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The potential of a confined closed greenhouse in terms of sustainable production, crop growth, yield and valuable plant compounds of tomatoes

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Summary

A confined closed greenhouse (CGH) was applied to save energy and to investigate how tomatoes respond to specific microclimatic conditions. As such, new dynamic set-points for precise climate control were used in the CGH compared to those applied in a conventional greenhouse. Based on the reduced ventilation frequency in the CGH, the results showed that higher levels of mean temperature, CO_2 concentration and relative humidity were achieved. Although the light interception was increased in the CGH, these changing microclimatic conditions resulted in higher rates of photosynthesis and an associated faster crop growth. This means that the mean plant height was increased by 1.5 m, which was the decisive factor to increase the total yield by 21.4 % in relation to that produced in the conventional greenhouse. The new microclimatic environment caused by the CGH promoted the accumulation of primary and secondary plant compounds in tomatoes such as soluble solids (by 9 %), lycopene (by 22 %), ß-carotene (by 21 %), phenolics (by 8 %) and L-ascorbic acid (by 26 %) compared to conventional produced tomatoes. Compared to existing greenhouse systems, the results suggested that a CGH can be used to produce tomatoes in a sustainable way, where the water use and the energy use efficiency can be improved by 71 % and 43 %, respectively.

Introduction

Generally, greenhouses have been developed to protect crops from phytosanitary problems and to extend the harvest season in order to provide the growing population with food (UNFPA, 2011). Additionally, these technical systems should also be used to produce food with a high quality standard, because the demand for improved quality of fruit and vegetable is increasing among consumers. One of the reasons for this amplified health awareness in society is the apparent relationship between the intake of horticultural products and numerous health benefits for consumers. These positive effects are attributed to different secondary plant compounds with antioxidant properties especially phenolic compounds, L-ascorbic acid and carotenoids, which can detoxify reactive oxygen species in the human body (Bazzano et al., 2002). This process is believed to be responsible for the suppression of the occurrence of chronic diseases, e.g., human prostate cancer and gastric cancer (Carr and Frei, 1999; Kotake-Nara et al., 2001). However, these high customer and market demands are overshadowed by the future production conditions in greenhouses. Among other things, the production processes in terms of fruit and vegetables require high amounts of energy for heating and freshwater for irrigation, where these traded goods are the most cost-intensive resources in greenhouse production due to the increase in fossil fuel and freshwater prices (Ozkan et al., 2007; Rout et al., 2008). This pricing policy is mainly based on the worldwide shortage of fossil fuels and freshwater resources (Vörösmarty et al., 2000; Shafiee and Topal, 2009).

Based on these facts, scientists invested much effort into the development of agronomic approaches for using renewable energies and new irrigation strategies, in order to reduce the consumption of fossil fuels and freshwater for greenhouse production. Amongst others, the solar energy is becoming used more and more for process energy in greenhouses, which can be collected in closed and semi-closed greenhouses using cold water from soil layers or rain water tanks, respectively (De Gelder et al., 2012; Dannehl et al., 2013b). After absorbing the excess heat using cooling fin heat exchangers installed under the roof in these greenhouses, the heat energy is stored in the aquifer or in rain water tanks used as short-term energy storage systems and can be reused in cooler periods by means of a heat pump (Bot, 2001; Dannehl et al., 2013b). This process results in decreasing levels of temperature and is accompanied by the dehumidification in greenhouses caused by condensation on the cooling fins (Campen and Bot, 2002). Although the energy use efficiency (EUE) and the water use efficiency (WUE) can be improved using these new technologies, high amounts of energy is needed for the heat pump to collect the sensible heat and latent energy in greenhouses (Dannehl et al., 2013b; Dannehl et al., 2014). This applies in particular to cooling processes if the heat stored in the short-term storage tank exceeds a temperature of 35 °C in the summer period.

In consideration of the cultivation period of tomatoes, it may be more effective to apply a combination of closed and semi-closed greenhouse systems including a heat pump in late winter, spring, late summer and autumn until the short-term storage tank is charged with heat. Thereby, it is assumed that the greenhouse can be cooled and the required energy for the basic load for heating up the greenhouse can be covered during the year. During summer, however, a fog system combined with a semi-closed operation mode named descending fog system (DescFog), which is operating without a heat pump, should be used for cooling processes (Dannehl et al., 2012). This combination of operation modes was applied in the present study and is referred to as confined closed greenhouse (CGH). Due to the new set-point strategies for cooling, heating, ventilation opening and CO_2-enrichment in the CGH, the microclimatic conditions can change in this system. In particular, it is expected that the average levels of temperature, relative humidity (RH) and CO_2-concentration will be increased as compared to a conventionally operating greenhouse. Furthermore, Dannehl et al. (2013b) found a light reduction by 11 % in the closed greenhouse, which was induced by the construction parts such as cooling fins under the roof. These mentioned conditions may cause stress in plants. It is well known that high temperatures and a reduced supply of RH, solar radiation or of CO_2 levels could have adverse effects on tomato plants, e.g., on photosynthesis, transpiration, fruit yield and secondary plant compounds with antioxidant properties (Dumas et al., 2003; Camejo et al., 2005; Van Der Ploeg and Heuvelink, 2005; Patane, 2011; Kläring and Krumbein, 2013). However, there is little information available regarding changes in plant growth, yield and secondary metabolites of tomatoes depending on a combination of higher temperatures, relative humidity and CO_2 concentrations during the cultivation period of tomatoes. Thus, this study focussed on the effects of changing microclimatic conditions in a CGH on photosynthesis, transpiration, vegetative plant growth, fruit yield, carotenoids, phenolic compounds and L-ascorbic acid of tomatoes. Furthermore, a

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sensory analysis regarding the internal fruit quality was conducted to test the influenced by the CGH on quality parameters such as juiciness, fruitiness and sweetness. Moreover, the effect of the CGH on the water consumption (WC), WUE and EUE was investigated, in order to estimate if plants can be produced in a sustainable way with such a greenhouse facility.

Materials and methods

Experimental set-up

The experiments were conducted in two different N-S oriented Venlo-type glasshouses at the Humboldt-Universität zu Berlin. One greenhouse, operated by a conventional microclimatic control strategy as used in practice (RGH) was compared with a CGH controlled system. Tab. 1 shows the structural differences between both greenhouses, which were described in more detail by Dannehl et al. (2013b). In both greenhouses the energy screens were closed at a global radiation of less than 3 W m^{-2}, in order to save energy. In the RGH, the floor level heating was set at 17 °C for day and night and the ventilation was opened above 23 °C to reduce the temperature inside the greenhouse. These processes were controlled using the application of proportional integral differences. The same control mechanisms were used in the CGH including new dynamic set-point strategies for cooling, heating, ventilation and CO_2 enrichment in comparison with the RGH. In this context, finned tube heat exchangers fixed under the roof of the CGH were coupled with an electrically operated heat pump and a rain water tank (300 m^3) used as short-term energy storage. This system was applied to collect high amounts of sensible heat energy and latent energy while cold water (5 °C) was flowing through the finned tube heat exchangers. The mentioned energy components were generated by the incoming solar energy and plant transpiration, as well as evaporation processes, respectively. This type of energy harvesting was used, in order to reuse the stored energy if necessary and for cooling processes in the CGH.

Tab. 1: Greenhouse characteristics as a function of the confined closed greenhouse (CGH) and the reference greenhouse (RGH)

Greenhouse construction	RGH	CGH
Gross acreage [m^2]	307	307
Greenhouse height [m]	6.7	6.7
Glazing roof	Single glass panes (4 mm)	Single glass panes (4 mm)
Glazing side walls	Double glass panes (16 mm)	Double glass panes (16 mm)
Energy screens (roof)	1	2
Energy screens (side walls)	No	1
Finned tube heat exchangers	No	16 (each 21.4 m)
Reversible heat pump	No	1 (120 kW HP[†]; 100 kW CP[††])
High pressure fog system	No	28 fog nozzles (150 bar)
Floor level heating	Yes	Yes
Tubular film blowers	No	Yes
Vegetation heating	No	Yes

HP[†] and CP[††] means heating power and cooling power, respectively.

In the present study, the closed and semi-closed operation phases in the CGH alternated several times during the cultivation of tomato plants as shown in Fig. 1. The closed and semi-closed operation phases from February to May and from mid-August to November were mainly used to charge the rain water tank with energy. As such, the water from this tank was used either direct without the heat pump (> 5 °C to 10 °C) or indirect with the heat pump (> 10 °C to 40 °C) for cooling processes in the CGH, which were started at an air temperature of 22 °C. While the ventilation was completely closed during the application period of the closed greenhouse, emergency ventilation above 27 °C was permitted during the semi-closed operation mode in spring and late summer, in order to avoid plant damage. As described earlier, the use of a heat pump requires high amounts of energy for cooling processes during summer. Therefore, an evaporative cooling system was applied in the CGH without using a heat pump from June to mid-August (Fig. 1). In this context, a high pressure fog system was installed above the plants to ensure a uniform distribution of the small droplets (10 µm) in the crop. In order to realize droplet evaporation and associated cooling processes, a coupled control for fog and ventilation was conducted using a microcontroller, which was connected between 23 °C and 27 °C measured in the plant population. To remove the energy rich water vapour from the roof region, the ventilation was opened with short time pulses and a minimum aperture (max. 10 %) at a RH of 80 % measured in the roof region. The fog system was interrupted at a RH of 80 % determined within the crop, in order to protect plants from diseases.

However, the warm water stored in the rain water tank was reused either for direct heating (40 °C to > 35 °C) or for indirect heating

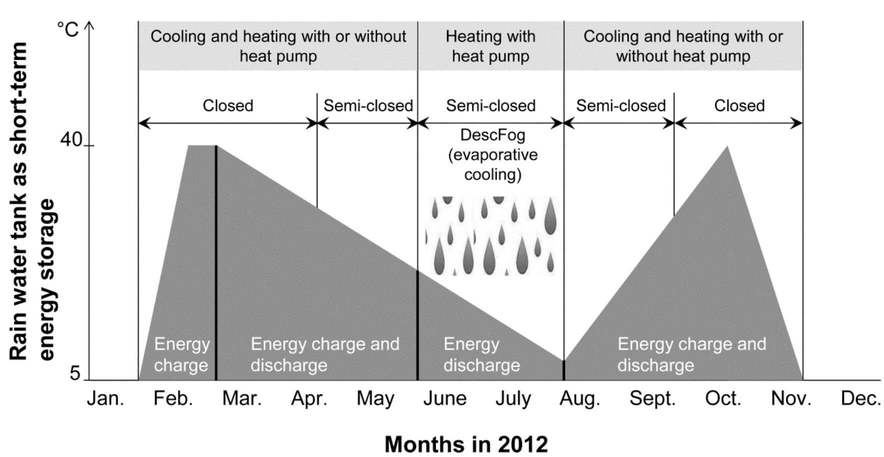

Fig. 1: Schematic diagram for closed and semi-closed operation phases in the confined closed greenhouse system and associated energy charge and discharge processes occurring in the short-term energy storage tank.

(35 °C to 8 °C) *via* a combination of the heat pump and heat exchangers mounted in the CGH, i.e., using tubular film blowers fixed under the nutrient solution gullies and a vegetation heating system installed in the plant population with a target temperature of 17 °C (day and night). This heating procedure in the CGH is accompanied by the discharge of the rain water tank (Fig. 1). When the stored energy was entirely used up, the energy supply for heating processes in the CGH was realized using a floor level heating system containing district heat as used in the RGH.
The CO_2 enrichment was applied in both greenhouses, which was kept at a level of 800 ppm during daylight hours. In this context, the CO_2 supply was stopped when the ventilation exceeded an opening of 10 %. To maintain the sought microclimatic conditions in the RGH and CGH, all the aforementioned set points for cooling, heating, ventilation, RH and CO_2 enrichment were controlled by data obtained from different sensors. The measurements were forwarded to a central control computer, where these were recorded every 30 seconds.

Cultivation of tomato plants and assessment of crop growth and yield

A closed hydroponic system with a recirculating nutrient solution was used to produce tomato plants (*Solanum lycopersicum* L. cv. Komeett) on a net-acreage of 260 m^{-2} per greenhouse. These were grown on high gullies in rock-wool slabs and watered using drip irrigation, which was started mainly after a light summation of 560 W m^{-2} for 150 seconds. To obtain a water overflow of 40 % after each irrigation cycle, the light summation for controlling the irrigation was regularly adjusted in each greenhouse. The nutrient solution was prepared by mixing fresh water and stock solution according to the mixture recipe of Göhler and Molitor (2002). Each greenhouse was equipped with twelve gullies, which were arranged in five double rows and two single rows with a length of 20 m. Each gully contained 40 plants grown at a distance of 0.5 m from each other.
The plants were transferred to the rock-wool slabs on 24th January 2012, when four leaves were formed. To calculate the leaf area index (LAI) in the sixth, seventh and eighth week after planting, a total of 20 plants per greenhouse was used to measure the leaf length and width of each leaf with a folding ruler. The measurements were inserted in an exponential function developed by Dannehl et al. (2013a) to estimate the leaf area of each individual leaf. The calculated area of these leaves was summed per plant, where the average leaf area regarding the evaluated plants was extrapolated to the entire plant population. This leaf area was divided by the net-acreage to obtain the LAI, which is expressed as m^2 m^{-2}. At the end of the experiments on 6th November 2012, the plant height of the same plants was measured after the stem of the plant was cut directly above the rock-wool slabs. Furthermore, the tomatoes were harvested and weighed weekly, as well as summed up to compare the total yield and the fruit mass per fruit in terms of both greenhouse facilities at the end of the investigations. The plant height, the fruit mass and the yield are expressed as m, g and kg m^{-2}, respectively.

Determination of photosynthesis, transpiration, EUE, WC and WUE

Ten leaf cuvettes of a leaf cuvette based gas exchanged system were arranged at the same heights in the canopy of both greenhouses to measure the photosynthesis (BERMONIS, Steinbeis GmbH & Co. KG for Technology Transfer; Berlin, Germany). To ensure the same measurements points in both greenhouses, the cuvettes were transferred weekly to the first fully developed leaf of different plants. The cuvettes consist of polyethylene which is transparent for the radiation frequency from 300 nm to > 3000 nm, where the boundary layer conditions inside the cuvettes are identical compared to those of a non-influenced leaf. The photosynthesis was measured every 30 seconds as mean CO_2-gas exchange ($GECO_2$) during the harvest period. As such, the flow rate of the air (Q), the CO_2 level difference between ambient air and the air in the cuvettes ($DiffCO_2$), the atmospheric pressure (p), the chamber area (ChA), the air temperature (T) and a constant (29.93), derived from the molar mass and the specific gas constant of CO_2, were used to calculate $GECO_2$ (Equation 1). $GECO_2$ was calculated as follows:

$$GECO_2 = \frac{Q \times DiffCO_2 \times p}{29.93 \times ChA \times T_{AIR}} \tag{1}$$

The mean value of $GECO_2$ was generated daily in terms of the daylight hours; these values are expressed as µmol CO_2 m^{-2} s^{-1}. Furthermore, the plant transpiration was measured with the same device using the same measuring principle and calculated according to Schmidt (1988). The flow rate of the air, the absolute humidity difference between the ambient air and that in the cuvettes (DiffAH), as well as the ChA was used in Equation 2 to compute the transpiration as follows:

$$Transpiration = \frac{Q \times DiffAH}{ChA} \tag{2}$$

The mean values of the transpiration were generated daily and expressed as mg H_2O m^{-2} s^{-1}.
The EUE is defined as the amount of energy required to produce one kg of tomatoes (MJ kg^{-1}) and was evaluated on three dates of the last three weeks of the experiments. To calculate the EUE for the CGH, the energy consumed (EC) for the circulation pumps (CP), for heat pump processes (HP) and for district heat (DH), the primary energy factor for electrical energy (PFEE) and for district heat energy (PFDH), the reuse of the stored energy (EE) and the total yield were considered as shown in Equation 3:

$$EUE = \frac{(EC_{DH} \times PFDH) + (\mathrm{EC_{CP+HP}} \times \mathrm{PFEE}) - (\mathrm{EE})}{Total\ yield} \tag{3}$$

The EUE calculated for the RGH was determined in the same manner as described in Equation 3, however, excluding the variables EC_{CP+HP}, PFEE and EE.
On three dates of the last three weeks of the investigations, the total water consumption (WC) consumed by the crop in each greenhouse during the cultivation period was calculated. This analysis included evapotranspiration losses and was determined using the difference between the amount of the recorded irrigation and that of the nutrient solution drained from the cultivation gullies. Based on these results, the WUE was calculated as a ratio between the total yield (kg m^{-2}) and WC (m^3 m^{-2}) and is expressed as kg fresh matter per m^{-3}.

Chemical analyses and sensory investigations of tomatoes

Three replicates containing 30 tomatoes were randomly harvested from different plants per greenhouse at the ripening stage 9. This procedure was repeated five times in five consecutive weeks from June to July to compare the average of five dates of three biological replicates. For the analyses, each sample collection per greenhouse was homogenised (KenwoodHB856, De'Longhi Deutschlang GmbH; Neu-Isenburg, Germany). The homogenised fresh material of each replication was used for the determination of the contents of fruit dry matter, secondary plant compounds, titratable acids (TA) and soluble solids (SSC) performed in duplicate.
Fresh mass and dry mass from all fruit samples were measured before and after drying in a ventilated oven for one day at 105 °C, respectively. The fruit dry matter content was calculated by the ratio of the dry mass to the fresh mass and is expressed as g kg^{-1}.

The L-ascorbic acid content (LAA) was determined using the enzymatic test kit (L-Ascorbate, Megazyme International Ireland; Bray, Ireland). Briefly, the tetrazolium salt MTT [3-(4,5-dimethylthiazolyl-2)-2,5-diphenyltetrazolium bromide] was reduced by LAA to a formazan compound (MTT-formazan) under the presence of phenazinium methylsulfate. MTT-formazan was detected spectrophotometrically at a wavelength of 578 nm. Other reducing substances were measured in the same way after removing LAA using ascorbic acid oxidase. The differences between both absorbance values were used to calculate the LAA content, which is expressed as g kg^{-1} fresh weight (FW).

Lycopene, ß-carotene and total phenolic contents were determined by spectrophotometry (Model 690, Gamma Analysen Technik GmbH; Bremerhafen-Lehe, Germany). Briefly, lycopene and ß-carotene contents in tomatoes were extracted using the method outlined by FISH et al. (2002), where this method was modified by DANNEHL et al. (2011). The hexane extracts of lycopene and ß-carotene were measured at wavelengths of 505 nm and 453 nm, respectively. Subsequently, the contents of carotenoids were calculated according to NAGATA and YAMASHITA (1992) and are expressed as g kg^{-1} FW.

The phenolics were extracted as described by CONNOR et al. (2002). For the analysis of the extracts, the Folin-Ciocâlteu method according to SLINKARD and SINGLETON (1977) was used. In this context, the modified procedure of this analysis was described exactly by DANNEHL et al. (2011). The results are expressed as g gallic acid per kg FW (g GAE kg^{-1} FW).

The TA content in tomatoes was determined by potentiometric titration with 0.05 mol L^{-1} NaOH by pH endpoint at 8.1 according to ASU-L-26.11.03-4 (1983). These analyses were performed using a pH meter (pH526, WTW; Weilheim, Germany) including a glass electrode (SenTix 41, WTW; Weilheim, Germany). The SSC was assayed using a digital refractometer (PR101, ATAGO; Karlsruhe, Germany), which detects reducing sugars and other soluble solids. The results of the analysis of TA and SSC were converted to one kg FW basis and are expressed as gram citric acid and gram SSC per kg FW, respectively.

On the last date of the chemical analyses in July, a whole batch of tomatoes at the ripening stage 9 was used for a sensory investigation, in order to assess the quality of tomatoes from the perspective of consumers. In this consumer acceptance test, 100 passers-by of different origin evaluated tomatoes from the RGH and CGH regarding flavour and mouthfeel attributes, such as fruity, watery, grassy, mealy, juicy, bitter, sour, sweet, tomato-like, and peel firmness. Additionally, the total quality, which includes all sensory attributes, was also assessed by the consumers. The intensity of all sensory impressions of the tomatoes was evaluated using an unstructured scale with the defined points 0 (low intensity) and 10 (high intensity). In this context, the consumers were trained over a period of 15 minutes to understand the meaning of the attributes and had to rinse their taste organ with water for neutralization. In all sensory tests, the tomatoes of each greenhouse were quartered before serving to the assessors on coded plates, where the consumers received as much tomato pieces as needed to evaluate them. These tests were performed at room temperature, 50 % RH and under artificial light conditions.

Statistical analysis

The effects of changing microclimatic conditions caused by the RGH and CGH on crop growth, tomato yield, plant physiological responses, as well as on the water and energy balance were evaluated using SPSS package version 19.0. All comparisons were calculated using t-test procedure, where asterisks indicate a significant increase at a significance level $*\alpha = 0.05$ and $**\alpha = 0.01$. Considering the harvest period, the results represent average values of 29 evaluation dates (n = 29) in terms of microclimatic conditions, transpiration rates, photosynthesis rates and fruit mass, except for the determination of LAI, WC, WUE and EUE (n = 3), as well as for chemical analyses of primary and secondary metabolites (n = 15). To compare both greenhouse systems regarding the plant height and the total yield at the end of the experiments, twenty plants and 400 plants were used, respectively. Before the flavour and mouthfeel attributes of tomatoes produced in the RGH and in the CGH were compared, a triangle test with one different and two alike tomato pieces was applied to consumers (n = 100). Since a data analysis using the chi-square test showed that the number of correct perceptions of consumers was significant ($\alpha = 0.01$), the t-test was used to compare sensory impressions of the consumers.

Results

Microclimatic conditions

In consideration of selected days, the comparisons of microclimatic conditions between the RGH and CGH are displayed in Fig. 2. At outside temperatures between 16.6 °C and 20.9 °C during the days of March, the ventilation in the RGH was opened of up to 54 %, whereas the ventilation in the CGH was completely closed due to the closed operation mode on these days. Based on this fact, the temperature in the RGH was maintained at 24 °C and that in the CGH at approximately 27 °C. Furthermore, the mentioned ventilation conditions led to higher levels of CO_2 and RH in the CGH, where maximum differences by up to 500 ppm and 22 % were observed, respectively, when compared to the RGH. However, the microclimatic conditions in both greenhouses changed depending on the warmer season in May but also due to the applied semi-closed operation mode in the CGH, which was operating with the heat pump to realize cooling processes. Based on the defined set-points regarding the ventilation opening in each greenhouse, the ventilation in the CGH was kept closed for a longer period than that in the RGH (Fig. 2). Two consequences of this were that the RH was more than 20 % higher and the CO_2 concentration was increased by up to 200 ppm in the CGH compared to the RGH, where this maximum CO_2 difference was only one third of the difference reached in the closed operation mode. Compared to the RGH, the higher levels of CO_2 in the CGH were accompanied by lower temperatures by up to 2.5 °C during the day. This effect was particularly based on the cooling process caused by the fined tube heat exchangers. Furthermore, the semi-closed operating DescFog system used for evaporative cooling in the CGH caused a lower ventilation frequency compared to that in the RGH during the summer period (Fig. 2). This ventilation behaviour provoked higher levels of CO_2 and RH in the CGH, which were maintained at 450 ppm and 85 %, respectively. However, the CO_2 concentration and the RH in the RGH were greatly limited to 250 ppm and 60 % at temperature peaks between 30 °C and 33 °C measured outside during the days in July. At the same days, the temperature inside the CGH could be lowered in the range between 2.5 °C and 4.4 °C compared to the outside conditions, whereas the temperature profile within the RGH was almost equal to that recorded outside. In contrast, the temperature values in the CGH were approximately 2 °C higher compared to those obtained in the RGH during the morning and evening hours due to the DescFog system and an associated ventilating at the earliest at 25 °C. The same applies to the closed operation mode used in late winter, spring and autumn, which was most pronounced with a maximum temperature difference of 2.8 °C around noon (Fig. 2). Considering these temperature differences between both greenhouses during the tomato cultivation, the average temperature in the CGH was significantly increased by 0.5 °C compared to the RGH (Tab. 2). The average value of the RH was not significantly affected. However, the mean CO_2 concentration in the RGH was significantly reduced by 132 ppm versus the CGH (Tab. 2), where this result was caused by the higher levels of ventilation in the RGH.

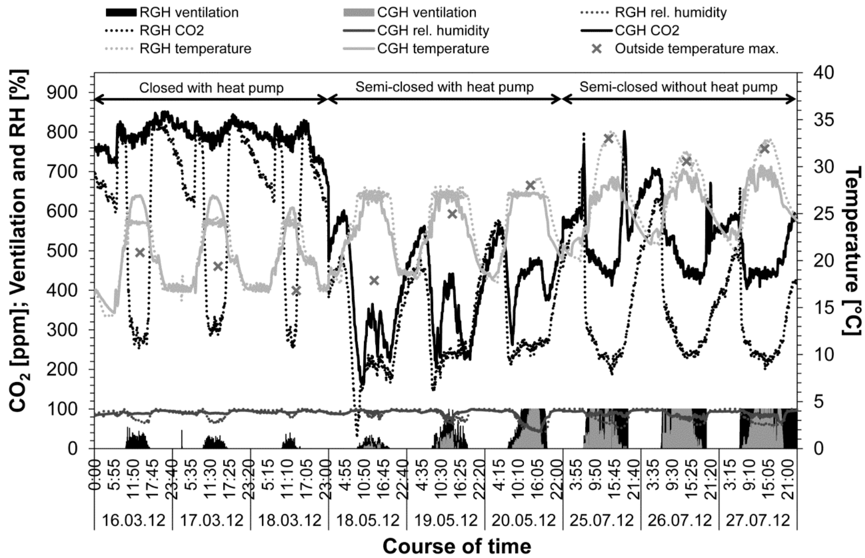

Fig. 2: Comparisons of microclimatic conditions and the ventilation behaviour between the reference greenhouse (RGH) and the confined closed greenhouse (CGH) in consideration of selected days during winter, spring and summer.

Tab. 2: Microclimatic conditions and plant responses of tomato plants caused by different climate control strategies

Characteristic	RGH	CGH	Significance
Relative humidity [%]	91.77	93.48	
Temperature [°C]	21.60	22.11	*
CO_2 [ppm]	525.72	657.87	*
Transpiration [mg H_2O m^{-2} s^{-1}]	21.54	14.07	*
Photosynthesis [μmol CO_2 m^{-2} s^{-1}]	4.39	5.31	*
Number of fruit [fruit m^{-2}]	188.59	242.15	*
Fruit mass [g]	107.27	116.05	*
Fruit dry matter content [g kg^{-1}]	60.00	60.00	
WC [m^3 m^{-2}]	0.81	0.57	*
WUE [kg fresh matter m^{-3}]	29.11	49.91	*
EUE [MJ kg^{-1}]	57.27	39.49	*

The table represents average values as a result during the harvest period (n = 29), except for WC, WUE and EUE (n = 3), as well as fruit dry matter content (n = 15). Asterisks indicate significant differences according to the t-test procedure at a significance level $p < 0.05$.

Photosynthesis and transpiration

Fig. 3 represents the daily mean photosynthesis and transpiration depending on different greenhouse systems during the harvest period. The photosynthesis was almost continuously higher in the CGH compared to the RGH, even though the solar radiation was reduced in the CGH described earlier. The effects of the weaker light quantity on photosynthesis were only noticeable in late April, where the photosynthesis caused by the closed operation mode in the CGH was markedly reduced by up to 100 % compared to the RGH. In contrast, the semi-closed operation mode including heat pump applied from calendar week 18 to 22 and from 34 to 39 resulted in a higher photosynthetic activity versus RGH (Fig. 3). These increased levels of photosynthesis varied between 32 % and 147 %. Similar differences in rates of photosynthesis were found owing to the application of the semi-closed operating DescFog system in the CGH from calendar week 23 to 33, however, to a smaller extent as shown before. As such, tomato plants grown in the CGH showed a maximum increase in photosynthesis by 65 % compared to those produced in the RGH. During the last two weeks of the experiments, no differences in photosynthesis were detected when the RGH and the closed operating CGH were compared. The latter outcomes are comparable to those found as results of transpiration measurements during the last two weeks of the investigations (Fig. 3). During the remaining harvest period, however, all applied operation modes in the CGH affected the plant transpiration in the same manner as shown in Fig. 3 (stacked bars). This means that the rates of plant transpiration were reduced by up to 58 % by the influence of the CGH when compared with the RGH. In consideration of the entire harvest period and compared to the RGH, the average value of the photosynthesis and that of the plant transpiration achieved in the CGH was significantly increased by 21 %, as well as significantly reduced by 35 %, respectively (Tab. 2).

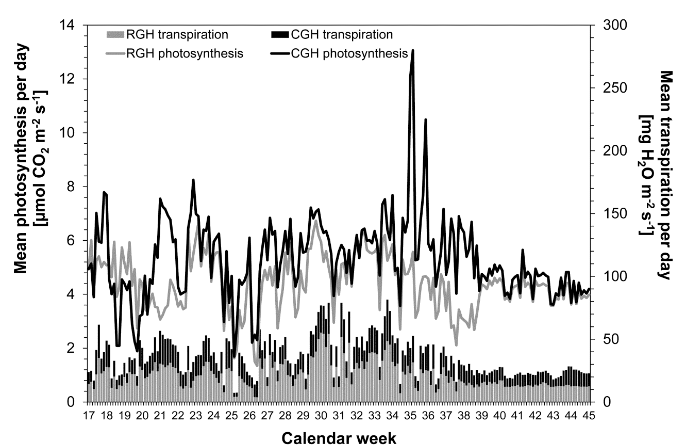

Fig. 3: The mean daily photosynthesis ($GECO_2$) and plant transpiration caused by the reference greenhouse (RGH) and the confined closed greenhouse (CGH) during harvest time.

Crop growth, WC, WUE and EUE

The influences of the RGH and the CGH on LAI, plant height and total yield are shown in Fig. 4. Eight weeks after planting, the prevailing microclimatic conditions in the CGH resulted in a significant increase in LAI (2.1 $m^2 m^{-2}$) compared to that measured in the RGH (1.8 $m^2 m^{-2}$). At the end of the experiment, the average plant height of plants grown in the CGH was significantly increased by 1.56 m when compared with the RGH. This result suggested that plants produced in the CGH grew faster, whereby 28.4 % more fruit per m^{-2} were formed (Tab. 2). Compared to the average fruit mass of 107.27 g attained in the RGH, the fruit mass of tomatoes matured in the CGH was significantly increased to 116.05 g, whereas the fruit dry matter content was not affected (Tab. 2). Based on these plant responses, the total yield caused by the CGH was significantly increased by 21.4 % in relation to the total yield produced in the RGH (Fig. 4). Furthermore, the microclimatic conditions in the CGH led to a significant reduction in WC by 30 % compared to that, which was consumed by plants grown in the RGH. Due to the higher WC and the lower total yield in the RGH, the WUE calculated for the CGH was significantly improved from 29.11 kg m^{-3} to 49.91 kg m^{-3} (Tab. 2). It was also demonstrated that the EUE achieved in the CGH was significantly improved by approximately 43 % compared to the RGH as consequences of the reuse of the stored energy in the rain water tank and the higher total yield (Tab. 2).

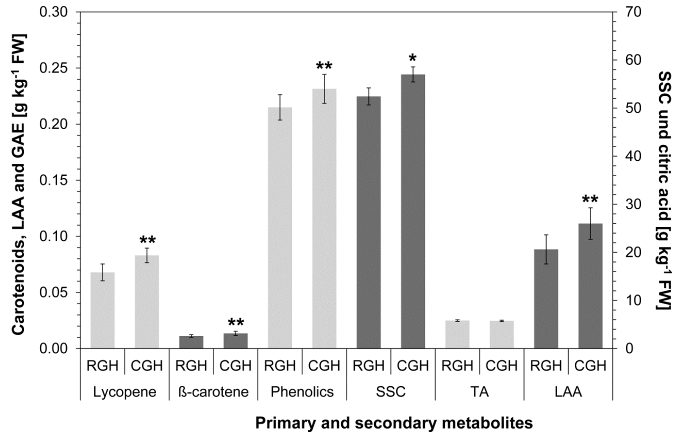

Fig. 5: Reference greenhouse (RGH) and confined closed greenhouse (CGH) mediated changes in contents of primary and secondary metabolites in tomatoes. Bars mean standard deviations and asterisks significant differences according to the t-test procedure at a significance level $*\alpha = 0.05$ and $**\alpha = 0.01$. The contents represent average values of five harvest dates of three biological replicates (n = 15).

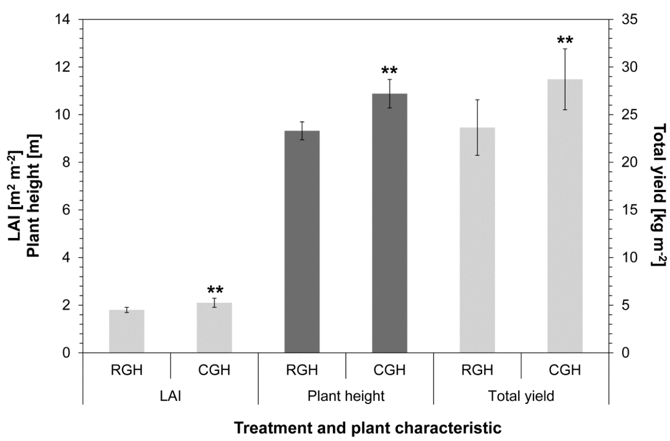

Fig. 4: Crop growth and total yield of tomato plants grown in the reference greenhouse (RGH) and in the confined closed greenhouse (CGH). All displayed comparisons were calculated using t-test procedure, where asterisks indicate a significant increase at a significance level $*\alpha = 0.05$ and $**\alpha = 0.01$ and bars standard deviations. The data represent average values of three replications, except for plant height (n = 2) and total yield (n = 2).

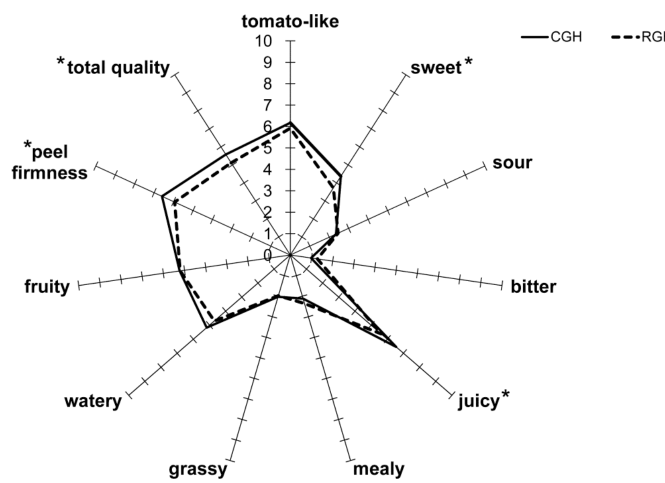

Fig. 6: Sensory investigation regarding flavour and mouthfeel attributes of tomatoes grown in the reference greenhouse (RGH) and in the confined closed greenhouse (CGH). All attributes were tested using t-test and represent the mean values of sensory impressions of 100 passers-by, where asterisks indicate a significant increase at a significance level $\alpha = 0.05$. The intensity of all sensory impressions is defined as 0 (low intensity) and 10 (high intensity).

Fruit quality and sensory investigations

It was found that the investigated primary and secondary metabolites containing in tomatoes were positively affected by the CGH. This means that the contents of SSC, lycopene, ß-carotene, phenolic compounds and LAA in tomatoes ripened in the CGH were significantly increased by 9 %, 22 %, 21 %, 8 % and 26 %, respectively, compared to those determined in fruit from the RGH (Fig. 5). These results were achieved not only on a fresh weight basis but also on a dry weight basis; because the fruit dry matter content in tomatoes did not differ in response to the corresponding greenhouse (Tab. 2). Otherwise, the content of TA remained unaffected depending on the application of different greenhouse systems. Furthermore, the microclimatic conditions caused by the CGH affected the intensity of some sensory attributes (Fig. 6). Mouthfeel attributes such as fruity, watery, grassy, mealy, bitter, sour and tomato-like were equally influenced in tomatoes, which were produced in the RGH and the CGH. However, the consumer perceived that the application of the CGH significantly intensified other flavour attributes in tomatoes such as sweet and juicy, but also the mouthfeel attribute defined as peel firmness (Fig. 6). In consideration of all sensory attributes, the consumers assessed the total quality of tomatoes grown in the CGH as significant higher compared to those matured in the RGH.

Discussion

Effects of different operation modes of greenhouses on photosynthesis, crop growth, yield, transpiration, WC, WUE and EUE

Generally, the applied operation modes in the CGH can effectively be used to decrease the inside temperature at high ambient temperatures, where this process is accompanied by higher levels of RH and CO_2 concentration. During the late April, the combination of higher levels of CO_2 and a diminished solar radiation in the CGH was not sufficient to increase the rates of photosynthesis compared to the RGH. This observation is consistent with the results reported by KLÄRING and KRUMBEIN (2013) and GOMEZ et al. (2013), who demonstrated that lower light conditions resulted in a decreased photosynthesis. In contrast, the rates of photosynthesis of plants grown under CGH conditions were higher compared to those achieved in the RGH during the remaining month of the harvest period (Fig. 3). These results were obtained, although the transmitted solar radiation in the CGH was reduced by 11 % compared to the RGH as described by DANNEHL et al. (2013b). Therefore, it was concluded that the higher levels of CO_2 concentration can contribute to a compensation of the mentioned light reduction in the CGH during the light intensive season. This conclusion complies with the evidences reported by VANOOSTEN et al. (1995) and HURD (1968), who showed a higher photosynthesis of tomato plants exposed to an elevated CO_2 and a reduced light environment. As reported by MORTENSEN (1987), the enhanced rates of photosynthesis are the basis for an increased plant growth, which was also demonstrated in the present study. As such, the LAI and the plant height of plants produced in the CGH were increased compared to those grown in the RGH, whereby more trusses can be formed. These plant responses can also be explained by the higher average temperature (22.11 °C) obtained in the CGH (Tab. 2). This assumption is consistent with the results found by ADAMS et al. (2001), who observed a faster plant growth and more produced trusses of tomato plants, when the temperature was increased from 21 °C to 22 °C. Furthermore, it was observed that changes in microclimatic conditions in the CGH did not promote the occurrence of fungal infestation or other tomato diseases. Therefore, not more plant protective agents must be used in the CGH compared to conventional production.

In the present study, the promoted photosynthesis of plants exposed to the CGH resulted in an enhanced assimilates supply followed by an accelerated plant growth, whereby the total yield and the fruit mass per fruit were increased by 21.4 % and 8.2 %, respectively (Fig. 4; Tab. 2). Similar results were found by KLÄRING and KRUMBEIN (2013), which were attributed to higher rates of photosynthesis. Since the fruit dry matter content per gram fresh weight was unaffected (Tab. 2), it was concluded that the higher fruit mass per fruit was most likely caused by a higher carbon fixation within the fruit than by an increased water accumulation due to higher levels of relative humidity as demonstrated by JOHNSON et al. (1992). Comparable yield responses as described in the present study were also found depending on an elevated mean temperature and CO_2 concentration (KIMBALL, 1983; REINERT et al., 1997; ADAMS et al., 2001), where these microclimatic conditions were similar to those measured in the CGH. Furthermore, KLÄRING and KRUMBEIN (2013) and MARCELIS et al. (2006) identified that the total yield of tomatoes depends on the light conditions, where the yields were diminished in the range between 0.54 % and 1.1 % per 1 % light reduction. These calculations do not agree with our data, because higher yields were obtained in the CGH even though the light transmission was reduced. Rather, it was found that a close relationship exists between the total yield and the average value of the photosynthesis, which was calculated under consideration of the entire harvest period (Tab. 2). As shown in the results section, the total yield and the average value of photosynthesis caused by the CGH resulted in a surplus of 21.4 % and 21 %, respectively. Therefore, it might be possible that a 1 % increment in photosynthesis results in a 1.02 % yield increase. In this context, ZELITCH (1982) summarized the results of various studies, which generally showed a positive correlation between photosynthesis and yields in terms of other plant species. To date, however, no investigations were found that refer to the estimation of tomato yields in relation to the photosynthesis.

In comparison of both greenhouses, the average RH tended to increase in the CGH, whereas the temporally differences in RH ranged between 20 % and 25 % in favour of the CGH (Tab. 2; Fig. 2). PATANE (2011) and LEONARDI et al. (2000) found that higher relative humidity conditions inhibited plant transpiration of tomato plants. Other studies showed that increased CO_2 concentrations led to decreasing stomatal conductance and rates of plant transpiration in C_3 species (WAGGONER and ZEILITCH, 1965; LOUWERSE, 1980). These results are fully consistent with our calculations. The differences in RH and CO_2 concentrations described earlier resulted in a decrease in transpiration of plants grown in the CGH (by 35 %) compared to those exposed to the RGH (Tab. 2). These reduced transpiration losses were crucial for the reduction of the number of irrigation cycles applied in the CGH, whereby the WC was lowered by 30 % when compared to the RGH (Tab. 2). This result combined with the higher total yield improved the WUE by 71 % of plants produced in the CGH. This variable was raised to a value of 49.91 kg m^{-3} in the CGH, whereas a WUE of 45.45 kg m^{-3} was achieved in CO_2 enriched Dutch greenhouses (VAN KOOTEN et al., 2008). Therefore, it is obviously possible to improve the WUE in other greenhouse facilities when the technical refinements applied in the CGH are integrated into existing systems.

Furthermore, it was demonstrated that the required energy for the basic load for heating up the CGH can be covered during the year using the collected energy from February to May and from mid-August to November. In this context, it was shown that the EUE in the CGH was improved by 43 % compared to the RGH, where this value was reached by the reuse of the stored energy, the energy screens and the increase in total yield (Tab. 2). The data showed that 39.49 MJ were necessary in the CGH to produce one kg of tomatoes. In Dutch greenhouses, however, the value of the EUE is much lower, where 25 MJ kg^{-1} were calculated (ELINGS et al., 2005). This difference is based on the warmer day and night temperatures in the Netherlands, whereby less energy is required to produce tomatoes, but also on this fact that the yield production in Dutch greenhouses is twice as high as shown in the present study.

Effects of different operation modes of greenhouses on fruit quality

Compared to the RGH, the contents of lycopene, ß-carotene, phenolic compounds, SSC and LAA were increased in tomatoes, which were exposed to the climate conditions in the CGH (Fig. 5). Therefore, it was concluded that the light reduction in the CGH did not negatively influence the contents of SSC in tomatoes or at least not during the light intensive season. This result is consistent with the observations made by GAUTIER et al. (2008) and KLÄRING and KRUMBEIN (2013), both of whom found that shaded plants did not result in a decrease in SSC. In this context, GAUTIER et al. (2008) reported that an increasing temperature from 21 °C to 26 °C did not affect the contents of SSC in tomatoes. That is why we excluded a temperature effect on the amount of SSC in tomatoes, which were produced with a small temperature difference occurring between the RGH and the CGH. The same applies to the influence of the RH on the SSC, because the temporally higher levels of RH in the CGH were not sufficient to dilute the SSC in tomatoes compared to those matured in the RGH (Fig. 5). However, BERTIN et al. (2000) reported that a higher RH was responsible for lower SSC in tomatoes, where these tomatoes were matured under summer Mediterranean conditions and an associated greater difference in levels of RH than in our own experiments. Rather, it seems that the higher levels of CO_2 concentration in the CGH triggered an increase in photosynthesis followed by an enhanced supply of assimilates, whereby more content of SSC was accumulated in tomatoes. These conclusions are supported by ISLAM et al. (2006), who found increased levels of SSC in different tomato cultivars, which were grown under doubling of the CO_2 concentration. Finally, this increase in SSC and the stronger peel firmness owing to the CGH was perceived by the consumers (Fig. 6). It is assumed that the stronger peel firmness was caused by the higher mean temperature in the CGH, where RIGA et al. (2008) described the same phenomenon in their study. However, no changes in sourness of tomatoes were noticeable by the consumers, where this result was confirmed using the chemical analyses (Fig. 5; Fig. 6).

The alterations in secondary metabolites were affected positively by the microclimate conditions in the CGH. Regarding the effects of light deficiency on secondary plant compounds in tomatoes, there are conflicting results from different studies that give negative and positive effects. TOOR et al. (2006), for instance, found that the total phenol content in tomatoes varied depending on the seasonal light conditions, whereas a reduction in the mean monthly solar radiation by 10 % did not influenced the levels of phenolic compounds. This light interception is approximately equal to that measured between the CGH and the RGH, which is the reason why a light effect on phenolics was excluded in the present study. In this context, other studies showed that tomatoes accumulated more lycopene, ß-carotene and LAA when they were ripened at high radiation intensities, where the solar radiation was increased by up to 97 % compared to the reference light conditions (LEE and KADER, 2000; GAUTIER et al., 2005; BRANDT et al., 2006). However, RAFFO et al. (2006), KLÄRING and KRUMBEIN (2013) and RIGA et al. (2008) did not observed variations in contents of carotenoids and LAA in tomatoes at light differences by up to 123 %. These results and the increasing contents of secondary metabolites caused by the CGH suggest that a light reduction by 11 % in the CGH was not sufficient to diminish the secondary plant compounds in tomatoes. Rather, it is assumed that the slightly higher mean temperature and the higher levels of CO_2 concentrations and associated higher rates of photosynthesis in the CGH (Tab. 2) were mainly responsible for the accumulation of carotenoids, phenolic compounds and LAA. This was concluded, because RAFFO et al. (2006) showed that the contents of several phenolic compounds in tomatoes were increased when the average temperature was raised by 0.5 °C. However, the LAA content remained unaffected at this temperature difference. KRUMBEIN et al. (2006) demonstrated that the content of carotenoids increased with elevated mean temperatures ranging between 18°C and 22 °C. It could also be possible that the temporally higher temperatures in the RGH led to an overheating of tomatoes, followed by an inhibition of the synthesis of lycopene as shown by DUMAS et al. (2003). Furthermore, it was found that CO_2 levels maintained between 550 ppm and 1000 ppm can be used to increase various phenolic compounds in strawberries and grapes (BINDI et al., 2001; WANG et al., 2003), whereas these higher CO_2 concentrations did not affect the carotenoid pattern in tomatoes (KRUMBEIN et al., 2006). Nevertheless, an elevated atmospheric CO_2 can generally increase the photosynthetic activity as shown in the CGH. In this context, LAA, phenolic compounds and carotenoids are synthesized from primary metabolites supplied through photosynthesis in plants (LEE and KADER, 2000; TREUTTER, 2010). Therefore, it might be possible that the higher rates of photosynthesis of plants grown in the CGH resulted in a higher carbohydrate supply, whereby more resources for carbon based secondary plant compounds were provided. This would explain the increased accumulation of secondary metabolites of tomatoes matured in the CGH compared to those ripened in the RGH.

Conclusion

It can be recommended for practitioners that a confined closed greenhouse can be used as horticultural approach to increase fruit quantity and quality. As such, the results suggested that changes in microclimatic conditions occurred in the CGH, whereby the rates of photosynthesis, the LAI, the plant height, the total yield and the accumulation of primary metabolites were increased. The same applies to the secondary plant compounds and associated contents of antioxidant activity, which most likely benefit human health. In this context, it needs to be investigated whether an individual climate factor or a general increase in photosynthesis is responsible for the accumulation of carotenoids, phenolic compounds and LAA in tomatoes. Furthermore, it was found that the CGH has the potential to guarantee the production of tomatoes in a sustainable way, where high amounts of water and energy can be saved. To attain all the mentioned advantages, the growers have to reduce the frequency of the ventilation and to accept higher mean temperatures, RH and CO_2 concentrations in the CGH during summer. Although it was demonstrated that a light reduction can be compensated by higher levels of CO_2, a lower light interception by shadow-casting mounting parts (e.g., energy screens) should be realized in greenhouses in order to produce even more tomatoes than shown in the present study.

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References

ADAMS, S.R., COCKSHULL, K.E., CAVE, C.R.J., 2001: Effect of temperature on the growth and development of tomato fruits. Ann. Bot. 88, 869-877.

ASU-L-26.11.03-4, 1983: Determination of the total acid content in tomato concentrate (potentiometric method). BVL.

BAZZANO, L.A., HE, J., OGDEN, L.G., LORIA, C.M., VUPPUTURI, S., MYERS, L., WHELTON, P.K., 2002: Fruit and vegetable intake and risk of cardiovascular disease in US adults: the first National Health and Nutrition Examination Survey Epidemiologic Follow-up Study. Am. J. Clin. Nutr. 76, 93-99.

BERTIN, N., GUICHARD, S., LEONARDI, C., LONGUENESSE, J.J., LANGLOIS, D., NAVEZ, B., 2000: Seasonal evolution of the quality of fresh glasshouse tomatoes under Mediterranean conditions, as affected by air vapour pressure deficit and plant fruit load. Ann. Bot. 85, 741-750.

BINDI, M., FIBBI, L., MIGLIETTA, F., 2001: Free Air CO_2 Enrichment (FACE) of grapevine (*Vitis vinifera* L.): II. Growth and quality of grape and wine in response to elevated CO_2 concentrations. Eur. J. Agron. 14, 145-155.

BOT, G.P.A., 2001: Developments in indoor sustainable plant production with emphasis on energy saving. Computers and Electronics in Agriculture 30, 151-165.

BRANDT, S., PEK, Z., BARNA, E., LUGASI, A., HELYES, L., 2006: Lycopene content and colour of ripening tomatoes as affected by environmental conditions. J. Sci. Food Agric. 86, 568-572.

CAMEJO, D., RODRIGUEZ, P., MORALES, A., DELL'AMICO, J.M., TORRECILLAS, A., ALARCON, J.J., 2005: High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. J. Plant Physiol. 162, 281-289.

CAMPEN, J.B., BOT, G.P.A., 2002: Dehumidification in greenhouses by condensation on finned pipes. Biosystems Eng. 82, 177-185.

CARR, A.C., FREI, B., 1999: Toward a new recommended dietary allowance for vitamin C based on antioxidant and health effects in humans. Am. J. Clin. Nutr. 69, 1086-1107.

CONNOR, A.M., LUBY, J.J., TONG, C.B.S., 2002: Variability in antioxidant activity in blueberry and correlations among different antioxidant activity assays. J. Am. Soc. Hortic. Sci. 127, 238-244.

DANNEHL, D., HUBER, C., ROCKSCH, T., HUYSKENS-KEIL, S., SCHMIDT, U., 2012: Interactions between changing climate conditions in a semi-closed greenhouse and plant development, fruit yield, and health-promoting plant compounds of tomatoes. Sci. Hortic. 138, 235-243.

DANNEHL, D., HUYSKENS-KEIL, S., EICHHOLZ, I., ULRICHS, C., SCHMIDT, U., 2011: Effects of direct-electric-current on secondary plant compounds and antioxidant activity in harvested tomato fruits (*Solanum lycopersicon* L.). Food Chem. 126, 157-165.

DANNEHL, D., ROCKSCH, T., SCHMIDT, U., 2013a: Modelling to estimate the specific leaf area of tomato leaves (cv. Pannovy). Acta Hort., accepted.

DANNEHL, D., SCHUCH, I., SCHMIDT, U., 2013b: Plant production in solar collector greenhouses – influence on yield, energy use efficiency and reduction in CO_2 emissions. J. Agr. Sci. 5, 34-45.

DANNEHL, D., SUHL, J., HUYSKENS-KEIL, S., ULRICHS, C., SCHMIDT, U., 2014: Effects of a special solar collector greenhouse on water balance, fruit quantity and fruit quality of tomatoes. Agric. Water Manage. 134, 14-23.

DE GELDER, A., DIELEMAN, J.A., BOT, G.P.A., MARCELIS, L.F.M., 2012: An overview of climate and crop yield in closed greenhouses. J. Hort. Sci. Biotech. 87, 193-202.

DUMAS, Y., DADOMO, M., DI LUCCA, G., GROLIER, P., 2003: Effects of environmental factors and agricultural techniques on antioxidant content of tomatoes. J. Sci. Food Agric. 83, 369-382.

ELINGS, A., KEMPKES, F.L.K., KAARSEMAKER, R.C., RUIJS, M.N.A., VAN DE BRAAK, N.J., DUECK, T.A., 2005: The energy balance and energy-saving measures in greenhouse tomato cultivation. Acta Hort. 691, 67-74.

FISH, W.W., PERKINS-VEAZIE, P., COLLINS, J.K., 2002: A quantitative assay for lycopene that utilizes reduced volumes of organic solvents. J. Food Compos. Anal. 15, 309-317.

GAUTIER, H., DIAKOU-VERDIN, V., BENARD, C., REICH, M., BURET, M., BOURGAUD, F., POESSEL, J.L., CARIS-VEYRAT, C., GENARD, M., 2008: How does tomato quality (sugar, acid, and nutritional quality) vary with ripening stage, temperature, and irradiance? J. Agric. Food Chem. 56, 1241-1250.

GAUTIER, H., ROCCI, A., BURET, M., GRASSELLY, D., DUMAS, Y., CAUSSE, M., 2005: Effect of photoselective filters on the physical and chemical traits of vine-ripened tomato fruits. Can. J. Plant Sci. 85, 439-446.

GÖHLER, F., MOLITOR, H.D., 2002: Erdelose Kulturverfahren im Gartenbau. Eugen Ulmer GmbH & Co., Stuttgart, Germany.

GOMEZ, S., GUENNI, O., BRAVO DE GUENNI, L., 2013: Growth, leaf photosynthesis and canopy light use efficiency under differing irradiance and soil N supplies in the forage grass Brachiaria decumbens Stapf. Grass Forage Sci. 68, 395-407.

HURD, R.G., 1968: Effects of CO_2 enrichment on growth of young plants in low light. Ann. Bot. 32, 531-542.

ISLAM, S., KHAN, S., GARNER, J.O., 2006: Elevated atmospheric CO_2 concentration enhances carbohydrate metabolism in developing *Lycopersicon esculentum* Mill. cultivars. Int. J. Agric. Biol. 8, 157-161.

JOHNSON, R.W., DIXON, M.A., LEE, D.R., 1992: Water relations of the tomato during fruit growth. Plant Cell Environ. 15, 947-953.

KIMBALL, B.A., 1983: Carbon dioxide and agricultural yield – An assemblage and analysis of 430 prior obserbvations. Agron. J. 75, 779-788.

KLÄRING, P., KRUMBEIN, A., 2013: The effect of constraining the intensity of solar radiation on the photosynthesis, growth, yield and product quality of tomato. J. Agro. Crop. Sci. 199, 351-359.

KOTAKE-NARA, E., KUSHIRO, M., ZHANG, H., SUGAWARA, T., MIYASHITA, K., NAGAO, A., 2001: Carotenoids affect proliferation of human prostate cancer cells. J. Nutr. 131, 3303-3306.

KRUMBEIN, A., SCHWARZ, D., KLÄRING, H.P., 2006: Effects of environmental factors on carotenoid content in tomato (*Lycopersicon esculentum* (L.) Mill.) grown in a greenhouse. J. Appl. Bot.-Angew. Bot. 80, 160-164.

LEE, S.K., KADER, A.A., 2000: Preharvest and postharvest factors influencing vitamin C content of horticultural crops. Postharvest Biol. Technol. 20, 207-220.

LEONARDI, C., GUICHARD, S., BERTIN, N., 2000: High vapour pressure deficit influences growth, transpiration and quality of tomato fruits. Sci. Hortic. 84, 285-296.

LOUWERSE, W., 1980: Effects of CO_2 concentration and irradiance on the stomatal behavior of maize, barley and sunflower plants in the field. Plant Cell Environ. 3, 391-398.

MARCELIS, L.F.M., BROEKHUIJSEN, A.G.M., MEINEN, E., NIJS, E.M.F.M., RAAPHORST, M.G.M., 2006: Quantification of the growth response to light quantity of greenhouse grown crops. Acta Hort. 711, 97-103.

MORTENSEN, L.M., 1987: CO_2 enrichment in greenhouses – crop responses. Sci. Hortic. 33, 1-25.

NAGATA, M., YAMASHITA, I., 1992: Simple method for simultaneous determination of chlorophyll and carotenoids in tomato fruit. J. Jpn. Soc. Food Sci. Technol. 39, 925-928.

OZKAN, B., FERT, C., KARADENIZ, C.F., 2007: Energy and cost analysis for greenhouse and open-field grape production. Energy 32, 1500-1504.

PATANE, C., 2011: Leaf area index, leaf transpiration and stomatal conductance as affected by soil water deficit and VPD in processing tomato in semi arid mediterranean climate. J. Agro. Crop. Sci. 197, 165-176.

RAFFO, A., LA MALFA, G., FOGLIANO, V., MALANI, G., QUAGLIA, G., 2006: Seasonal variations in antioxidant components of cherry tomatoes (*Lycopersicon esculentum* cv. Naomi F1). J. Food Compos. Anal. 19, 11-19.

REINERT, R.A., EASON, G., BARTON, J., 1997: Growth and fruiting of tomato as influenced by elevated carbon dioxide and ozone. New Phytol. 137, 411-420.

RIGA, P., ANZA, M., GARBISU, C., 2008: Tomato quality is more dependent on temperature than on photosynthetically active radiation. J. Sci. Food Agric. 88, 158-166.

ROUT, U.K., AKIMOTO, K., SANO, F., ODA, J., HOMMA, T., TOMODA, T., 2008: Impact assessment of the increase in fossil fuel prices on the global energy system, with and without CO_2 concentration stabilization. Energ. Policy 36, 3477-3484.

SCHMIDT, U., 1988: Die Temperatur des Pflanzenbestandes als Regelgröße für die Klimaregelung im Gewächshaus unter besonderer Berücksichtigung der Heizungsregelung. Ingenieurhochschule Berlin-Wartenberg.

SHAFIEE, S., TOPAL, E., 2009: When will fossil fuel reserves be diminished? Energ. Policy 37, 181-189.

SLINKARD, K., SINGLETON, V.L., 1977: Total phenol analysis: Automation and comparison with manual methods. Am. J. Enol. Vitic. 28, 49-55.

TOOR, R.K., SAVAGE, G.P., LISTER, C.E., 2006: Seasonal variations in the antioxidant composition of greenhouse grown tomatoes. J. Food Compos. Anal. 19, 1-10.

TREUTTER, D., 2010: Managing Phenol Contents in Crop Plants by Phytochemical Farming and Breeding-Visions and Constraints. Int. J. Mol. Sci. 11, 807-857.

UNFPA, 2011: State of world population 2011. People and possibilities in a world of 7 billion. Information and External Relations Division of the United Nations Population Fund, New York.

VAN DER PLOEG, A., HEUVELINK, E., 2005: Influence of sub-optimal temperature on tomato growth and yield: a review. J. Hortic. Sci. Biotech. 80, 652-659.

VAN KOOTEN, O., HEUVELINK, E., STANGHELLINI, C., 2008: New developments in greenhouse technology can mitigate the water shortage problem of the 21st century. Acta Hort. 767, 45-52.

VANOOSTEN, J.J., WILKINS, D., BESFORD, R.T., 1995: Acclimation of tomato to different carbon-dioxide concentrations – relationships between biochemistry and gas-exchange during leaf development. New Phytol. 130, 357-367.

VÖRÖSMARTY, C.J., GREEN, P., SALISBURY, J., LAMMERS, R.B., 2000: Global water resources: vulnerability from climate change and population growth. Science 289, 284-288.

WAGGONER, P.E., ZEILITCH, I., 1965: Transpiration and stomata of leaves. Science 150.

WANG, S.Y., BUNCE, J.A., MAAS, J.L., 2003: Elevated carbon dioxide increases contents of antioxidant compounds in field-grown strawberries. J. Agric. Food Chem. 51, 4315-4320.

ZELITCH, I., 1982: The close relationship between net photosynthesis and crop yield. Bioscience 32, 796-802.

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