Short- and Long-term Stomatal Responses to Fluctuations in Environment in Southern European Greenhouses

S. CHAMONT*, D. STRAINCHAMPS and S. THUNOT

Station d'Agronomie, INRA Bordeaux, BP81, 33883 Villenave d'Ornon Cedex, France

Received: 6 April 1994 Accepted: 5 August 1994

Stomatal behaviour in cucumber (*Cucumis sativus* L.) was analysed and modelled as a function of different greenhouse environmental parameters, under variable summer conditions. Solar radiation was the main regulating factor. During the day, large atmospheric vapour pressure deficit increased transpiration which was followed by a reduction in stomatal aperture, suggesting the presence of a feedback response to water stress. However, stomatal behaviour was more sensitive to high atmospheric vapour pressure deficit when this was accompanied by a rapid decrease of solar radiation. The response to the difference between leaf and air temperature was also influenced by air vapour pressure deficit and duration of plant exposure to high evaporative demand. Calculation of the crop water stress index showed that the air vapour pressure deficit of 1 kPa used in the control treatment probably caused water stress and induced some hardening, a necessary condition for adaptation to summer climate in southern Europe. The importance of the interaction between climatic parameters and plant response in greenhouse environmental management is analysed. Classical models of stomatal resistance are also discussed.

Key words: *Cucumis sativus* L., stomata, transpiration, leaf temperature, modelling, greenhouse environment, vapour pressure deficit, solar radiation.

INTRODUCTION

The new generation of greenhouse environmental control systems uses crop growth models for on-line optimization (Tantau, 1989). The aim of these models is to predict and describe short term plant reaction and long term plant growth. The low water holding capacity of substrates employed in soilless culture requires the evapotranspiration estimate to be predicted on a short time scale.

Exchanges of CO₂ and H₂O between the plant and atmosphere are mainly controlled by stomata, though the relationship between stomatal behaviour and environmental conditions is extremely complex. Numerous studies have shown that radiation, air vapour pressure deficit, leaf and air temperature, air CO₂ concentration and plant water status regulate stomatal behaviour under steady state conditions (Jarvis and Morison, 1981; Stanghellini, 1987).

Suboptimal climatic conditions result in poor development of the cucumber crop, inducing stomatal closure and decreasing crop transpiration (Javoy, Letard and Pelletier, 1990). In greenhouses, the water vapour lost by a developed crop canopy is the major source of evaporative cooling, allowing control of air temperature and vapour pressure deficit (Boulard *et al.*, 1991; Boulard and Baille, 1993). Therefore, efficient control of the greenhouse environment during summer represents the major challenge for greenhouse management.

Several authors (Bakker, 1991a; Jolliet and Bailey, 1992)

have studied the effect of air humidity on transpiration and stomatal conductance in cucumber, sweet pepper and tomato grown under greenhouse conditions. However, these studies represent northern climatic conditions with low solar radiation (R_s) and small vapour pressure deficit (D_a). Thus, Gijzen, Vegter and Nederhoff (1990) postulate that stomatal resistance is constant in the validation of a crop photosynthesis model for greenhouse-grown cucumber. In southern Europe, the summer climate is very variable but with greater solar radiation and vapour pressure deficit. Greenhouse climate control has to be adapted to take advantage of higher solar radiation. As evaporative demand increases with intensity of solar radiation, stomatal closure may be caused by (a) a decrease of leaf water potential because transpiration is greater than water absorption, or (b) the leaf-air vapour pressure difference (Grantz, 1990). However, in soilless culture, water is not considered to be a limiting factor in the root substrate since optimal water supply is ensured by frequent checking of the volume of drainage water (de Graaf, 1988). In contrast to tomato, cucumber is very sensitive to large vapour pressure deficit and is known to have a substantial water requirement. Janoudi, Widders and Flore (1993) observed that continuous high vapour pressure deficit induced stomatal closure in pickling cucumber grown in soil. This requirement for a humid climate may be attributed to its origins from the foothills of the Himalayas. Thus, Javoy *et al.* (1990) showed that the use of a fog-system in greenhouses resulted in a considerable yield improvement of a cucumber crop. However, Yang *et al.* (1990) did not find a significant correlation between stomatal conductance and other environmental variables, other than with solar energy, even

* For correspondence at: Station d'Agronomie, INRA, BP81, 33883 Villenave d'Ornon Cedex, France.

though the greenhouse conditions were similar to those observed in southern Europe.

This paper analyses greenhouse-grown cucumber plants under summer conditions and has three main objectives. First, to analyse the effect of vapour pressure deficit on plant transpiration in relation to other parameters (i.e., solar radiation and duration of plant exposure). Second, to evaluate the effect of environmental parameters on stomatal behaviour. Third, to define the optimal environment by calculating the crop water stress index (Jackson, 1982).

MATERIALS AND METHODS

Plant material and greenhouse facilities

Two successive experiments were carried out using cucumber (*Cucumis sativus* L.) cv. Regina. In the first, seeds were sown in rockwool cubes on 21 Apr. 1993 and measurements made from 10 to 19 May 1993. In the second, seeds were sown on 20 Jul. 1993 and measurements made from 4 to 9 Aug. 1993. After cotyledon expansion, or at the beginning of the week of measurement, seedlings were placed in two different environments, and were regularly watered with a standard nutrient solution. In the control condition, D_a was maintained at or below 1 kPa using a mist-sprayer. In the 'dry climate' D_a was never higher than 2.2 kPa or 3.5 kPa in the first and second experiments, respectively. Environments in the two greenhouses were controlled by a climate computer (CV 250 from Priva B.V.). Both greenhouse air temperatures were similar owing to adapted venting set-points. However, greenhouse daytime air temperature was 2–4 °C higher in the second dry climate ($D_a \leq 3.5$ kPa) experiment. Climate parameters (global radiation, air temperature, vapour pressure deficit) were recorded every 5 min. Radiation (R_g) within the greenhouse was estimated by multiplying the external global radiation by a light transmission factor of 0.7 (Baille, pers. comm.).

Measurement of temperature and transpiration

Leaf temperature was measured with five copper-constantan thermocouples (wire diameter 0.127 mm), placed on the abaxial leaf surface (centre), and connected to a Campbell data-logger (execution interval: 10 s, mean of 5 min). The air temperature reference was measured as the mean of five replicated measurements using a shaded, non-ventilated thermocouple in the first experiment, and was the dry air temperature of the greenhouse ventilated psychrometer in the second experiment.

Plant transpiration was monitored by periodically weighing two or three plants placed in the centre of the greenhouse. Transpiration in the dry climate was measured on plants taken from the control condition at the beginning of the experiment (short term exposure, first trial) and on plants transferred after cotyledon development (long term exposure, second trial). Weighing balances, with an accuracy of ± 1 g, were connected to a computer and data recorded every 10 min. Average hourly transpiration rate (E) was calculated from three successive data points. Leaf area was measured at the beginning and end of the experiment.

Calculation and measurement of stomatal resistance

The Penman–Monteith equation is derived for horizontally homogeneous vegetation, so it fails to predict the evaporation rates of a sparse canopy. For this reason, stomatal conductance (r_s) is calculated from Fick's law as follows:

$$E = (q_{\text{leaf}} - q_{\text{air}}) / (r_a + r_s) \quad (1)$$

where E is the transpiration rate (g m^{-2} leaf area s^{-1}), q_{leaf} and q_{air} the absolute humidities (g m^{-3}) of leaf and air respectively, and r_a (s m^{-1}) is the aerodynamic resistance to water vapour exchange. The absolute humidity of the leaf assumes that water vapour inside the stomatal pores is saturated at the measured leaf temperature.

From Segner (1984), r_a is approximated as follows:

$$h_a = 1.95 \times |T_l - T_a|^{0.25} / l \quad (2)$$

and since cucumber leaves are amphistomatous

$$r_a = \rho C_p / 2h_a \quad (3)$$

where h_a is the heat transfer coefficient ($\text{W m}^{-2} \text{°C}^{-1}$), T_l and T_a the leaf and air temperature respectively, l the leaf dimension characteristic (Yang *et al.*, 1990), ρ is the air density and C_p the air specific heat at constant pressure. For the leaf resistance calculation, r_a was taken as a constant throughout the experiment and had a value of 40 s m^{-1} and 30 s m^{-1} for the first and the second experiment respectively. During both experiments, stomatal conductances were measured with a steady state continuous flow porometer (LCA3 from Analytical Development Company) and a dynamic diffusion porometer (Delta-T Devices).

Calculation of Crop Water Stress Index

First, net radiation (Rn) is calculated per unit leaf area as follows:

$$Rn = H + \lambda E \quad (4)$$

and

$$H = \rho C_p \times (T_l - T_a) / r_a \quad (5)$$

where λ is the latent heat of vaporization and H is the sensible heat flux. Second, crop water stress index ($CWSI$) is calculated as follows:

$$CWSI = (\Delta_{\text{max}} - \Delta l) / (\Delta_{\text{max}} - \Delta_{\text{min}}) \quad (6)$$

where Δ_{min} is calculated for $r_s \rightarrow \infty$, and

$$\Delta_{\text{min}} = \rho_a \times Rn / \rho C_p \quad (7)$$

Δ_{max} is calculated for $r_s = 0$, and

$$\Delta_{\text{max}} = r_a \times Rn / \rho C_p \times [\gamma / (\gamma + \Delta)] - D_a / (\gamma + \Delta) \quad (8)$$

$$\Delta l = T_l - T_a$$

where γ is the psychrometric constant and Δ is the slope of the saturated vapour pressure-temperature relation and is evaluated at ambient air temperature since $T_l - T_a$ is not very large (Jackson, 1982).

RESULTS

Effects of radiation and vapour pressure deficit on transpiration rate

In the humid condition of both experiments ($D_a \leq 1$ kPa), variation in global radiation could explain most of the variation of transpiration. As proposed by Yang

FIG. 1. Effect of air vapour pressure deficit (D_a) on relation between global radiation (R_g) and transpiration rate (E), data from 13 May 1993. $D_a \leq 1$ kPa ($\circ$), $D_a \leq 2.2$ kPa ($\bullet$), regression on the humid environment (—) with $D_a \leq 1$ kPa, model is $y = 0.421x + 44.1$ with $r^2 = 0.905$ and where x is global radiation.

FIG. 3. Effect of D_a on stomatal resistance (r_s) measured by porometry. A, Data from 13 May 1993, $D_a \leq 1$ kPa ($\square$), $D_a \leq 2.2$ kPa ($\blacksquare$). Bars represent standard error of four measurements. B, Data from 4 Aug. 1993, $D_a \leq 1$ kPa ($\square$), $D_a \leq 3.5$ kPa ($\blacksquare$). Bars represent standard error of six measurements.

FIG. 2. Effects of D_a on residual transpiration, residuals equal actual values for $D_a \leq 2.2$ kPa minus model. A, Data from 19 May 1993. Model calculated for $D_a \leq 1$ kPa is $y = 0.26x + 37.1$ with $r^2 = 0.84$ and where x is global radiation and y is residual. Linear relation is $y = 205x - 145.7$ with $r^2 = 0.846$ and where x is vapour pressure deficit, data ($\bullet$), relation (—). B, Data from 13 May 1993. Model calculated for $D_a \leq 1$ kPa is taken from Fig. 1, data ($\bullet$), free-hand curve (---).

FIG. 4. Diurnal course of stomatal resistance, r_s calculated from Fick's law, points are means from five successive values. A, Data from 12 May 1993, $D_a \leq 1$ kPa (○), $D_a \leq 2.2$ kPa (●), global radiation in the greenhouse, R_g (—). B, Data from 8 Aug. 1993, $D_a \leq 1$ kPa (○), $D_a \leq 3.5$ kPa (●), R_g (—).

et al. (1990), daytime leaf transpiration was related to solar radiation (Fig. 1) by a linear relation. For the data from 13 May, E is related to x by the following model:

$$y = 0.421x + 44.1 \quad (9)$$

where x is global radiation (W m^{-2}) and $r^2 = 0.905$. Figure 1 also shows that transpiration rate increased further with higher D_a , though the effect was very variable and not linearly related to radiation. In order to analyse the effect of vapour pressure deficit on transpiration under dry climate, residual transpiration was calculated from the model. Residuals represented the differences between actual values obtained in the dry climate and predicted ones calculated from the transpiration model. Figure 2 shows a different pattern of the relation of residuals with D_a . On 19 May, residuals increase linearly with vapour pressure deficit (Fig. 2A). On 13 May, residuals only increased during the morning (first part of the curve, Fig. 2B) then decreased from 300 to $-50 \text{ g m}^{-2} \text{ s}^{-1}$ while D_a varied slightly from 1.8 to 2.2 kPa during the midday and afternoon respectively. From these results, D_a could not be simply included in a model of transpiration. Moreover, if there was a tendency

FIG. 5. Effect of D_a on r_s plotted vs. R_g . Data from 7 Aug. 1993, $D_a \leq 1$ kPa (○), $D_a \leq 3.5$ kPa (●), regression on the humid environment (—) with $D_a \leq 1$ kPa, model is $y = r_{\min} + 122.4 \exp(-0.021x)$ with $r_{\min} = 33.6$, $r^2 = 0.902$ and where x is the global radiation.

of D_a to increase transpiration during the daytime, the effect was the opposite during the night i.e., leaf transpiration rate was slightly lower in the greenhouse with higher D_a during the night ($25 \text{ g m}^{-2} \text{ h}^{-1}$ instead of $30 \text{ g m}^{-2} \text{ h}^{-1}$).

Effects of air vapour pressure deficit and radiation on stomatal resistance

The resistances calculated by Fick's law were similar to those measured by porometry (Figs 3 and 4). Thus, when D_a was lower than 1 kPa, measured stomatal resistances were $20\text{--}40 \text{ s m}^{-1}$ (Fig. 3B) while those calculated were $25\text{--}60 \text{ s m}^{-1}$ (Fig. 4B). When D_a was higher, r_s increased. The most important effect of D_a was seen in Fig. 4B, which shows that r_s was equal to 90 s m^{-1} at 1200 h when D_a was 3.5 kPa compared to stomatal resistance of 35 s m^{-1} in the control condition ($D_a \leq 1$ kPa). Second, variation in solar radiation had an important effect on r_s in the dry environment during the daytime. Figures 4A and B show that cloudy periods induced stomatal closure (from 70 to 200 s m^{-1} between 1230 h to 1430 h in the first experiment). The r_s increase was not so important when vapour pressure deficit remained below 1 kPa and was rather stable in the first experiment. Similarly, during the first experiment, we observed cyclic stomatal variations from the control value to values which were $50\text{--}100 \text{ s m}^{-1}$ higher in the dry environment ($D_a \leq 2.2$ kPa), for the other days with variable lighting. These variations followed those of global radiation (data not shown). On the other hand, nocturnal stomatal resistance in both experiments tended to be higher for the diurnal dry climate plants.

Concerning the regulation of transpiration in the control condition, diurnal stomatal variations could be explained mainly by the level of global radiation entering the greenhouse (Fig. 5). The following equation (similar to that

FIG. 6. Effect of D_a on residual resistance. Residuals equal actual values minus resistance model. A, Data from 19 May 1993, model for $D_a \leq 1$ kPa is $y = r_{min} + 187.1 \exp(-0.0267x)$ with $r_{min} = 113.8$, $r^2 = 0.921$ and where x is the global radiation, data (●), linear regression (—), $y = -110.7x + 136.9$ with $r^2 = 0.82$ and where x is D_a . B, Data from 7 Aug. 1993, model is calculated for $D_a \leq 1$ kPa (see Fig. 5), data (●), linear regression (—), $y = -35.6x + 160.6$ with $r^2 = 0.76$ and where x is D_a . C, Data from 13 May 1993, model is $y = r_{min} + 206.4 \exp(-0.0063x)$ with $r_{min} = 51.4$, $r^2 = 0.92$ and where x is global radiation. D, Residual variations (●), R_g (—) and D_a (.....) as a function of time, data from 13 May 1993.

proposed by Yang *et al.*, 1990) modelled stomatal resistance (y):

$$y = r_{min} + 122.4 \exp(-0.021x) \quad (10)$$

with $r_{min} = 33.6\ s\ m^{-1}$ and $r^2 = 0.902$ and where r_{min} is the minimal resistance and x is the global radiation ($W\ m^{-2}$). The parameters of this equation varied slightly from day to day. Moreover, r_{min} of the first experiment tended to be higher even though daily air temperature (23–29 °C) was lower than in the second experiment (26–36 °C).

If the solar radiation could account for stomatal resistance behaviour, then high vapour pressure deficit increased stomatal resistances, the effect being enhanced at low radiation (Fig. 5). In order to analyse the effect of vapour pressure deficit on stomatal resistance in a dry environment, residual resistance was calculated from the model. As previously, residuals were the differences between actual values obtained in the dry condition and predicted ones calculated from the stomatal resistance model. Different patterns are shown in Fig. 6. Two examples with the same stomatal behaviour are shown in Fig. 6A and B from both

experiments (19 May and 7 Aug., respectively). In these cases there was a negative and linear correlation of residual resistance with D_a . Slope varied from day to day. However, the continuous linear relation was not always observed. Figure 6C shows an example from 13 May where the inverse relation between residual resistance and D_a was only seen in the first part of the day. Then, stomatal resistance tended to increase in the afternoon even though D_a was quite constant. In this part of the day, Fig. 6D shows that residual resistance varies greatly with a maximum at 1500 h after a cloudy period. More generally, the relation between residual resistance and D_a was obtained in the last three or four hours of the day while solar radiation was decreasing from 200–300 $W\ m^{-2}$ to zero in both experiments.

Effects of air vapour pressure deficit and radiation on leaf temperature

Diurnal course of leaf-air temperature difference with different vapour pressure deficits are plotted in Fig. 7A and

FIG. 7. Effect of D_a on diurnal course of leaf-air temperature difference, $T_l - T_a$. A, Data from 13 May 1993, $D_a \leq 1$ kPa (○), $D_a \leq 2.2$ kPa 'adapted plants' (●), global radiation in the greenhouse, R_g (—). B, Data from 7 Aug. 1993, $D_a \leq 1$ kPa (○), $D_a \leq 3.5$ kPa (●), R_g (—).

B. During both experiments, we observed that leaf-air temperature difference decreased at the beginning and end of the day becoming positive at noon (+1 to +2 °C) when D_a was low (1 kPa). In contrast, the temperature difference was larger (−2 to −5 °C) at noon when D_a was high (2.2 and 3.5 kPa) and plants were adapted to this climate since the cotyledons showed full expansion. The higher the vapour pressure deficit the larger was leaf to air temperature difference. For plants placed in the dry environment for a few days (since the beginning of experiment, i.e., short term exposure), temperature difference was intermediate (0 to −1.5 °C, see Fig. 8C). During the night, leaf temperature was slightly cooler than air (0 to −0.5 °C) which was in accordance with the nocturnal transpiration rate.

If leaf-air temperature difference is plotted *vs.* global radiation (Fig. 8A,B) different relations are observed. In both experiments, when $D_a \leq 1$ kPa, leaf-air temperature difference was very similar to that calculated by Marcelis (1989) and could be modelled by the following equation:

$$T_l - T_a = 0.0056x \times \ln(0.0022x) \quad (11)$$

where x is the global radiation and $r^2 = 0.65$ – 0.85 for the different days of the first experiment. Leaf-air temperature

FIG. 8. Effect of D_a on the relation between global radiation and leaf-air temperature difference, $T_l - T_a$. A, data from 13 May 1993, $D_a \leq 1$ kPa (○), $D_a \leq 2.2$ kPa (●). B, Data from 7 Aug. 1993, $D_a \leq 1$ kPa (○), $D_a \leq 3.5$ kPa (●). C, 'Unadapted plants' to $D_a \leq 2.2$ kPa, data from 13 May 1993.

FIG. 9. Diurnal course of crop water stress index (*CWSI*) and global radiation, R_g (---) with small and large vapour pressure deficit. A, Data from 14 May 1993, $D_a \leq 1$ kPa (.....), $D_a \leq 2.2$ kPa (—). B, Data from 7 Aug., $D_a \leq 1$ kPa (.....), $D_a \leq 3.5$ kPa (—).

difference was also plotted *vs.* radiation when D_a increased to 3.5 kPa (second experiment, Fig. 8B). This difference increased greatly during the morning then became less important in the afternoon. It changed rapidly from -5 to -3 °C even though solar radiation was increasing slightly from 500 to 600 W m^{-2} . In the example shown in Fig. 8B, both plant types (i.e., short and long term exposure to air humidity stress) have the same leaf temperature.

Effect of vapour pressure deficit on crop water stress index

A comparison of the *CWSI* in the two different environment in both experiments (Fig. 9A and B) showed that this index was lower if $D_a \leq 1$ kPa while leaf temperature tended to be higher than air temperature. The lowest value was observed in the afternoon and was 0.25–0.30 for the first experiment. In the second experiment, the *CWSI* of control plants was lower and varied from 0.1 to 0.25 for the period 1000 to 1800 h. In the dry environment, *CWSI* was higher in the first than in the second experiment even though D_a was lower. We also noticed that this index fluctuated with sunlight in Fig. 9A. These values suggested moderate water stress in plants cultivated under a high

evaporative demand. This data could be associated with a slightly reduced stomatal opening in both experiments.

DISCUSSION

In this paper, we have shown that cucumber stomata are very sensitive to environmental conditions. Thus, stomata may be a good parameter for on-line control of the greenhouse environment. The minimum stomatal resistances measured and calculated under our experimental conditions are very low compared to those obtained previously for greenhouse cucumber, using porometry, by Bakker (1991*b*) and van de Sanden and Veen (1992). This discrepancy is most probably due to differences in radiation which are very much higher in our experiments.

Simple methods for estimating stomatal resistance to water vapour transfer as a function of environmental parameters have been put forward by Avissar *et al.* (1985), Stanghellini (1987) and Boulard *et al.* (1991). These authors propose a multiplication function where r_s results from environmental variables in the absence of a synergistic effect between them:

$$r_s = r_{\min} \times f_1(R_g) \times f_2(D_a). \quad (12)$$

Under our experimental conditions, we see that global radiation accounts for 85–95 % of stomatal resistance [eqn (10) and Fig. 5]. This is in accordance with the modelling of transpiration and leaf to air temperature difference as a function of radiation [eqn (9) and (11)]. Quantification of the effect of vapour pressure deficit is more difficult. Two different types of result have been obtained in this paper. A long term effect is shown after several days of exposure to dry environment (second crop) where large D_a (3.5 kPa) does not allow complete stomatal opening during the day (Fig. 4B). This is in accordance with other published data (Schulze, 1986; Stanghellini, 1987) where increases in vapour pressure deficit generally induce stomatal closure.

However, stomatal response to D_a is quite complex. First, nocturnal stomatal resistance is higher in both experiments as a consequence of diurnal dry environment. Second, after just a few days of exposure to $D_a \leq 2.2$ kPa (first experiment), daily resistance is not continuously higher than the control condition (Fig. 4A). Third, when we analyse the effect of vapour pressure deficit on the diurnal variation of stomatal resistance, we obtain different patterns. The least common is an inverse effect of D_a to that mentioned above (Fig. 6A, B). Increase in vapour pressure deficit induces stomatal opening. This is very different from what is generally assumed. However, this phenomenon can only be observed during parts of day (Fig. 6C). As a matter of fact, the positive effect of a higher D_a on stomatal aperture is always linked to increasing solar radiation. In the same way, a concomitant decrease of D_a and R_g induces a steep rise in stomatal resistance at the end of the day. One possible explanation would be an interaction between radiation level and evaporative demand with a synergistic effect on stomatal aperture. This hypothesis may be supported by the effect of variation in sunlight observed in response to high vapour pressure deficit. Thus, large D_a increases stomatal sensitivity to cloudiness (Fig. 4A and B). Moreover, stomatal response

to high D_a is mainly correlated with variation in sunlight (Fig. 6D). Knapp and Smith (1990) reported a high stomatal sensitivity to rapid changes in photosynthetic photon flux (PPF) of fast growing species. On the contrary, Kaufmann (1976), has shown that in slow growing species a more noticeable stomatal closure occurs at low PPF with an increase in the absolute humidity difference.

Thus, stomatal resistance cannot be simply modelled as a function of D_a [eqn (12)]. Other factors probably need to be included. When vapour pressure deficit is increasing for a long time (i.e., for more than 1 or 2 h) the rise in transpiration rate is transitory, as we observed in residuals of the transpiration model [eqn (9) and Fig. 2B]. The most likely cause of this behaviour is stomatal closure following high transpiration rate as shown in the increase of residual resistance in Fig. 6C. Since the possibility of a water deficit in the root environment may be excluded under soilless conditions, we can suppose that an increase in transpiration rate, caused by high vapour pressure deficit, would not be entirely compensated by an increase in root absorption rate or xylem water conductance (Meinzer and Grantz, 1990). On the other hand, wilting of *Impatiens pallida* reported by Schulz, Smith and Wu (1993) may be compared to the one commonly observed of a cucumber crop in bright sunlight after a period of dull and humid days. Within natural settings, these authors confirm the postulate (Cowan and Farquhar, 1977) where stomatal aperture optimizes the amount of CO_2 assimilated to water lost by transpiration. Models for greenhouse climate control are primarily concerned with the prediction of the rate of crop photosynthesis in relation to environmental parameters. Our results highlight the need to include gas exchange optimization in these models.

Leaf temperature is a good indicator of transpiration. Latent heat of water vaporization allows dissipation of the solar energy absorbed by the leaf (Stanghellini, 1987). In our data obtained in the first experiment, leaf temperature varies greatly when plants are submitted to a moderate atmospheric stress (2.2 kPa) for a long (Figs 7A and 8B) or a short period (Fig. 8C). When plants are submitted to a high D_a from the time of cotyledon expansion, the cooler leaf temperature may indicate that transpiration is greater and stomatal aperture less limited by the evaporative stress compared to other plants which have been under the same environment for just a few days. This difference between plant types is not observed when vapour pressure deficit is higher (second experiment). In the first case, is there an adaptation to the mild evaporative stress? This kind of response may be compared to that related by Schulze and Hall (1982) for *Triticum* where response of leaf conductance to leaf water potential is linked to crop conditions (greenhouse or field) and which has been interpreted as resulting from osmotic adjustment or exposure to a previous stress. In contrast, Kawamitsu, Yoda and Agata (1993) has shown that the reduction of stomatal conductance in rice, with a long term humidity pretreatment, is not reversible.

CWSI was successfully used by Baille and Baille (1993) to evaluate the effect of a fog-system on a rose crop grown on substrate. In the absence of humidity stress ($D_a \leq 1$ kPa), cucumber shows a higher stress index (Fig. 9A) than the

rose crop (Baille and Baille, 1993). However, as for minimal stomatal resistance, CWSI is lower in the second experiment even though air temperature is much higher. For higher vapour pressure deficit ($D_a \leq 2.2$ or 3.5 kPa), CWSI is nearly equal to or slightly higher than the control. However, in the second experiment high D_a increases the crop water stress index in the afternoon. This is in accordance with the hypothesis of cumulative stress. As for this index, we may consider that the stress which is shown by stomatal closure under high D_a conditions, is only mild stress. Does cucumber have a capacity for adaptation to high evaporative demand? It appears that our control treatment ($D_a \leq 1$ kPa) represents an atmospheric stress. Thus, Bakker, Welles and van Uffelen (1987) have shown that cucumber yield is negatively and linearly correlated with vapour pressure deficit from 0.5 to 0.9 kPa.

For cucumber grown in southern European greenhouses, it would appear that some atmospheric stress is necessary for the adaption of plants to important environment variations (Javoy *et al.* 1990). Our measurements have been carried out on small plants, but tall, more developed plants may be more affected by atmospheric stress. A larger leaf area means an increase of plant evaporative capacity and a longer xylem pathway for water transport from the roots to the top of the plant (vertical trained crop). In contrast, a higher transpiring area increases greenhouse air humidity which consequently reduces evaporative demand. Another important consequence of maintaining a low vapour pressure deficit within the greenhouse environment is an easier control of air temperature and therefore protection of plants against heat stress.

ACKNOWLEDGMENTS

This work was supported by the Conseil Régional d'Aquitaine. Authors gratefully acknowledge helpful discussions with Dr A. Baille and wish to thank Dr Ch. Valancogne for his programs for balance-computer communication and porometry data analysis, and S. Dayau for her technical assistance with the data logger programming.

LITERATURE CITED

- Avisar R, Avisar P, Mahrer Y, Bravdo BA. 1985. A model to simulate response of plant stomata to environmental conditions. *Agricultural and Forest Meteorology* 34: 21–29.
- Baille M, Baille A. 1993. Greenhouse soilless crops in mediterranean countries: the need for a better environmental control (air, substrate). In: Martinez PF, ed. *Environmental constraints in protected cultivation: possibilities for new growing techniques and crops*. CEE Agrimed Research Program, Report EUR 15123, 91–106.
- Bakker JC, Welles GWH, van Uffelen JAM. 1987. The effect of day and night humidity on yield and quality of glasshouse cucumbers. *Journal of Horticultural Science* 62: 363–370.
- Bakker JC. 1991a. Leaf conductance of four glasshouse vegetable crops as affected by air humidity. *Agricultural and Forest Meteorology* 55: 23–26.
- Bakker JC. 1991b. Effects of humidity on stomatal density and its relation to leaf conductance. *Scientia Horticulturae* 48: 205–212.
- Boulard T, Baille A. 1993. A simple greenhouse climate control model incorporating effects of ventilation and evaporative cooling. *Agricultural and Forest Meteorology* 65: 145–157.
- Boulard T, Baille A, Mermier M, Villette F. 1991. Mesures et

- modélisation de la résistance stomatique foliaire et de la transpiration d'un couvert de tomate de serre. *Agronomie* **11**: 259–274.
- Cowan IR, Farquhar GD. 1977. Stomatal function in relation to leaf metabolism and environment. *Symposia of the Society for Experimental Biology* **31**: 471–505.
- Gijzen H, Vegter JG, Nederhoff EM. 1990. Simulation of greenhouse crop photosynthesis: validation with cucumber, sweet pepper and tomato. *Acta Horticulturae* **268**: 71–80.
- de Graaf R. 1988. Automation of the water supply of glasshouse crops by means of calculating the transpiration and measuring the amount of drainage water. *Acta Horticulturae* **229**: 219–231.
- Grantz DA. 1990. Plant response to atmospheric humidity. *Plant, Cell and Environment* **13**: 667–679.
- Jackson RD. 1982. Canopy temperature and crop water stress. In: Hillel D, ed. *Advances in irrigation*. London: Academic Press, **1**: 43–85.
- Janoudi AK, Widders IE, Flore JA. 1993. Water deficit and environmental factors affect photosynthesis in leaves of cucumber (*Cucumis sativus*). *Journal of American Society for Horticultural Science* **118**: 366–370.
- Jarvis PG, Morison JIL. 1981. The control of transpiration and photosynthesis by the stomata. In: Jarvis PG, Mansfield TA, eds. *Stomatal physiology*. Cambridge: Cambridge University Press, 247–279.
- Javoy M, Letard M, Pelletier B. 1990. Le concombre en culture hors sol. Les éléments de conduite. *Infos CTIFL Hors série Cultures légumières sur substrats*, 53–68.
- Joliet O, Bailey BT. 1992. The effect of climate on tomato transpiration in greenhouses: measurements and models comparison. *Agricultural and Forest Meteorology* **58**: 43–62.
- Kaufmann MR. 1976. Stomatal response of Englemann spruce to humidity, light, and water stress. *Plant Physiology* **57**: 898–901.
- Kawamitsu Y, Yoda S, Agata W. 1993. Humidity pretreatment affects the responses of stomata and CO₂ assimilation to vapor pressure difference in C₃ and C₄ plants. *Plant and Cell Physiology* **34**: 113–119.
- Knapp AK, Smith WK. 1990. Stomatal and photosynthetic responses to variable sunlight. *Physiologia Plantarum* **78**: 160–165.
- Marcelis LFM. 1989. Simulation of plant-water relations and photosynthesis of greenhouse crops. *Scientia Horticulturae* **41**: 9–18.
- Meinzer FC, Grantz DA. 1990. Stomatal and hydraulic conductance in growing sugarcane: stomatal adjustment to water transport capacity. *Plant, Cell and Environment* **13**: 383–388.
- van de Sanden PACM, Veen BW. 1992. Effects of air humidity and nutrient solution concentration on growth, water potential and stomatal conductance of cucumber seedlings. *Scientia Horticulturae* **50**: 173–186.
- Schulz KE, Smith M, Wu Y. 1993. Gas exchange of *Impatiens pallida* Nutt. (Balsaminaceae) in relation to wilting under high light. *American Journal of Botany* **80**: 361–368.
- Schulze ED, Hall AE. 1982. Stomatal responses, water loss and CO₂ assimilation rates of plants in contrasting environments. In: Lange OL, Nobel PS, Osmond CB, Ziegler H, eds. *Physiological plant ecology II. Water relation and carbon assimilation. Encyclopedia of Plant Physiology*. Berlin: Springer Verlag, **12B**: 181–230.
- Schulze ED. 1986. Carbon dioxide and water vapor exchange in response to drought in the atmosphere and in the soil. *Annual Review of Plant Physiology* **37**: 247–274.
- Seginer I. 1984. On night transpiration of greenhouse roses under glass or plastic cover. *Agricultural and Forest Meteorology* **30**: 257–268.
- Stanghellini C. 1987. *Transpiration of greenhouse crops, an aid to climate management*. PhD dissertation, Wageningen: Agricultural University.
- Tantau HJ. 1989. On-line climate control. *Acta Horticulturae* **248**: 217–222.
- Yang X, Short TH, Fox RD, Bauerle WL. 1990. Transpiration, leaf temperature and stomatal resistance of a greenhouse crop. *Agricultural and Forest Meteorology* **51**: 197–209.