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Daily temperature drop prevents inhibition of photosynthesis in tomato plants under continuous light

E.N. IKKONEN[*], T.G. SHIBAEVA[*,+], E. ROSENQVIST[**], and C.-O. OTTOSEN[***]

Institute of Biology, Karelian Research Centre, Russian Academy of Sciences, Pushkinskaya 11, 185910 Petrozavodsk, Russia[*]
Department of Plant and Environmental Sciences, University of Copenhagen, Hoejbakkegaard Alle 9, DK-2630 Taastrup, Denmark[**]
Department of Food Science, Aarhus University, Kirstinebjergvej 10, 5792 Årslev, Denmark[***]

Abstract

The negative effects of continuous light (CL) seen in tomato plants are often claimed to be linked to effects of offsetting the diurnal rhythm. In this study we tested whether a short-term daily temperature drop prevents the decreased photosynthetic performance seen in tomato plants grown under CL. Tomato (*Lycopersicon esculentum* Mill.) plantlets were grown at constant temperature of 26°C under 16-h day (16D) or 24-h day (24D) at 150 μmol m^{-2} s^{-1} PPFD. Some 24D plants were treated daily by 2 h temperature drop from 26 to 10°C (24D+DROP). Physiological disorder, such as severe leaf chlorosis, a large decrease in net photosynthetic rate, maximal quantum yield of PSII photochemistry, and the effective quantum yield of PSII photochemistry were observed in 24D, but not in 16D and 24D+DROP plants. The daily 2-h drop in temperature eliminated a negative effect of CL on photosynthesis and prevented the development of leaf chlorosis in tomato plants. This could be due to a change in carbohydrate metabolism as the short drop in temperature might allow maintenance of the diurnal rhythms.

Additional key words: chlorophyll fluorescence; gas exchange; leaf area; photodamage; stomatal conductance.

Introduction

Growing plants under continuous light (CL) is a way of producing crops economically in controlled environment. Using a 24-h photoperiod with relatively low PPFD can reduce both initial and operational costs for plant production (Ohyama *et al*. 2005). The use of CL in production systems ultimately depends on the cost-to-benefit ratio. High value products such as horticultural commodities, *e.g*. tomatoes, could potentially benefit from cultivation under CL since the light requirement for the year-round production is high under northern latitudes (Velez-Ramirez *et al*. 2011). However, the cultivated tomato cultivars are known to be sensitive to CL and develop leaf injuries under CL (Hillman 1956, Bradley and Janes 1985, Cushman *et al*. 1995). The longer periods of exposure to CL negatively affect several photosynthetic parameters, such as the net photosynthetic rate, quantum yield, maximum rate of Rubisco carboxylation, and maximum rate of electron transport (Van Gestel *et al*. 2005, Pettersen *et al*. 2010). The CL-induced injuries overall expressed as chlorosis and the mechanisms by which the photosynthesis is downregulated under CL are still poorly understood (Sysoeva *et al*. 2010, Velez-Ramirez *et al*. 2011).

It was suggested that temperature fluctuations might prevent the CL-induced injury. The circadian rhythms are affected by both temperature and light fluctuations that increase the turnover of carbohydrate metabolism and reduce CL-related damage (Velez-Ramirez *et al*. 2011, Kjaer *et al*. 2012). Previous studies have shown that diurnal

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[+]Corresponding author; e-mail: shibaeva@krc.karelia.ru
Abbreviations: C_a – ambient CO_2 concentration; C_i – intercellular CO_2 concentration; Chl – chlorophyll; CL – continuous light; DM – dry mass; DROP – daily short-term temperature decrease; F_0 – minimal fluorescence yield of the dark-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_m' – maximal fluorescence yield of the light-adapted state; F_v – variable fluorescence; F_v/F_m – maximal quantum yield of PSII photochemistry; g_s – stomatal conductance; LA – leaf area; P_N – net photosynthetic rate; R_D – dark respiration rate; α – apparent quantum yield of photosynthesis; Φ_{PSII} – effective quantum yield of PSII photochemistry.
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fluctuations in air temperature (thermoperiod) might prevent the CL-induced injury in several *Solanaceae* species including eggplant, potato, and tomato (Hillman 1956, Tibbitts *et al*. 1990, Omura *et al*. 2001, Ohyama *et al*. 2005). Similar to the thermoperiod, a daily short-term intensive temperature drop was effective in preventing or moderating the CL-induced injury in tomato, but in contrast to a thermoperiodic temperature pattern, the temperature drop had no effect on the developmental rate of plants (Sysoeva *et al*. 2012).

We hypothesized that a daily temperature drop allows tomato plants grown at 24-h photoperiod to exhibit greater photosynthetic performance. Thus, the aim of our study was to examine the effect of a daily short period of low temperature on the photosynthetic parameters and growth of tomato plants grown under CL.

Materials and methods

Tomato seeds were germinated in Petri dishes on filter papers moistened with distilled water and placed in darkness at an air temperature of 28°C for 3 d (day 0–2) in a growth chamber (*VKSH–73*, *Agrophysical Research Institute RAAS*, St. Petersburg, Russia). Germinated seeds were sown in plastic containers (7 × 7 cm) with sand and placed in the growth chambers at photoperiods of 16 and 24 h with (PPFD of 150 μmol m^{-2} s^{-1} provided by high-pressure mercury lamps (*HPL-N 400W*, *Philips*, Eindhoven, Germany) [midrange daily light integral (DLI) was 8.64 and 12.96 mol m^{-2} d^{-1}, respectively], air temperature of 26°C, and relative air humidity of 60%. Plants were watered daily, using a complete nutrient solution (based on 1 g L^{-1} of $Ca(NO_3)_2$, 0.25 g L^{-1} of KH_2PO_4, 0.25 g L^{-1} of $MgSO_4 \cdot 7H_2O$, 0.25 g L^{-1} of KNO_3, trace quantity of $FeSO_4$, and pH 6.0–6.3).

From day 8, when the seedlings had fully expanded cotyledons, to day 36, plants were grown in the same growth chambers under the following conditions: (*1*) the constant temperature of 26°C and 16-h day (16D); (*2*) the constant temperature of 26°C and 24-h day (24D); and (*3*) daily 2 h temperature drop (10°C) treatment and 24-h day (24D+DROP), where the temperature was maintained at 26°C for 22 h and 10°C for 2 h. The temperature changes from 26 to 10°C and reverse occurred within 30 min.

The leaves were visually rated for the degree of chlorosis. Plant dry mass (DM) was determined by oven drying samples at 105°C for 24 h and the leaf area (LA) was measured on day 36 with a scanner (*Perfection V33*, *Epson America*, Long Beach, USA) connected to PC with corresponding software (*AreaS 2.1*). Chlorophyll (Chl) *a* and *b* concentrations were measured following extraction with 96% ethanol on day 18 and 36. The light absorbance of the extract was determined spectrophotometrically at 665 nm (Chl *a*) and 649 nm (Chl *b*) (*SF-2000*, *OKB Spektr*, Russia). The concentration was calculated according to Lichtenthaler and Wellburn (1983).

The Chl fluorescence was measured using a portable chlorophyll fluorometer *MINI-PAM* (*Walz*, Effeltrich, Germany) on the 2nd and 5th fully expanded leaves on day 18 and 36. The maximal quantum yield of PSII photochemistry was calculated as $F_v/F_m = (F_m - F_0)/F_m$ after 20 min of dark adaptation. The effective quantum yield of PSII photochemistry was measured at PPFD of 150 μmol m^{-2} s^{-1} and calculated as $\Phi_{PSII} = \Delta F/F_m' = (F_m' - F)/F_m'$. Net photosynthetic rate (P_N), stomatal conductance (g_s), and the ratio of intercellular to ambient CO_2 concentration (C_i/C_a) were measured with a *HCM-1000* portable photosynthesis system (*Walz*, Effeltrich, Germany) on the 5–7th fully expanded leaves on day 36. The temperature response of photosynthesis was measured at 10, 15, 20, 25, and 35°C at PPFD of 1,000 μmol m^{-2} s^{-1}. The apparent quantum yield of photosynthesis (α) was calculated as the slope of the linear portion of the light response curve at PPFD of 0, 20, and 50 μmol m^{-2} s^{-1} (Pasian and Lieth 1989). Respiration rate (R_D) was measured after 15-min acclimation to darkness.

Two similar trials were used. All results were presented as means ± SE ($n \geq 4$). Data were tested for normality and homogeneity of variance using Chi-square test and *Levene*'s test in *Statistica* (*v. 8.0.550.0*, *StatSoft, Inc.*). Differences between treatments for P_N, g_s, C_i/C_a, α, and R_D were tested with two-way analysis of variance (*ANOVA*), using an experimental run (growth temperature/photoperiod) and measured temperature as factors and within each measurement temperature or date of measurement with one-way *ANOVA* using experimental run (treatment effects) or date of measurement as factors.

Results

The 24D+DROP plants were shorter and exhibited higher DM compared to 24D and 16D plants (Table 1). In both 16D and 24D+DROP plants, no physiological disorders were observed, while leaves of 24D plants showed a classical mottling and later also severe chlorosis (Fig. 1). All true leaves of 24D plants developed these injuries. The injuries appeared after day 10 and succeeding leaves were gradually affected. The experimental run (treatment effects) as a factor showed a significant effect on the Chl (*a*+*b*) content in tomato leaves (Table 2). The leaves of 24D plants had the lowest Chl (*a*+*b*) content on day 36 (P<0.0001 for both 24D+DROP and 16D plants, Table 1). From day 18 to day 36, the Chl (*a*+*b*) content increased by 30% in 16D, decreased in 24D due to both Chl *a* and

Table 1. Plant dry mass (DM), leaf area (LA), chlorophyll (Chl) *a* and *b*, Chl (*a*+*b*), Chl *a*/*b*, maximal quantum yield of PSII photochemistry (F_v/F_m), effective quantum yield of PSII photochemistry (Φ_{PSII}) at PPFD = 150 μmol m^{-2} s^{-1} and ratio of intercellular to ambient CO_2 concentration (C_i/C_a) at PPFD = 1,000 μmol m^{-2} s^{-1} in tomato plants grown at 16-h day and 26°C (16D), 24-h day and 26°C (24D), 24-h day, 26°C and a daily short-term (2 h) temperature drop to 10°C (24D+DROP). Means ± SE ($n \geq 4$). *Different letters* within each parameter indicate statistical differences at $P<0.05$, as a result of *posthoc Bonferroni* analysis within a one-way analysis of variance (*ANOVA*). *Uppercase letters* compare differences between treatments and *lowercase letters* compare differences between days of measurement within each parameter.

Parameter	Day	16D	24D	24D+DROP
DM [g]	36	1.56 ± 0.08^{AB}	1.00 ± 0.06^{B}	1.97 ± 0.13^{A}
LA [cm^2]	36	555.5 ± 27.6^{A}	264.5 ± 13.9^{B}	525.5 ± 12.2^{A}
Chl (*a*+*b*) [mg g^{-1}(DM)]	18	13.7 ± 0.2^{Ab}	11.9 ± 0.2^{Ba}	12.7 ± 0.7^{Aba}
	36	17.1 ± 0.1^{Aa}	5.6 ± 0.6^{Cb}	12.7 ± 0.7^{Ba}
Chl *a* [mg g^{-1}(DM)]	18	10.4 ± 0.1^{Aa}	8.7 ± 0.1^{Ba}	9.3 ± 0.4^{Ba}
	36	10.2 ± 0.3^{Aa}	4.3 ± 0.5^{Bb}	5.8 ± 0.3^{Bb}
Chl *b* [mg g^{-1}(DM)]	18	3.3 ± 0.1^{Ab}	3.2 ± 0.1^{Aa}	3.5 ± 0.3^{Ab}
	36	6.9 ± 0.4^{Aa}	1.3 ± 0.1^{Cb}	5.0 ± 0.4^{Ba}
Chl *a*/*b*	18	3.2 ± 0.1^{Aa}	2.7 ± 0.1^{Bb}	2.8 ± 0.1^{Ba}
	36	1.5 ± 0.1^{Bb}	3.4 ± 0.1^{Aa}	1.1 ± 0.1^{Bb}
F_v/F_m	18	0.803 ± 0.005^{Bb}	0.784 ± 0.006^{Ba}	0.821 ± 0.005^{Aa}
	36	0.826 ± 0.001^{Aa}	0.648 ± 0.038^{Bb}	0.836 ± 0.018^{Aa}
Φ_{PSII}	18	0.687 ± 0.012^{Bb}	0.682 ± 0.011^{Ba}	0.712 ± 0.005^{Aa}
	36	0.770 ± 0.005^{Aa}	0.540 ± 0.031^{Bb}	0.709 ± 0.013^{Aa}
C_i/C_a	36	0.59 ± 0.03^{A}	0.54 ± 0.05^{A}	0.46 ± 0.03^{A}

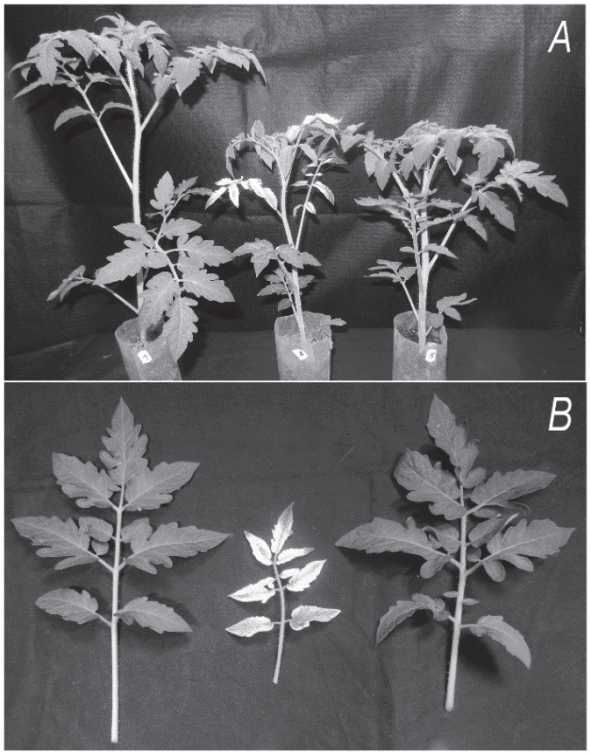

Fig. 1. Intact (*A*) and fifth leaves (*B*) of tomato plants grown at 16-h day and 26°C (16D, *left*), 24-h day and 26°C (24D, *middle*), 24-h day, 26°C, and a daily short-term (2 h) temperature drop to 10°C (24D+DROP, *right*) on day 36.

Chl *b*,but did not change in 24D+DROP, as the decrease in Chl *a* content was compensated by increased Chl *b* content in the 24D+DROP leaves. At day 18, all treatments resulted in the high Chl *a*/*b* ratio, with 16D being significantly higher than those two CL treatments. After 36 days, the ratio decreased considerably in the 16D and 24D+DROP plants, while it increased in 24D plants.

There were significant differences between treatments in F_v/F_m on both days (Table 2). The 24D plants exhibited lower F_v/F_m than those of the16D and 24D+DROP plants (Table 1). From day 18 to day 36, the F_v/F_m values increased in 16D, decreased in 24D, and were not affected in the 24D+DROP plants. The experimental run as a factor significantly affected the Φ_{PSII} values on both day 18 and 36; the Φ_{PSII} was the highest in the 24D+DROP plants on day 18 and the lowest in the 24D plants on day 36 (Table 1).

The experimental run as a factor had strong effect on P_N at 15, 20, and 25°C (Table 2). The temperature sensitivity of P_N differed depending on the photoperiod and the growth temperature regime (Fig. 2*A*). P_N was not significantly affected by temperature in the 24D leaves, but was significantly lower in the 24D compared with the 16D and 24D+DROP leaves (Table 2). The 24D+DROP leaves showed P_N values significantly lower than the 16D leaves only at 25°C. Similar differences in photosynthetic response to temperature were observed under all used PPFD (data not shown). The g_s was not significantly affected by temperature in the 24D and 24D+DROP leaves (Table 2). There was no difference between the 24D and 24D+DROP leaves in g_s at any temperature, but g_s was significantly higher in the 16D than in 24D and 24D+DROP leaves at 15, 20, and 25°C (Fig. 2*B*, Table 2). The experimental run as a factor had no significant effect

Table 2. Statistical analysis (F-value and significance level) on gas-exchange characteristics of tomato leaves grown at 16-h day, 26°C (16D), 24-h day, 26°C (24D), 24-h day, 26°C, and a daily short-term (2 h) temperature drop to 10°C (24D+DROP). Asterisks denote significance levels: * – $P<0.05$, ** – $P<0.01$, *** – $P<0.001$; NS – not significant; T – effects are calculated for day 36.

Variable	Experimental run effect at measurement temperature *F* *P*					Meas. T effect *F* *P*
	10°C	15°C	20°C	25°C	35°C	
P_N [μmol(CO_2) m^{-2} s^{-1}]	3.0 NS	7.4*	9.5*	27.0**	1.0 NS	
16D						36.9***
24D						0.7 NS
24D+DROP						3.5*
g_s [mmol(H_2O) m^{-2} s^{-1}]	–	16.4***	12.4**	15.3**	0.3 NS	
16D						5.6*
24D						1.0 NS
24D+DROP						0.7 NS
α [mol(CO_2) mol(photon) $^{-1}$]	360.7***	15.7**	18.5**	5.7*	163.5***	
16D						4.8*
24D						1.1 NS
24D+DROP						43.0***
R_D [μmol(CO_2) m^{-2} s^{-1}]	0.9 NS	0.8 NS	0.6 NS	38.6***	215.1***	
16D						30.6***
24D						65.7***
24D+DROP						73.1***

on the C_i/C_a ratio, but the C_i/C_a ratio was lower in the 24D+DROP leaves (Table 1).

Light and temperature conditions had the strong effect on the apparent quantum yield (α) (Fig. 2*C*). The α values were significantly lower in the 24D compared to 16D and 24D+DROP leaves within the full temperature range, but there were no differences in α between the 16D and 24D+DROP leaves at all temperatures except 10°C (Table 2). The α was affected by temperature in 16D and 24D+DROP, but not in the 24D leaves (Table 2). The temperature response of R_D displayed an exponential increase with increasing temperature (Fig. 2*D*). The differences in R_D between the 16D, 24D, and 24D+DROP leaves were significant only at 25 and 35°C (Table 2); R_D in the 24D+DROP was higher than those in the 16D and 24D leaves.

Discussion

The temperature regime significantly affected growth and photosynthetic performance of tomato plants grown under CL. Plants grown under CL and the constant temperature developed typical CL leaf injuries seen as mottled and chlorotic leaves, while the CL accompanied with the daily 2-h temperature drop had no effect on the photosynthetic processes, no injuries and even enhanced vegetative growth were observed. In noninjured leaves of the 16D and 24D+DROP plants, the total Chl concentration increased or was maintained, which was accompanied by a decrease in the Chl *a*/*b* ratio indicating the increased relative size of the LHCII (Anderson *et al*. 1988). The decreased total Chl content in the injured 24D leaves was accompanied by the elevated Chl *a*/*b* ratio. It suggests that individual PSII complexes developed smaller LHCII during CL at constant temperature and this disintegration of the antenna part of the photosynthetic machinery under CL at constant temperature also resulted in the lower F_v/F_m. Those plants showed also much lower P_N and g_s. However, despite decreasing g_s, the C_i and the C_i/C_a ratio in leaves of the 24D plants at high light were the same as in the 16D plants, which indicated that no stomatal limitation of photosynthesis occurred at 24-h day and constant temperature. The decrease in F_v/F_m values in the 24D plants reflects damage to the PSII, which appears very fast (days) after subjecting tomatoes to CL (Haque, personal communication). Degradation of photosynthetic pigments reduced the carboxylation efficiency as well as α in the 24D plants, which also corresponds to nonstomatal limitations of photosynthesis. The CL affects physiology of plants by continuously supplying energy and signals (Velez-Ramirez *et al*. 2011), which makes difficult to identify one component that is uniquely responsible for changes in photosynthetic performance of plants under CL. The daily short-term temperature drop allowed maintaining the photosynthetic rates at a level close to the 16D plants. The decrease in P_N in the 24D+DROP plants at optimal temperature might be attributed to partial stomatal closure since no indications of nonstomatal limitations to photosynthesis were observed at high light. One of the reasons of the high photosynthetic rates, the absence of the damage to PSII,

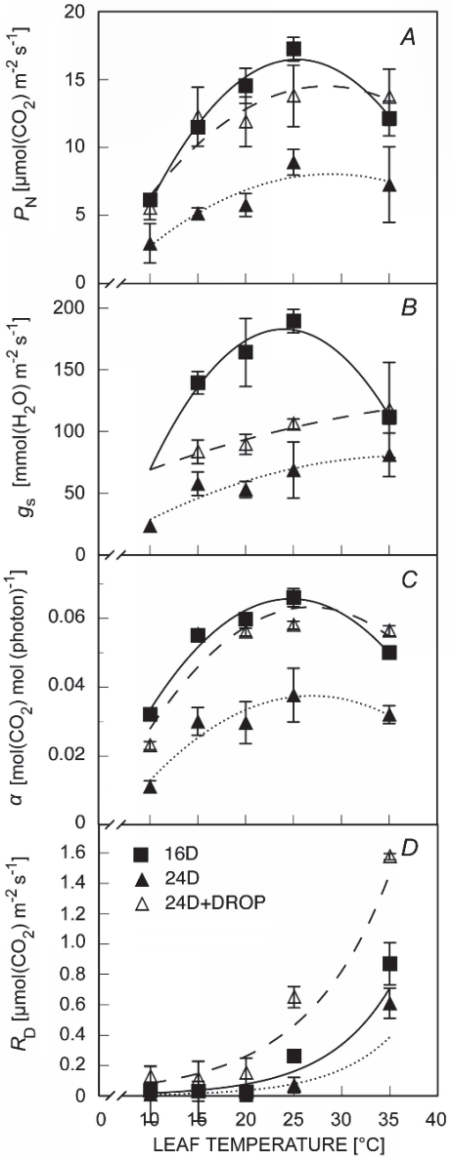

Fig. 2. The temperature response of net photosynthetic rate (P_N) (*A*), stomatal conductance (g_s) (*B*) at PPFD = 1,000 µmol m^{-2} s^{-1}, apparent quantum yield (α) (*C*), and respiration rate (R_D) (*D*) in tomato leaves grown at 16-h day and 26°C (16D), 24-h day and 26°C (24D), 24-h day, 26°C, and a daily short-term (2 h) temperature drop to 10°C (24D+DROP) on day 36. Fitted lines for 16D, 24D, and 24D+DROP, respectively, are: $y = -0.044\ x^2 + 2.27\ x - 12.38$ $R^2 = 0.98$, $y = -0.014\ x^2 + 0.86\ x - 4.40$ $R^2 = 0.88$, $y = -0.023\ x^2 + 1.343\ x - 4.65$ $R^2 = 0.87$ (P_N, *A*); $y = -0.58\ x^2 + 27.85\ x - 151.5$ $R^2 = 0.95$, $y = -0.070\ x^2 + 5.21\ x - 16.58$ $R^2 = 0.88$, $y = -0.032\ x^2 + 3.41\ x + 38.15$ $R^2 = 0.96$ (g_s, *B*); $y = -0.000\ x^2 + 0.007\ x - 0.025$ $R^2 = 0.97$, $y = -9\ E-05\ x^2 + 0.004\ x - 0.025$ $R^2 = 0.90$, $y = -0.000\ x^2 + 0.006\ x - 0.027$ $R^2 = 0.84$ (α, *C*); $y = 0.004\ e^{0.147\ x}$ $R^2 = 0.80$, $y = 0.001\ e^{0.158\ x}$ $R^2 = 0.80$, $y = 0.026\ e^{0.114\ x}$ $R^2 = 0.88$ (R_D, *D*).

and a lack of Chl degradation in CL+DROP plants might be a higher antioxidant activity induced as a result of nonspecific plant response to hardening temperature (Chapin 1991). This could also be caused by an activation of the alternative respiratory pathway reducing the production of reactive oxygen species and the Chl degradation (Van Aken *et al*. 2009). Both 24D and 24D+DROP plants inevitably experienced an imbalance between the light energy absorbed through photochemistry *vs*. the energy utilized through metabolism. At subcellular level, the restoration of donor-acceptor balance in chloroplasts of the 24D+DROP plants might be explained by the appearance of additional acceptors oxidizing electron carriers, so efficient photosynthesis can be maintained by protecting the photosynthetic electron transport chain from excess light (Noguchi and Yoshida 2008). The increase in R_D in the 24D+DROP leaves might be caused by a shift to the alternative oxidase respiratory pathway or due to differential accumulation of starch (Kjaer *et al*. 2012). Additional studies are needed to determine whether the alternative oxidase is activated by the short-term temperature drop.

At the whole plant level, photosynthetic acclimation to excessive light might be modified by the balance between assimilate sources and sinks. The daily short-term low temperature treatment under CL induced a formation of resistant ultrastructure of chloroplasts and cells, increased density of membranes, *etc.* (Klimov *et al.* 1997), accompanied by sink strengthening stabilizing the source-sink balance. Changes in the composition of photosynthetic products (mainly starch or other carbohydrates) may control the source-sink balance (Klimov *et al.* 1990). Sink strengthening may occur due to synthesis of more energy-consuming products, for example, unsaturated fatty acids, as plant respond to daily short-term exposures to low temperature by increasing the content of unsaturated fatty acids (Markovskaya *et al*. 2009). We assume that such 'product regulation' of the source-sink balance took place, when the 24D plants experienced a low temperature for a short period.

The results confirmed a complex relationship between carbohydrate metabolism, source-sink relations, and growth rate and revealed the complex dynamic processes during short-term acclimation towards altered environmental responses of plants in fluctuating environments (Kjaer *et al*. 2012). It is likely that the disturbed source-sink balance in plants grown under CL might be restored by strengthening of sinks at the different levels of plant structural hierarchy, and/or by enhancement of antioxidant activity and/or alternative oxidase activation. This study showed that the daily short-term low temperature treatments eliminated the inhibiting effect of CL on the photosynthetic performance of tomato plants.

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