively 14.1, 22.6, and 38.2 sec cm^{-1} . The ratios of these values to the corresponding stomatal diffusive resistances to CO_2 were 2.1, 6.4, and 1.8 for cucumber, tomato, and pepper, respectively.

4.3.2. *Effect of drought on gas exchange properties of cucumber and pepper in saturating light and darkness*

The change in photosynthesis, transpiration, dark respiration, leaf water potential, stomatal diffusive resistance to water vapour, and mesophyll resistance to CO_2 diffusion for cucumber and sweet pepper in relation to days after the last watering is shown in Figure 9. In the figure photosynthesis and transpiration are also presented as a percentage of the well watered controls. Ten days after suspension of watering, the plants were rewatered and this point is denoted by an arrow in the figure. The above parameters corresponding to the day after rewatering, are also shown in the figure.

For cucumber, the photosynthesis rate of the control was 4.73 $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$. It declined to a value of 0.17 $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ after six days of stress. No net photosynthesis was observed for the 8th and 10th days of stress whereas one day after rewatering, net photosynthesis was 1.4 $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$. Diminution of transpiration was also observed when the watering was suspended. From Day 6 to Day 10, at which photosynthesis did not occur, transpiration was also at its lowest rate. After rewatering, it recovered to a value of 0.34 $\text{g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$ (29% of the control rate) in one day. The dark respiration rate for the control was 0.38 $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, or 8% of control net photosynthesis at light saturation. The respiration rate started to rise slowly at the onset of stress and showed a larger increase from Day 4 to 6. It had a higher rate (taking the absolute values) than the net photosynthesis for Days 6, 8, and 10. The recovery value was similar to that observed for the highest stress level.

Variation of stomatal diffusive resistance to water vapour followed those of the transpiration. The control r_s value was 6.58 sec cm^{-1} . It reached a maximum of 70.3 for Day 8 and declined to 53.0 at Day 10, before rewatering. The recovery of this parameter was not complete one day after rewatering. As shown in the upper part of Figure 9, mesophyll resistance increased from 34.5 sec cm^{-1} at the onset of water stress to a value of 447 after six days of stress.

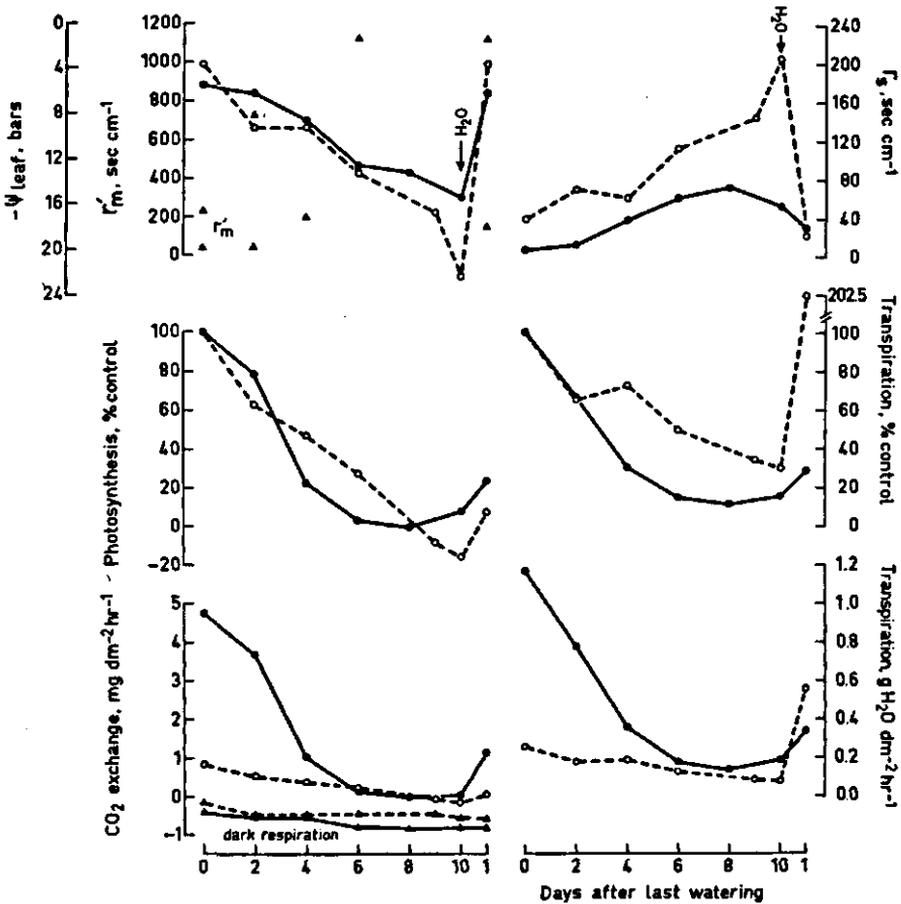


FIG. 9. Variations in CO_2 exchange rate, transpiration, leaf water potential (ψ_{leaf}), stomatal diffusive resistance to water vapour (r_s), and mesophyll resistance (r_m) for cucumber (closed symbols) and pepper (open symbols) in relation to days after the last watering. The arrows indicate rewatering of the severely stressed plants.

Values of Days 8 and 10 reached infinity. The recovery value was 144 sec cm^{-1} . The control treatment had a leaf water potential of -5.5 bars. After two days of stress, this value fell to -6.2 bars. The subsequent diminution was sharper until a value of -15.4 bars was measured at Day 10. One day after rewatering, a value of -6.2 bars was observed. Therefore, the recovery value was just below that of the control. The middle part of Figure 9 shows that at Day 2 the transpiration rate had a larger decline than that of photosynthesis. For the later days, the percentual decline of photosynthesis was higher than that of transpiration. The transpiration rate of the control in this experiment is comparable to those reported in 4.3.1., but photosynthesis rate was lower. The measurements of these parameters for the present experiment were carried out in the

afternoon, and sharp increases in mesophyll resistance following a diurnal rhythm (see also Figure 17) could have decreased the photosynthetic rate more than that of transpiration.

For sweet pepper, net photosynthesis of the control was $0.87 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, which seems to be very low. There was a steady decline in this parameter until only respiration was measured at Days 9 and 10. One day after rewatering, photosynthesis recovered to 31% of the control level. The respiration rate for the control was $0.16 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, which was 18% of the net photosynthesis. The rate increased to 0.45 at the second day of stress, decreased slightly for the 4th day, and increased thereafter. The increasing pattern did not reverse one day after rewatering. The transpiration rate was $0.26 \text{ g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$ for the control and declined to 0.18 after two days of stress. The rate for the fourth day of stress was higher than that of the second. Since values for leaf water potential were the same for both Days 2 and 4, a variability in experimental samples for these days was suspected to be the reason for the higher transpiration rate at Day 4. The rate declined from Day 4 to Day 10. The recovery rate was $0.53 \text{ g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$, or 202% of the control rate. Although similar rates had been observed in the phytotron experiments for pepper (Figure 1), for the results in Figure 9 this rate seems to be excessive. No explanation can be given for this relatively high rate. The control treatment had a leaf water potential of -3.7 bars. Except for Day 4, there was a steady decline in this parameter until a value of -22.4 was reached at Day 10. One day after rewatering, the leaf water potential reached a value of -3.6 bars, slightly exceeding that of the control. Variations in the stomatal diffusive resistance followed those of the transpiration. The control value of r_s was 37.0 sec cm^{-1} which was very high, and explains the low transpiration rate. The highest value of r_s occurred at Day 10 and was 205 sec cm^{-1} . The post watering recovery value was lower than that of the control, resulting in the higher transpiration rate observed. Similar to that of cucumber, the mesophyll resistance increased with increasing stress. The control value was 226 sec cm^{-1} , which was very high. Values of Day 2 and 6 were 725 and 1119 sec cm^{-1} respectively. No value for Day 4 is given in Figure 9 because two replicates had infinity values while the average for the other two was 296 sec cm^{-1} . The recovery value was 1116 sec cm^{-1} . The control rates of photosynthesis and transpiration in Figure 9 for pepper are lower than those shown in Figures 7 and 8. The rates in Figure 9 correspond to afternoon measurements only and as discussed in Chapter 5, gas exchange rates in the afternoon were always lower than those in the morning. Cultivar differences could have also contributed to the discrepancies of Figure 9 and Figures 7 and 8. The rates shown in Figures 7 and 8 correspond to cultivar Agronomico 8 whereas those in Figure 9 belong to cultivar California Wonder.

Figure 9 demonstrates that the rates of photosynthesis and transpiration in cucumber were higher than those in pepper. The values of stomatal diffusive resistances were higher in pepper as compared to cucumber and so were the mesophyll resistances. Leaf water potentials in pepper were observed to be

higher than those of cucumber. This has been consistently observed previously and explanations were offered in Chapter 2. In Figure 9, larger declines in leaf water potential for pepper, as compared to cucumber, are even more striking in view of the expectedly higher soil moisture values (due to lower transpiration rates) for the same days after the last watering. Pepper seems to wilt at lower plant water potentials. In the present experiment, drooping of the lower leaves occurred at -15.4 and -22.4 bars for cucumber and pepper, respectively. However, in ten days of stress the leaf water potential of cucumber decreased only 9.9 bars as compared to 18.7 bars for pepper.

4.3.3. *Effect of drought and irradiance on gas exchange properties of cucumber, tomato, and sweet pepper*

Some gas exchange properties of cucumber leaves, as affected by water stress, are plotted against different levels of irradiance in Figure 10. For cucumber, the terms control, medium stress, severe stress, and recovery are hereafter applied to treatments having average leaf water potentials of -5.7 , -8.2 , -12.6 , and -7.2 bars respectively. Transpiration and photosynthetic rates of the control treatments, already shown in Figures 7 and 8 respectively, are repeated here to greatly facilitate comparisons with other treatments. The control reached light saturation for photosynthesis at 70 Wm^{-2} and for severe stress maximum photosynthesis occurred at 25.5 Wm^{-2} . The reduction of photosynthesis in stressed plants was greater at high light as compared to low light. Upon rewatering, photosynthesis recovered to a greater extent in low light as compared to high light. The efficiency of light energy utilization for photosynthesis was apparently decreased for stressed plants. The light compensation point for the stress treatments increased compared to that of the control. At the higher levels of irradiance, there was a decreasing trend for photosynthesis in the control and was even more conspicuous for recovery, medium stress, and severe stress treatments. For control and recovery treatments, transpiration rates increased as irradiance was raised. After reaching the highest rates at 84 and 75 Wm^{-2} , the transpiration rates of medium and severe stress treatments decreased with increasing irradiance. Among the treatments, the differences in transpiration at high light were more pronounced than those at low light. For different treatments, dark transpiration ranked in the same order as that in light. The dark stomatal diffusive resistance for control was 21.2 sec cm^{-1} . In the light, it varied between 2.28 and 3.98 sec cm^{-1} . Minimum r_s values for recovery, medium stress, and severe stress were 4.98 , 16.8 , and 45.7 sec cm^{-1} respectively. The r_s values of severe stress treatment showed a decline at 75 Wm^{-2} followed by an increase up to 175 sec cm^{-1} at 260 Wm^{-2} .

For pepper, the same parameters are shown in Figure 11. In this experiment the control, medium stress, severe stress, and recovery treatments had average leaf water potentials of -4.7 , -10.4 , -18.4 , and -5.1 bars respectively. For control plants, photosynthesis saturation occurred at 29 Wm^{-2} , and then decreased with further increases in irradiance beyond 82 Wm^{-2} . Photosynthesis

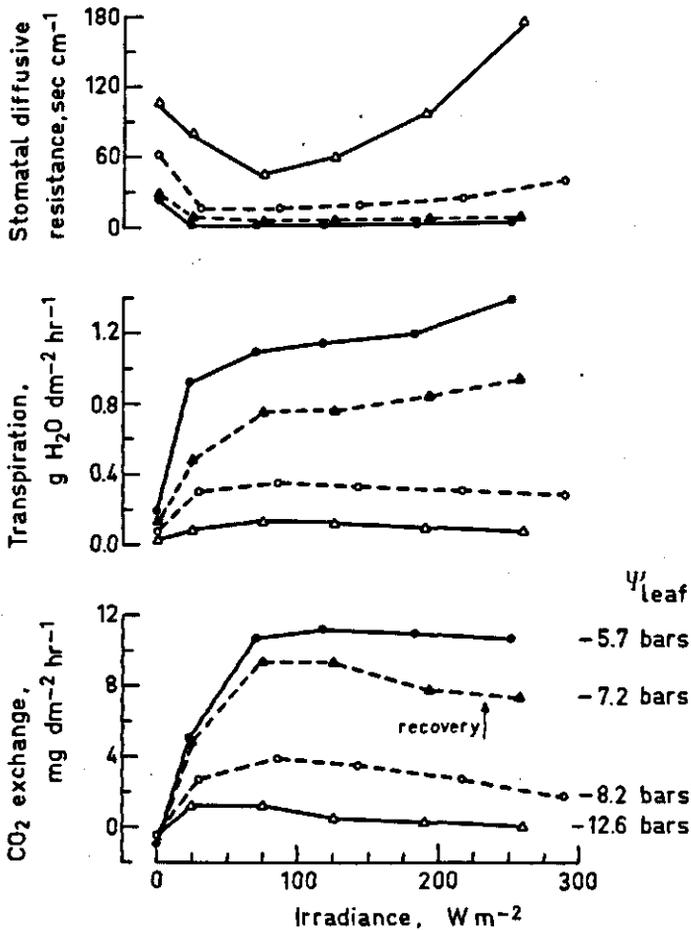


FIG. 10. Carbon dioxide exchange rate, transpiration, and stomatal diffusive resistance to water vapour of cucumber leaves as affected by water stress and irradiance.

for medium and severe stress showed an optimum at 29 Wm^{-2} followed by a decrease in the former and a steady level in the latter. The maximum photosynthesis for recovery occurred at 75 Wm^{-2} and decreased at higher light levels. The light compensation point increased for recovery and severe stress treatments.

The transpiration rate showed a sharp increase at 29 Wm^{-2} followed by a reduction at 82 Wm^{-2} and a subsequent gradual rise with higher irradiance levels. The recovery rate increased slightly over that of the dark value up to an irradiance of 126 Wm^{-2} and showed a further rise for the last two levels of irradiance. The medium and severe stress treatments showed almost the same rate of transpiration throughout the whole range of light intensities, the value being in the order of $0.1 \text{ g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$ in both cases. The dark

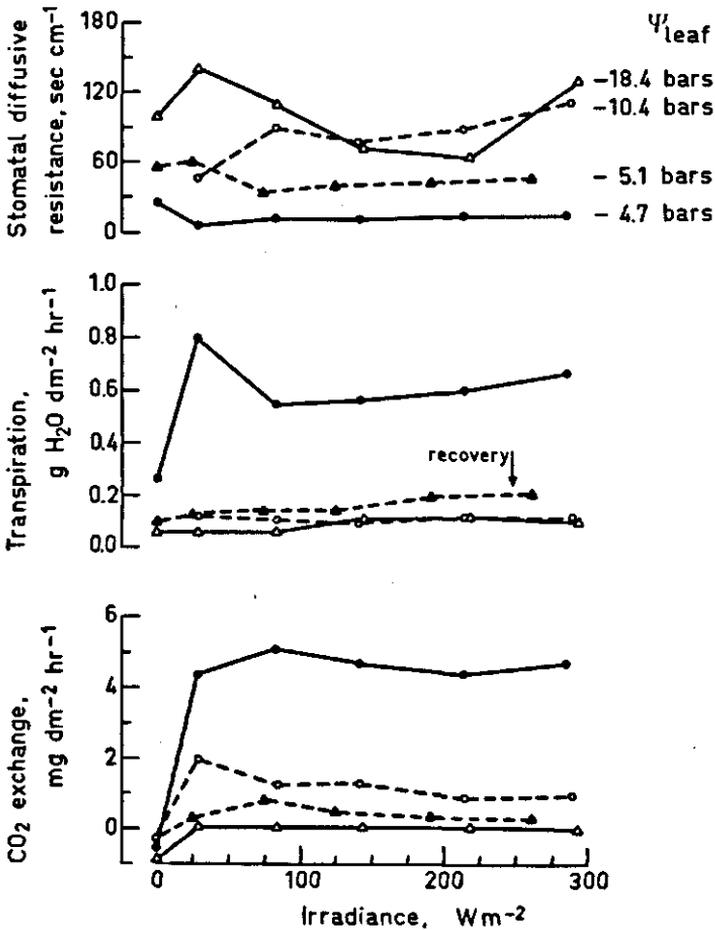


FIG. 11. Carbon dioxide exchange rate, transpiration, and stomatal diffusive resistance to water vapour of pepper leaves as affected by water stress and irradiance.

r_s for the control was 26.4 sec cm^{-1} . It declined to 5.90 sec cm^{-1} at 29 Wm^{-2} , rose to 12.2 sec cm^{-1} at 82 Wm^{-2} , and eventually had a value of 14.2 sec cm^{-1} at the highest irradiance measured. The minimum r_s value for recovery was 34.0 sec cm^{-1} , or 2.4 times higher than that of the maximum for the control value in light. The r_s values of medium stress gradually increased with increasing levels of irradiance. For severe stress, r_s increased over that of the dark value (0 Wm^{-2}), showed a decrease until an irradiance level of 218 Wm^{-2} had been reached, and increased again at the highest level of irradiance.

For tomato, some gas exchange parameters of control and severely stressed plants are shown in Figure 12. The control and severe stress treatments had leaf water potentials of -3.2 and -15.3 bars, respectively. A photosynthetic light saturated level was not clearly observed for the control. Photosynthesis

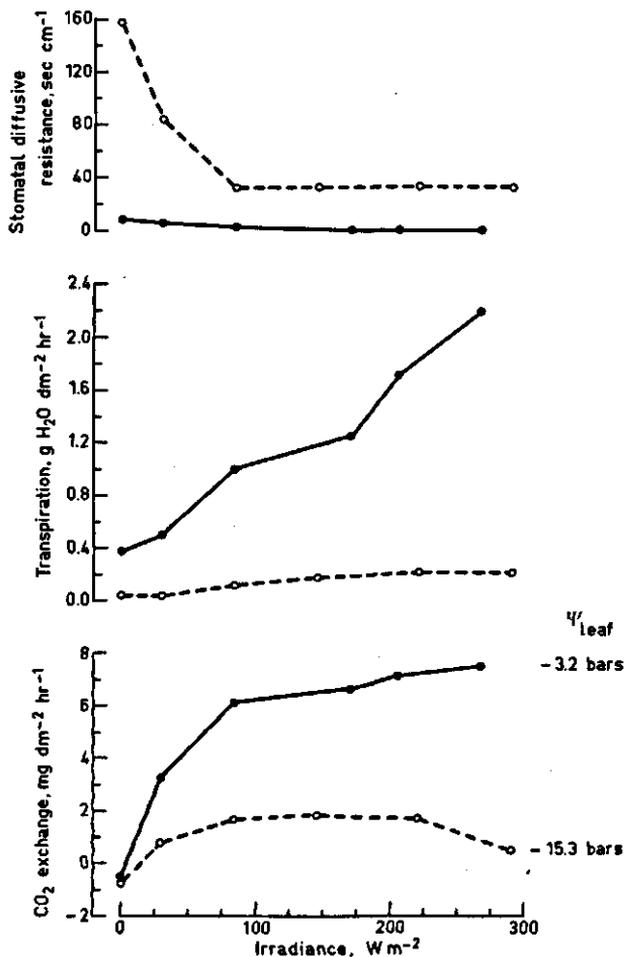


FIG. 12. Carbon dioxide exchange rate, transpiration, and stomatal diffusive resistance to water vapour of tomato leaves as affected by water stress and irradiance.

showed a rising pattern with higher levels of irradiance. For stressed plants, maximum CO_2 exchange occurred at $146 W m^{-2}$ and subsequently decreased with increasing irradiance. Transpiration rates for both control and stressed plants increased with higher levels of irradiance and the increase was more pronounced in the control treatment. Dark transpiration of the control was 7.7 times higher than that of the stressed plants. The dark r_s values for control and stress treatments were 10.5 and 156 $sec cm^{-1}$ respectively. For both treatments, this parameter decreased with increasing levels of irradiance up to $83 W m^{-2}$. For control treatment, a subsequent slight decrease was observed while the opposite happened for the stressed plants. At $83 W m^{-2}$, the r_s values for the control and stress treatments were 3.70 and 40.8 $sec cm^{-1}$ respectively.

TABLE 5. Calculated minimum mesophyll resistances (r'_m in sec cm^{-1}) for different treatments in cucumber, pepper, and tomato. The corresponding stomatal diffusive resistances to CO_2 (r'_s in sec cm^{-1}) are also presented.

Plant	Control		Medium stress		Severe stress		Recovery	
	r'_m	r'_s	r'_m	r'_s	r'_m	r'_s	r'_m	r'_s
Cucumber	14.1	6.80	32.0	28.7	120	78.1	13.3	9.81
Pepper	38.2	20.8	79.1	133	infinity	240	153	70.1
Tomato	22.6	3.52	—	—	43.0	73.6	—	—

In Table 5 the calculated minimum mesophyll resistances with the corresponding stomatal diffusive resistances to CO_2 are presented. Among the three species, tomato had the lowest r'_s and pepper the highest r'_m . For all the three species, both r'_s and r'_m increased with drought.

Figure 13 shows the ratios of photosynthesis/transpiration for cucumber, pepper, and tomato at the highest irradiance level as a function of leaf water potential. For cucumber and pepper, the ratio decreased with decreasing leaf water potential, while for tomato an increase was observed. The recovery ratio in cucumber was comparable to that of the control while in pepper it was not. For potentials lower than -10.4 bars, ratios in pepper were higher than those in cucumber.

4.4. DISCUSSION

In previous chapters, effects of drought on transpiration and internal characteristics of plants were described. As mentioned in section 4.1., it was of interest to measure transpiration and photosynthesis simultaneously in order to find out whether these processes show the same sensitivity towards drought. Moreover, as drought may occur in the field, a knowledge regarding recovery of these processes is highly important. The measurements were made on single attached leaves. By suspending watering for different durations plants with various water potentials were obtained. In the following the effects of radiation on transpiration and photosynthesis in cucumber, tomato, and pepper will be discussed as well as the effects of drought on these processes, their recovery, and water use efficiencies.

4.4.1. Effects of radiation on gas exchange properties in favourable moisture conditions

In general, a photoactive opening of the stomates occurred for cucumber, tomato, and pepper in the range of 0 to 100 Wm^{-2} , which was reflected in a rapid rise in transpiration (Figure 7). Above 100 Wm^{-2} , cucumber and pepper demonstrated a small increase in stomatal diffusive resistance and tomato a small decline. Due to the small changes in the resistance pathway, the increase

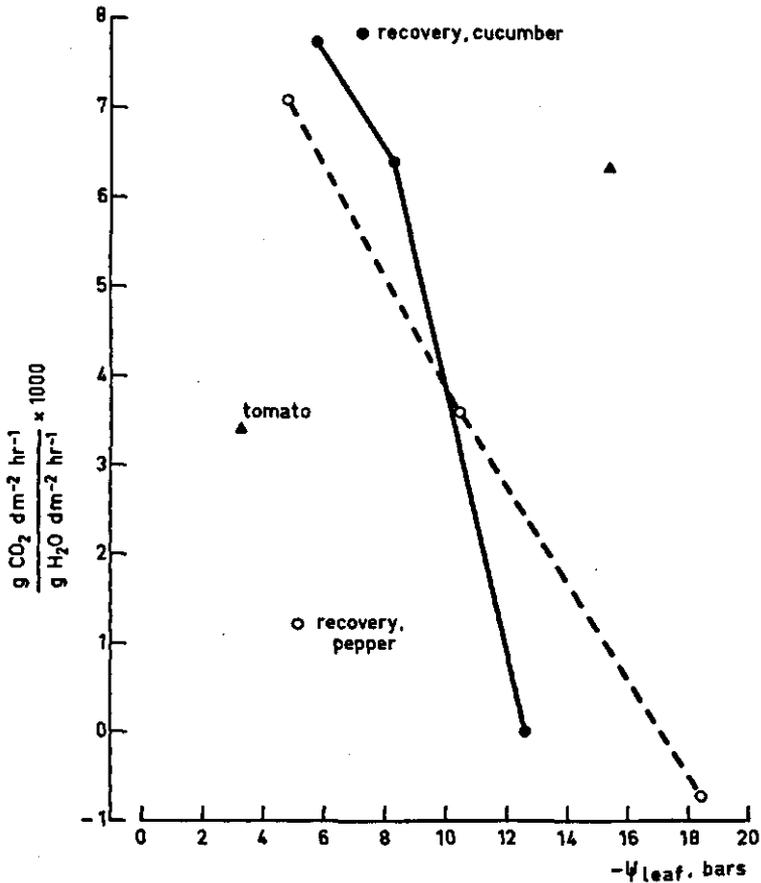


FIG. 13. Ratios of photosynthesis to transpiration as affected by water stress for cucumber, pepper, and tomato.

in radiation above 100 Wm^{-2} caused a pronounced increase in leaf temperature, which led to a small increase in the vapour pressure gradient and thus in transpiration. At the highest irradiance, the sequence in the rate of transpiration from a high value to a low one was for tomato, cucumber, and pepper. Tomato showed the lowest resistance and the lowest leaf temperature followed by cucumber and pepper.

The increase in photosynthesis in the range of 0 to 100 Wm^{-2} was affected by decrease in the stomatal and mesophyll resistances. For example in cucumber, the stomatal diffusive resistance in the range of 0 to 100 Wm^{-2} decreased from 21 to 2.5 sec cm^{-1} and mesophyll resistance declined from 45 to 15 sec cm^{-1} . Photosynthesis for cucumber and pepper was already light saturated at approximately 100 Wm^{-2} because values of r_s and r_m did not change at the neighbourhood of that irradiance. Tomato showed a continuous increase in the rate of photosynthesis with higher light intensities due to a

continuous decline in the resistance pathway. At the highest light intensity the sequence in the rate of photosynthesis from a high to a low value was for cucumber, tomato, and pepper. This sequence is not the same as that for transpiration. The lower mesophyll resistance of cucumber caused a higher rate of photosynthesis compared to tomato. The higher r'_m than r'_s values for the three species is indicative that photosynthesis is affected relatively less by stomata under conditions of CO₂ limitations. Considering the r'_m and r'_s values of the three species (section 4.3.1.), photosynthesis of tomato should be least sensitive to stomatal movements and that of pepper the most. This is because r'_s values contribute least to the total resistance pathway of CO₂ in tomato and most, in pepper. Water stress is then expected to cause photosynthetic reduction in pepper, cucumber, and tomato in this decreasing order of magnitude. This would be the case if mesophyll resistance was constant or was affected less than stomatal resistance at the onset of water stress. The actual experimental data dealing with these phenomena are discussed later in this chapter.

At light saturation, differences in leaf photosynthesis among species as proposed by EL-SHARKAWY and HESKETH (1965) are due to: (1) the existence of respiratory CO₂ leakage into intercellular leaf spaces and/or out of leaves, (2) stomatal diffusive resistances associated with lack of stomata on the top surface of some leaves, and (3) difference between warm-climate and cool-climate species, which is thought to be associated with some internal characteristics of leaves. Dark respiration in cucumber was higher than in pepper (Figures 8 and 9), and therefore is not presumed to have positively contributed to a higher rate of photosynthesis in cucumber. Pepper is known to possess appreciable (but not specified) photorespiration (JANES, 1973). Data of DUNIWAY and SLATYER (1971) showed that photorespiration in tomato was 28 to 36% of that of photosynthesis. Data for photorespiration in cucumber are lacking to warrant a comparison. However, the differences in photosynthesis at light saturation among the three species could at least partially be ascribed to differences in photorespiration and CO₂ leakage into intercellular spaces.

The second point mentioned above by EL-SHARKAWY and HESKETH (1965) is also considered. It is known that cucumber is an amphistomatous plant while tomato is hypostomatous (AL-ANI and BIERHUIZEN, 1971). Microscopic examination showed that sweet pepper is hypostomatous too. The amphistomatous nature of cucumber leaf could explain the highest photosynthetic rate as compared to tomato and pepper (Figure 8). However, transpiration of cucumber was lower than that of tomato (Figure 7). Also, differences in photosynthetic activity between tomato and pepper cannot be explained on this basis because both species are hypostomatous. It should be mentioned that a generalization such as that made by EL-SHARKAWY and HESKETH (1965) about the warm-climate and cool-climate species cannot be applicable to cucumber, tomato, and pepper because these species are all warm-season crops. However, the internal characteristics reflecting higher mesophyll resistances in tomato and pepper as compared to cucumber (Figure 8) could account for the photosynthetic differences.

In comparing the data of Figures 7 and 8 and control values of Figure 9 to those in the literature, considerations should be given to experimental procedures, genotypes, and plant conditions. The data of cucumber and pepper (Figures 7 and 8) are averages of morning and afternoon measurements while those of tomato are for morning measurements only. As mentioned in section 4.1., less emphasis was put on tomato measurements for the reasons given in that section. For these species it is generally observed that gas exchange rates in the afternoon are lower than in the morning. These photoperiodic effects are discussed in Chapter 5. Demonstration of this phenomenon can be made from the data of the present chapter. For example, the photosynthetic rates of controls for cucumber and pepper plants in Figure 9 (measured only in the afternoon) are lower than those in Figure 8 (averages of morning and afternoon measurements). In the case of pepper, cultivar differences could partly account for the discrepancy.

Experimental conditions (such as direction of changing the light steps) could affect the results in gas exchange measurements. The lack of a definite photosynthesis light saturation for tomato in Figure 8 could be due to the fact that the light steps were applied downwards from 300 to 0 Wm^{-2} . TATSUMI and HORI (1969) studied the effect of irradiance applied in two directions on photosynthesis of cucumber, tomato, and pepper. They stated that the light-photosynthesis relationship was little affected in cucumber between upwards and downwards administration of light steps. With a downwards application of light, photosynthesis of tomato in their experiment continuously increased with higher light intensities in the same way observed in Figure 8.

Conditions prevailing in the assimilation chambers may affect the experimental results. For example, air flow rates affect the values of air boundary layer resistance. Low rates increase the humidity and decrease the CO_2 concentration, decreasing both transpiration and photosynthesis as a result of declining the gradients. The higher rates of photosynthesis ($17.8 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$) for cucumber reported by GAASTRA (1959) as compared to those in the present paper could be partially due to the higher flow rates in his experimental set-up. Air flow rate in his set-up was 700 l hr^{-1} as compared to 570 l hr^{-1} for the apparatus employed here.

Plant conditions and genotypes have effects on the rate of photosynthesis. For sweet pepper, STEER and PEARSON (1976) reported photosynthesis rates of 7.2 and $21.6 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ for old and young leaves, respectively. The plants were in the fruiting stage and their higher rates of photosynthesis (compared to those reported here) could be partially due to the existence of strong sinks, as exemplified by the results of LOVEYS and KRIEDEMANN (1974) with grapes. Cultivars could differ in their rate of photosynthesis as shown for tomato by AUGUSTINE et al. (1976). Such a cultivar difference is manifest in this paper for the two varieties of pepper used. For the control plants of California Wonder in Figure 9 (measured in the afternoon), the rate of photosynthesis is lower than the afternoon samples for cultivar Agronomico 8 shown in Figure 19. The experimental conditions used for the gas exchange measurements were

comparable for the control and water stressed plants for each set of experiments in this chapter. The above conditions notwithstanding, the effects of water stress on gas exchange properties could be discussed then, and the remainder of this chapter is allocated to this purpose.

4.4.2. Gas exchange properties as affected by drought

In the following paragraphs, the effects of drought on the gas exchange properties of cucumber, tomato, and pepper will be discussed. Both light saturated and light limited conditions will be examined. Consideration will be given to the recovery of gas exchange properties of cucumber and pepper after stressed plants are rewatered.

For the light saturated conditions, the discussion will be centred on the contention that drought reduces the rate of photosynthesis by: (1) stomatal closure, (2) higher respiratory rates, (3) increasing mesophyll resistances, and (4) impeding assimilate transport out of the stressed leaves. For the three species, the parallel decreases in the rates of photosynthesis and transpiration shown in Figures 9, 10, 11, and 12 indicate that the stomatal closure is closely linked with decrement of photosynthesis. Such effects are of common occurrence, as reported in the literature and reviewed in section 4.1. As Figures 10 and 11 show, the administration of higher light intensities to droughted plants of cucumber and pepper, did not necessarily bring about more stomatal opening; rather, further closure occurred at the higher levels of irradiance, implying that the closing effect of drought overrides the opening effect of light. This is reminiscent of the results of WILLIS and BALASUBRAMANIAM (1968) with pelargonium.

Although stomatal closure is linked with decrements of photosynthesis, it does not necessarily imply a completely causal relationship (SLATYER, 1973). If only the closing of stomata was the influencing factor in reduction of photosynthesis in the present experiments, then according to formula (2) the percentage decrease in photosynthesis would be lower than that of transpiration. As Figure 9 shows, there were higher percentual decreases in photosynthesis, as compared to transpiration, at high water stress levels for cucumber and pepper. Involvement of other mechanisms besides stomatal closure is implicit in this connection. Since the air boundary layer resistance to CO_2 diffusion is assumed to remain constant (it was found to be in the order of 1 sec cm^{-1}), the mesophyll resistance should have increased at higher stress levels. Before examining the variations of r'_m as influenced by drought, consideration should be given to the method used to calculate this parameter, as was also stressed in section 4.1. Given the instrumental and experimental set-ups, the internal CO_2 levels had to be assumed as zero to make the calculations possible. However, the internal CO_2 levels cannot correctly be assumed as zero because photorespiration and CO_2 fixation in chemical reactions will necessitate values greater than zero (LEOPOLD and KRIEDEMANN, 1975, p. 27). Moreover, internal CO_2 levels have been shown to increase as a result of water stress (HEATH, 1969, p. 180). Therefore, the r'_m values given in Figure 9 and Table 5 are bound

to be overestimated at least for stress and recovery treatments. Nevertheless, they are useful guidelines in appreciating the nonstomatal effects of water stress on photosynthesis for the three species. Figure 9 and Table 5 show that the mesophyll resistance of cucumber and pepper increased with higher water stress. Tomato also showed an elevated r'_m value in stressed plants (Table 5). DUNIWAY and SLATYER (1971) reported that in tomato mesophyll resistance increased as the leaf water potential fell below -12 bars. SLAVIK (1975) reviewed the literature concerning the effects of water stress on mesophyll resistance. He concluded that the problem of relative contribution of stomatal and intercellular resistances to CO_2 transport during water stress is still far from being resolved. He observed that low water deficits have some small effects on intercellular resistances, which become high only when relative water content is low. LAWLOR and MILFORD (1975) reported that in sugarbeet the rate of photosynthesis was directly related to leaf conductance, except in severely stressed plants ($\psi < -20$ bars), in which the stress had a more direct effect on photosynthesis. Although it is maintained that the r'_m values reported in the present paper could be overestimated, the results nevertheless show that these values in cucumber, tomato, and pepper had a distinct sensitivity to water stress. Similar results were reported by O'TOOLE et al. (1976) for *Phaseolus vulgaris*. They showed that an increase in mesophyll resistance occurred when for its calculation the internal CO_2 was assumed to be either zero or equal to compensation point. However, the rise in r'_m was more pronounced in the former case.

The effects of drought on the internal control of photosynthesis was not the same for the three species. Figure 9 shows that the percentual reduction of photosynthesis in pepper is more than in cucumber, after ten days of stress. However, after the same period of stress, the transpiration rates for cucumber and pepper were respectively 16 and 31% of the controls. Nonstomatal mechanisms, had then greater effect in reducing photosynthesis in pepper, as compared to cucumber. This is further corroborated by the data presented in Table 5, taken from other experiments. Application of the same criteria to the data for tomato in Figure 12 would reveal that the internal control of photosynthesis in tomato was the least affected by drought, as compared to the other two species. The difference in the sensitivities of photosynthesis and transpiration to drought in the three species are further reflected in Figure 13. The ratio assimilation/transpiration was termed 'water economy of assimilation' by LARCHER (1960). For cucumber and pepper, water economy of assimilation deteriorated upon drought. Tomato improved its water economy as stress was imposed. This was due to its high mesophyll control over photosynthesis, as shown in Figure 8 and discussed before. The mesophyll resistance in this species did not increase with stress as much as in the other two, and therefore an improvement of water economy of assimilation with water stress was expected for it.

The decrease in the rate of photosynthesis as affected by drought could be partially due to enhancement of respiratory processes. Figures 9 and 12 give

examples of increases in the dark respiration for cucumber, pepper, and tomato. The increase in respiration could have been due to an increase in soluble carbohydrates as a result of stress. This explanation was proposed by WESSELIUS and BROUWER (1972), who observed an increase in corn respiration rate with onset of drought. BRIX (1962) stated that carbohydrates could be used as respiratory substrates regardless of water stress. However changes in dark respiration as affected by water stress seem to be species dependent (HEATH, 1969, p. 179) and there could be cultivar differences, as is evident by a comparison of Figures 9 and 11 which show that the values in dark respiration for the two pepper cultivars employed in these experiments were different. Since the dark respiratory processes could also continue in light (ZELITCH, 1975), the reduction of photosynthesis in light could be partly a result of this phenomenon, when drought occurs in plants. A possibly higher photorespiration for stressed plants could further decrease the net rate of photosynthesis. DUNIWAY and SLATYER (1971) reported that photorespiration for stressed tomato plants was higher than the dark respiration. Further observations on different species under drought seem to be needed to justify a definite conclusion on this aspect.

Decreased translocation of assimilates out of the stressed leaves could have also resulted in reduction of photosynthesis. LEOPOLD and KRIEDEMANN (1975, p. 69) maintained that assimilate translocation out of a leaf is especially sensitive to moisture stress, whereas movement within the vascular system is not as severely affected. Figures 10, 11, and 12 show that for the stress treatments in cucumber, pepper, and tomato the rates of photosynthesis declined at higher light intensities after having reached a maximum rate at low or intermediate light. These decrements are proposed to be either due to a reduced translocation of photosynthates out of leaves and/or enhancement of photorespiration. TINUS (1974) stated that photorespiration was a function of irradiance and had a Q_{10} of 3.5.

All the photosynthesis-light curves in the present investigation showed that light saturated photosynthesis was more sensitive to desiccation than light limited photosynthesis. The results are in accordance with those reported by PIETERS and ZIMA (1975) for desiccated poplar leaves. According to BOYER and BOWEN (1970), for droughted plants reduction of light saturated photosynthesis is through diffusional limitations while for light limited reductions, other mechanisms are involved. PIETERS and ZIMA (1975) maintained that at low light the photosynthetic rates are controlled by enzymatic systems which respond more slowly to desiccation, and therefore the reduction of photosynthesis as affected by drought is expected to be less in low light as compared to high light. The authors cited literature examples indicating that in intact cells and isolated chloroplasts, NADP and PGA reductions and photophosphorylation were impaired only slightly with water losses up to 50%.

Factors affecting the recovery of plants after a period of water stress were cited in the introduction of this chapter. BOYER (1971) studied the photosynthetic recovery of sunflowers after a drought period, and concluded that

two factors inhibited the recovery after a period of low water potentials. They were the incomplete recovery of leaf water potentials, and the incomplete stomatal opening in light. The recovery values of leaf water potentials reported in this chapter for cucumber and pepper were almost comparable to the control values (Figures 9, 10, and 11); however, the rates of transpiration still lagged behind those of controls (except for pepper in Figure 9, for which an explanation for its unusually high value could not be given). This implies an aftereffect of water stress on the stomates of these species, as discussed in Chapter 2. For cucumber, the recovery of photosynthesis paralleled that of the transpiration and values of r'_m were not far above those of the control. In pepper however, photosynthesis did not recover to the same extent as transpiration. For both species these phenomena were reproducible, as shown for different experiments in Figures 9, 10, 11, and 13 and Table 5. Therefore, there could have been persisting damage to the photosynthetic apparatus of pepper, disabling it to recover after rewatering. This damage made even the recovery of the low light photosynthesis level impossible, as shown in Figure 11. For cucumber, however, the low light photosynthesis level was readily recovered, as shown in Figure 10. BOYER (1971) showed that for sunflower the recovery of photosynthesis in low light was essentially complete for photochemical activity even for plants desiccated to a leaf water potential of -17 bars. Since low light photosynthesis is at least partially controlled by enzymatic system which is only slightly sensitive to drought (PIETERS and ZIMA, 1975), its recovery after rewatering should be fast, as was observed in the present investigation for cucumber and reported for sunflower by BOYER (1971).

5. DIURNAL VARIATIONS IN SOME PLANT PARAMETERS UNDER GLASSHOUSE AND CONSTANT ENVIRONMENTAL CONDITIONS

5.1. INTRODUCTION

Observations on diurnal variations of plant parameters in changing and constant environmental conditions will help to enhance our understanding of the interrelationship among environmental factors and plant responses. In field conditions, such observations might be of help in satisfying irrigation needs of plants.

Studies with field crops have generally indicated the influence of climatic factors (especially radiation) on changes in plant parameters, particularly plant water potential. REICOSKY et al. (1975) reported that for a well watered corn plant, the water potential depended more on radiation than vpd. In one of their measurements, the diurnal variation in vpd lagged five hours behind that of the plant water potential. There was a time lag between the recovery in plant water potential of stressed and well watered plants in the late afternoon as well. An increase in the rhizosphere resistance due to a decreased hydraulic conductivity of the soil during the day was thought to be the reason. MARTIN and DOUGHERTY (1975) observed that at sunrise the ear water potential of irrigated and unirrigated wheat was similar, being in the order of -3 bars, but the leaf water potential of unirrigated plants had decreased to -20 bars by 1200 hr, irrespective of the evaporative demand of the atmosphere. Over the same period, the leaf water potential of irrigated plants dropped to -10 bars. Therefore an important resistance could be located in the water uptake pathway. Irrigation could only partly prevent the fall in water potential of wheat leaves during the day. For corn plants, TURNER (1975) observed that the change in plant water potential from maximum near sunrise to minimum in the afternoon was greater in dry soil than that in wet soil. Stomata hardly closed in the upper canopy and therefore plant water potentials decreased. He maintained that maize was not efficient in preventing the development of low plant water potentials. JORDAN and RITCHIE (1971) observed that for cotton, a minimum plant water potential occurred at 1300 to 1400 hr, corresponding to maximum solar and net radiations. Stomatal diffusive resistance decreased from 40 to 2.5 sec cm⁻¹ within two hours after sunrise and remained near the minimum between 0900 and 1700 hr.

Diurnal variations in some plant parameters have also been reported for a few horticultural plants. The results of HOPMANS (1974) with carnation, chrysanthemum, pepper, and strawberry indicated a drop in plant water potential from morning to mid-day or even later and a subsequent recovery afterwards. SMART and BARRS (1973) reported that for both irrigated and non-irrigated plants of peaches, prunes, citrus, and grapes the minimum values of leaf water

potential occurred soon after mid-day. For all species, radiation was the most important environmental factor in determining the change in plant water potential, while vpd was the least important. The importance of radiation in determining the plant water potential was also stressed by KLEPPER (1968). She observed that leaf water potentials were lower at the east side of pear trees as compared to the west side in the morning, and the opposite was true in the afternoon. She also reported that irrigated and non-irrigated grape vines showed no differences in their leaf water potential values during the day. A closure of stomata in the droughted plants was considered to be the reason for maintenance of water potential although no data were given for the stomatal movements. PLAUT et al. (1975) did a comprehensive study on diurnal variations in some plant and gas exchange parameters of rose in a glasshouse. They reported that for wet and dry treatments, shoot water potential decreased gradually from early morning until 1000–1100 hr, remained at a minimum value throughout mid-day, and increased in the afternoon. No correspondence was found between diurnal changes of shoot water potential and stomatal aperture. They attributed this discrepancy to a difference between shoot water potential and the water potential of the leaves in which stomatal aperture was determined. For both wet and dry regimes, maximal stomatal opening occurred at 1000 hr followed by a closure thereafter. This closure, especially around mid-day, seemed to be independent of radiation and temperature. Carbon dioxide fixation patterns did not follow those of shoot water potential, and no difference in CO₂ fixation in the morning was observed between dry and wet treatments.

For constant environmental conditions, there are only a few literature reports on diurnal variation of plant parameters and those are confined to gas exchange parameters only. HOPKINSON (1964) observed that the rate of photosynthesis in cucumber reached its maximum level during the first two hours of photoperiod and declined thereafter. He stated that the rise in the first two hours was due to stomatal opening. The reduction later on was thought to be due to partial stomatal closure associated with changes in leaf turgor and loss of phosphorous and nitrogen from the leaves. A continuous supply of inorganic phosphorous is needed for the movement of sucrose into and within sieve tubes to maintain the production of 2-phosphoglycerate in photosynthesis. For *Vicia faba*, PEARSON (1974) reported that photosynthesis was maximum during the first hour of photoperiod and minimum during the last two hours. The variation was shown to depend more on changes in mesophyll resistance than that in stomatal resistance. Much of the daily fluctuations in photosynthesis appeared to be governed by either carboxylation reaction or transport of products away from the chloroplasts. PALLAS (1973) studied the diurnal variation of transpiration and photosynthesis (measured in a closed system) in cotton, pepper, peanut, soybean, and bermudagrass. Except for bermudagrass, a diurnal variation of photosynthesis and transpiration showed increasing patterns in the early hours of photoperiod followed by declines in the later hours. Changes in photosynthesis were not exclusively

controlled by stomata. Therefore, endogenous changes in diffusion resistance and/or biochemical activities were suggested as the controlling mechanisms. However, biophysical and biochemical causes of those circadian rhythms were not explained.

The following series of experiments were performed to study diurnal variations in some plant parameters for tomato, cucumber, and pepper. Diurnal variations of some water relations parameters were studied in a glasshouse for tomato and pepper. Gas exchange measurements throughout the photoperiods were carried out for tomato (two cultivars), cucumber, and pepper. To investigate the effects of drought on these properties, both well-watered and stressed plants were used for the measurements.

5.2. MATERIALS AND METHODS

For the ease of reference, materials and methods of the measurements in the glasshouse will be written separately from those in a controlled environment.

5.2.1. *Glasshouse measurements*

Plants of tomato cv. Moneymaker and sweet pepper cv. California Wonder were grown in the summer of 1975 in the glasshouse in which the measurements took place. Two treatments were considered for each species. These were a control, consisting of well watered plants, and stressed plants which received no water for three days (tomato) or four days (pepper). The measurements in the glasshouse started early in the morning and continued until darkness. Measurements of environmental conditions were recorded continuously; those related to plant parameters were carried out in 2-hour intervals.

Irradiance was measured with a Kipp Solarimeter connected to a Kipp Solarimeter Integrator CCI and a Sodecoprinter. Air temperature and humidity were recorded by a thermohygrograph. Evaporation rates were determined by eight piche evaporimeters.

The plant measurements were made on leaf water potential, stomatal diffusive resistance, and transpiration rate. Leaf water potential was measured by a Scholander pressure chamber. The stomatal resistance of leaves was determined with a diffusion porometer built as described by KANEMASU et al. (1969) and calibrated according to STIGTER et al. (1973). The transpiration rate was measured by weighing the pots. Stomatal diffusive resistance and leaf water potential were measured on the 5th leaf of the two species. Sometimes the 10th leaf of pepper was included for these measurements. For each species, five replicates were used. At the time of measurements, tomato and pepper plants were respectively 36 and 67 days old. Dates of measurements were 28 and 29 August 1975 for tomato and pepper, respectively.

5.2.2. *Experiments at constant environmental conditions*

Plants of cucumber cv. Fertila, sweet pepper cv. Agronomico 8 from Brazil, Meded. Landbouwhogeschool Wageningen 77-6 (1977)

and tomato cultivars Moneymaker and Damartin (a cultivar grown locally in the sub-tropical area of South-West Iran) were raised during the summer of 1975 in a glasshouse and were transferred to the 25°C climate room of the phytotron described by DOORENBOS (1964). The irradiance, temperature, and vapour pressure deficit were 29.3 Wm⁻², 24.7°C, and 8.7 m bars, respectively. A 16-hr photoperiod was given between 1630 and 0830 hr. The controls were watered every 48 hours and the stressed had not been receiving water for 5, 8, and 6 days respectively for cucumber, pepper, and tomato at the time of gas exchange measurements. These different drought periods were imposed based on preliminary observations, and were meant to develop the same degree of stress in the three species. During the gas exchange measurements, the plants were 4, 8, and 5 weeks old for cucumber, pepper, and tomato, respectively. The age of the plant was chosen depending on the respective rate of development, which was fastest for cucumber and slowest for pepper.

For gas exchange measurements, the appropriate plants were transferred each day to the gas exchange assembly described by LOUWERSE and VAN OORSCHOT (1969) at the Centre for Agrobiological Research. A brief account of the set-up is given in section 4.2.1. The gas exchange measurements started at 1700 hr and were continued throughout the night in order to avoid changing the previous photoperiod received in the phytotron. After placing the leaves into the leaf chambers, 300 Wm⁻² irradiance was applied for the duration of the measurements. After photoperiod termination, the leaves were taken out of the chambers and their water potentials were measured by a pressure chamber. For cucumber, pepper, and tomato, the 3rd, 5th, and 4th leaves were used, respectively. Duplicate samples were used for gas exchange measurements in each species. At the start of the photoperiod, the leaf water potential for parallel plants of well watered cucumber, pepper, tomato cv. Moneymaker, and tomato cv. Damartin were -5.8, -2.7, -4.0, and -4.0 bars, respectively. For stressed plants the corresponding values were -10.9, -12.7, -14.0 and -14.4 bars.

5.3. RESULTS

The results obtained for tomato and pepper in a glasshouse in which the climatic conditions showed a diurnal pattern will be described separately from those in constant environment with cucumber, tomato, and pepper.

5.3.1. *Glasshouse measurements*

For the ease of reference, the results of tomato and pepper experiments are presented separately.

5.3.1.1. *Tomato*

The diurnal variations of some environmental conditions and various plant parameters are shown in Figure 14. The environmental parameters included air temperature, vapour pressure deficit of the air, irradiance, and evapora-

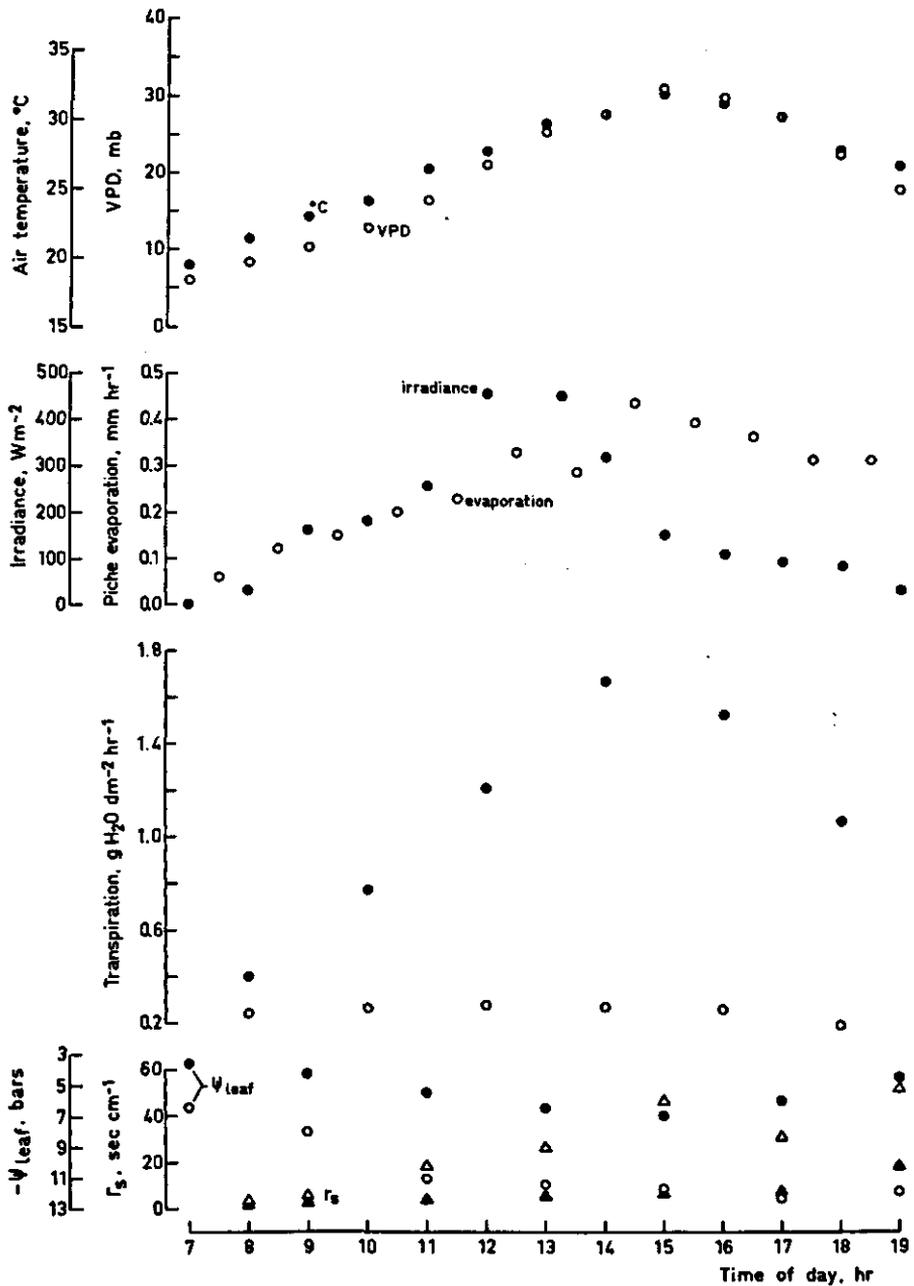


FIG. 14. Diurnal variations in some environmental (air temperature, vpd, irradiance, and piche evaporation) and plant parameters (transpiration, ψ_{leaf} , and r_s) for the tomato experiment. For plant parameters, open and closed symbols respectively represent stress and control treatments.

tion measured by piche evaporimeters. The plant parameters consisted of transpiration rate, stomatal diffusive resistance, and leaf water potential. Air temperature was 19.5°C at 0700 hr and increased to a maximum value of 32.0°C at 1500 hr. It then decreased to 26.0°C at 1900 hr. Vapour pressure deficit followed a similar trend as that of air temperature and was 6.12, 31.34 and 18.47 m bars at 0700, 1500 and 1900 hr, respectively. Irradiance increased from zero at 0700 hr to a maximum of approximately 450 Wm⁻² at noon, declining afterwards to a value of 40 Wm⁻² at 1900 hr. Throughout the day, the sky was completely cloudless, giving a smooth diurnal pattern in radiation. The solarimeter was placed near the plants inside the glasshouse so that its measurement gave a better reflection of the radiation received by the plants. During the day occasionally a sudden drop in radiation occurred due to the shading of the solarimeter cup by the glasshouse structure. These drops are not depicted in Figure 14. The above mentioned data at each hour of the day were obtained from a continuous recording of the climatic factors. Hourly measurements of piche evaporation were also made at the same time, and the difference between each measurement and the previous one reflects the evaporation during an hourly period. The data are therefore plotted at the midpoint of two consecutive measurements. Except for a discontinuous drop at 1330 hr, piche evaporation increased from a value of 0.06 mm hr⁻¹ at 0730 hr to a maximum value of 0.44 mm hr⁻¹ at 1430 hr, declining gradually later on to a rate of 0.32 mm hr⁻¹ at 1830 hr.

Plant parameters for stress and control treatments are shown by open and closed symbols respectively. The transpiration rate of the control was always higher than that of the stress treatment. The rate of the control after sunrise increased to a maximum at 1400 hr and declined thereafter. The values at 0800, 1400 and 1800 hr were 0.40, 1.68, and 1.08 g H₂O dm⁻² hr⁻¹, respectively. The diurnal variations in transpiration followed that of the air temperature, vapour pressure deficit, and piche evaporation, whereas a phase lag with radiation was evident. For stressed plants, the transpiration rate did not show similar fluctuations. The rate was steadily low throughout the day. The values at 0800 and 1800 hr were respectively 0.24 and 0.20 g H₂O dm⁻² hr⁻¹, being lower than the other values during the day. The values from 1000 to 1600 hr ranged between 0.27 and 0.29 g H₂O dm⁻² hr⁻¹.

The stomatal diffusive resistance of the control increased steadily throughout the day from a minimum of 1.59 sec cm⁻¹ at 0800 hr to a maximum of 18.4 sec cm⁻¹ at 1900 hr. Stressed plants showed a similar but more pronounced trend except at 1700 hr. The *r_s* values for the stressed treatment were higher than those of the control and ranged from 2.93 sec cm⁻¹ at 0800 hr to 52.5 at 1900 hr.

The leaf water potential of the control decreased until 1500 hr and showed an increasing pattern afterwards. Values at 0700, 1500, and 1900 hr were -3.6, -6.9, and -4.4 bars, respectively. For the stressed plants, a decline occurred from -6.4 bars at 0700 to -12.3 bars at 1700 hr. At 1900 hr a value of -11.9 bars was measured.

5.3.1.2. Pepper

A similar experiment as that described above was carried out with pepper during the next day (29 August 1975). The results are shown in Figure 15. Air temperature, vapour pressure deficit, solar radiation, and piche evaporation showed a similar trend as those in Figure 14. Transpiration rates of control and stress treatments were both $0.13 \text{ g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$ at 0800 hr. For both treatments, the rates increased to a maximum value at 1500 hr and declined afterwards. For control treatment at 1500 and 1900 hr, the rates were 1.05 and $0.44 \text{ g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$ respectively. The corresponding rates for stress treatment were 0.62 and 0.28.

The stomatal diffusive resistances for control and stress treatments were 0.94 and 4.60 sec cm^{-1} , respectively, at 0800 hr. The resistances for both treatments were similar at 0900 and 1100 hr. For control treatment, a maximum value of 93.2 sec cm^{-1} occurred at 1500 hr and decreased to 28.6 sec cm^{-1} at 1900 hr. For stress treatment, a maximum value of 95.2 sec cm^{-1} occurred at 1300 hr, decreasing to 29.4 sec cm^{-1} at 1900 hr.

The leaf water potential of the control increased from -2.9 at 0700 hr to -2.3 bars at 1100 hr, decreased to a minimum value of -3.7 bars at 1500 hr, and recovered to -2.6 bars at 1900 hr. For stress treatment, this parameter decreased from -3.7 bars at 0700 hr to a minimum of -7.3 bars at 1700 hr. Its value at 1900 hr was -6.0 bars.

5.3.2. Measurements at constant environmental conditions

The effects of light duration on transpiration, photosynthesis, stomatal diffusive resistance to water vapour and mesophyll resistance to CO_2 diffusion for well watered plants of tomato cultivars Moneymaker and Damartin are shown in Figure 16. Photosynthesis and transpiration of stressed plants are also shown in the figure. During the whole period of 16 hours, the air temperature varied between 27 and 29°C . A light intensity of 300 Wm^{-2} was given, which was considered to be a saturating value. The cultivar Damartin is grown locally in the Khuzestan Province (sub-tropical) of Iran. This cultivar was presumed to be more drought resistant than Moneymaker and it was of interest to measure its gas exchange properties under drought for a comparison to those of Moneymaker. After one hour of photoperiod, transpiration rates of the controls in Moneymaker and Damartin were 1.75 and $1.55 \text{ g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$ respectively. As the photoperiod proceeded, the transpiration rates declined, reaching values of 0.55 and $0.50 \text{ g H}_2\text{O dm}^{-2} \text{ hr}^{-1}$. Transpiration rates in Damartin were generally lower than those of Moneymaker. The stomatal diffusive resistance in the former was higher and increased from 3.38 sec cm^{-1} in the first hour to 18.9 sec cm^{-1} after 16 hours of continuous light. The corresponding values for Moneymaker were 2.49 and 13.6 sec cm^{-1} . The rate of photosynthesis of the controls also showed a decline throughout the photoperiod. For Moneymaker it reduced from $9.28 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ during the first hour to $4.04 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ after a light duration of 16 hours. For Damartin the corresponding values were 8.97 and 3.68 mg CO_2

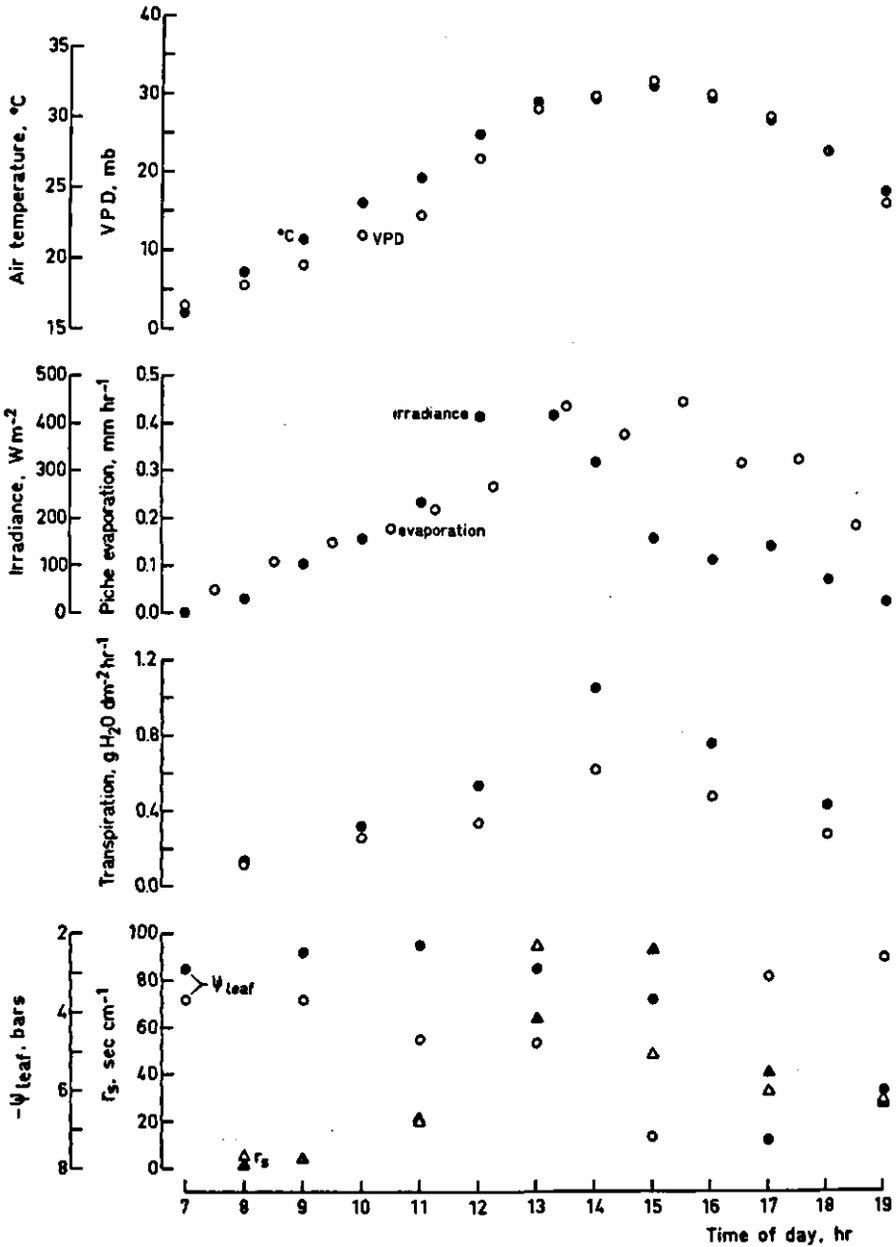


FIG. 15. Diurnal variations in some environmental (air temperature, vpd, irradiance, and piche evaporation) and plant parameters (transpiration, ψ_{leaf} , and r_s) for the pepper experiment. For plant parameters, open and closed symbols respectively represent stress and control treatments.

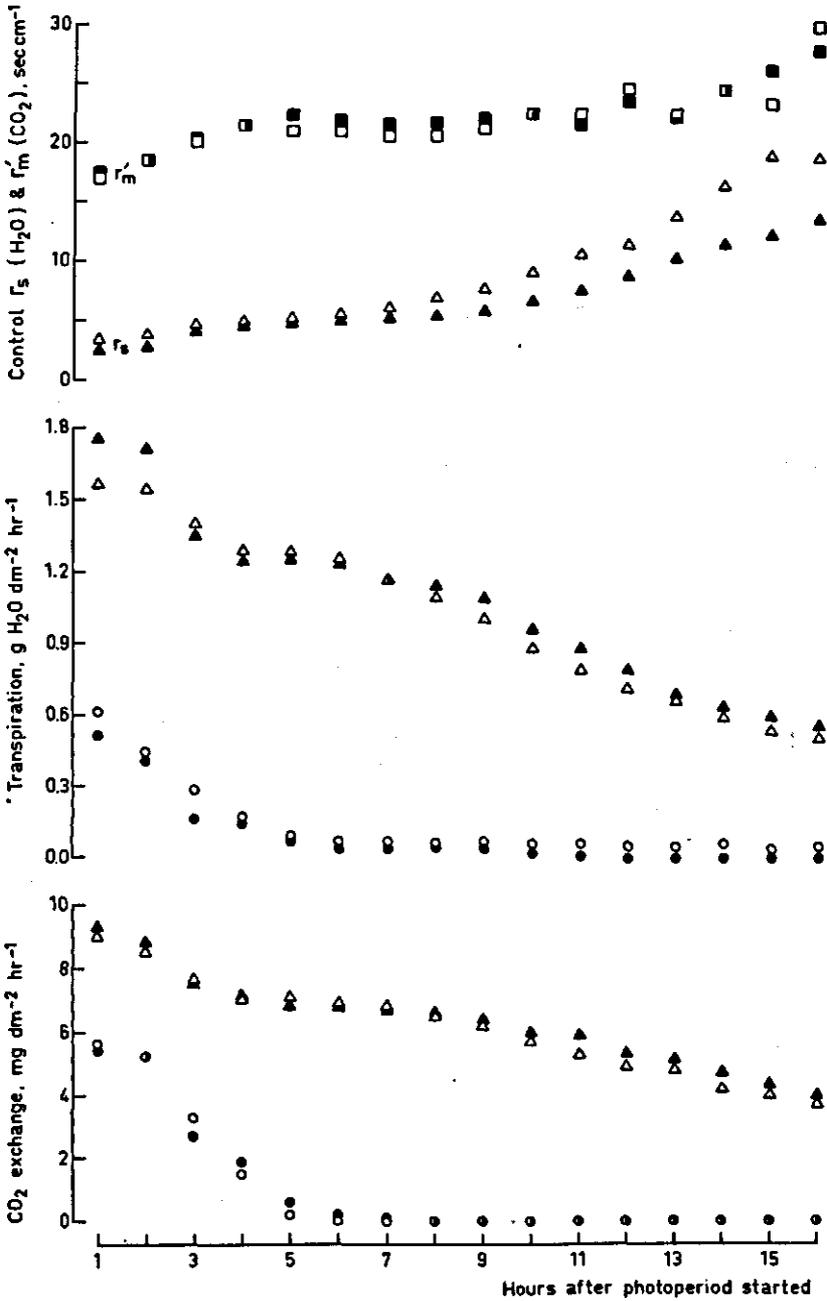


FIG. 16. Changes in CO_2 exchange rate, transpiration, stomatal and mesophyll resistances of tomato cultivars Moneymaker (closed symbols) and Damartin (open symbols). Stress treatments are symbolized by circles. For controls, leaf water potentials were -3.9 and -4.6 bars for Moneymaker and Damartin respectively, while the corresponding potentials for stressed plants were -14.2 and -12.3 bars.

$\text{dm}^{-2} \text{hr}^{-1}$. Both cultivars showed an increasing pattern in the mesophyll resistance from the first hour to the fifth one. The resistance remained more or less constant until the 11th hour and then increased again. For Money-maker, r'_m values at the first and 16th hour were 17.6 and 28.1 sec cm^{-1} , while those of Damartin were 17.0 and 30.1 sec cm^{-1} . The transpiration of stressed plants declined to negligible rates from the first to the fifth hour of photoperiod. For this treatment Damartin had slightly higher rates. Photosynthesis showed a similar decline over the same period. For the last nine hours, zero rates were maintained. The control treatment in Money-maker had a higher leaf water potential than that of Damartin (-3.9 and -4.6 bars respectively). After six days of no watering, the leaf water potential of Money-maker and Damartin decreased to -14.2 and -12.3 bars respectively. The lower rates of transpiration and higher r_s values of Damartin as compared to Money-maker, could have helped to maintain higher leaf water potentials in the former cultivar. Damartin, then, showed a higher degree of stomatal control.

Figure 17 shows the effect of light duration on transpiration, photosynthesis, stomatal diffusive resistance to water vapour, and mesophyll resistance to CO_2 diffusion for well watered plants of cucumber and pepper. Photosynthesis and transpiration of stressed plants are also shown in the figure. Transpiration rates of control plants were always higher for pepper as compared to cucumber. This was true also for photosynthesis except at the first hour. Stomatal diffusive resistances of pepper were lower than cucumber. These results are contradictory to those indicated in Chapter 4 which reported higher rates of photosynthesis and transpiration for cucumber as compared to pepper. The pretreatments given to the plants in the present experiment were different from those in Chapter 4. This difference could have caused the discrepancy between the two sets of results. Transpiration rates of stressed cucumber plants were higher than those of pepper while their photosynthesis rates were lower. For control and stress treatments in both species, transpiration and photosynthesis rates decreased throughout the photoperiod. For well watered plants of pepper and cucumber, transpiration rates decreased from 1.62 and 1.31 $\text{g H}_2\text{O dm}^{-2} \text{hr}^{-1}$ at the first hour to 0.33 and 0.28 at the 14th hour. The change in photosynthesis rates were from 6.6 at the first hour to 2.44 $\text{mg CO}_2 \text{dm}^{-2} \text{hr}^{-1}$ at the 14th hour for pepper and from 7.76 to 0.57 for the same period in cucumber. The corresponding values in stomatal diffusive resistances were 3.60 and 30.3 sec cm^{-1} for pepper and 4.91 and 38.1 sec cm^{-1} for cucumber. Mesophyll resistance in pepper showed a fluctuating pattern throughout the photoperiod, but there was an upward trend. The minimum value was 24.3 sec cm^{-1} at 1.5 hours from the start of the photoperiod and increased to 40.8 sec cm^{-1} at the 13th hour. For cucumber, r'_m increased from 17.3 sec cm^{-1} at the first hour to 677 sec cm^{-1} at the 15th hour. In stressed plants, the proportional decline in photosynthesis was higher than transpiration. During 15 hours of photoperiod, transpiration fell from 0.32 to 0.12 $\text{g H}_2\text{O dm}^{-2} \text{hr}^{-1}$ for cucumber and from 0.30 to 0.05 for pepper. Corresponding values in photosynthesis of stressed pepper were 3.65 and zero and for cucumber 0.80

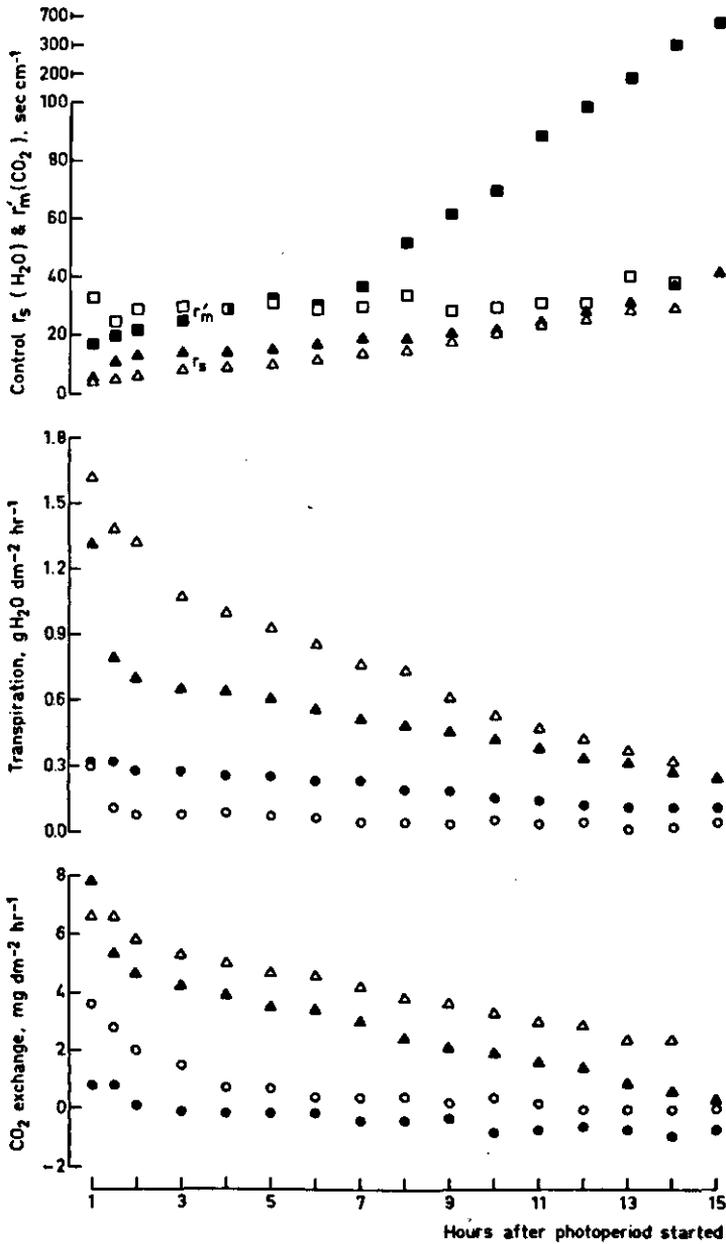


FIG. 17. Changes in CO_2 exchange rate, transpiration, stomatal and mesophyll resistances of cucumber (closed symbols) and pepper (open symbols). Stress treatments are symbolized by circles. For controls, leaf water potentials were -5.1 and -5.7 bars in cucumber and pepper respectively, while the corresponding potentials for stressed plants were -17.9 and -15.5 bars.

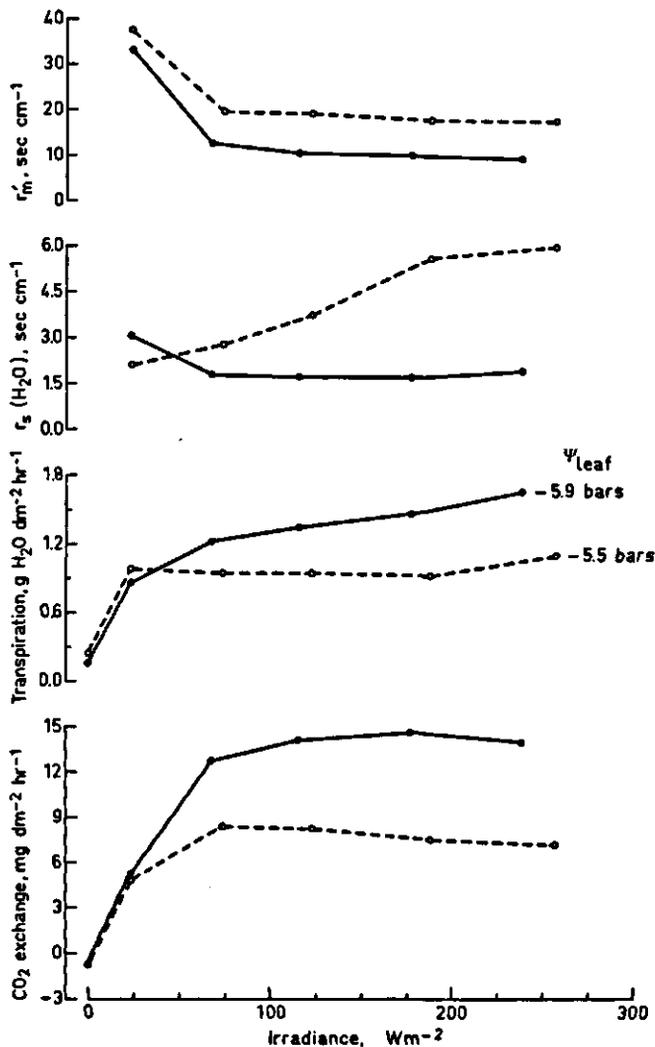


FIG. 18. Some gas exchange properties of cucumber plants measured in the morning (closed symbols) and in the afternoon (open symbols).

and $-0.71 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ with still some lower values encountered during the photoperiod.

To visualize the effects of sampling time on gas exchange rates, the data of Figures 7 and 8 for cucumber and pepper were divided into their morning and afternoon components and are presented in Figures 18 and 19. Figure 18 shows that the morning photosynthesis rates for cucumber were higher than the afternoon rates in spite of the slightly lower leaf water potential in the morning samples. The r_s and r'_m values were lower in the morning. The afternoon r_s values increased with increasing radiation. The same trend can be

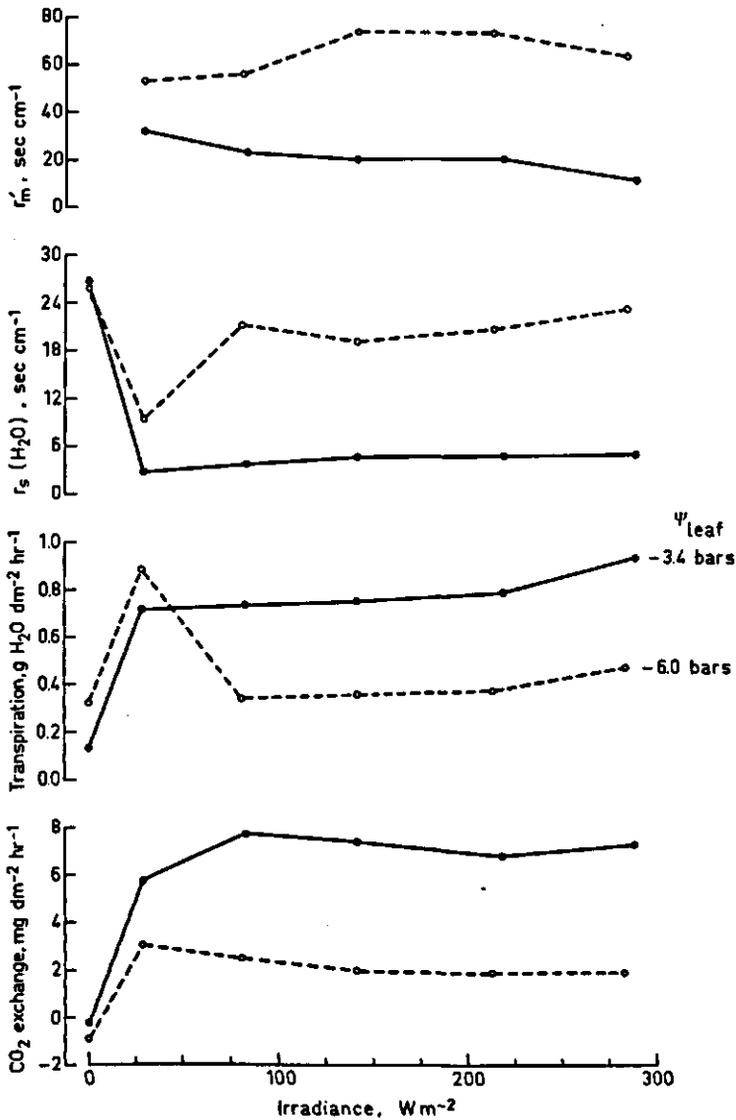


FIG. 19. Some gas exchange properties of pepper plants measured in the morning (closed symbols) and in the afternoon (open symbols).

seen in Figure 19 for pepper, except for the higher transpiration rate for afternoon samples at 29 W m^{-2} . The fact that transpiration rates declined above 29 W m^{-2} , could be due to diurnal stomatal closure. The afternoon leaf water potentials were 2.6 bars lower than the morning samples, which could at least partly explain the stomatal closure.

5.4. DISCUSSION

The results of glasshouse experiments are discussed separately from those of constant environmental conditions.

5.4.1. *Glasshouse experiments*

The experiments carried out with tomato (on 28 August 1975, Figure 14) and pepper (on 29 August 1975, Figure 15) demonstrate that the trend in radiation, piche evaporation, air temperature and vapour pressure deficit of the air for both days was almost identical. Maximum values in radiation occurred at noon, whereas a phase lag in the maximum value of piche evaporation, temperature, and vpd of approximately three hours existed. The correlation coefficients among the atmospheric factors and between these factors and rate of transpiration are indicated in Table 6. Transpiration of tomato and pepper showed a maximum value at approximately 1400 hr (Figures 14 and 15) and Table 6 shows that its correlation with radiation is less as compared to the other climatic parameters (except in stressed tomato). For stressed tomato plants, the large increase in stomatal resistance effected by drought seems to have overridden any effect of the evaporative conditions of the atmosphere.

The introduction to this chapter contains literature reports emphasizing that radiation is of primary importance in bringing about diurnal changes in water relations parameters. Those reports are mainly concerned with field situations whereas the experiments discussed in this section were carried out in a glasshouse. Shading by glasshouse structures could have prevented a more pronounced effect of light. However, radiation could have been affecting the plant parameters more indirectly through variations of temperature and vpd.

Examinations of the trends of r_s and leaf water potential values show some interesting features. The control treatment of tomato had the lowest r_s value early in the morning. It gradually increased during the day and after 1700 hr a sharp increase occurred because of light limitation or the length of the photo-period, which will be discussed later. The water potential of the leaf decreased from -3 bars in the morning until a minimum of -7 bars at 1500 hr. Due to the decrease in evaporative demand and stomatal closure, thus decreasing transpiration, a recovery in leaf water potential occurred after 1500 hr. The stress treatment showed the same stomatal resistance as the control early in the morning, but the increase in r_s during the day until 1500 hr was much more pronounced. Early in the morning, leaf water potential of stress treatment was lower than the control. The subsequent decline in leaf water potential was more pronounced in droughted plants as compared to the well watered plants. After 1500 hr, stomatal opening occurred, and its value at 1700 hr was the same as that at 1300 hr. This opening could be attributed to a decline in the evaporative demand. Due to this stomatal opening, leaf water potential became lower again, showing a slight recovery later on at 1900 hr.

For pepper, the stomatal diffusive resistances in both control and stress

TABLE 6. Correlation coefficients (accompanied by the number of observations, n) among radiation, air temperature, vpd, and rate of transpiration (for control and stressed treatments) for tomato (measured on 28 August 1975) and pepper (measured on 29 August 1975). For $n = 6$, r values equal to or higher than 0.73 and 0.89 are respectively significant at 5 and 1% levels, and for $n = 13$ at the same levels of significance, r values should be equal to or higher than 0.48 and 0.64.

	Radiation Wm^{-2}	Air temperature $^{\circ}C$	vpd m bar	Transpiration (control) $g H_2O dm^{-2} hr^{-1}$	Transpiration (stress) $g H_2O dm^{-2} hr^{-1}$
a. Tomato					
Radiation	-	0.43, $n = 13$	0.35, $n = 13$	0.50, $n = 6$	0.71, $n = 6$
Air temperature	0.43, $n = 13$	-	0.97, $n = 13$	0.98, $n = 6$	0.26, $n = 6$
vpd	0.35, $n = 13$	0.97, $n = 13$	-	0.96, $n = 6$	0.20, $n = 6$
Transpiration (control)	0.50, $n = 6$	0.98, $n = 6$	0.96, $n = 6$	-	0.40, $n = 6$
Transpiration (stress)	0.71, $n = 6$	0.26, $n = 6$	0.20, $n = 6$	0.40, $n = 6$	-
b. Pepper					
Radiation	-	0.60, $n = 13$	0.51, $n = 13$	0.54, $n = 6$	0.53, $n = 6$
Air temperature	0.60, $n = 13$	-	0.98, $n = 13$	0.90, $n = 6$	0.89, $n = 6$
vpd	0.51, $n = 13$	0.98, $n = 13$	-	0.91, $n = 6$	0.89, $n = 6$
Transpiration (control)	0.54, $n = 6$	0.90, $n = 6$	0.91, $n = 6$	-	0.99, $n = 6$
Transpiration (stress)	0.53, $n = 6$	0.89, $n = 6$	0.89, $n = 6$	0.99, $n = 6$	-

treatments were minimum in the morning and started to increase as the day progressed. For both treatments, an opening trend was noticed in the afternoon. The variations were closely related to those of vpd. This is reminiscent of the results reported by CONDE and KRAMER (1975) for *Opuntia compressa*. The r_s values in that species followed the vpd irrespective of the dark and light periods. In Figure 15 transpiration followed the vpd in both control and stress treatments (correlation coefficients of 0.91 and 0.89 respectively). Since the rates were smaller in stressed plants, some degree of stomatal control is expected to have occurred. This could be only true for the measurements at 1300 hr, when the r_s value of stress treatment was higher than control and the transpiration rate was lower. For measurements at 1500 and 1700 hr, a contradiction is apparent. It is to be considered that the transpiration rates are measurements relating to the whole plants over two hours while r_s values are based on single leaf measurements. The lower leaves of stressed plants could have had higher resistances. JORDAN et al. (1975) reported that in stressed cotton plants stomatal closure proceeded from the oldest leaves to the youngest. The changes in stomatal reactivity were not solely the result of alteration in K^+ or ABA concentration. They maintained that the nature of those age related changes remained unclear. The leaf water potentials in control treatments showed an increase up to 1100 hr. The difference could be due to the use of smaller plants at 0900 and 1100 hours. Although the plants were chosen for uniformity, there is always a possibility of fallibility in visual judgement.

The low transpiration rates in the morning would perhaps not cause a reduction in leaf water potentials, since absorption by roots of well-watered plants could make up for the transpirational losses. However, a minimum leaf water potential of -3.7 bars occurred at 1500 hr, concomitant with highest transpiration rate. For later hours, decrease in rates of transpiration led to a recovery of leaf water potentials to -2.6 bars at 1900 hr. For stressed plants, leaf water potentials were -3.7 bars at 0700 hr and therefore an equilibration of soil and plant water potentials at the previous night had not occurred. If we assume that the leaf water potential at 1900 hr of the previous day was -6 bars (this is a minimum value since that of the present day at 1900 hr was -6 bars), it seems that even at leaf water potentials of this order of magnitude, an increased resistance in soil-plant system in absorption and translocation of water had occurred. This resistance could be attributed more to plants than soil as discussed in Chapter 2. Perhaps it is partly due to this resistance that the levels of leaf water potential in stressed plants fell to a minimum of -7.3 bars at 1700 hr. The transpiration losses were not made up for by absorption of water. However, a partial but belated recovery in potentials occurred at 1900 hr, five hours after transpiration started to decline.

Since the meteorological conditions on the two days of measurements for tomato and pepper were fairly similar, a comparison of the plant behaviour in the two species could then be warranted on that basis. For control plants, transpiration rates in tomato were always higher than pepper. This was also

shown in Chapters 2 and 4. Since transpiration rates of tomato were higher than those of pepper, leaf water potential in stressed tomato plants became lower than stressed pepper plants although stress duration was shorter in tomato. Although it is maintained that the r_s values of single leaf in the present experiment did not fully account for the variations in transpiration, it is nevertheless evident that r_s values for tomato are lower than those of pepper. The stomata of pepper then would seem to be more sensitive to variations in vpd than those of tomato in well watered plants. For tomato and pepper the correlation coefficients between r_s and vpd were 0.33 and 0.87 respectively. The r_s values in stressed pepper followed the vpd variations better than those of stressed tomato. However, as tomato was more severely stressed than pepper, it would be expected that its stomata would follow a more distinct closing pattern throughout the day and not follow the vpd all of the time.

Leaf water potentials of tomato were lower than those of pepper in well watered plants. This has been repeatedly observed in the previous experiments and explanations were offered in Chapter 2. For the present experiment, although pepper did not receive water for four days, as compared to three days for tomato, the leaf water potentials of the former were higher than the latter. At the time of the experiments, the plant ages for tomato and pepper were 36 and 67 days respectively. For this age, the top/root ratio for tomato is higher than that of pepper (VAN DER POST, 1968). This factor, as well as the higher transpiration rates of tomato, has caused then more reduction in the leaf water potential in this species, as compared to pepper.

5.4.2. *Scheduling irrigation based on variations in plant water potential*

In Chapter 2, leaf water potential was assessed as the best parameter indicating plant water status. Since this parameter also has an important bearing on many plant physiological processes, it would seem logical to schedule irrigation based on this parameter. Since values of leaf water potential depend on the time of sampling, as shown in the present chapter, a procedure should be adopted in which the diurnal variations have been accounted for. A pre-determined 'critical' value of ψ_{leaf} should be established, below which irrigation is necessary in order to avoid unfavourable effects on plant growth. Since variations in plant water potential are brought about by changes in transpiration, a process which is dependent on a variety of environmental factors including radiation, temperature, vpd, and windspeed, it seems appropriate to predict plant water potentials based on variations in those environmental factors (SMART and BARRS, 1973). For this purpose, a multiple regression analysis is necessary in which environmental factors are treated as independent variables. To avoid dependent variables in the analysis and also to make calculations as simple as possible, the only variables considered in the following analysis are radiation and temperature. Vapour pressure deficit is a function of temperature, and showed the same trend as that in temperature (Figures 14 and 15) and therefore will not be considered as a factor in the following equations. Temperature is also dependent on radiation, but it was in-

TABLE 7. Leaf water potentials as a function of solar radiation (R) and air temperature (T) for well-watered and stressed plants of tomato and pepper. The measurements were carried out in a glasshouse on 28 and 29 August 1975 for tomato and pepper, respectively.

Plant	Treatment	Regression equation of plant water potential on temperature and radiation	r ψ .RT
Tomato	Control	$\psi = 1.35 - 0.0025 R - 0.23 T$	0.97
Tomato	Stress	$\psi = 2.13 + 0.0014 R - 0.48 T$	0.90
Pepper	Control	$\psi = -1.28 + 0.0032 R - 0.08 T$	0.69
Pepper	Stress	$\psi = 1.76 + 0.0118 R - 0.33 T$	0.93

cluded in view of the low correlation coefficients it had with radiation (Table 6). Since the measurements were carried out in a glasshouse, windspeed would not be presumed as an important factor, here, although it might be of importance in the field. Table 7 shows the regressions of leaf water potential on radiation and temperature for well watered and stressed tomato and pepper plants. The lower correlation coefficient for well watered pepper plants is obviously due to the increase in leaf water potential from 0900 till 1100 hr (Figure 15). Equations similar to those in Table 7 could be used for scheduling irrigation if the following points are considered. Firstly, a critical plant water potential for each species should be defined. Since leaf growth is very sensitive to drought, the critical water potential could be based on this parameter, or, since the present procedure is meant for practical applications, the critical water potential is suggested to be taken at values below which significant yield decrements occur and recovery of water potentials to normal values becomes difficult. Secondly, the forecast weather conditions regarding radiation and temperature are fed into the equations. Thirdly, when calculated values fall below those of the critical levels, irrigation should be carried out. Equations such as those in Table 7 should be determined for different stages of plant growth and irrigation cycle. The stages in irrigation cycles could be divided on the basis of pan or piche evaporation, measured from the last irrigation, or any other criterion preferred by the irrigator.

Table 8 shows the actual water potential measurements of well watered and stressed tomato and pepper plants. Meteorological data of both days of measurements (Figures 14 and 15) were used to calculate values of water potentials for different treatments. As could be expected because of their high correlation coefficients, equations in Table 7 give reasonably close approximation of leaf water potential variations if the current method for scheduling irrigation was to be used. If for example critical leaf water potentials of -10 bars for tomato and pepper were to be assumed, only the stressed tomato plants should have been irrigated for imminent weather conditions similar to those in Figures 14 and 15.

5.4.3. Changes in gas exchange parameters in constant environments

Two series of experiments were carried out to study the gas exchange para-

TABLE 8. Diurnal variations of actual and calculated leaf water potentials of tomato and pepper (control and stress) plants. For calculated values, radiation and air temperature data of 28.8.75 (Day 1) and 29.8.75 (Day 2) were fed to the equations of Table 7.

	Plant	Treatment	0700	0900	1100	1300	1500	1700	1900
Actual	Tomato	Control	-3.6	-4.3	-5.4	-6.4	-6.9	-5.9	-4.4
Day 1	Tomato	Control	-3.2	-4.4	-5.5	-6.3	-6.5	-6.0	-4.8
Day 2	Tomato	Control	-2.4	-3.9	-5.3	-6.6	-6.6	-6.0	-4.6
Actual	Tomato	Stress	-6.4	-8.0	-11.0	-11.6	-11.7	-12.3	-11.9
Day 1	Tomato	Stress	-7.2	-8.6	-10.1	-11.7	-12.9	-12.2	-10.2
Day 2	Tomato	Stress	-5.5	-7.9	-9.8	-12.4	-13.0	-11.9	-9.7
Actual	Pepper	Control	-2.9	-2.5	-2.3	-2.9	-3.7	-3.1	-2.6
Day 1	Pepper	Control	-2.5	-2.6	-2.5	-2.9	-3.3	-3.1	-3.1
Day 2	Pepper	Control	-2.8	-2.5	-2.5	-2.7	-3.2	-3.3	-3.2
Actual	Pepper	Stress	-3.7	-3.7	-4.7	-4.8	-7.2	-7.3	-6.0
Day 1	Pepper	Stress	-4.8	-4.0	-4.0	-5.2	-7.1	-7.2	-6.5
Day 2	Pepper	Stress	-3.6	-4.1	-4.0	-5.7	-7.1	-6.6	-6.3

meters in a constant environment. In the first series, cucumber, pepper and two cultivars of tomato were measured in the gas exchange assembly at a temperature range of 27–29°C and a light intensity of 300 Wm⁻² for durations of 15 or 16 hours (Figures 16 and 17). In the second series, cucumber and pepper plants were taken in the morning and in the afternoon from a climate room and subsequently measured at various light intensities for a relatively short time in the gas exchange assembly. Figures 18 and 19 show the effect of light on cucumber and pepper for morning and afternoon samples.

Figures 16 to 19 show that in well watered plants transpiration and photosynthesis decrease when the photoperiod proceeds. The reductions which were due to an increase in r_s and r'_m were not solely a consequence of decreasing plant water potentials. It is likely that in pepper (Figure 19) the low leaf water potential during the afternoon could have caused the increase in r_s and r'_m . The water potentials in tomato (Figure 16) and that in cucumber (Figure 17) are normal values measured in well watered plants. Moreover, the water potential in cucumber (Figure 18) during the afternoon was actually higher than that in the morning. Therefore a decrease in transpiration and photosynthesis during the later hours of a photoperiod could not be generally brought about by a decrease in plant water potential.

It is possible that in well watered plants photorespiration at high light intensities increased as photoperiod proceeded. Photorespiration is a common feature of C₃ plants (TINUS, 1974) and it could be even more enhanced by a slow transport of photosynthetic products away from the CO₂ fixation sites. An increase in photorespiration then could have raised the internal CO₂ levels, causing stomatal closure. Hence the decrease in transpiration could be explained by an increase in r_s , and that in photosynthesis by r_s and a decreased

CO₂ gradient. Photosynthesis could also decrease by an increase in mesophyll resistance. It should be re-emphasized that the rise in the calculated r_m values could have been overestimated, since internal CO₂ levels were assumed to be zero, not a valid assumption if photorespiration becomes important. An examination of Figures 18 and 19 reveals that the light limited phase of photosynthesis was less affected in the afternoon samples compared to light saturated phase. Photorespiration is a function of light intensity (TINUS, 1974), and therefore the diffusional limitations brought about by photorespiration would be more pronounced at higher levels of irradiance.

Transpiration rates of stressed cucumber plants were higher than those of stressed pepper, although the corresponding photosynthesis rates were lower (Figure 17). In fact, for cucumber plants only photorespiration was measured. Since the leaf water potentials were very low in both species (-17.9 and -15.5 bars for cucumber and pepper respectively), it seems that transpiration was only cuticular, especially after the second hour of photoperiod in cucumber. The exhibition of photorespiration by cucumber makes it difficult to assess the role of mesophyll resistance in controlling photosynthesis in stress conditions. For stressed plants of Figures 16 and 17, reductions in photosynthesis throughout the photoperiods could have occurred as discussed in Chapter 4. The possible mechanisms are: (1) stomatal closure; (2) increases in mesophyll resistances; (3) impeded translocation of photosynthates; and (4) photorespiration.

For the stressed tomato cultivars in Figure 16, photosynthesis and transpiration rates were mostly similar in the two cultivars for the duration of photoperiod. Control transpiration rates in Damartin were slightly below that of Moneymaker and the corresponding stomatal diffusive resistances were higher. It is clear that the cultivar Damartin which is grown in South-West Iran was not any more adapted to drought conditions than Moneymaker in the conditions of this experiment.

Figures 16 and 17 show that transpiration and photosynthesis did not follow the same pattern in stressed plants as compared to well-watered plants over the photoperiods. During the first five hours of photoperiod, percentual declines in the rates of photosynthesis and transpiration were higher in stressed plants as compared to well-watered plants. After this period, the rates were steadily low in stressed plants and continued to decline in well-watered plants. This confirms that in water relations experiments, time of sampling could greatly affect the results. Measurements taken only at one point in the photoperiod cannot completely define the general status of plants. For example as observed in Chapter 2, stomatal resistances measured at only one point in the photoperiod did not always correlate with soil water potentials; whereas with calculated r_s values, based on transpiration rates over the entire photoperiod, better correlations with soil water potential were observed.

SUMMARY

The ever increasing importance of water as a critical resource for agricultural production has encouraged more research on water relations in recent years. Most attention has been paid to field crops and less information is available for horticultural crops, especially vegetables. The results of studies on water relations of cucumber, tomato, and pepper are reported and discussed in this thesis.

Drying cycle experiments were carried out with tomato, cucumber, and sweet pepper at two temperatures and three light intensities in order to: (1) examine suitability of some plant parameters as criteria for expression of plant water status; (2) investigate which parameter is most suitable as a basis for timing of irrigation; and (3) observe the change of various parameters during a drying cycle as affected by environment. Measurements were carried out on transpiration rate, stomatal diffusive resistance (r_s), leaf temperature, plant and soil water potentials, and relative water content. The transpiration rate at 25°C was in general higher than that at 21°C due to the higher vapour pressure deficit (vpd) at the former temperature. For all the three species, a more pronounced stomatal closure was demonstrated at 25°C as compared to that at 21°C when drought was imposed on the plants. This result could be due to the fact that at 25°C the vpd and/or the internal CO₂ concentration was higher. Various levels of irradiance did not invoke different responses of stomata or transpiration rates throughout the drying cycles. The difference among the three light intensities used are thought to have been too small to show distinct responses. Moreover, relatively low intensities were used in this series of experiments. The measured r_s values did not always correlate significantly with soil water potentials because r_s measurements were carried out on single leaves at only one point in the photoperiod and the measurements were also affected by other environmental factors, such as humidity, prevailing during the measurements. Calculated r_s values showed better correlations with soil water potential, presumably because transpiration rates of the whole plants over the entire photoperiod were used for their calculation. Relative water content and leaf water potential correlated significantly with soil water potential. Among the plant parameters studied, the plant water potential as measured with the pressure chamber, was judged as the most suitable parameter expressing plant water status.

Some physical aspects of the internal plant water relations were considered for the three species. The measured parameters were relative water content, sap electrical conductivity, and leaf water potential and its components (osmotic, pressure, and matric potentials). The contribution of matric potential to the total plant water potential was considerable. Neglecting the matric component would result in unrealistically low levels of pressure potential for the three species. Tomato was considered to have the best osmotic and matric

adjustments, followed by cucumber and pepper. Sap osmotic potential and electrical conductivity were found to be significantly correlated with leaf water potential. Electrical conductivity was considered as an easy and accurate method to determine the osmotic potential indirectly. From the regression of relative water content on leaf water potential, cucumber, tomato, and pepper showed, in this order, decreasing drought resistance. Examination of some other parameters, however, such as osmotic and matric adjustments and reduction of photosynthesis in stress conditions, confirmed a better drought resistance property to tomato, followed by cucumber and pepper. Relative position of cucumber and tomato in drought resistance was discussed. For all the criteria examined, pepper was considered to be the least drought resistant. It was concluded that a better understanding of the drought resistance mechanisms in plants is required.

Carbon dioxide exchange and transpiration rates were measured in a gas exchange assembly in two series of experiments. In the first series, measurements were carried out on cucumber and pepper at light saturation and in darkness. In the second series, photosynthesis-light curves for cucumber, tomato, and pepper were obtained. For both series, well-watered as well as stressed plants were used. Both photosynthesis and transpiration were reduced as stress set in. It was shown that both stomatal and nonstomatal mechanisms were involved in the reduction of photosynthesis. For all the three species, an increase in mesophyll resistance was observed as a result of water stress. In experiments with different levels of irradiance, it was observed that the stress-induced reduction of photosynthesis was more pronounced at light saturation compared to low light. After showing some initial opening reaction to light, the stomata of stressed plants showed a closing pattern, especially for cucumber and pepper, regardless of irradiance levels. It was proposed that the closing effect of drought overrode the opening effect of light. Severely stressed plants of cucumber and pepper were rewatered to study their recovery. Photosynthesis did not reach the pre-stress level one day after rewatering, this was due to an aftereffect of drought on stomata in cucumber and pepper and a damage to the photosynthetic system in pepper.

Diurnal changes in water relations parameters were measured in a glasshouse for tomato and pepper. In a constant environmental condition, gas exchange rates were monitored throughout the photoperiod for cucumber, pepper, and two cultivars of tomato. Both well-watered and stressed plants were used for the above measurements. In the glasshouse, transpiration, leaf water potential, stomatal diffusive resistance, as well as the diurnal changes in environmental factors such as radiation, temperature, vpd, and evaporation were measured. It was observed that the diurnal variation in leaf water potential followed that of transpiration. Changes in the whole plant transpiration were not necessarily accounted for by the r_s values measured on single leaves. Multiple regression relationships were obtained for plant water potentials on radiation and temperature and suggestions were made to their use in timing of irrigation. In a constant environmental condition, all species showed maxi-

mum rates of transpiration and photosynthesis during the first hour of the photoperiod. The rates steadily declined thereafter, and the decline was more pronounced in stressed plants. A decrease in leaf water potential could not account for these diurnal phenomena, and other internal control mechanisms were thought to be involved. It has been suggested that photorespiration increased under the high irradiance employed. Internal CO₂ levels then increased, causing stomatal closure, leading to a decline in transpiration. Photosynthesis also decreased through both stomatal closure and a decrease in the CO₂ gradient. Increases in mesophyll resistance in the case of cucumber and pepper also occurred.

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SAMENVATTING

In toenemende mate wordt de watervoorziening als een beperkende factor voor een optimale agrarische productie ondervonden. Hierdoor is onderzoek naar de waterhuishouding van de plant de laatste jaren sterk gestimuleerd. Veel aandacht over dit onderwerp werd besteed aan landbouwgewassen, terwijl weinig informatie beschikbaar is over de tuinbouwgewassen, speciaal bij groenten. In dit proefschrift zijn de resultaten van een onderzoek over de waterhuishouding van komkommer, tomaat en paprika besproken.

Proeven werden uitgevoerd, waarin gedurende een uitdrogingscyclus van de grond bij twee temperaturen en drie lichtintensiteiten verschillende plantparameters in komkommer, tomaat en paprika werden gemeten om: 1) te onderzoeken welke plantparameters gebruikt kunnen worden om de waterhuishouding van de plant te beschrijven; 2) na te gaan welke parameter het meest geschikt is als criterium, om het tijdstip van irrigatie te bepalen; 3) gedurende een uitdrogingscyclus de invloed van klimaatsfactoren op de verschillende plantparameters te bestuderen. Metingen werden uitgevoerd aan de transpiratiesnelheid, de stomataire diffusieweerstand (r_s), de bladtemperatuur, de waterpotentiaal van de plant en van de grond en het relatieve watergehalte van het blad. Door het hogere waterdampdeficit van de lucht bij 25°C was de transpiratiesnelheid bij deze temperatuur meestal hoger dan die bij 21°C. Uitdroging veroorzaakte bij 25°C in hogere mate een sluiting van de huidmondjes. Dit resultaat zou het gevolg kunnen zijn van een hoger waterdampdeficit en/of een hogere interne CO₂-concentratie. Tijdens een uitdrogingscyclus werd geen effect van de lichtintensiteit op de huidmondjesweerstand en de transpiratie waargenomen. Het verschil tussen de drie toegepaste lichtintensiteiten was waarschijnlijk te klein voor een respons. Bovendien werden in deze reeks proeven betrekkelijk lage lichtintensiteiten toegepast. De gemeten r_s -waarden waren niet altijd significant gecorreleerd met de waterpotentiaal van de grond, omdat de metingen van de huidmondjesweerstand aan afzonderlijke bladeren op één tijdstip in de lichtperiode werden uitgevoerd. Klimaatfluctuaties van de geconditioneerde ruimte in het fytotron tijdens de meting, vooral die van de luchtvochtigheid, bleken in hoge mate de openings-toestand van de huidmondjes te beïnvloeden. De stomataire weerstand r_s , berekend uit de transpiratie van de plant gedurende de gehele lichtperiode vertoonde een betere correlatie met de waterpotentiaal van de grond. Het relatieve watergehalte en de waterpotentiaal van het blad waren significant gecorreleerd met de waterpotentiaal van de grond. De waterpotentiaal van de plant, gemeten met een 'pressurechamber' bleek de meest geschikte parameter te zijn om de waterhuishouding van de plant weer te geven.

Enige fysische aspecten over de interne waterhuishouding van deze drie species werden nader bestudeerd. De gemeten parameters waren het relatieve watergehalte van het blad, het elektrisch geleidingsvermogen van het perssap

van bladeren, de waterpotentiaal van het blad en haar componenten, de drukpotentiaal (turgor), de osmotische en de matrix-potentiaal. De bijdrage van de matrixpotentiaal aan de totale waterpotentiaal van de plant was aanzienlijk. Het verwaarlozen van deze component zou resulteren in een onwaarschijnlijk lage drukpotentiaal van de drie species. Tomaat bleek de meest gunstige aanpassing van de osmotische en matrixpotentiaal te vertonen, gevolgd door komkommer en paprika. De osmotische potentiaal en het elektrisch geleidingsvermogen van het perssap bleken significant gecorreleerd te zijn met de waterpotentiaal van het blad. De bepaling van het elektrisch geleidingsvermogen van het sap zou een gemakkelijke en nauwkeurige methode kunnen zijn om op indirecte wijze de osmotische potentiaal vast te stellen. Uit de regressie tussen het relatieve watergehalte en de waterpotentiaal van het blad bleek, dat de gewassen komkommer, tomaat en paprika, in deze volgorde, in droogteresistentie afnemen. Op basis van enige andere parameters, zoals de aanpassing van de osmotische en de matrixpotentiaal en de afname van de fotosynthese bij droogte, is de volgorde in droogteresistentie echter: tomaat, komkommer en paprika. De relatieve positie in droogteresistentie van komkommer en tomaat werd besproken. Een beter inzicht in het mechanisme van de droogteresistentie wordt noodzakelijk geacht.

In twee proefseries werd de nettofotosynthese en de transpiratie simultaan gemeten door registratie van de gasuitwisseling. In de eerste serie werden metingen uitgevoerd met komkommer en paprika bij lichtverzaadiging en in het donker. In een tweede serie werden gegevens over komkommer, tomaat en paprika verkregen bij verschillende lichtintensiteiten. In beide series werden planten vergeleken, waarin tijdens de meting het vochtgehalte van de grond optimaal of suboptimaal was. Bij uitdroging daalde de fotosynthese- en de transpiratiesnelheid. Aangetoond werd, dat zowel stomataire als niet-stomataire mechanismen betrokken waren bij de afname van de fotosynthese. Uitdroging veroorzaakte een toename van de mesofylweerstand bij de drie species. Uit proeven met verschillende lichtintensiteiten bleek dat uitdroging bij lichtverzaadiging de afname van de fotosynthese meer beïnvloedde dan die bij een lage lichtintensiteit. Hoewel de huidmondjes bij uitdroging aanvankelijk in de lichtperiode een openingsreactie vertoonden, werd vooral bij komkommer en ook bij paprika spoedig een sluiting waargenomen, ongeacht de lichtintensiteit. Verondersteld wordt, dat het effect van droogte op de sluiting van de huidmondjes groter is dan de openingsreactie van het licht. Transpiratie en fotosynthese van komkommer en paprika werden ook gemeten aan planten, welke na een sterke uitdroging geïrrigeerd werden om hierdoor een inzicht over de reversibiliteit van deze processen te verkrijgen. De fotosynthese bereikte een dag na irrigatie niet het oorspronkelijk niveau van de controle. Dit werd toegeschreven aan een nawerking van droogte op de huidmondjesopening in komkommer en paprika en tevens aan een beschadiging van het fotosynthetisch apparaat in paprika.

Bij tomaat en paprika werd onder natuurlijke omstandigheden in een kas de dagelijkse gang van verschillende parameters bestudeerd. In constante kli-

maatsomstandigheden werd bij lichtverzadiging de gasuitwisseling van komkommer, paprika en twee tomatenrassen continu geregistreerd. Planten, voorzien van voldoende water en planten, onderhevig aan uitdroging, werden voor bovengenoemde metingen gebruikt. In de kas werd de transpiratie, de waterpotentiaal van het blad en de stomataire diffusieweerstand gedurende de dag gemeten, evenals de lichtintensiteit, de temperatuur, het dampdrukdeficit en de Piche-evaporatie. De waterpotentiaal van het blad gedurende de dag en de transpiratie vertoonden eenzelfde verloop. Veranderingen in de transpiratie van de gehele plant komen niet noodzakelijkerwijze overeen met de r_s -waarden, gemeten aan afzonderlijke bladeren. Door middel van meervoudige regressieberekeningen werd de waterpotentiaal van de plant gecorreleerd met de lichtintensiteit en de temperatuur. Tevens zijn suggesties gedaan om de gevonden correlaties te benutten voor het bepalen van het tijdstip voor irrigatie. Onder constante klimaatsomstandigheden vertoonden de drie species een maximale transpiratie- en fotosynthesesnelheid gedurende het eerste uur van de lichtperiode. Daarna nam de transpiratie- en fotosynthesesnelheid geleidelijk af. Deze afname was meer geprononceerd bij planten in een toestand van uitdroging. De daling in transpiratie en fotosynthese werd niet veroorzaakt door een afname in de waterpotentiaal van het blad, zodat andere interne controlemechanismen hierbij een rol spelen. De veronderstelling is geopperd, dat de fotorespiratie toeneemt, waardoor de interne CO_2 -concentratie stijgt, sluiting van de huidmondjes optreedt en de transpiratiesnelheid hierdoor daalt. De daling van de fotosynthese zou het gevolg zijn; enerzijds door een sluiting van de huidmondjes en anderzijds door een verlaging van de CO_2 -gradiënt. Bij komkommer en paprika werd een toename van de mesofylweerstand waargenomen.

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