Water Use Efficiency in *Cucumis sativus* L. in Response to Daily Short-Term Temperature Drop

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Abstract

This study investigates the effect of daily short-term (2 h) low temperature treatment (12 °C) (DROP) on photosynthetic water use efficiency (WUE) at leaf level of cucumber plants. The DROP treatment caused an increase of WUE in the leaves treated by DROP during their early growth (D1), but not in leaves which were already mature during the treatment (D2). The WUE increase in D1 compared to D2 leaves was due to higher net photosynthetic rate at low temperature or lower transpiration rate at common temperature. The elongation of the DROP treatment from early growth stage until full maturation of leaves did not lead to an additional increase in WUE compared to the leaves treated by DROP only during their early growth.

Keywords: water use efficiency, photosynthesis, transpiration, leaf developmental stage, low temperature

1. Introduction

Photosynthetic water use efficiency (WUE), calculated as the ratio between photosynthetic and transpiration rates, shows ability of plants to assimilate CO_2 per unit water loss (Bacon, 2004). This efficiency parameter determines whether a plant leaf optimizes the ratio of carbon gain to water transpired as environmental conditions change (Swarthout et al., 2009). The plants with higher WUE are able to assimilate more carbon at low volumes of water transpired, allowing them to safely develop under conditions of soil water deficit (Bacon, 2004). However, high WUE can constrain plant growth as a result of increased allocation of nitrogen to photosynthetic enzymes or by constricting net photosynthetic rate (Huxman et al., 2008).

The regulation of stomatal aperture is central to the water use efficiency of plants (Bacon, 2004), particularly under conditions of limited water supply (Swarthout et al., 2009; Kudoyarova et al., 2013; Cheikh M'hamed et al., 2015). Stomatal guard cells integrating environmental signals generate a stomatal aperture to optimize water loss and carbon dioxide gain under a given set of environmental conditions (Bacon, 2004). Because a decrease in stomatal conductance generates a proportionally greater decrease in transpiration than CO_2 assimilation, such variation provides the WUE increase. Furthermore, increased photosynthetic capacity may cause the WUE rise (Medek et al., 2011; Gremer et al., 2012).

The improvements in the water use efficiency act as an important special class of drought tolerance mechanisms (Jones, 2004). High WUE plants besides being more tolerant to water deficit were shown to have higher carbon gain at low temperatures with times of low evaporative demand (Gremer et al., 2012). The increased net photosynthetic rate for high WUE species was shown to associate with increased investment into electron transport relative to maximum carboxylation rate (Huxman et al., 2008). The greater sink for electron transport, helping to avoid photoinhibition and to alleviate low temperature stress for plant species (Yamori et al., 2013), is one of adjustment for acclimation of photosynthesis to low temperature (Way & Yamori, 2014). Acclimation of photosynthetic apparatus to cold has been shown to associate closely with plant cold tolerance (Rapacz et al., 2007, 2008). The adjustments, that confer cold acclimation, are strikingly similar to those that result in a high WUE score, such as changes in the balance between electron transport and carboxylation rates, structural changes at leaf level and high leaf nitrogen content (Gremer et al., 2012).

Daily short-term temperature drop (DROP) to hardening values was shown to enhance cold resistance in some plant species (Markovskaya et al., 2011). DROP-treated cucumber plants were found to have changed response of stomatal conductance to temperature (Ikkonen et al., 2012). As the DROP treatment stimulated changes in

stomatal aperture and enhanced plant cold resistance, that can be associate with an acclimation of the photosynthetic apparatus to low temperature, we suggested that photosynthetic WUE of cucumber plants may be enhanced in response to the daily short-term temperature drop.

Recent studies have found that developmental stage of leaves plays significant role in their capacity for thermal acclimation of photosynthesis (Campbell et al., 2007; Gorsuch et al., 2010). Mature leaves exposed to cold are unable to alter their structure, chemical composition, and the enzyme activity to the extent required for full adaptation (Loveys et al., 2003). Not only some photosynthetic but also transpiration modifications under stress, as was shown for condition of limited soil water supply, are dependent on the plant/leaf developmental stage (Ge et al., 2012). We hypothesized that the leaf developmental stage may be reflected in modulation of photosynthesis and transpiration losses in response to the DROP treatment and it may lead to some differences in WUE at leaf level. Therefore, the objective of this study was a comparative evaluation of photosynthetic water use efficiency in cucumber leaves which were affected by daily short-term night temperature drop during their early growth and in leaves which were already mature during the DROP treatment.

2. Materials and Methods

2.1 Plant material and Growth Conditions

Seeds of *Cucumis sativus* L., "Zozulja", were germinated in Petri dishes on filter papers moistened with distilled water placed in darkness at 28 °C for 2 d. Sixty germinated seeds were sown in 7 × 7 cm individual plastic containers with sand in a growth chamber (Vötsch, Germany). An 12 h day/12 h night temperature regime of 23/20 °C was imposed, with 60-70% relative humidity throughout and 150 µmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) provided by fluorescent tubes. Plants were watered daily, using a complete nutrient solution (based on 1 g L^{-1} Ca(NO$_3$)$_2$, 0.25 g L^{-1} KH$_2$PO$_4$, 0.25 g L^{-1} MgSO$_4$·7H$_2$O, 0.25 g L^{-1} KNO$_3$, trace quantity of FeSO$_4$ and pH 6.0-6.3). All plants were separated at four equal parts. When the second leaf was about to emerge one part of plants was shifted for 2 hours (DROP treatment) within 6 days to a growth cabinet (Snijders Microclima 1750; Snijders Scientific BV, The Netherlands) maintained at 12 °C. These plants/leaves were called D1. After completion of 6 day DROP treatment, the plants were grown at the initial conditions until full maturation of the second leaf.　The second part of plants was transferred to 12 °C for 2 hours within 6 days when the second leaf was about 70% of the area of the fully expanded leaves. These plants/leaves were called D2. During 6 day DROP treatment the D2 leaves reached maturity. The third part of plants was DROP-treated within 12 days from the day when the second leaf was about to emerge until it full maturation (D3). Warm control plants were grown similarly, but with no cold treatment. After the second leaf had fully matured (for D1 plants that were returned to initial warm conditions with no cold treatment and for D2 and D3 plants after completion of period with DROP treatment), we then quantified either rates of net photosynthesis, or a range of structural characteristics.

2.2 Measurements

Light-saturated photosynthesis (P_N), transpiration (E), stomatal conductance (g_s), the intercellular CO$_2$ concentration (C_i) and leaf vapour pressure deficit were measured on fully expanded second leaves at three temperatures (12, 23 and 38 °C) using a HCM-1000 Portable Photosynthesis System (Walz, Effeltrich, Germany). The parameters were measured on separate plants (n = 4-6) at each temperature. Readings were taken at 1200 µmol m^{-2} s^{-1}, after it had been determined that this level was saturating, but not damaging, especially for the plants experienced cold treatment. All measurements took place on leaves that had been exposed to at least 2 h of daytime illumination. Water use efficiency (WUE) was defined as the ratio of P_N to E.

After all gas exchange measurements the plants were harvested and divided into leaves, stems and roots; these were dried at 105 °C for 24 h and weighted. Before drying, total leaf area (LA) was measured with a scanner (Perfection V33, Epson, China) connected to personal computer with corresponding software (AreaS 2.1). Leaf, stem, and root dry weights were used to calculate the following: total plant dry weight (DW) (sum of leaf, stem and root dry weights), leaf weight ratio (LWR) (leaf dry weight : total plant dry weight), stem weight ratio (SWR) (stem dry weight : total plant dry weight), root weight ratio (RWR) (root dry weight : total plant dry weight). The leaf water content was calculated as the percent difference between fresh mass and oven dried mass divided by the fresh mass (Weatherley, 1950).

2.3 Statistical Analysis

Two similar trials were run. All results are presented as means ± SE (n ≥ 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 the treatments means were tested with one-way ANOVA followed the least significance

difference (LSD) test with P < 0.05 level of significance. The means were differentiated for each measurement temperatures. A two-way analysis of variance was used to test for the main effect of treatments and measurement temperature on the parameters. Correlation analysis for plant parameters and WUE was performed using Fit Model function.

3. Results

The temperature as a factor had strong effect on both the net photosynthetic rates per unit leaf area (P_N) and transpiration rate (E) (Table 1). There were significant differences between treatments in P_N, but not in E (Table 2). The rates of P_N were 50% higher in D1 and D3 than in control and D2 leaves at 12 °C (P < 0.001). The treatment had no significant effect on of P_N or E measured at 23 °C. The P_N and E rates were higher by 30 and 20%, respectively, in D3 leaves and not differed between control, D1 and D2 leaves at 38 °C.

Table 1. Statistical data (F-value and P-value) of two-way ANOVA for the leaf parameters shown in Table 2 and Figure 1

Variables	Treatment Effect		Meas. temp. Effect		Treatment × Meas. temp. Effect	
	F	P	F	P	F	P
P_N	5.19	0.0044 **	87.9	0.0000 ***	1.84	0.1197 ns
E	2.23	0.1020 ns	584.6	0.0000 ***	4.32	0.0023 **
WUE	5.20	0.0008 ***	68.0	0.0000 ***	5.40	0.0000 ***
g_s	2.90	0.0235 *	1.17	0.3180 ns	4.76	0.0001 ***
C_i/C_a	3.22	0.0135 *	67.2	0.0000 ***	4.17	0.0003 ***
DW	5.37	0.0087 *				
LA	6.91	0.0014 *				
LWR	2.24	0.1125 ns				
SWR	0.08	0.9697 ns				
RWR	1.50	0.2405 ns				

Note. Asterisks denote significance levels: *P < 0.05, ** P < 0.01, ** P < 0.001; ns, not significant; Meas. temp, measurement temperature; P_N, net photosynthetic rate; E, transpiration rate; WUE, water use efficiency; g_s, stomatal conductance; C_i/C_a, the ratio of intercellular to ambient CO_2 concentration; DW, plant dry weight; LA, leaf area; LWR, leaf weight ratio; SWR, stem weight ratio; RWR, root weight ratio.

Table 2. Net photosynthetic (P_N) and transpiration (E) rates in cucumber leaves grown at 23°C with no cold treatment (control) or treated daily by short-term (2 h) temperature drop to 12°C within 6 days when the leaves were young (D1), mature (D2) or during the period (12 days) from leaf emergence until full maturation (D3)

	Control	D1	D2	D3
P_N (µmol CO_2 m^{-2} s^{-1}) at 12 °C	4.2 ± 0.3[a]	6.3 ± 0.1[b]	4.5 ± 0.2[a]	6.3 ± 0.5[b]
P_N (µmol CO_2 m^{-2} s^{-1}) at 23 °C	10.4 ± 0.9[a]	9.6 ± 0.5[a]	10.6 ± 0.7[a]	10.9 ± 1.1[a]
P_N (µmol CO_2 m^{-2} s^{-1}) at 38 °C	9.5 ± 0.2[a]	10.2 ± 0.2[a]	9.1 ± 0.3[a]	12.2 ± 0.8[b]
E (mmol m^{-2} s^{-1}) at 12 °C	1.4 ± 0.1[a]	1.5 ± 0.1[a]	1.3 ± 0.2[a]	1.7 ± 0.3[a]
E (mmol m^{-2} s^{-1}) at 23 °C	2.9 ± 0.3[a]	2.4 ± 0.6[a]	2.6 ± 0.2[a]	2.4 ± 0.5[a]
E (mmol m^{-2} s^{-1}) at 38 °C	7.4 ± 0.6[a]	8.7 ± 0.3[b]	7.3 ± 0.1[a]	9.0 ± 0.5[b]

Note. Means ± SE (n ≥ 4). Different letters within each parameter indicate statistical differences at P < 0.05, as a result of the least significance difference (LSD) test within a one-way analysis of variance (ANOVA).

The treatment and measurement temperature as a factors had significant effect on WUE of cucumber plants (Table 1). The temperature response of WUE did not differ between the treatments (Figure 1A). The WUE values reduced when the measurement temperature decreased from 23 to 12 °C or increased to 38 °C regardless

of the treatment, at that the lowest WUE levels being reached at 38 °C. The D1 and D3 plants maintained similar WUE at all measurement temperatures. The elongation of the DROP treatment from the initial developmental stage until full maturation of leaves (D3) did not lead to an additional increase in WUE compared to D1 plants. Moreover no differences in WUE were observed between control and D2 plants. At the temperature of 23 °C the D1 and D3 plants had WUE level 30-40% higher compared to control and D2 plants. The same differences between the counterparts were maintained at 12 °C, but no significant differences in WUE between treatments were recorded at 38 °C.
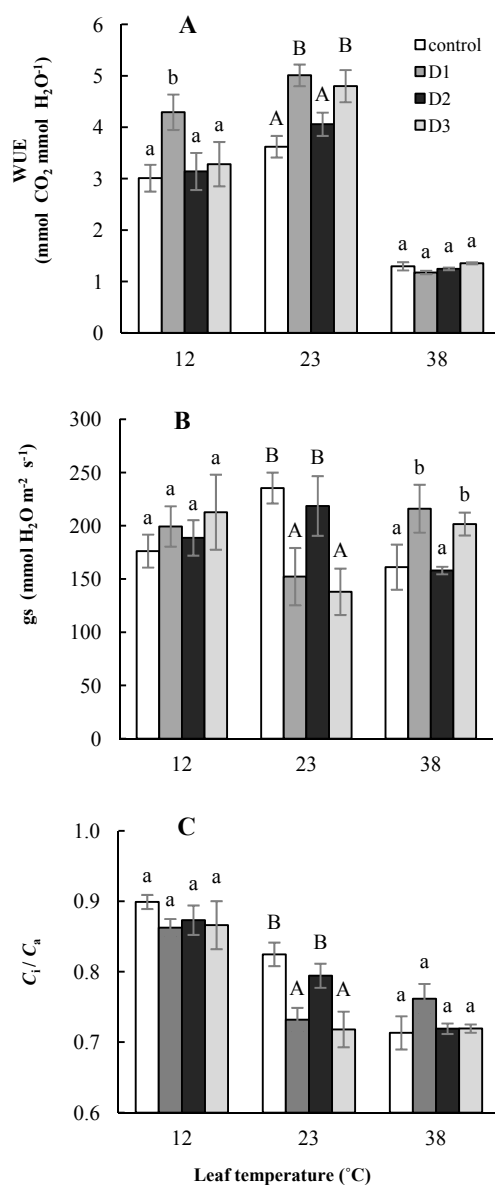

Figure 1. Water use efficiency (A), stomatal conductanse (B) and the ratio of intercellular (C_i) to ambient (C_a) CO_2 concentration (C) for cucumber leaves grown at 23 °C (control) and treated daily by short-term (2 h) temperature drop to 12 °C within 6 days when the leaves were young (D1), mature (D2) or during the period (12 days) from leaf emergence until full maturation (D3)

Table 3. Plant dry weight (DW), leaf area (LA), plant organ biomass partitioning (LWR, leaves; SWR, stems; RWR, roots) of cucumber grown at 23 °C with no cold treatment (control) or treated daily by short-term (2 h) temperature drop to 12 °C within 6 days when the leaves were young (D1), mature (D2) or during the period (12 days) from leaf emergence until full maturation (D3)

	Control	D1	D2	D3
DW (g)	1.18 ± 0.07^b	1.07 ± 0.09^{ab}	1.22 ± 0.11^b	0.86 ± 0.03^a
LA (cm^2)	514.2 ± 20.5^b	483.6 ± 41.8^{ab}	496.3 ± 60.2^b	387.0 ± 16.4^a
LWR	0.670 ± 0.011^a	0.634 ± 0.010^a	0.638 ± 0.030^a	0.650 ± 0.010^a
SWR	0.162 ± 0.006^a	0.159 ± 0.013^a	0.148 ± 0.007^a	0.172 ± 0.009^a
RWR	0.168 ± 0.07^a	0.207 ± 0.016^b	0.177 ± 0.009^a	0.197 ± 0.014^b

Note. Means ± SE (n ≥ 4). Different letters within each parameter indicate statistical differences at P < 0.05, as a result of the least significance difference (LSD) test within a one-way analysis of variance (ANOVA).

The temperature response of stomatal conductance (g_s) was different depending on the treatment (Figure 1B). When measured at 12 or 38 °C, g_s tended to decrease in control and D2 leaves and increase in D1 and D3 leaves compared to that measured at 23 °C. Growth temperature had strong effect on the g_s values (Table 1). On average, g_s was 36% lower and 24% higher at 23 °C and 38 °C, respectively, in D1 and D3, than in control and D2 leaves. There was no significant difference between the treatments when the g_s values were measured at 12 °C. Whereas the C_i to C_a ratio did not differ throughout the treatments at measurement temperatures of 12 or 38 °C, at 23 °C the D1 and D3 leaves exhibited values of C_i/C_a that were, on average, 12% lower than those of control and D2 leaves (Figure 1C).

There was significant effect of the treatments on DW and LA (Table 1). Control and D2 plants had higher DW than D3 plants (Table 3). LA was greater for control and D2 plants. There were no significant differences in LA between control and D2 plants and between D1 and D3 plants. The plants did not differ significantly in LWR, SWR and RWR between the treatments, but D1 and D3 plants tended to have larger RWR than control or D2 plants.

Table 4. Simple correlation coefficients (*r*) between the WUE values and leaf relative traits of cucumber plants

Variables	12 °C	23 °C	38 °C
P_N	0.72 *	0.11 ns	0.45 ns
E	-0.27 ns	-0.82 *	-0.11 ns
g_s	-0.20 ns	-0.82 *	-0.31 ns
C_i/C_a	-0.91 *	-0.94 *	-0.73 *
DW	-0.93 *	-0.84 *	-0.49 ns
LA	-0.86 *	-0.78 *	-0.59 *
LWR	-0.37 ns	-0.57 ns	0.62 *
SWR	-0.26 ns	-0.41 ns	0.26 ns
RWR	0.89 *	0.95 *	-0.32 ns

Note. Asterisks * denote significance levels P < 0.05; ns, not significant; P_N, net photosynthetic rate; E, transpiration rate; g_s, stomatal conductance; C_i/C_a, the ratio of intercellular to ambient CO_2 concentration; DW, plant dry weight; LA, leaf area; LWR, leaf weight ratio; SWR, stem weight ratio; RWR, root weight ratio.

Table 4 shows simple correlation coefficients between WUE and other variables. The relationships between WUE and P_N, E, g_s were strongly affected by temperature at which the parameters were measured. The WUE values had positive correlation with P_N at 12 °C and with E at 23 °C. The relation between WUE and the C_i/C_a values was similar at all measurement temperatures. DW and LA were found to be negatively correlated with WUE at all temperatures and RWR was positively correlated with WUE at 12 and 23 °C.

4. Discussion

This study sought to quantify the impact of growth temperature conditions and leaf developmental stage on water use efficiency being one of the physiological characters indicating plant adaptation to stresses. Significant differences in photosynthetic WUE were found between plants treated daily by the short-term temperature drop and non-treated plants, and that variations depended on the leaf developmental stage at the time of the treatment (Figure 1A).

The increase of the WUE values appears to be the result of enhanced photosynthesis or decreased transpiration. In this study higher WUE values for DROP plants at optimum temperature were associated with lower transpiration losses, while high WUE at low temperature were due to higher photosynthetic rates (Tables 2 and 4). The enhanced net photosynthetic rates and WUE in D1 and D3 leaves at low temperature are consistent with previous research of Gremer et al. (2012), shown that high WUE species are more efficient at processing incoming light and exhibit higher net photosynthetic rate, and these advantages are greatest at low temperature. Thus, according to Gremer et al. (2012) enhancing photosynthesis at lower temperature in DROP plants can reduce water stress by increasing photosynthetic activity at low transpiration.

The observed changes in WUE for DROP plants are consistent with physiological differences associated with photosynthetic acclimation of leaves at various stages of development. The DROP treatment caused the WUE increase when it was imposed on young, but not mature leaves. The leaves developed at low temperature have been found to exhibit enhanced metabolic rates, associated with changes in leaf morphology and anatomy (Loveys et al., 2003; Campbell et al., 2007; Gorsuch et al., 2010; Atkinson et al., 2010). Greater acclimation has been found to occur when leaves develop at low temperature in contrast to mature leaves what were shifted to low temperature (Loveys et al., 2003). In this study the reason for increased photosynthetic activity causing the WUE enhance at low temperature in D1 and D3 in contrast to D2 leaves could be in some differences in their ability to acclimate to alternating temperatures. Greater ability to acclimate to low temperature in leaves, treated by the daily temperature drop at the early stage of their development, was associated with some structural changes, such as the decrease of leaf area and increase of root weight ratio (Table 3).

At the optimum measurement temperature the P_N rates were close to similar between treatments, but the E rates tended to be lower in D1 and D3 than in control and D2 leaves, which could cause the increase of WUE. This is supported by strong negative correlation between WUE and E (Table 4). The decrease in E for D1 and D3 leaves was associated with some stomatal closing and decrease of intercellular CO_2 content (Figures 1B and 1C). The lower values of C_i/C_a ratio in D1 and D3 leaves could be not only due to the reduction of stomatal conductance, but also an active inclusion of CO_2 into the carbon metabolism. The decrease of C_i to C_a ratio in these leaves did not affect their P_N rates likely because of the increased photosynthetic capacity of DROP leaves. The stomatal conductance decrease in D1 and D3 leaves could be caused by some changes in hydraulic anatomy of plants. It was documented that plants have narrower conduit radius at the colder growth temperature (Medek et al., 2011) and even a small reduction in conduit radius may cause large reduction in vascular hydraulic conductance (Zwieniecki et al., 2001). One of the ways to maintain sufficient leaf water content in plants with narrow conduits might be partial stomatal closure (Medek et al., 2011), caused by abscisic asid (ABA) accumulation or its repartitioning in plants (Talanova & Titov, 1994; Kudoyarova et al., 2011). ABA not only controls stomatal aperture but also stimulates plant root growth (Kudoyarova et al., 2013). The D1 and D3 plants had higher RWR and WUE compared to D2 and control plants. Increased RWR, partial stomatal closure and enhanced photosynthetic capacities of leaves treated by DROP at their early developmental stage may reflect the role of ABA in WUE increase at leaf level in cucumber plants.

The control of water use could be realized not only by a modification of xylem diameter or root system biomass but also an alteration of leaf area (Blum, 2009). Since WUE is closely connected with leaf morphology (Bacon, 2004), reduced leaf area plays a role in moderation of water use by plants and allows expressing high WUE values (Blum, 2009). The inhibition of D1 and D3 leaf growth (Table 3) could limit water use of these plants resulting in increased WUE. The smaller leaf area considering as a plant response on limited water supply in soil, along with the stomatal closing, provides the rational use of water by plants (Kudoyarova et al., 2013). Furthermore, the limitation of leaf growth is often associated with higher mesophyll photosynthetic activity (Bacon, 2004), that is confirmed by this study. The negative correlation of WUE and leaf area values for all measurement temperatures (Table 3) in this study allows suggesting that reduced leaf area is one of the ways of WUE increase in leaves treated by DROP during their early developmental stage.

Despite the fact that instantaneous measures of physiological performance are not always connected with population dynamics, these measures can provide specific information on how species respond to short-term

variation in environmental conditions (Nippert et al., 2007). Daily short-term low temperature treatment, as have been shown in this study for cucumber plants, can maximize photosynthetic rates at low temperature. However, this modification of photosynthetic performance, accompanied by some structural changes at leaf and plant level, appeared only when the DROP treatment was imposed on young leaves. The differences in the response of photosynthesis to low temperature provide one of the physiological explanations for differences in plant cold tolerance. The cucumber leaves being young during the DROP treatment showed temperature acclimation of photosynthesis, which along with some structural changes, such as increased proportion of root biomass, reduced leaf area and, apparently, changed hydraulic anatomy caused the increase of water use efficiency in these plants, what theoretically reflects the enhance of plant resistance to soil water deficit. Thus, based on the results of this study, we conclude that daily short-term temperature drop can stimulate an increase of WUE at leaf level if the temperature drop was imposed on young leaves. If mature leaves experienced daily short-term low temperature the photosynthetic WUE value is not increased due to the fact that these leaves are unable to modify their structure to provide a more economical use of water. Interestingly, if young leaves experienced the DROP, the elongation of exposure of plants to short-term low temperature treatment until full leaf maturation did not lead to an additional increase in water use efficiency.

Acknowledgements

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