Diurnal Temperature Variations Significantly Affect Cucumber Fruit Growth

Hans-Peter Kläring¹ and Angela Schmidt

Department Modelling, Leibniz Institute of Vegetable and Ornamental Crops, Theodor-Echtermeyer-Weg 1, 14979 Grossbeeren, Germany

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Abstract. Decreasing the temperature in heated greenhouses significantly reduces heat costs and CO₂ emissions. However, the thermophile cucumber is known to be very sensitive to low temperatures. In particular, fruit growth decreases considerably as temperature declines. Nevertheless, reports show that cucumber can be grown successfully at low night temperatures. To explain this phenomenon, it is necessary to investigate the effect of the diurnal temperature variation on fruit growth. Fruit-bearing cucumber plants were grown in two experiments, either at a constant low temperature during the light and dark phase of 15 or 16 °C or at an extremely low temperature during the dark phase of 10 or 11 °C with an increase to 24 or 25 °C during the middle of the light phase resulting in a daily average of 15 or 16 °C, respectively. Introducing the diurnal temperature variation considerably increased fruit growth compared with cultivation at a constant temperature. The vegetative dry matter, however, was greater at a constant than at variable temperatures. Therefore, the total dry matter appeared to be unaffected by the treatments, meaning that photosynthesis was unaffected. Model calculations indicate that the relationship between temperature and fruit growth is not linear in the low-temperature range. For practical applications, it can be concluded that short daily periods with high temperature can mitigate the negative effect of low night temperature on fruit growth and yield.

Decreasing the temperature in heated greenhouses significantly reduces heat energy consumption and thus heat costs and CO₂ emissions (Elings et al., 2005). However, growth of the plants may also decrease, with major implications for yield. The thermophile cucumber is known to be very sensitive to low temperature. In particular, fruit growth rate is considerably decreased as temperature declines (Marcelis, 1993), especially when the temperature is low during the early stages of fruit development (Marcelis and Baan Hofman-Eijer, 1993). Nevertheless, reports show that cucumber can be grown successfully at low night temperatures of 11–14 °C (Heißner and Drews, 1986). One reason for this phenomenon could be that diurnal temperature variations have an additional effect on dry matter partitioning and fruit growth.

There are several studies on the effect of diurnal temperature variations on plant

growth, mostly in pot plants (e.g., Blanchard and Runkle, 2011; Erwin and Heins, 1995; Myster and Moe, 1995) but also in vegetable plants (e.g., Agrawal et al., 1993; Si and Heins, 1996; Xiong et al., 2011). However, latter authors mainly considered the vegetative growth stage. As is also typical for most species, Grimstad and Frimanslund (1993) demonstrated that for cucumber, increasing the difference between day and night temperature (DIF) increased stem elongation and leaf area while leaf unfolding rate was unaffected. A negative DIF had the opposite effect.

Some energy-saving approaches suggest temperature integration strategies. These approaches are based on the assumption that low temperatures in medium time periods can be compensated for by higher temperatures in later periods, and that only the average temperature is essential for plant growth and yield. The possibility of exploiting such temperature integration systems has been published for several vegetable crops such as cucumber (Slack and Hand, 1983), sweet pepper (Bakker and Van Uffelen, 1988), and tomato (De Koning, 1990). These strategies usually use fixed time periods for achieving a certain average temperature independent of daily temperature variations.

Sophisticated models which include a temperature effect in the simulation of dry matter distribution and fruit growth of cucumber do not consider daily temperature variations (Augustin, 1984; Marcelis, 1994a). One likely reason is that these models estimate

fruit growth on the basis of daily sink/source relations. The source here is the assimilate pool recharged by photosynthesis, which is difficult to handle on, say, hourly terms. In addition, no data about the effects of daily temperature variations on fruit growth in cucumber are available. There was no need to include these effects in previous studies, because the models satisfactorily simulated fruit growth and yield (Augustin, 1984; Marcelis and Gijzen, 1998). However, the models were not used to simulate yield under low-temperature conditions.

This study investigates the effect of the temperature variation on fruit growth in two growth chamber experiments. In contrast to previous articles (e.g., Marcelis and Baan Hofman-Eijer, 1993), which investigated a temperature range from 17 to 35 °C, which is typical for conventional cucumber production, we considered a lower temperature range. In addition, we varied the diurnal course of the temperature. Diurnal temperature variations on a low level but with high amplitudes usually occur when reducing the set point for heating to reduce the consumption of heat energy (Kläring et al., 2015).

Materials and Methods

Cucumber plants (*Cucumis sativus* L.) cv. Torreon (Enza Zaden, Enkhuizen, The Netherlands) were grown in containers filled with aerated nutrient solution. The nutrient solution was prepared by mixing deionized water and fertilizers according to De Kreijl et al. (1997). The plants were then hung by their shoots on a wire and the roots were set in polyethylene containers with the nutrient solution. The nutrient solution taken up by the plants was replenished every 2 to 3 d. In one experiment (Expt. 1), a total of seven containers filled with 8 L of nutrient solution were arranged in each of three growth chambers with a base area of 1 m² (Vötsch, Balingen, Germany). AGRO SON-T 400 W (Philips, Amsterdam, The Netherlands) high-pressure sodium discharge lamps and SVA (Osram, Munich, Germany) krypton bulbs served as light sources. The photosynthetic photon flux density (PPFD) at plant level was 300 μmol·m⁻²·s⁻¹ during an 11-h light phase and 80 μmol·m⁻²·s⁻¹ during a 1-h transition period to the dark phase in the morning and the evening. The temperature of the air in the chamber was 18 °C at night and 20 °C during the day; the relative humidity was 80% day and night. The CO₂ concentration in the chamber dropped to 300 μmol·mol⁻¹ during the light phase and increased to ≈440 μmol·mol⁻¹ in the dark phase due to the lack of a CO₂ supply facility. In a second experiment (Expt. 2), 19 plants in 15-L containers were arranged in two growth cabinets with a ground area of 10 m² (York, Mannheim, Germany) and grown at 325 μmol·m⁻²·s⁻¹ PPFD during the light phase and 100 μmol·m⁻²·s⁻¹ in the transition period. The relative humidity was 80% and the temperature during day and night was 25 and 23 °C, respectively. The CO₂ concentration was

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¹Corresponding author. E-mail: klaering@igzev.de.

controlled during the light phase at 400 $\mu\text{mol}\cdot\text{mol}^{-1}$ and increased to 450 $\mu\text{mol}\cdot\text{mol}^{-1}$ in the dark phase.

In both experiments, all side shoots of the plants were removed as they appeared. In Expt. 1, all flowers were removed except for one flower in leaf axil eight and 10. Plants were topped after 12 leaves. When the flowers in the 10th leaf axils appeared, one plant per chamber was harvested. Then the temperature in the three chambers was set to 16/16 °C during the dark and light phase in the first chamber, to 13/19 °C in the second chamber, and to 11 °C during the dark phase with an increase to 25 °C in the middle of the light phase in the third chamber (Fig. 1). All treatments resulted in a daily average of 16 °C. In Expt. 2, plants were topped after 22 leaves and one fruit each was allowed to grow in leaf axil 13, 14, 16, 17, 19, and 20. When the fruit length in the 20th leaf axil had reached ≈ 6 cm and that in the 13th axil 15 cm, three plants per cabinet were harvested, and the temperature in one cabinet was lowered to 15 °C day and night. In the second cabinet, it was set to 10 °C during the dark phase and increased to 24 °C in the middle of the light phase (Fig. 1).

Lengths (LF, cm) of the single fruits were measured during fruit growth and fruit mass (M_{est} , g) was estimated using an allometric

relationship established previously in earlier experiments:

$$M_{\text{est}} = 0.076 \cdot \text{LF}^{2.5} \quad [1]$$

At the end of the experiments, the masses (M_{mea} , g) of the single fruits were measured, correction factors (f_{cor} , 1)

$$f_{\text{cor}} = \frac{M_{\text{mea}}}{M_{\text{est}}} \quad [2]$$

were determined and the estimated masses of the fruits during their development were corrected using these factors. Finally, the plants were completely harvested and the masses of their components were determined before and after drying in a ventilated oven for 2 d at 80 °C. In Expt. 2, the lengths of all leaves (LL, m) were measured and leaf areas (LA, m^2) were estimated using an allometric relationship (Kläring et al., 2007):

$$\text{LA} = 1.75 \cdot \text{LL}^{2.34} \quad [3]$$

Treatments were compared using Fisher's F procedure followed by Tukey's T procedure at a significance level of $\alpha = 0.05$. In addition, relative fruit growth rates were calculated for weekly increments in fruit mass and related to the fruit mass in the middle of this period.

In Expt. 1, one of the 12 fruits of treatment 11/25 °C was not included in the analysis because its length was exceptionally large compared with all other fruits at the start of the treatments. In Expt. 2, one of the 16 plants of treatment 15/15 °C was omitted due to a damaged root which was likely a result of a malfunction of the air supply to the container.

Results

Diurnal temperature variation significantly affected cucumber fruit growth. At a low 24-h average of 16 °C, introducing a DIF of 6 K in Expt. 1 increased fruit growth by 21% and a DIF from the night to the middle of the light phase of 14 K by 66% compared with a constant 16 °C (Fig. 2A). In Expt. 2 at 1 K lower temperatures, this difference was on average for all fruits 49% (Fig. 2B). Differences in the absolute growth rates were present during the entire fruit growth period (Figs. 2A and B). Increasing the DIF resulted even in enhanced relative growth rates for all fruit sizes in both experiments (Figs. 3A and B).

In terms of fruit dry matter, these differences were 18%, 52%, and 31%, respectively, due to the inverse relationship between the fruit dry matter content and DIF (Tables 1 and 2). A significantly higher dry matter fraction was allocated to the fruit at DIF 14 K than at DIF 0 K in both experiments at the expense of the dry matter distributed to the vegetative components of leaf, stem, and root. Total dry matter, however, was not found to be affected (Tables 1 and 2). The increase in leaf dry matter from DIF 14 to 0 K was an effect of increasing leaf dry matter content (Tables 1 and 2). However, the increase from the start value to the end value at DIF 14 K was mainly affected by an increase in leaf fresh weight (data not shown).

Particularly in Expt. 2, no increase in leaf dry matter contents during growth at DIF 14 K was found (Table 2). Similar results were found for the stem (Tables 1 and 2). Root growth was reduced by about 40% with increasing DIF but leaf growth by only 20%, resulting in leaf-to-root ratios of 3.1, 2.6, and

Fig. 1. Daily temperature course of the treatments in Expt. 1 (black lines) and Expt. 2 (gray lines). The 24-h average temperature in all treatments was 16 °C in Expt. 1 and 15 °C in Expt. 2.

Fig. 2. Growth of cucumber fruits depending on the daily temperature course. In Expt. 1 (A), night/day temperatures were 16/16 °C, 13/19 °C, or 11 °C at night with an increase to 25 °C in the middle of the day; all resulted in a 24-h average of 16 °C. In Expt. 2 (B), night/day temperatures were 15/15 °C or 10 °C at night with an increase to 24 °C in the middle of the day; both resulting in a 24-h average of 15 °C. Data points relate to a single fruit. They are average values of two fruits on six plants (A) and of fruit in the 13th or 20th leaf axil on 15 (constant temperature) and (variable temperature) 16 plants (B), respectively. The bars indicate standard error of the mean when they are greater than the symbol.

Fig. 3. Relative fruit growth depending on the daily course of temperature. In Expt. 1 (A), night/day temperatures were 16/16 °C, 13/19 °C, or 11 °C at night with an increase to 25 °C in the middle of the day; all resulted in a 24-h average of 16 °C. In Expt. 2 (B), night/day temperatures were 15/15 °C or 10 °C at night with an increase to 24 °C in the middle of the day; both resulting in a 24-h average of 15 °C. Each point is the mean relative fruit growth rate of all fruits of the treatment estimated for a period of about a week as the difference between the natural logarithm of fruit mass at the start and end of the period divided by number of days in the period.

Table 1. Dry matter and dry matter content of plant components depending on the daily temperature course in Expt. 1. Night/day temperatures were 16/16 °C, 13/19 °C, or 11 °C at night with an increase to 25 °C in the middle of the day; all resulting in a 24-h average of 16 °C. Values followed by the same letter do not differ significantly according to Tukey's T-procedure at a significance level of $\alpha = 0.05$.

Characteristic	Start value	Value at night/day temp, °C		
		11/25	13/19	16/16
Leaf dry matter, g	17.5 b	25.3 ab	30.7 a	30.3 a
Stem dry matter, g	4.65 b	6.67 a	6.86 a	7.10 a
Root dry matter, g	5.59 c	8.13 bc	11.93 ab	13.50 a
Fruit dry matter, g	— ^z	45.4 a	35.3 ab	29.9 b
Total dry matter, g	27.7 b	85.5 a	84.8 a	80.8 a
Leaf dry matter content, mg·g ⁻¹	74.2 c	85.6 bc	95.7 ab	102.6 a
Stem dry matter content, mg·g ⁻¹	62.7 c	72.7 b	80.2 a	80.8 a
Root dry matter content, mg·g ⁻¹	37.5 b	49.5 a	40.0 ab	42.6 ab
Fruit dry matter content, mg·g ⁻¹	— ^z	33.8 b	37.0 a	38.7 a

^zFruit dry matter was negligible and included in the stem dry matter.

Table 2. Dry matter and dry matter content of plant components depending on the daily course of temperature in Expt. 2. Night/day temperatures were 15/15 °C or 10 °C at night with an increase to 24 °C in the middle of the day; both resulting in a 24-h average of 15 °C. Values followed by the same letter do not differ significantly according to Tukey's T procedure at a significance level of $\alpha = 0.05$.

Characteristic	Start value	Value at night/day temp, °C	
		10/24	15/15
Leaf area, m ²	2.07 b	2.04 b	2.19 a
Leaf dry matter, g	61.8 c	76.3 b	96.9 a
Stem dry matter, g	12.9 b	13.8 b	15.7 a
Root dry matter, g	20.5 b	23.6 b	41.6 a
Fruit dry matter, g	11.2 c	135.4 a	108.1 b
Total dry matter, g	106.4 b	249.2 a	262.3 a
Leaf dry matter content, mg·g ⁻¹	87.4 b	89.8 b	110.3 a
Stem dry matter content, mg·g ⁻¹	75.4 c	79.8 b	87.9 a
Root dry matter content, mg·g ⁻¹	32.1	34.5	34.5
Fruit dry matter content, mg·g ⁻¹	45.4 a	32.4 c	36.5 b

2.3 g·g⁻¹ at DIFs 14, 6, and 0 K in Expt. 1, and 3.2 and 2.3 g·g⁻¹ at DIFs 14 and 0 K in Expt. 2, respectively. Interestingly, the leaf-to-root ratio at DIF 14 K did not drift noticeably from the values at the treatment start, namely 3.1 and 3.0 g·g⁻¹ in Expts. 1 and 2. In Expt. 2, the leaf area did not change during growth at DIF 14 K, but slightly increased at a constant 15 °C. Nevertheless, the specific leaf area decreased during the treatments from 3.35 dm²·g⁻¹ of dry matter to 2.26 and 2.67 dm²·g⁻¹ at DIFs 0 K and 14 K, respectively.

Discussion

Most of the effects of increasing DIF with the same 24-h average temperature are similar to those observed for an increase in the

24-h average temperature, such as increasing fruit growth rate (Marcelis and Baan Hofman-Eijer, 1993), increasing dry matter fraction allocated to the fruit (Kläring and Kyuchukova, 2007; Marcelis, 1993), increasing leaf-to-root ratio (Kläring and Kyuchukova, 2007), and decreasing dry matter content of fruit (Marcelis, 1992).

The temperature increase during the light phase obviously overcompensated for the negative effect on fruit growth at the lower temperature during the dark phase. This means that either the base temperature for fruit growth is higher than 13 °C or the effect of temperature on fruit growth is not linear.

The piecewise linear relationship between the mean hourly fruit growth (F , g·h⁻¹) during

the experimental period and the temperature (T , °C) can be expressed as

$$F = \begin{cases} a_0 \cdot (T - a_1) & \text{if } T - a_1 > 0 \\ 0 & \text{else} \end{cases} \quad [4]$$

where a_0 and a_1 are parameters. These parameters can be estimated by trial and error with the goal of meeting the average final fruit mass of the treatments 16/16 and 11/25 °C in Expt. 1. This results in a base temperature a_1 of 14.1 °C, and could explain the observed phenomenon in Expt. 1 (Table 3). Estimating the fruit mass of fruits grown at 13/19 °C using a_0 and a_1 would not contradict the piecewise linear approach Eq. [4] (Table 3). To apply this relationship to Expt. 2 with different conditions, parameter

Table 3. Parameters for the effect of temperature on the mean-hourly single-fruit mass-increment estimated from treatments 16/16 °C and 11/25 °C of Expt. 1 (a_0 , a_1) and corrected for Expt. 2 using treatment 15/15 °C (a_0^*), and final calculated mean single-fruit mass of treatment 13/19 °C and 10/24 °C in Expts. 1 and 2, respectively, using the estimated parameters.

Characteristic	Piecewise linear function	Exponential function
Parameter a_0	0.323	0.781
Parameter a_1	14.125	0.190
Parameter a_0^*	0.979	1.090
Calculated single-fruit mass at 13/19 °C, kg	0.500	0.452
Relative to measured fruit mass	1.06	0.95
Calculated single-fruit mass at 10/24 °C, kg	1.374	0.753
Relative to measured fruit mass	2.10	1.15

a_0 was modified to a_0^* to meet the measured fruit mass at 15/15 °C. However, estimating the fruit mass of the treatment at 10/24 °C using parameters a_0^* and a_1 then resulted in a 110% overestimation of the measured value (Table 3).

The empirical exponential relationship between F and T can thus be calculated as

$$F = a_0 \cdot e^{a_1 \cdot T} \quad [5]$$

Parameters a_0 , a_1 , and a_0^* can be estimated the same as for Eq. [4]. Using this relationship and parameters a_0^* and a_1 , the fruit mass of the treatment 10/24 °C in Expt. 2 was then overestimated by only 15% (Table 3). Similar results can be obtained with other (empirical) nonlinear relationships such as

$$F = a_0 \cdot T^{a_1} \quad [6]$$

where the measured fruit mass of treatment 10/25 °C was overestimated by 22% (data not shown).

Thus, a nonlinear approach such as Eq. [5] or Eq. [6] explains the data of both experiments much better in the low-temperature range of the experiments than the piecewise linear Eq. [4] with an estimated base temperature of 14.1 °C. In addition, this base temperature is very high. In his cucumber growth model, Marcelis (1994a) assumed a linear temperature effect on fruit growth with a base temperature of 10 °C, which was derived from measurements between 17.5 and 30 °C (Marcelis and Baan Hofman-Eijer, 1993). Both the linear approach of Marcelis and the exponential estimates in this study are empirical, and therefore valid only in the temperature range of the corresponding experiments. Therefore, there is no contradiction between the nonlinear temperature effect on fruit growth at low temperatures and the linear effect observed at moderate and high temperatures.

Similar results can be found in the literature for the tomato. Gent (1988) and Gent and Ma (1998) obtained in greenhouse experiments that plants grown at a DIF of 9 or 14 K yielded more than those grown at a DIF of 3 or 5 K, respectively, which was mainly due to a faster fruit ripening and a larger single fruit mass. It was generally accepted that virtually no tomato growth can be expected below 12 °C (Criddle et al., 1997; Van der Ploeg and Heuvelink, 2005). However, experiments demonstrated a significant fruit growth and development even in the range of a daily average of 12 °C (Kläring et al., 2015). In addition, Adams et al. (2001)

derived a base temperature of 5.7 °C for fruit growth and development in tomato from measurements in a temperature range from 14 to 26 °C. They also used a nonlinear function to describe the effect of temperature on the time of the fruit development.

Cutting the top of the plants and removing all side shoots kept the plant photosynthesis and thus the assimilate source for fruit growth in both treatments comparable. Therefore, conclusions on the effects of diurnal temperature variations on the development of leaves and roots and the further development of the crop cannot be definitely drawn. At the low temperatures under moderate light conditions in the growth chambers and cabinets the plants were sink limited rather than source limited. In the growth cabinets, a leaf area index of $\approx 3 \text{ m}^2 \cdot \text{m}^{-2}$ was comparable with conditions in commercial greenhouses.

Regarding roots, root dry matter per leaf area with a value of $11.7 \text{ g} \cdot \text{m}^{-2}$ is above the range of 7.6 and $10.1 \text{ g} \cdot \text{m}^{-2}$ Marcelis (1994b) reported for fruit-bearing plants at 18 °C, at almost equal daily radiation integrals and nonrestricted growth of the vegetative compartments. This indicates that any growth inhibition in the long term due root size limitations is not to be expected. A tremendous increase in root growth was also reported when sinks in the form of fruit were removed from the plants (Kläring et al., 2014; Marcelis, 1994b). Therefore, sink limitations in the shoot are likely the cause of the larger root size for plants at constant temperatures compared with those at variable temperatures.

Regarding the leaves, one may expect that the response of leaf growth on temperature also follows a nonlinear function in the low-temperature range, but this remains to be proven in further experiments. The findings by Grimstad and Frimanslund (1993) that a positive DIF enhances leaf growth relative to a single constant DIF points in this direction. The cause of the higher dry matter content in leaves, stems, and fruits of the constant low temperature relative to the variable temperatures was most probably the restriction in the formation of new leaves and stem sections and the lower extension rate of the fruits. A significant increase in dry matter content of leaves, stems, and fruits due to a lack of sinks for assimilates caused by fruit removal was also observed by Marcelis (1994b) and Kläring et al. (2014).

Heißenner and Drews (1986) showed that cucumber plants grow well at night heating

set points of 11 °C and produce, with some delay, the same yield compared with plants cultivated at night heating set points of 17 °C. However, the heating set point during the day was 20 °C, which results in a remarkable DIF of 9 K without taking into account a further temperature increase on sunny days. In addition, similar low night temperatures and large DIFs are the typical conditions in unheated Mediterranean greenhouses during the winter season where cucumbers have been produced successfully. Thus, under practical conditions, low average temperatures with low DIFs rarely occur. However, increasing the greenhouse insulation at night by closing layers of thermal screens reveals the application of higher night heating set points and can make lower or even negative DIFs profitable from an energy-saving viewpoint in northern countries. When considering both approaches regarding the effect of temperature on fruit growth—linear above a base temperature Eq. [4] and nonlinear Eq. [5]—it follows that a negative DIF should also improve the fruit growth compared with a DIF of 0 K at low average temperature. This, however, remains to be tested. In that case, the very low temperature during the light phase may have a negative effect on photosynthesis. In the experiments in this study, any temperature effect on net photosynthesis can be excluded because the total dry matter of the plants by the end of the experiments was unaffected by the treatments (Tables 1 and 2).

Summary and Conclusions

Short daily periods with high temperature can mitigate the negative effect of low night temperature and even of low 24-h average temperature on fruit growth and yield. This opens up the simple possibility of reducing heat costs in greenhouse cucumber production by lowering the set point for temperature control during the night and using the solar radiation for warming the greenhouse air during the day. In southern regions, cucumbers can also be produced in unheated greenhouses if the air temperature in the greenhouse at night does not drop below 10 °C.

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