IMPACT OF ATMOSPHERIC CO_2 ENRICHMENT ON SOME ELEMENTS OF MICROCLIMATE AND PHYSIOLOGY OF LOCALLY GROWN MAIZE

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Abstract. Higher atmospheric CO_2 concentration may influence positively plant production once the substrate for photosynthesis and gradient increase between the ambient air and mesophyll cells. Plants respond not only to change in surrounding CO_2 concentration, but to modifications of their micro-environment. Modelling approach was applied to investigate the relation of plants and some elements of microclimate to increased CO_2 levels. Other influences of global warming included in the study indirectly by running warmer and dryer sample days than the average measured locally during the past decades. Depending on growth in CO_2 concentration increases in inside canopy air temperatures were between 0.12 and 0.37°C. The warmer plants could have less effective transpiration cooling resulted from higher stomatal resistances. It decreased the water vapour pressure of the air inside the plant stand. In spite of partly stomatal closure, abundant carbon-dioxide concentration raised the intensity of photosynthesis. However if elevated CO_2 concentration takes place, the other additional influencing factors as warming, change in precipitation amount and its distribution, plant adaptation processes etc. may offset the production benefits of increasing level of CO_2. More detailed investigations are needed to complete our imaginations about future consequences of possible climate variations, mainly in local level.

Keywords: *global warming, simulation, microclimate, physiology of maize*

Introduction

Global atmospheric CO_2 concentration has been increasing since the beginning of the industrial revolution in the mid-18th century and is predicted to double at some time in the mid- or late 21st century [16], [22]. Humans emitted 6 gigatons of carbon per year into the atmosphere from fossil fuel burning and cement production during the 1990's, yet only about half of this carbon accumulated in the atmosphere. Of the remainder, about half was absorbed by the oceans and half by terrestrial ecosystems [13], [26].

Ecological responses to CO_2 enrichment and climate change are expressed at several interacting levels: photosynthesis and stomata movement at leaf level, energy and gas exchanges at the canopy level, photosynthate allocation at the plant level, and water budget and carbon cycling at the ecosystem level [6].

Increasing level of CO_2 concentration has effect through modification of stomata behaviour on photosynthesis, water use efficiency and crop yield, etc. Stomata movements may change in response to elevated CO_2. A doubling CO_2 concentration reduces the conductance at the leaf level by 30-40%, although large differences among species exist [25], [8], [30], [36], [28] and values as high as 50-70% decrease can be found in the literature [27] with similar response between C3 and C4 species [18], [8], [24], [28]. Two responses of crops to elevated CO_2 are an increase in the rate of photosynthesis and a decrease in stomatal conductance [36]. The increase in net photosynthesis in C3 species has been reported as high as 50-100% when CO_2 concentration doubles compared to 10% in C4 species [36].

The partitioning of net radiation on the leaves under elevated CO_2 concentration is modified due to decrease in stomatal conductance, which causes a decrease in transpiration leading to an increase in leaf temperature [20], [15], [28]. The temperature of the leaf surface may rise 0.5 - 1.7°C only due to doubling CO_2 concentration [11], [12], [21], [31] or even up to 3°C, depending on the specie and the weather [27]. Higher leaf temperatures may have important consequences on the longevity and photosynthetic capacity of the individual leaves and at the canopy level, as ageing may be accelerated and shortening the growing season [9], [21], [31].

[17], [18] and [19] estimated that a doubling CO_2 concentration, holding other factors constant, could lead to a 34±6% increase in agricultural yields of C3 plants and a 14±11% in C4 plats with a 95% confidence interval.

In the present study the simulation of the effects of increased carbon dioxide on some of the elements governed by stomatal movements were focused. For our researches, we applied the Crop Micrometeorological Simulation Model (CMSM) of [10] modified by [7], [1]. The inputs of the model were collected at Keszthely Agrometeorological Research Station to get information about locally grown maize response to increased CO_2 levels. The local tendency of other elements of global warming were included in the study by the selection of dry and hot sample days to model run.

Materials and methods

The model

The theory of the CMSM is the calculation of the radiation distribution among different environmental processes. The sensible heat flux (H_i) in the i^{th} layer is:

$$H_i = \rho c_p \left[T_{L,i} - T_{a,i}\right] / r_{H,i} \qquad \text{(Eq. 1)}$$

where ρ is the density of the air, c_p is the specific heat of the air on constant air pressure, $T_{L,i}$ is the temperature of the plant, $T_{a,i}$ is the air temperature, $r_{H,i}$ is the resistance against heat transmission.

The latent heat flux (λE_i) in the i^{th} layer can be calculated as follows:

$$\lambda E_i = \left(\rho c_p / \gamma\right)\left(e_{s,T_{L,i}} - e_{a,i}\right) / r_{V,i} \qquad \text{(Eq. 2)}$$

where γ is the psychometric constant, $e_{s,T_{L,i}}$ is the saturation water vapor pressure at actual plant temperature, $e_{a,i}$ vapor pressure of the air, $r_{V,i}$ is the resistance against the entrance of moisture into the layer.

Simulation of crop- and air temperatures and humidity of the air

After calculation of the sensible and latent heat, the estimation of the air temperature in the i^{th} layer ($T_{a,i}$) and vapor pressure ($e_{a,i}$) in the i^{th} layer were as follows [10]:

$$T_{a,i} = T_{a,i-1} + H_i R_i / \rho c_p \qquad \text{(Eq. 3)}$$

$$e_{a,i} = e_{a,i-1} + \lambda E_i * R_i / (\rho c_p / \gamma) \qquad \text{(Eq. 4)}$$

where R_i is a value characteristic to resistance in the ith layer. When i=1, $T_{a,i-1}$ and $e_{a,i-1}$ are the temperature and water vapour pressure from the separated standard meteorological measurement, respectively. The zero level (if i=1, i-1 is the level zero) is the place of the measurement of the meteorological elements.

The model estimates the crop temperature ($T_{L,i}$) in the ith layer according to the following equitation:

$$T_{L,i} = T_{a,i} + (H_i - H_{i-1}) * r_{H,i} / \rho c_p \qquad \text{(Eq. 5)}$$

Simulation of leaf resistance and photosynthesis

Basis of assumption of leaf resistance simulation is that mass transport processes – both water vapour and carbon dioxide – occur via stomata, so that the ratio between their resistances is equal to the ratio between their diffusivities. In case of maize a linear relationship exists between net CO_2 assimilation and inverse leaf resistance at constant CO_2 concentration of substomatal cavity. This connection served to simulate the leaf resistance, since net CO_2 assimilation can be deducted precisely from the absorbed short wave radiation [10]. Exceeding the saturation point of CO_2 assimilation (200 J m^{-2} s^{-1} for sunny maize leaves) the leaf resistance approaches its minimum value [29]. Rate of net CO_2 assimilation (F) was considered empirically by [32] as follows:

$$F = (F_m - F_d)[1/\exp(R_v \varepsilon / F_m)] + F_d \qquad \text{(Eq. 6)}$$

where Fm is the maximum rate of net assimilation, F_d is the dark respiration, R_v is the absorbed short wave radiation (per LAI), ε is the slope of the curve of F-R_v at low light intensities, or efficiency ($17.2 \cdot 10^{-9}$ kg J^{-1} light in maize).

At calculation of F_m the influence of leaf age and ambient CO_2 concentration were simplified and their average values were applied. Dependence of leaf temperature was considered as a dependence on ambient air temperature. Dark respiration was at about -0.1 of F_m [10]. To calculate maize leaf resistance Eqn. (6) can be written as:

$$F = \frac{1.83 \cdot 10^{-6}(C_e - C_r)}{1.66 r_{leaf} + 1.32 r_{b,h}} \rightarrow r_{leaf} = \frac{1.83 \cdot 10^{-6}(C_e - C_r)}{1.66F} - 0.795 \ [\text{s m}^{-1}] \qquad \text{(Eq. 7)}$$

where $r_{b,h}$ is the boundary layer resistance for heat, 1.66 is the ratio between diffusivities (for CO_2 and H_2O), $1.83 \cdot 10^{-6}$ converts CO_2 concentration into kg CO_2 m^{-2} at 20°C, Ce is the external CO_2 concentration, Cr is assumed as 'regulatory' CO_2 concentration, 1.32 originates from calculation of boundary layer resistance for CO_2.

The inputs of the model were site and plant specific parameters (plant height, leaf density in three layers), different soil characteristics (soil moisture content and physical properties) and hourly meteorological data from local measurements. From the outputs the crop- and air temperatures, the air humidity, the leaf resistance and photosynthesis were presented on the border of the upper third of plant height in the study. This is the place of cob formation, where the intensity of physiological processes is the highest.

The meteorological data were provided by the local (Keszthely) standard QLC-50 automatic weather station [5]. Regarding soil moisture, the monthly average for July of the past decade (-10 bar of soil water potential at Keszthely) included basically in the model. The plant characteristics (plant height, LAI and leaf density) were also measured at Keszthely during the last three decades. Our test plant was maize with short growing season having the largest growing area for maize in Hungary.

We chose a hot day of July for presentation of model-runs, because these characteristics represent the possible future weather tendency in our location as a result of global warming. The 'control' run for the present had 380 ppm ambient air CO_2 concentration. In addition we created three scenarios, which correspond well with the IPCC scenarios [13]. Scen. 1., 2. and 3. had 540, 760 and 970 ppmv CO_2 concentrations, respectively. The Scen. 2. presented the double of the present value.

Following the findings of [14], who confirmed the conservation of the ratio of intercellular and ambient air CO_2 concentrations, we kept the value of the intercellular gas concentration in one third of the ambient one [31].

The validation of the model outputs (crop temperature, stomatal resistance, elements of microclimate, photosynthesis) were carried out earlier by [2], [3], [4], [23]. Modification regarding meteorological input data processing was published earlier by [4].

Results

The elements of microclimate with crop temperature

The air temperature inside the canopy was influenced by the altered CO_2 levels (*Fig. 1*). In daily mean the scenarios produced 0.12 to 0.37°C (0.4-1.3%) rise in it, respect the control. In the evening hours there were milder or no variation in inside canopy air temperatures between the CO_2 treatments. During daylight higher variations were simulated for inside canopy air temperatures at elevated CO_2 levels. From sunrise to sunset, in the first scenario the air temperature increased by 0.22°C in average.

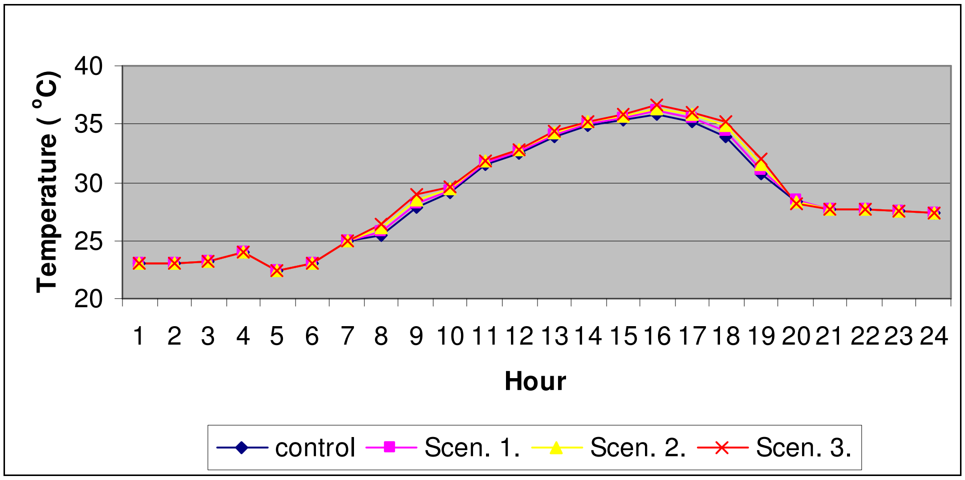

Figure 1. *Simulated inside canopy air temperatures of different CO_2 scenarios (CO_2 concentrations of the ambient air were control: 380 ppmv; Scenario 1: 540 ppmv; Scenario 2: 760 ppmv, doubled CO_2; Scenario 3: 970 ppmv)*

In case of doubled CO_2 level, the air temperature predicted by the model was 0.5°C higher in daytime hours than the control run. Using the third scenario, we established the air temperature growth in 0.74°C (2.4%) for the daytime hours. In this scenario the maximum deviation appeared at 18 o'clock (1.36°C).

According to model assumption the basis of calculation crop- and air temperatures was almost the same. Due to this similarity, there was no surprise finding in the same tendency of the two investigated temperatures (*Fig. 2*). At constant soil water level, the maize' crop temperature increased with rising atmospheric CO_2 concentration. The changes in crop temperatures were less pronounced than variation in air ones. The probably reason of it might have been the complexity of crop temperature, where the impact of moisture level was also important. The increases in daytime mean (8-19 o'clock) crop temperatures were about the half of the air one; 0.09, 0.24 and 0.39°C at 540, 760 and 970 ppmv CO_2 levels, respectively.

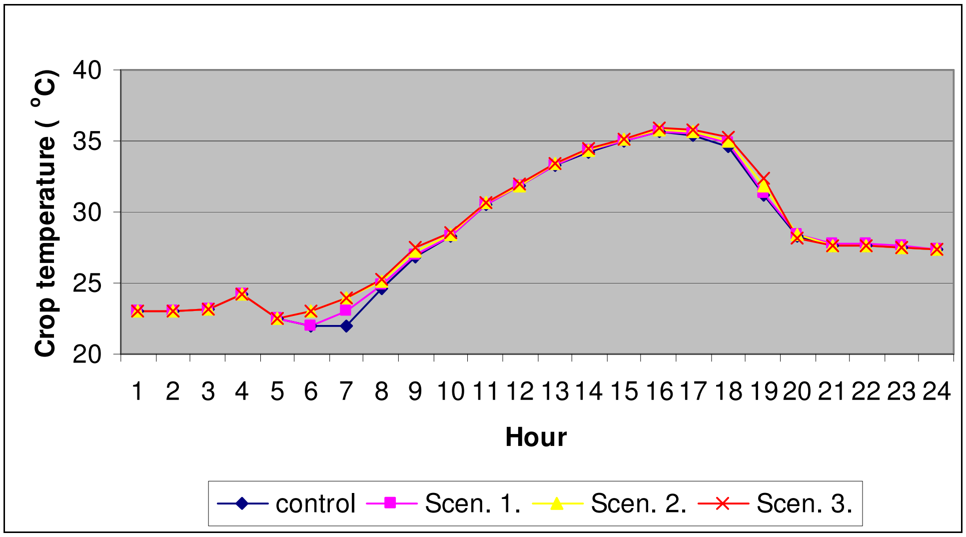

Figure 2. *Daily variation in simulated crop temperatures according to different CO_2 levels (CO_2 concentrations of the ambient air were control: 380 ppmv; Scenario 1: 540 ppmv;Scenario 2: 760 ppmv, doubled CO_2; Scenario 3: 970 ppmv)*

Beside the inside canopy air temperature we examined another microclimate parameter that is the water vapor pressure inside the plant stand. Transpiration is not only effected by the stomatal opening, but also by the driving force for exchange the water vapor from the leaf surface to the surrounding atmosphere. One of the parameters characterizing the air moisture content is the water vapor pressure of the air. Our simulated data were close to each other, and the water vapor pressure was decreasing by the increasing CO_2 level. We found that the more the CO_2 level was, the less the water vapor pressure in the canopy, comparing to control. In the first scenario (540 ppmv) the maize canopies' vapor pressure decreased by 0.9% (0.23 mbar) for daytime hours (8-19 o'clock), respect the present CO_2 conditions. In case of second scenario, the model predicted 2.88% (0.76 mbar) less vapor pressure at cob layer in daylight average. In the third scenario 4.14% (1.09 mbar) decrease was estimated in the mean from sunrise to sunset (*Fig. 3*). The largest differences arose close to sunset, at the time close to stomata closure. We do not know the reason of less humidity content of the second and third scenarios at 19 o'clock. This alteration was in accordance with stomatal movements of the above scenarios. As this difference appeared at 19 o'clock only, we did not want to rush to a false conclusion.

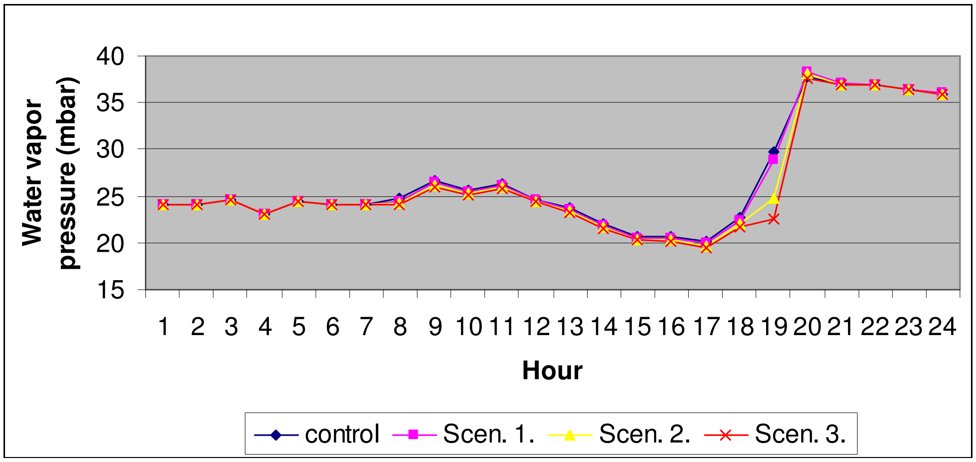

Figure 3. *Changes in simulated water vapour pressures in maize canopy (cob level) at increasing CO2 concentrations (CO2 concentrations of the ambient air were control: 380 ppmv; Scenario 1: 540 ppmv; Scenario 2: 760 ppmv, doubled CO2; Scenario 3: 970 ppmv)*

Probably the small negative differences between the different model runs for canopy's water vapour pressure can be associated with the slight increase in plant temperatures. Increase in crop temperature presumably associated with less source of cooling water, and the intensity of transpiration might have been also lower. Declined amount of water loss caused decreased vapour pressures inside the maize stand of extra amount CO_2.

Physiological processes in maize

Studies in physiological processes of plants need assumption change from canopy level to the level of plant or leaf [31]. Among the parameters that influence yield formation we examined the variations in leaf resistance and photosynthetic intensity.

There are two processes that CO_2 concentration must influence through modifying the stomatal resistance: the photosynthetic intensity and transpiration. Photosynthesis is the only way on the Earth to produce organic matter from inorganic elements using the energy of sunlight. The basic material of photosynthesis is the atmospheric carbon-dioxide content. This gas reaches the place of the biochemical processes through the stomata. For this reason stomatal resistance is a limiting factor for the penetration of CO_2 in the leaf, but also regulates the getting out of the water vapor, so the transpiration. To achieve the highest yield, the plant needs to balance the pore opening, where the entering of CO_2 is not limited for photosynthesis and the water loss is also moderate.

Variation in stomatal resistance

The effect of elevated CO_2 was the highest for stomatal resistances (*Fig. 4*). In the evening hours the stomata were closed in every treatment (not shown in the Fig.). Significant differences between the model runs appeared beside low radiation intensities.

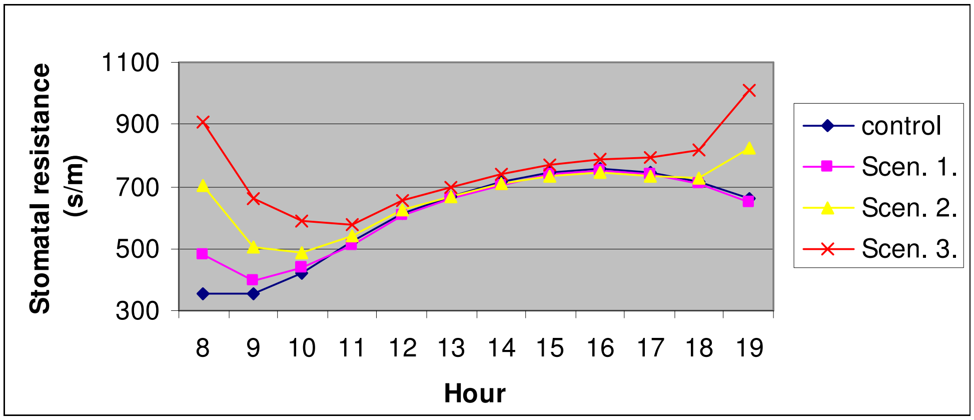

Figure 4. *Diurnal variation in simulated stomatal resistances in maize at different CO2 levels (CO2 concentrations of the ambient air were control: 380 ppmv; Scenario 1: 540 ppmv; Scenario 2: 760 ppmv, doubled CO2; Scenario 3: 970 ppmv)*

In case of Scen. 1., the stomatal resistance rose in the morning hours with 17.99%, but from 11 to 18 o'clock it was almost the same as the control. The daytime mean increase in stomatal resistance was 3.53% comparing to the control treatment. According to the second scenario (doubled level), the resistance showed a rise of 15.38% in daytime average (8-19 o'clock). Similarly to the previous run, there were significant differences in resistances between the periods of low radiation intensities. During high radiation (between 14 and 17 o'clock) the stomatal resistance was predicted to be almost the same as the control run. In case of the last CO_2 scenario, model predicted an increase of 32.72% in daytime average, but between 11 and 18 o'clock the rise was only 6.7%, respect the control.

The higher resistances at elevated CO_2 levels harmonized to warmer crop temperatures and declined transpiration that could result in lower vapour pressures inside the canopies.

Intensity of photosynthesis and respiration

Even if the rise of the stomatal resistance might limit the penetrating quantity of CO_2 in the leaf, the higher concentration of the gas caused a more intensive photosynthesis.

In case of the first scenario photosynthetic intensity grew by 25.43% on daytime average (8-19 o'clock), but this increase exceeded 30% between 13 and 15 o'clock. Doubling the present CO_2 level model run predicted 51.75% higher photosynthetic intensity for the daytime hours. Beside high sun radiation (10-17 o'clock) the increase exceeded 60% on average. Using the third scenario photosynthetic intensity raised by 70% in daytime mean, but between 11 and 16 o'clock this growth was higher than 90%, respect the control run (*Fig. 5*).

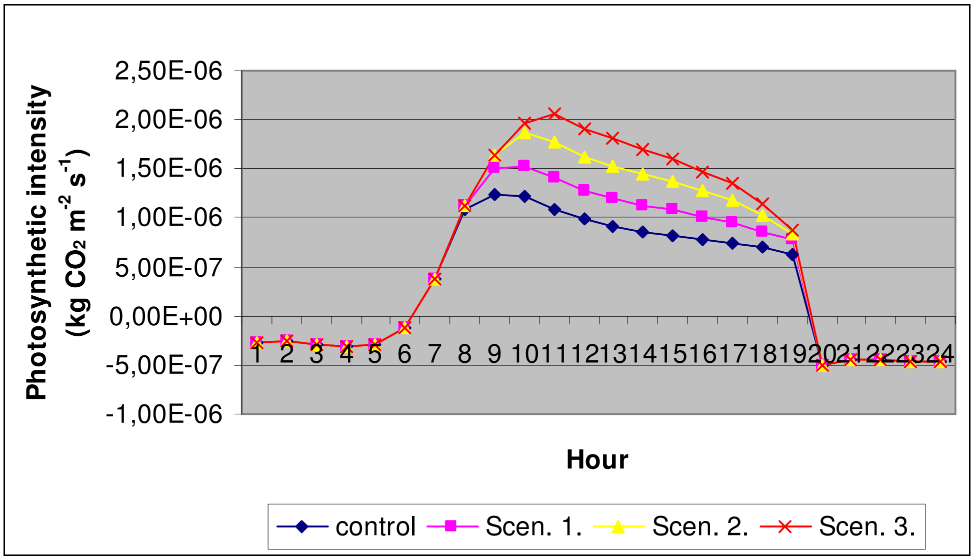

Figure 5. *Simulated photosynthetic intensity of maize at modified levels of* CO_2
(CO_2 *concentrations of the ambient air were control: 380 ppmv; Scenario 1: 540 ppmv; Scenario 2: 760 ppmv, doubled* CO_2*; Scenario 3: 970 ppmv)*

Elevating atmospheric carbon-dioxide concentration stimulated photosynthesis even if the stomatal resistance increased, so stomata were more closed.

In the night there was no significant difference in respiration of different CO_2 treatments.

Conclusions

Among the elements of global climate change the study was focused on the investigation of increased ambient air CO_2 level. This is the component of global warming that probably bound to happen in the near future. The other element, the air temperature rise was taken into account indirectly with choosing proper sample days for model run. As the variation in precipitation is the most uncertain element of future prognoses, input data of moderately dry periods included in the study. Increased level of CO_2 influenced all the analyzed elements of microclimate and physiological processes.

The inside canopy air- and crop temperatures became warmer at rising CO_2 levels. Although it is presently not known how different crops respond to the increase in leaf and canopy temperatures [31], they may have important consequences for the longevity and photosynthetic capacity of the leaves [21]. The relation between temperatures and ratio of biochemical processes is well known. Exceeding the optimum temperature range of given physiological process could lead to depression of its intensity.

Water vapour pressure inside the maize stand declined moderately. It may be associated with the increased stomatal resistances resulted from growth in ambient CO_2 concentration. Any change in air humidity interact transpiration by affecting the “driving force”, the vapour pressure deficit of the air. This modification may also hurt the components of energy balance of leaves, the ratio of sensible and latent heat fluxes. It is important to note, that air temperature rise alone due to global warming is able to stimulate the transpiration [31].

In spite of decreased pore openings due to higher CO_2 concentrations, the intensity of photosynthesis increased. The size of variation was much pronounced as it has been published earlier for C_4 plants [28]. Direct influences on some plant properties linked to CO_2 concentration variation discussed here must be taken into account as well. Other indirect influences of global warming related with shortage of available soil water, temperature rise may even dominate. Further studies are needed to collect more information about the interactions between plants and their environment in leaf- plant- and canopy levels as well.

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