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Effect of high temperature on photosynthesis and transpiration of sweet corn (*Zea mays* L. var. *rugosa*)

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Abstract

Four temperature treatments were studied in the climate controlled growth chambers of the Georgia Envirotron: 25/20, 30/25, 35/30, and 40/35 °C during 14/10 h light/dark cycle. For the first growth stage (V3-5), the highest net photosynthetic rate (P_N) of sweet corn was found for the lowest temperature of 28−34 μmol m^{-2} s^{-1} while the P_N for the highest temperature treatment was 50−60 % lower. We detected a gradual decline of about 1 P_N unit per 1 °C increase in temperature. Maximum transpiration rate (E) fluctuated between 0.36 and 0.54 mm h^{-1} (≈5.0−6.5 mm d^{-1}) for the high temperature treatment and the minimum E fluctuated between 0.25 and 0.36 mm h^{-1} (≈3.5−5.0 mm d^{-1}) for the low temperature treatment. Cumulative CO_2 fixation of the 40/35 °C treatment was 33.7 g m^{-2} d^{-1} and it increased by about 50 % as temperature declined. The corresponding water use efficiency (WUE) decreased from 14 to 5 g(CO_2) kg^{-1}(H_2O) for the lowest and highest temperature treatments, respectively. Three main factors affected WUE, P_N, and E of *Zea*: the high temperature which reduced P_N, vapor pressure deficit (VPD) that was directly related to E but did not affect P_N, and *quasi* stem conductance (QC) that was directly related to P_N but did not affect E. As a result, WUE of the 25/20 °C temperature treatment was almost three times larger than that of 40/35 °C temperature treatment.

Additional key words: maize; *quasi* stem conductance; transpiration rate; vapor pressure deficit; water use efficiency.

Introduction

The optimal temperature for warm season maize is 15−20 °C for planting and 20−30 °C for the regular growing season (Bird *et al.* 1977). Under field conditions the combination of high temperatures and inadequate moisture has caused severe damage to yield. As dry weather continues, more maize fields may show signs of moisture stress. Temperature is the primary factor driving maize development within a fairly broad range and stress is identified by marked leaf rolling. The root development above optimum soil temperature of 20−25 °C was inhibited in general, but especially near the soil surface (Shaw and Newman 1985) by very low soil water content within the upper dry layer. Air temperatures above the optimum (22.5−27.0 °C) during the grain development resulted in reduced grain yields (Dale 1983, Thompson 1986, Commuri and Jones 2001).

The net photosynthetic rate (P_N) of maize increases with temperature up to a maximum around 35 °C, then decreases at higher temperatures (Lizaso *et al.* 2005). Vinocur and Ritchie (2001) indicated the necessity of using the apex temperature in thermal time calculations for an accurate understanding of maize development. A decreased leaf P_N at high temperatures is believed to be largely due to reduced efficiency in photosystem 2, rather than an increase in maintenance dark respiration or a decrease in leaf area (Prange *et al.* 1990). In general, C_4 plants (including maize) have higher temperature optima for photosynthesis and growth than C_3 plants (Bird *et al.* 1977) and thus are better adapted to warmer climates (Kim *et al.* 2007). To estimate the impact of dry hot weather on maize yield potential, we studied the effects of extreme temperatures on its development and gas exchange. The gas exchange rate provides a highly sensitive measure of the degree of temperature stress to which

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the maize is exposed. The manner in which maize canopy is developed under high temperatures and the corresponding contribution to P_N and transpiration rate (E) has not been quantified. Very limited experimental data is available on the relationship between extreme high temperatures and gas exchange by maize. The data is specifically relevant to predict the influence of global warming on biomass production. It is also important for crop model development and evaluation (Hoogenboom 2000). The temperature dependencies used in models have largely been developed from data collected in field trials and greenhouses (Ingram and McCloud 1984), and using temperature gradients with altitude (Manrique and Bartholomew 1991). In these studies, variations in temperature are reduced but there is no true control of temperature. Measurements on a single leaf provide the basis for scaling carbon exchange from leaf to canopy and earth system models (Farquhar *et al.* 1980, Bernacchi *et al.* 2003). The scaling requires using leaf temperature over a wider temperature range than that for which experiments are usually designed. The objective of this study was to evaluate the effect of high temperature on P_N, E, and water use efficiency (WUE) of sweet corn in a climate controlled environment.

Materials and methods

Plants and measurements: Four climate controlled chambers in the Georgia Envirotron facility (Ingram *et al.* 1998) were used for this study. In each chamber 42 sweet corn plants (*Zea mays* L. var. *rugosa* cv. Seneca) were grown from 21 November 2006 to 9 February 2007, a total of 80 d. The plants were grown in 1 500 cm^3 plastic containers (Passioura 2006), with dimensions of 16 and 12 cm for upper and lower diameter, respectively, and a height of 11.5 cm. Air-dried Georgia sand with particle size up to 0.5 mm was employed as growth media; the bulk density of the sand varied between 1 100 and 1 300 kg m^{-3}. *Miracle Gro* fertilizer (24−8−16 % NPK) was used during the entire growth period and was applied with the irrigation water. An application of 13 g in each container was equivalent to 150−170 kg(N) ha^{-1}. The seeds were planted at a depth of approximately 5 cm and the containers were irrigated with one dripper at a rate of 1 000 cm^3 h^{-1}. Irrigation was triggered four times per day (at 06, 10, 14, and 18 h) for 15 min at the initial stage and was changed to 30 min/irrigation at a later stage. The containers were positioned near the walls of the chambers leaving the center open for measuring activities. Irrigation through the drippers was controlled by a computer. The major properties of the individual treatments are summarized in Table 1.

Following a preliminary germination test at different temperatures, we selected the 25/20 °C treatment as the nursing temperature for all plants in the study. This temperature was applied from planting through emergence until all plants reached the growth stage of V1. At this stage the temperature in the individual chambers was changed according to the proposed treatments. The day light and night time hours lasted 14 and 10 h, respectively (from 06:00 to 20:00 daylight and the rest of the day was kept dark).

For measuring the various environmental and plant parameters the *PTM-48M* or Photosynthesis and Transpiration Monitor (*PhyTech*, Israel) was used. The system contains four self-clamping leaf chambers (*LC-4A*), which successively every 30 min were closed for two min while monitoring P_N, E, and additional environmental variables that are listed hereafter. The samples were analyzed with an infrared CO_2 analyzer and the results were stored in a built-in data logger. The additional sensors of the *PTM-48M* include: *ATH-2* Air Temperature and Humidity Sensor, *SMS* Soil Moisture Sensor, *SF-4M* Sap Flow Relative Rate Sensor, two *LT* leaf temperature sensors, a photon flux meter (model *LI-190SB*, *LI-COR*, Lincoln, NE, USA) measuring. PAR (photosynthetic active radiation) and global radiation were measured by a pyranometer (*LICOR 250* light meter). The combined measurements of canopy temperature and relative humidity enabled the monitor's software to determine the leaf to air vapor pressure deficit (VPD). Photosynthesis data from four leaf chambers as well as data from the additional sensors were automatically recorded every 30 min around-the-clock.

Organization of *PTM* records and supporting data collection: In each chamber the *PTM* was measured for a 24−48 h period. At the end of the measuring period the device was transferred to a neighboring temperature treatment in a different chamber. A very large number of *PTM* measurements were collected (≈2 000 records). Each set of 24 h provided 48 data records of a treatment and was determined as a "project". Its given ID was the date and the hour of its start for a total of 30 projects. For example, the name of a project that started on 1 February 2007 at 09:00 and lasted until 2 February at 10:00 was automatically given the name 20070201_0900, so that it was easier at a later to locate the data and to conduct analysis.

Data analysis:
Elapsed time analysis: The effect of temperature on P_N, E, WUE, and transpiration coefficient (TC = H_2O/CO_2 = 1/WUE) was analyzed as a function of elapsed time throughout a 24-h period. The average value from four replications of these processes was plotted as a function of time in order to demonstrate the differences between the four temperature treatments in chambers 1, 2, 3, and 4 (Table 1).

Table 1. Average physical properties of the chambers. In each chamber we employed 14 h light (D) with high temperature and 10 h dark (N) with low temperature. The dark conditions are marked by zero radiation. Radiation flux increased with height at a polynomial rate: $y = 0.017\ x^2 - 0.700\ x + 420.5$; $r^2 = 0.922$. Photosynthetic photon flux density (PPFD) measured near the plants increased with height at a polynomial rate: $y = 0.010\ x^2 - 0.788\ x + 163.9$; $r^2 = 0.88$. Wind speed was measured in the center of the chamber.

Chamber	1		2		3		4	
Temperature treatment [ºC]	25	20	25	20	25	20	25	20
	D	N	D	N	D	N	D	N
Dew point temperature [ºC]	−32.0	−1.9	−25.6	−28.8	2.7	−17.1	−54.0	−52.0
Saturated vapor pressure [kPa]	3.4	1.4	4.0	1.7	4.5	3.2	6.0	3.8
Radiation [W m^{-2}]	315	0	300	0	292	0	310	0
PPFD [μmol m^{-2} s^{-1}]	611	0	743	0	564	0	645	0
Area [m^2]	6.5		3.5		6.5		6.5	
Height [m]	2.1		1.8		2.1		2.1	
Wind speed [m s^{-1}]	0.15		0.15		0.15		0.15	
Area [m^2]	6.5		3.5		6.5		6.5	
Height [m]	2.1		1.8		2.1		2.1	

Envelope analysis: One way that was recently used to construct a relevant P_N-temperature response function is the envelope analysis. The envelope data analysis or Eppley curve is used to model data that has a high interval of ranges due to the influence of several parameters. This data analysis methodology is commonly used in oceanographic (Behrenfeld and Falkowski 1997, Brush *et al.* 2002) and photosynthesis (Yurista 1999, Bernacchi *et al.* 2002, Ben-Asher *et al.* 2006) studies. The envelope data analysis creates upper curves that delimitate the upper limits of the scatter plot data, therefore containing inside (of this envelope) all the points of the scatter plot. This technique, based on the upper envelopes of the data, was used to determine the maximum P_N only as a function of various temperatures. Other factors that affected the measurements, such as local water stress, or lower irradiance at a specific site, or incomplete leaf cover by its chamber would concomitantly limit full gas exchange. The upper envelope technique allows for considering only the temperature as the independent variable. For this analysis the P_N as a function of temperature was determined for positive values during daytime (light) hours.

Statistical analysis: The P_N and E measurements were taken simultaneously with four replications and analyzed for standard deviation (SD). The *SigmaPlot* (version *10.0*, *Systat Software*, Chicago, IL, USA) was used to perform Student's *t*-test from which we calculated for significance and least significant difference (LSD).

Results and discussion

Environmental conditions in the growth chambers: From emergence to harvest the incident PAR averaged 32±2.3 mol m^{-2} d^{-1} for a constant 14 daylight hours. The global radiation was 12.4±1 MJ m^{-2} d^{-1}. For comparison, the respective photosynthetic photon flux density (PPFD) values were 640±76 μmol m^{-2} s^{-1} and 247±26 W m^{-2}, while peak PPFD was 1 080±45 μmol m^{-2} s^{-1} and global irradiance was 629±26 W m^{-2} at 13:00 h EST in January. In Fig. 1 the concentration of CO_2 within the growth chamber is displayed next to the daily temperature course.

Due to efficient aeration, the CO_2 concentrations of the two treatments did not differ much, with a bit higher concentration at the lower temperature treatment, surprisingly. The abrupt change between light and dark time is clearly distinct. A sharp temperature decrease was observed when the lights went off and temperature was reduced by 5 °C in both the high and low temperature treatments. The CO_2 concentration also changed rapidly from about 300 cm^3 m^{-3} during the daylight hours to 400 cm^3 m^{-3} at dark hours. In closed un-aerated chambers it could be expected that under extreme 40/35 °C conditions, losses due to maintenance and dark respiration would increase the CO_2 concentration within the chamber. For example, Kim *et al.* (2007) found that dark respiration rates increased with temperature and were maximal at 35/29 °C. However, due to appropriate aeration they did not comply with the expected higher CO_2 concentration in the high temperature treatment.

The effect of temperature on photosynthesis:

Single leaf P_N: At the first growth stage (V3-5), the highest P_N was measured under the lowest temperature treatment, ranging between 28 and 34 μmol m^{-2} s^{-1} (Fig. 2). The 30/25 °C temperature treatment presented a 30 % lower P_N than the 25/20 °C treatment. After the 40/35 °C treatment, P_N was 50−60 % lower than at 25/20 °C treatment. The high temperature clearly inhibited P_N. In general, the two lower sections of Fig. 2 show a gradual decline of about 1 P_N unit per 1 °C increase in temperature. During the second measuring cycle

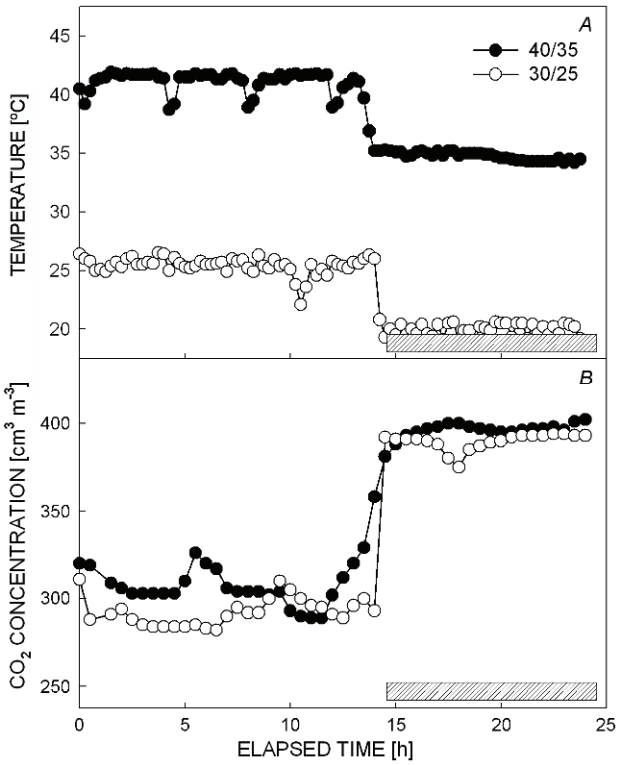

Fig. 1. (*A*) Daily time course of the lowest (25/20 °C) and highest (40/35 °C) temperature treatments. (*B*) CO_2 concentrations under the above two temperature treatments. *Gray boxes* mark the dark hours.

(Fig. 2, V9-10) the rate of P_N of the low temperature treatment was reduced to 25−30 μmol m^{-2} s^{-1} while the P_N of the plants under 30/25 °C increased. The trend of increasing P_N for 30/25 °C and decreasing rate of the 25/20 °C was also detected during the third stage (R1). The P_N of the plants under 40/35 °C remained low and nearly constant, at 10−15 μmol m^{-2} s^{-1} during the experiment period. As expected, the nocturnal P_N was negative with an average of about −2 μmol m^{-2} s^{-1}.

All treatments demonstrated the abrupt change from light to dark conditions. These results are corroborated by a research of Hew *et al.* (1969) who reported that P_N of a sunflower leaf in a closed system exhibited a proportional decrease with temperature increases from 19 to 34 ºC. Baker *et al.* (1992) reported that grain yield of rice decreased from 10.4 to 1.0 Mg ha^{-1} with increasing temperature from 28/21/25 °C to a 37/30/34 °C, a decrease of about nine productivity units per increase of 9 °C. Timlin *et al.* (2006) also found a decrease of about one productivity unit per increase of 1 °C. In their study the maximum daily cumulative C gain was about 0.9 g(C) plant^{-1} d^{-1} for the 24 °C temperature. The temperatures of 28 and 32 °C produced lower maximum rates, about 0.25−0.35 g(C) plant^{-1} d^{-1}. The daily course of CO_2 accumulation is displayed in Fig. 3.

The totals during the V3-5 period were 1.54, 1.12, 0.89, and 0.66 mol m^{-2} for the 25/20, 30/25, 35/30, and 40/35 ºC treatments, respectively. The suboptimal conditions created by the 40/35 ºC treatment were harmful

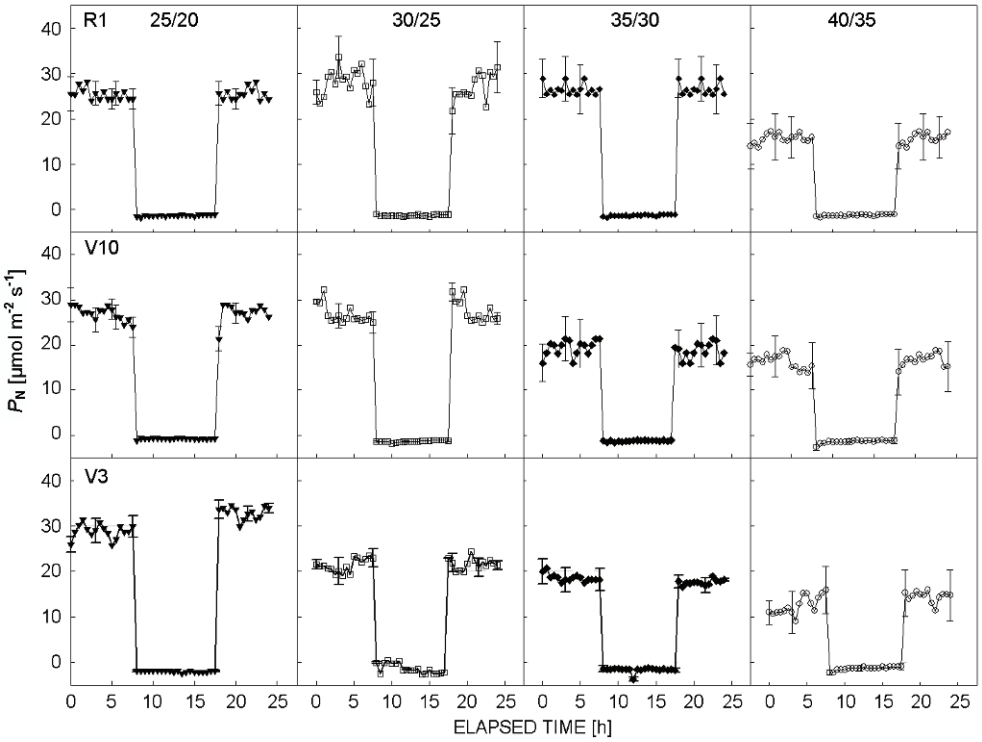

Fig. 2. Net photosynthetic rate (P_N) at growth stages V3-5, V9-10, and VT-R1. *The numbers on the top of the figure* indicate day/night temperature. *The bars* are standard errors.

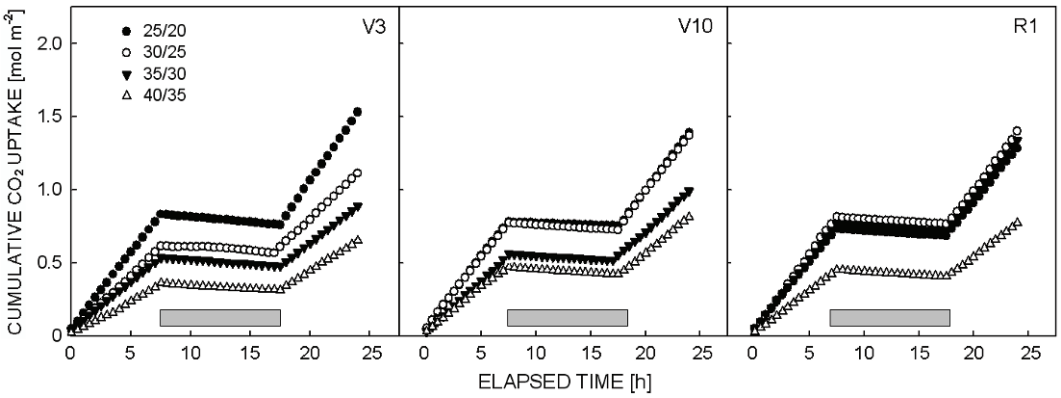

Fig. 3. Cumulative CO_2 uptake under four temperature treatments in growth chambers. Means of 4 determinations. *The gray squares* mark the dark hours through which the cumulative uptake slightly declines due to night respiration.

throughout the entire growing period. The accumulated CO_2 of two treatments (30/25, 35/30) increased with time by 20−40 % above their initial value and the 25/20 °C treatment decreased with time by 10−15 %. Thus the highest P_N was about 40 μmol m^{-2} s^{-1} and it was measured when the temperature was 30−32 °C (Fig. 4).

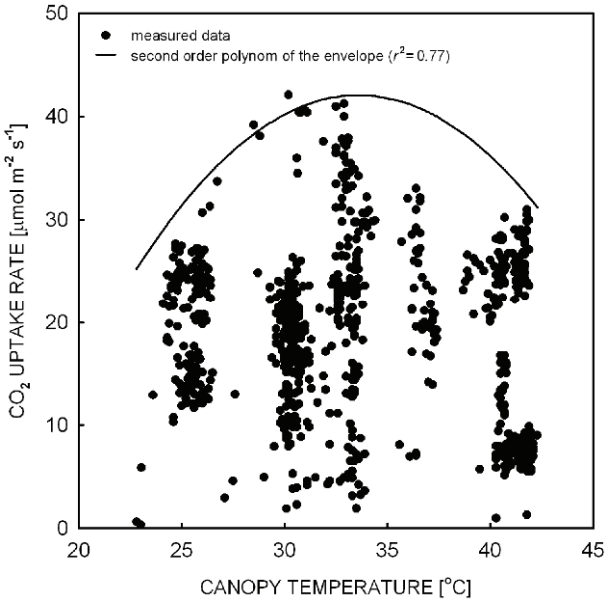

Fig. 4. Temperature dependence of the net photosynthetic rate (P_N) for *Zea mays* L. var. *rugosa*. Data were obtained at 30 min intervals under various temperatures, environmental and experimental conditions; 1 028 data points are displayed. The envelopes for the rising portions were analyzed using Eq. 1 and parameter values are summarized in Table 2.

Optimal temperature for photosynthesis: Experimental design with temperature in growth chambers suffers some lack of continuity with regards to the selection of optimal temperatures. For this reason we could not determine the temperature that maximizes the P_N. To bridge between the arbitrarily selected treatments and to obtain continuity between the four temperatures, we used all the positive P_N and produced a scatter diagram from which we obtained an envelope function that combined all the positive P_N values. When the only factor limiting P_N was the temperature, we drew an upper limit border that enclosed the entire set of data (Fig. 4).

The large number of data points for positive P_N at various temperatures (over 1 000) together with their inherent scatter enabled upper envelope functions to be created. In Fig. 4, as the canopy temperature increased from 22 °C to the optimal value of about 32 °C, P_N gradually rose to about 42 μmol m^{-2} s^{-1}. Temperatures above the optimal for P_N were associated with its reduction. The upper envelope, when factors other than temperature (such as incomplete cover of the leaf by the measuring chambers and/or environmental factors such as nutritional or water deficiency) would not be limiting P_N, was then fitted for the rising portion of the curve using the exponentially-based Arrhenius equation (Nobel 2005):

$$\text{Rate} = B\, e^{-A/RT} \quad (1)$$

where B is a constant, A is the apparent activation energy [kJ mol^{-1}], R is the gas constant [8.314 J mol^{-1} K^{-1}], and T is the absolute temperature [K]. Using an Arrhenius plot [lnP_N *vs*. 1/T], A, which represents the minimum energy for the reaction, was estimated (Table 2). These values are within the range determined for a diverse group of species using different methodologies (Ben-Asher *et al*. 2006). The energy barrier to start the reaction of some photosynthetic enzymes is relatively small compared to the representatives of C_3 and the CAM pathways. The apparent activation energy obtained by Kim *et al*. (2007) for maize (C_4) was also smaller than those of the other pathways (C_3 and CAM), but it was somewhat higher than the data obtained from the above envelope analysis. However, beyond the optimal temperature (Fig. 4) the production was decreased, as we actually observed in the photosynthetic measurements.

The effect of temperature on *E*:
Diurnal transpiration: The maximum E was found for

the high 40/35 °C treatment and during the 14 daylight hours it fluctuated from 100 to 150 mg(H_2O) m^{-2} s^{-1} (0.36−0.54 mm h^{-1}), while the minimum transpiration fluctuated from 70 to 100 mg(H_2O) m^{-2} s^{-1} (0.25−0.36 mm h^{-1}) for the low 25/20 °C treatment (Fig. 5). The respective total transpiration for 24-h cycle ranged from 4 to 7 mm. A declining (non significant) effect with the progress of growth stages was therefore detected (Table 3).

The reference evapotranspiration, E0, was estimated using the FAO-56, Penman Monteith model (Allen *et al.* 1998). It increased from 4.7, through 5.5 and 5.6, to 6.3 mm d^{-1} with an increase in temperature from 25 °C through 30 °C, and 35 °C to 40 °C. Due to the vapor pressure gradients, *E* during the dark hours was also detected even when irradiance was zero. This lower limit, *e.g.* during the dark hours, varied between 5 and 7 mg m^{-2} s^{-1} (0.20−0.25 mm for 10 dark hours). The standard deviation was 0.5 mg m^{-2} s^{-1} and the CV was 0.33.

Further study of the data presented in Figs. 4 and 5 shows that the maximum P_N was measured when *E* was at its minimum and *vice versa*. Separate peaks of P_N and *E* are contrary to expectations, because the pathway for diffusion of CO_2 into leaves is similar to the pathway for diffusion of H_2O out of leaves. Both are linearly affected by stomatal conductance. Thus the two processes, maximum P_N and maximum *E*, are expected to happen at the same time (Slatyer 1960, de Wit 1978). As the *PTM* also provides additional measurements, we used the sap flow and VPD data in order to study this disagreement.

Quasi* stem conductance (QC) and *E: Stem conductance is a key parameter to assess limitations to P_N, *E*, and growth potential. It is needed in models of carbon and water flux at scales ranging from leaf to full ecosystem. The general expression for *E* can be written in terms of Fick's first law as it applies to our measurement sensors:

$$\text{relative flux density} = \text{conductance} \times \text{force} \quad (2)$$

Relative flux density [dimensionless] was measured with a sensor based on relative sap flow (*SF-4M*, Sap Flow Relative Rate Sensor). Thus, a term "*quasi* stem conductance" [kPa^{-1}] can be defined by the following ratio:

$$QC = \text{relative flux density } VPD^{-1} \quad (3)$$

where VPD = leaf to air vapor pressure deficit [kPa]. It represents the force in Eq. (2). The ratio between relative sap flow and VPD thus represents the ratio between transpiration and its driving force. We used the term QS [kPa^{-1}] because the flux is given in relative units rather than in physical units. Qualitatively, however, it shows when the stomata exhibit major opening. Under non-water-stressed conditions for the 25/20 °C treatment, irradiation was sufficient to generate wide apertures for the stomata and thus, as displayed in Fig. 6, QC was maximized.

In particular, the CO_2 conductance was at its maximum, leading to high P_N. The H_2O conductance was also at its maximum but the low VPD, which was associated with low temperature, resulted in low *E*.

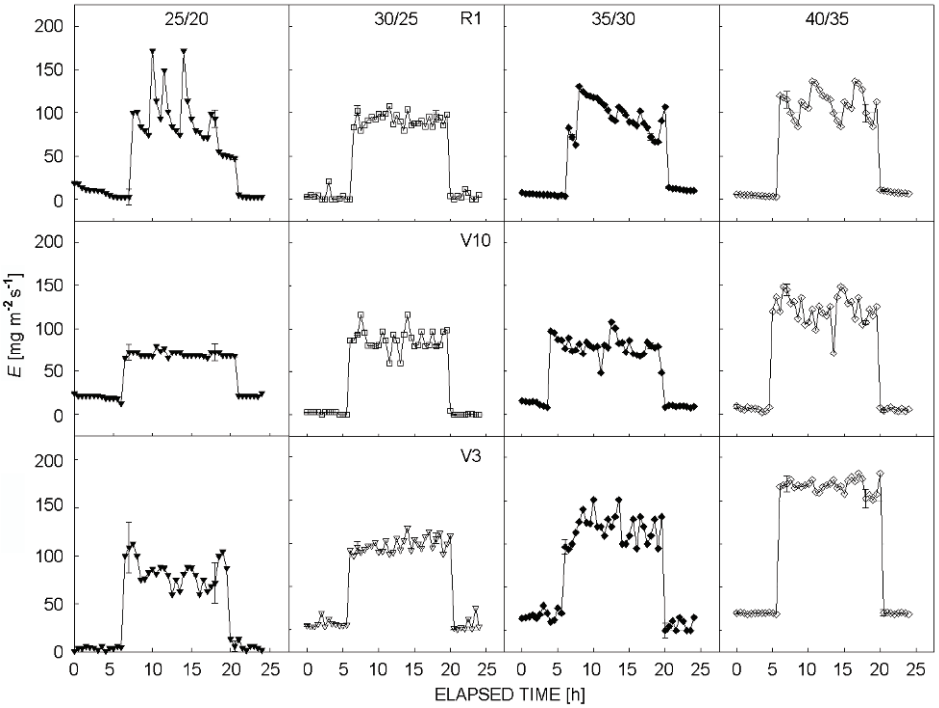

Fig. 5. Transpiration rate (*E*) at three growth stages: V3-5, V9-10, and VT-R1. *The numbers at the top of the figure* indicate day/night time temperature. *The bars* are standard errors. *E*: 100 mg m^{-2} s^{-1} = 0.36 mm h^{-1}.

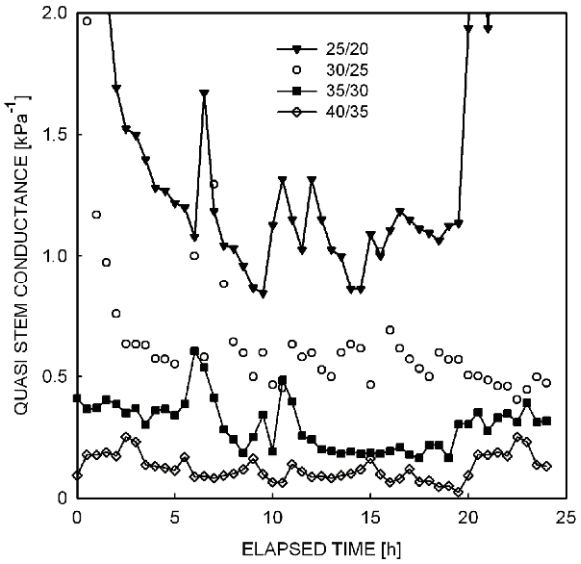

Fig. 6. The course of the *quasi* stem conductance as a function of elapsed time under four temperature treatments that are specified on the top of the figure.

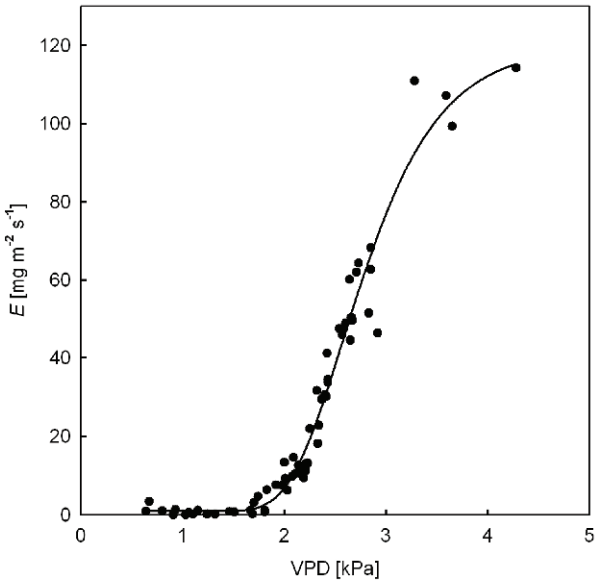

Fig. 7. Transpiration rate (E) as a function of VPD. Data from the 40/35 °C treatment.

Table 2. Activation energy [kJ mol^{-1}] for photosynthesis of several crops. Calculated from the upper envelopes of the responses of net photosynthetic rate to temperature (except Kim *et al.* 2007).

Plant	Activation energy
Maize (C_4; this experiment)	24.5
Maize (Kim *et al.* 2007)	26−27
Wheat (C_3; Ben-Asher 2006)	150
Salinity stressed wheat (Ben-Asher 2006)	250
Pitaya cactus (CAM; Ben Asher *et al.* 2006)	50−100

Contrary to the stress conditions (Fig. 6), for the high temperature treatment (40/35 °C) QC was minimal but the high VPD strengthened the driving force to increase E (Fig. 7). This figure shows that VPD was the dominant factor that controlled E in the controlled chamber. To further emphasize the role of VPD in the transpiration process, it is worth mentioning that transpiration also occurred during nighttime hours even without the irradiative energy source. Indeed, E decreased sharply when the dark period started but as mentioned above, it was not zero. Moreover, in spite of the low QC in the 40/35 °C treatment, the high E is also an indication that the major factor that affected E was the large VPD. The weak linkage between P_N and E that was displayed here is expected to magnify the differences between the treatments in terms of WUE.

The effect of temperature on WUE: In Table 3 the daily cumulative values for P_N and E were converted to appropriate units in order to calculate the mass (economical) and the mol (biophysical) basis of WUE. In the mass units system (Table 3) it can be seen that while E was reduced by about 30 % with reduced temperature, P_N increased by about 50 % and the corresponding WUE decreased from 14 g(CO_2) kg^{-1} per kg(H_2O) in the lowest temperature treatment to 5 g(CO_2) kg^{-1} per kg(H_2O) in the highest temperature treatment; a decrease of about 280 %. In terms of biophysical units, WUE of the 25/20 °C treatment was about 6 mmol(CO_2) mol^{-1}(H_2O) compared with 2 mmol(CO_2) mol^{-1}(H_2O) for the 40/35 °C treatment. The transpiration ratio was thus about 170 mol(H_2O) mol^{-1}(CO_2) while the plants in the 40/35 °C treatment required some 500 mol(H_2O) in order to produce one molecule of fixed CO_2.

Concluding remarks: Three main factors affected the P_N and E of maize in this experiment. One was the high temperature which reduced P_N. The second was VPD; it was directly related to E but did not affect P_N. Third was QC that was directly related to P_N but did not affect E. Thus, when QC was low during daylight hours for the high temperature treatments, P_N was low, while, due to high VPD under these conditions, E was high. As a result, WUE of the high temperature treatment was low. Contrarily, high QC during light hours and low temperatures did not affect E of the 25/20 °C treatment (non-stressed plants) but enhanced the P_N. As a result the WUE of the non-stressed plants was almost three times greater than that of 40/35 °C treatment. Our new findings on the relationship between P_N and E will be the basis for further studies on the response of the sweet corn to various humidity and [CO_2]. Also, our experimental data will be used to characterize the temperature response of crop models.

Table 3. Temperature effect on water use efficiency and its components. Temperature treatments day/night [ºC]. E0 − reference evapotranspiration estimated from FAO-56, Penman-Monteith model (Allen *et al*. 1998).

	Stage	25/20	25/20	25/20	25/20	LSD(0.05)
Mass (economic) basis calculations:						
CO_2 [g m^{-2} d^{-1}]	V3	66.0	48.4	39.6	30.8	30.0
	V10	61.6	61.6	44.0	35.2	
	R1	57.2	61.6	57.2	35.2	
	Average	*61.6*	*57.2*	*46.9*	*33.7*	
H_2O [kg m^{-2} d^{-1}]	V3	4.05	5.4	6.4	7.1	0.4
	V10	4.48	4.5	5.0	6.8	
	R1	4.52	4.6	5.1	5.8	
	Average	*4.4*	*4.8*	*5.5*	*6.6*	
E0		4.8	5.5	5.6	6.3	
WUE mass basis [g(H_2O) kg^{-1}(CO_2)]	V3	16.3	9.0	6.2	4.4	
	V10	13.8	13.7	8.8	5.2	
	R1	12.7	13.5	11.2	6.1	
	Average	*14.2*	*11.9*	*8.5*	*5.2*	
Transpiration coeff. [kg(H_2O) kg^{-1}(CO_2)]	V3	61.4	111.6	161.6	228.9	
	V10	72.7	73.1	113.6	193.2	
	R1	79.0	73.9	89.2	164.8	
	Average	*71.0*	*86.2*	*121.5*	*195.6*	
Mol (physicochemical) basis calculations:						
CO_2 [g m^{-2} d^{-1}]	V3	1.5	1.1	0.9	0.7	0.69
	V10	1.4	1.4	1.0	0.8	
	R1	1.3	1.4	1.3	0.8	
	Average	*1.4*	*1.3*	*1.1*	*0.8*	
H_2O [kg m^{-2} d^{-1}]	V3	225.0	300.0	355.6	391.7	22.0
	V10	248.9	250.0	277.8	377.8	
	R1	251.1	252.8	283.3	322.2	
	Average	*241.7*	*267.6*	*305.6*	*363.9*	
WUE mass basis	V3	0.0067	0.0037	0.0025	0.0018	
	V10	0.0056	0.0056	0.0036	0.0021	
	R1	0.0052	0.0055	0.0046	0.0025	
	Average	*0.0058*	*0.0049*	*0.0035*	*0.0021*	

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