Effects of temperature and photoperiod on photosynthesis in everbearing strawberry

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Abstract

There is little knowledge about photosynthesis in everbearing strawberry cultivars. We therefore grew three everbearing strawberry cultivars in daylight phytotron compartments at temperatures of 9, 15, 21 and 27 °C and photoperiods of 10 h (SD) and 20 h (LD). After three weeks, the rates of dark respiration and photosynthesis and their acclimation were measured in cv. Favori. Photosynthesis of plants grown in the various conditions was measured as CO_2-uptake with an infrared gas analyzer at increasing irradiances (50-1000 µmol quanta m^{-2} s^{-1}) and temperatures ranging from 9 to 27 °C. In the dark, CO_2-production (dark respiration) increased with increasing measuring temperature and was always largest in plants grown at low temperature (9 °C) with no significant effect of photoperiod. Photosynthetic CO_2-uptake was lowest at almost all irradiances in plants grown at 9 °C, and with no clear effect of growth temperatures in the 15-27 °C range. At saturating irradiances (500-1000 µmol), CO_2-uptake increased with increasing measuring temperatures, reaching a plateau at about 21 °C for plants grown at 15-27 °C in SD and at 21-27 °C in LD. For plants grown at 15 °C in LD, the maximum CO_2-uptake rate was obtained at 27 °C. Light response curves showed that CO_2-uptake increased with increasing irradiance and measuring temperatures and that the irradiance effect was markedly enhanced by increasing growth temperature. Maximum uptake rates were lowest for plants grown at 9 °C at both photoperiods and highest for plants grown at 15 °C in SD. Comparison of plants of 'Altess', 'Favori' and 'Murano' at 500 µmol irradiance and 21 °C revealed no significant differences in photosynthetic efficiency between the cultivars. Generally, the everbearing strawberry cultivars showed considerable photosynthetic plasticity to temperature within the 9-27 °C range, although with an overall optimum at 15-21 °C.

Keywords: *Fragaria*, photoperiod, photosynthesis, temperature acclimation

INTRODUCTION

Plant growth results from interactions among different processes such as photosynthesis, respiration, long-distance transport, plant water relations, and mineral nutrition (Lambers et al., 2008). Photosynthesis implies the use of solar light energy for synthesis of complex carbon compounds, primarily sugars; the energy stored in these compounds can be used later to power cellular processes connected to growth and development (Taiz et al., 2015). Among the various factors that regulate photosynthesis, and concomitantly growth and development, those associated to the environment, i.e. temperature, photoperiod and light intensity, are predominant in species such as strawberry (Sønsteby et al., 2016). Strawberry plants, an important berry crop in Norway, has been subject of extensive research, with special focus on its physiology and genetics, and the literature in the field has been reviewed (Heide et al., 2013). Despite the extensive research available on the environmental regulation of some physiological events in strawberry such as flower bud formation and the transition from vegetative to reproductive development, the environmental regulation of vegetative growth has received less attention (Sønsteby et al., 2016). Furthermore, the literature on how different temperature and

photoperiod regimes affect photosynthesis, how this acclimates under different measuring conditions (e.g. increasing measuring temperature, irradiance and the interactions between measuring- and growing temperatures) and the possible differences between cultivars is scarce.

The increasing interest for new strawberry cultivars, such as everbearing cultivars 'Favori', 'Murano', 'Delizzimo' and 'Altess', gives the opportunity to extend the already short growing season in Norway. This, and the lack of studies on the physiological regulation of plant growth and development of these cultivars, in particular the effect of temperature and photoperiod on photosynthesis and how this acclimates to different measuring temperatures motivated this study. The aim was to test the effect of increasing growing and measuring temperatures on photosynthesis, their possible interactions and differences among three cultivars.

MATERIALS AND METHODS

Plant material and handling

Young runner plants of everbearing strawberry cultivars 'Favori', 'Murano' and 'Altess' were harvested in late April from stock plants grown in a greenhouse at a minimum temperature of 20 °C and a photoperiod of 20 h. The runners were rooted directly in 9 cm plastic pots and after 14 days they were moved in day-light compartments at the phytotron at the Norwegian University of Life Sciences at Ås (59° 40´ N, 10° 40´ E) and exposed to constant temperatures of 9, 15, 21 and 27 °C and photoperiods of 10 and 20 h. Plant trolleys were positioned randomly in the daylight rooms because of everyday movements to and from the adjacent photoperiodic treatment rooms. Temperature was controlled in all rooms to ±1 °C and a water vapor pressure deficit of 530 Pa was maintained at all temperatures.

In the light compartments, the plants received natural daylight for 10 h per day (8:00-18:00 h), with additional lighting (125 µmol quanta/m^2 s by high-pressure metal halide lamps, 400W Philips HPI-T) when the photosynthetic photon flux (PPF) fell below 150 µmol/m^2 s (as on cloudy days). Long day- treated plants got day length extension provided by low-intensity incandescent light bulbs (approximately 7 µmol/m^2 s PPF), with the dark period centered around midnight (22:00h to 2:00 h). Short day- treated plants were in the dark from 18:00 h to 8:00 h. The daylight extension amounted to less than 2% of the total daily light radiation, thus the plants receiving nearly the same daily light integral in both photoperiods.

After three weeks of temperature and photoperiod treatments, the measurements described below were performed.

CO_2 gas exchange

CO_2 exchange was measured with an infrared gas analyzer (LI-6400XT Portable Photosynthesis System) in conjunction with a leaf chamber fluorometer (Licor 6400-40) (Li-Cor, Lincoln, NE, USA). For cv. Favori, light response curves were measured by exposing the middle leaflet of the youngest fully developed leaf to red light with 10% blue light at stepwise irradiances of 0, 50, 100, 250, 500 and 1000 µmol photons/m^2 s and block temperatures of 9, 15, 21 and 27 °C. The CO_2 concentration was kept at 400 ppm. For experiment 1 with the three cultivars, the block temperature in the cuvette and irradiance was set constant at 21 °C and 500 µmol photons/m^2 s, respectively. In general, one measurement for each light level/temperature was taken after a 1-3-min, equilibration time on three plants per treatment (n=3). Quantum yield of CO_2- uptake (ϕCO_2) based on incident light was computed from the linear portion of the light response curves (0-100 µmol photons/m^2 s) using the function 'Slope' on Microsoft Excel (Microsoft, USA).

Statistical analysis

For the statistical analyses of the data, homoscedasticity and normality assumptions were tested prior to running generalized linear models (Ryan-Joiner test for normality and Levene's test for homoscedasticity), and response parameters were transformed if required. Statistical

analyses were run in Minitab v18 (Minitab Inc., State College, PA, USA). Means and standard error (± 1SE) of all studied parameters were calculated.

RESULTS

Effect of growth temperature and photoperiod on CO_2-uptake in three everbearing strawberry cultivars

The photosynthetic CO_2-uptake was lowest at 9 °C and highest at 27 °C (Figure 1). Significant differences were found for temperature and for the combined effect of temperature * photoperiod. Uptake at 9 °C was significantly lower than 27- and 15 °C, but not than 21 °C. As for the combined effect, uptakes at 27 °C/LD and 15 °C/SD were significantly higher than 9 °C/LD. No significant effect was found for the variables: cultivar and photoperiod or for the combined effect of cultivar * temperature, cultivar * photoperiod nor cultivar * temperature * photoperiod (data not shown).

Effect of growth temperature and photoperiod on CO_2-uptake in 'Favori' strawberry plants

The effect of growing temperature and photoperiod on photosynthesis, at increasing irradiances (0, 50, 100, 250, 500 and 1000 µmol) and block temperatures (9, 15, 21 and 27 °C) was tested and the results are summarized in Figure 2 and Table 1. In the dark, CO_2 production (dark respiration) increased with increasing measuring temperatures and was largest in low-temperature- grown plants (9 °C). CO_2-uptake was also lowest at almost all irradiances for plants grown at 9 °C and with an increasing trend at increasing measuring temperatures in the range 15-27 °C. Lower uptake rates than 9 °C- grown plants were seen for LD/27 °C- grown plants at irradiances of 250-1000 µmol measured at 9 °C. At saturating irradiances (500-1000 µmol), CO_2-uptake increased with increasing measuring temperatures, reaching a plateau at about 21 °C, for 15-27 °C/SD- and 21-27 °C LD- grown plants. Table 1 summarizes the results of the ANOVA.

The light response curves in figure 3 and data from Table 1 show that, in general, photosynthetic CO_2-uptake increased with increasing irradiance and measuring temperatures. The uptake rates were lowest for 9 °C- grown plants regardless of the photoperiod, except at 9 °C measuring T for 27 °C- grown plants. At 500 µmol irradiance, the maximum uptake was obtained for at 15 °C growing T in SD at all measuring T (highest recorded was 13.57 µmol/m^2 s). For LD-grown plants the maximum uptake seen was at a growing T of 21 °C and measured in the range 15-21 °C. At 27 °C measuring T, the maximum uptake was observed for 15 °C- grown plants in both SD and LD. At the maximum irradiance tested, 1000 µmol, the highest mean uptake was about 11% higher than at 500 µmol, that is 15.2 µmol/m^2 s for 15 °C/SD- grown plants measured at 27 °C. For dark respiration, no significant effect of photoperiod was obtained. The effect of growing- and measuring temperatures and their interaction was significant (Table 1), the values being the largest for 9 °C- grown plants, measured at 27 °C, and the lowest for 27 °C- grown plants measured at 9 °C. As for the interaction between growing and measuring T, plants grown at 9-15 °C, measured at high temperatures (21-27 °C) were significantly different from the rest of the combinations (mean values ranged from -3.1 to -2.57 µmol/m^2 s).

Similarly, no significant effect of photoperiod was found for CO_2-uptake at saturating irradiances (500-1000 µmol) and the effects of growing and measuring T, their interaction and the interaction growing T * photoperiod were significant (Table 1). As shown in Figure 2, upper and lower panels at 1000 µmol/m^2 s, there was a combined effect of measuring and growing temperature. At 9 °C measuring T, differences in uptake rates were considerably smaller between all growing T than at 27 °C. At higher measuring T, 15-27 °C- grown plants had significantly higher rates than 9 °C- grown plants (13.41-15.20 and 6.9- 7.94 µmol/m^2 s, respectively) for both photoperiods. The quantum yield of CO_2-uptake increased with increasing measuring temperatures for SD-grown plants and 9-15 °C/LD- grown plants. However, no significant effect of temperatures (neither growing- nor measuring) was obtained.

Table 1. Dark respiration, photosynthesis and quantum yield of CO_2-uptake in 'Favori' strawberry plants grown at various temperatures and photoperiods and measured at increasing temperatures. ϕCO_2 was computed from the linear portion of the light response curves (0-100 µmol photons m^{-2} s^{-1}).

			PPFF (µmol photons m^{-2} s^{-1})			
Measuring T (°C)	**Growth T (°C)**	**Photoperiod (h)**	**Dark respiration**	**500**	**1000**	**ϕCO_2**
9	9	SD	-1.62_{bcd}	5.03_{de}	6.74_{fg}	0.042
9	15	SD	-0.99_{ab}	7.72_{cd}	8.74_{def}	0.058
9	21	SD	-0.66_{a}	4.96_{de}	6.42_{fg}	0.043
9	27	SD	-0.73_{a}	5.10_{e}	5.00_{g}	0.048
15	9	SD	-1.77_{cd}	6.99_{cd}	7.60_{def}	0.048
15	15	SD	-1.12_{bcd}	11.51_{ab}	12.17_{bc}	0.065
15	21	SD	-1.23_{abc}	8.91_{b}	9.62_{cd}	0.061
15	27	SD	-1.01_{ab}	9.58_{bc}	9.92_{cde}	0.063
21	9	SD	-2.65_{e}	6.59_{cd}	7.38_{def}	0.049
21	15	SD	-2.49_{e}	13.36_{a}	14.85_{ab}	0.069
21	21	SD	-1.73_{cd}	12.48_{a}	13.86_{ab}	0.065
21	27	SD	-1.28_{abcd}	12.85_{a}	13.99_{ab}	0.064
27	9	SD	-2.82_{e}	5.72_{de}	6.90_{efg}	0.049
27	15	SD	-2.47_{e}	13.57_{a}	15.20_{a}	0.062
27	21	SD	-1.89_{cd}	12.79_{a}	14.39_{ab}	0.065
27	27	SD	-1.89_{d}	12.49_{a}	13.61_{ab}	0.066
9	9	LD	-1.28_{bcd}	5.53_{de}	6.10_{fg}	0.044
9	15	LD	-1.09_{ab}	6.27_{cd}	6.97_{def}	0.051
9	21	LD	-0.75_{a}	6.12_{de}	6.86_{fg}	0.050
9	27	LD	-0.58_{a}	4.50_{e}	4.97_{g}	0.045
15	9	LD	-1.68_{cd}	7.58_{cd}	8.39_{def}	0.052
15	15	LD	-1.59_{bcd}	10.15_{ab}	10.70_{bc}	0.063
15	21	LD	-1.21_{abc}	10.42_{b}	11.16_{cd}	0.064
15	27	LD	-0.87_{ab}	8.37_{bc}	9.40_{cde}	0.059
21	9	LD	-3.20_{e}	7.92_{cd}	8.59_{def}	0.055
21	15	LD	-2.73_{e}	9.99_{a}	10.94_{ab}	0.061
21	21	LD	-1.70_{cd}	12.61_{a}	13.63_{ab}	0.068
21	27	LD	-1.30_{abcd}	12.12_{a}	13.35_{ab}	0.064
27	9	LD	-3.30_{e}	6.68_{de}	7.94_{efg}	0.055
27	15	LD	-2.73_{e}	12.23_{a}	14.01_{a}	0.064
27	21	LD	-1.80_{cd}	11.81_{a}	13.03_{ab}	0.058
27	27	LD	-1.90_{d}	12.18_{a}	13.41_{ab}	0.061
Probability level of significance (ANOVA)*						
Source of variation						
Growing T (A)			<0.005	<0.005	<0.005	n.s.
Measuring T (B)			<0.005	<0.005	<0.005	n.s.
A * B			<0.005	<0.005	<0.005	n.s.
Photoperiod (C)			n.s.	n.s.	n.s.	n.s.
A * C			<0.005	n.s.	n.s.	n.s.
B * C			n.s.	n.s.	n.s.	n.s.
A * B * C			n.s.	n.s.	n.s.	n.s.

Data are means of three replicates (n=3). Means within the same column that do not share a letter are significantly different (*P*-value≤ 0,005). n.s. not significant.

DISCUSSION

Effect of growth temperature and photoperiod on CO_2-uptake in three everbearing strawberry cultivars

CO_2-uptake rates for the three cultivars tested were similar and no significant differences were obtained between them. This may indicate that the photosynthetic system of these cultivars responds similarly, and that extrinsic factors such as temperature may be more important to photosynthesis than genotype (remembering that these cultivars are genetic variations of the same species, namely *Fragaria x ananassa*). The effect of growing temperature on uptake and the combined effect of temperature and photoperiod were significant. Uptake for 9 °C-grown plants was significantly lower than for 15-27 °C-grown plants. Since photosynthetic CO_2-uptake is driven by enzymatic reactions, at low temperatures, the rate of the enzymatic reactions is lower (Taiz et al. 2015), so that plants grown at low temperatures may acclimate their photosynthetic machinery to a lower thermal optimum than high-temperature-grown- plants. In addition, it may take some time before their photosynthetic functions are acclimated to higher temperatures, i.e. increase their thermal optimum to CO_2 assimilation (Bunce, 2000). Since in the present study photosynthesis was measured at 21 °C, just a couple of minutes after taking the plants out of the growing chambers at their respective temperatures, the lack of a long enough acclimation period may account for the low values obtained. Increasing growing temperatures in the range of 15-21 °C gave increased uptake, and from 21- to 27 °C a slight decrease (Figure 1). Similarly, increasing temperatures promote enzymatic activity leading to CO_2-uptake, so an increased uptake is expected, especially when the temperature at which photosynthesis was measured (21 °C) is in the range of growing temperatures for the plants studied (15-27 °C).

Effect of growth temperature and photoperiod on CO_2-uptake in 'Favori' strawberry plants at increasing irradiances and measuring temperatures

Photosynthesis at increasing irradiances in the range 0-1000 µmol, increased linearly from dark until reaching a plateau (Figure 2). In the dark (0 µmol m^{-2} s^{-1}), CO_2-uptake was negative because no photosynthesis occurs, and mitochondrial respiration continued, producing CO_2 instead (Taiz et al. 2015). The significant effect obtained of the growing and measuring temperature and their interactions on dark respiration was expected, as it has been reported in the literature (Taiz et al. 2015). The highest respiration values were found at increasing measuring temperatures, for low temperature- grown plants, or decreasing for high temperature-grown plants (Figure 2). Similar results have been reported by Keys et al. (1977) and Lawlor et al. (1987) for wheat plants grown under controlled environment.

The effect of measuring and growth temperature on quantum yield was not statistically significant, this meaning that the plants tested had similar efficiencies of CO_2 uptake in the light limiting part of the light response curves. However, there was a clear significant effect of measuring and growing temperatures on CO_2-uptake at saturating irradiances (Figure 3, 500-1000 µmol, Table 1). As for the results discussed above for the three cultivars measured at 500 µmol and 21 °C, uptake increased with increasing measuring and growing temperatures. Increasing measuring temperatures in the range 15-27 °C for plants grown in the same temperature range resulted in increasing CO_2 assimilation. Increased rate of enzymatic activity due to increased temperature may be the reason for these results. In addition, the maximum photosynthetic CO_2- uptake rates were obtained for 15 °C grown plants measured at 27 °C, a range of temperatures previously reported by Bunce (2000) as the optimum among eight cool and warm climate herbaceous crops and weed species grown at 15 and 25 °C.

CONCLUSIONS

The following conclusions can be drawn from the present study:

- Dark respiration increased with increasing measuring temperature and was always largest in plants grown at 9 °C.
- Photosynthetic CO_2-uptake was lowest at almost all irradiances in plants grown at 9 °C.
- At saturating irradiances (500-1000 μmol), CO_2-uptake increased with increasing measuring temperatures, reaching a plateau at about 21 °C for plants grown at 15-27 °C in SD and at 21-27 °C in LD.
- Light response curves showed that CO_2-uptake increased with increasing irradiance and measuring temperatures and that the irradiance effect was markedly enhanced by increasing growth temperature.
- The everbearing strawberry cultivars tested showed considerable photosynthetic plasticity to temperature within the 9-27 °C range, although with an overall optimum at 15-21 °C.

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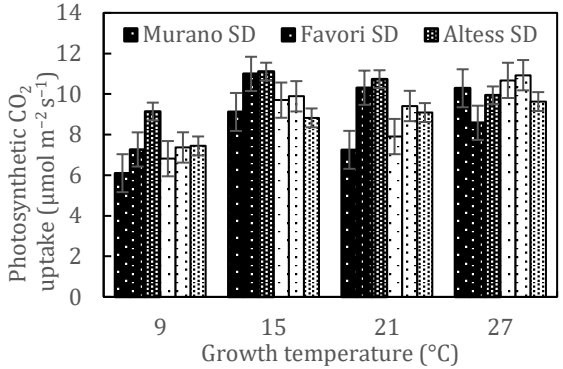

Figure 1. Photosynthetic CO_2- uptake in three everbearing strawberry cultivars grown at 9, 15, 21 or 27 °C in 10 (SD) or 20 h (LD). Vertical bars on each column represent standard errors, n=3.

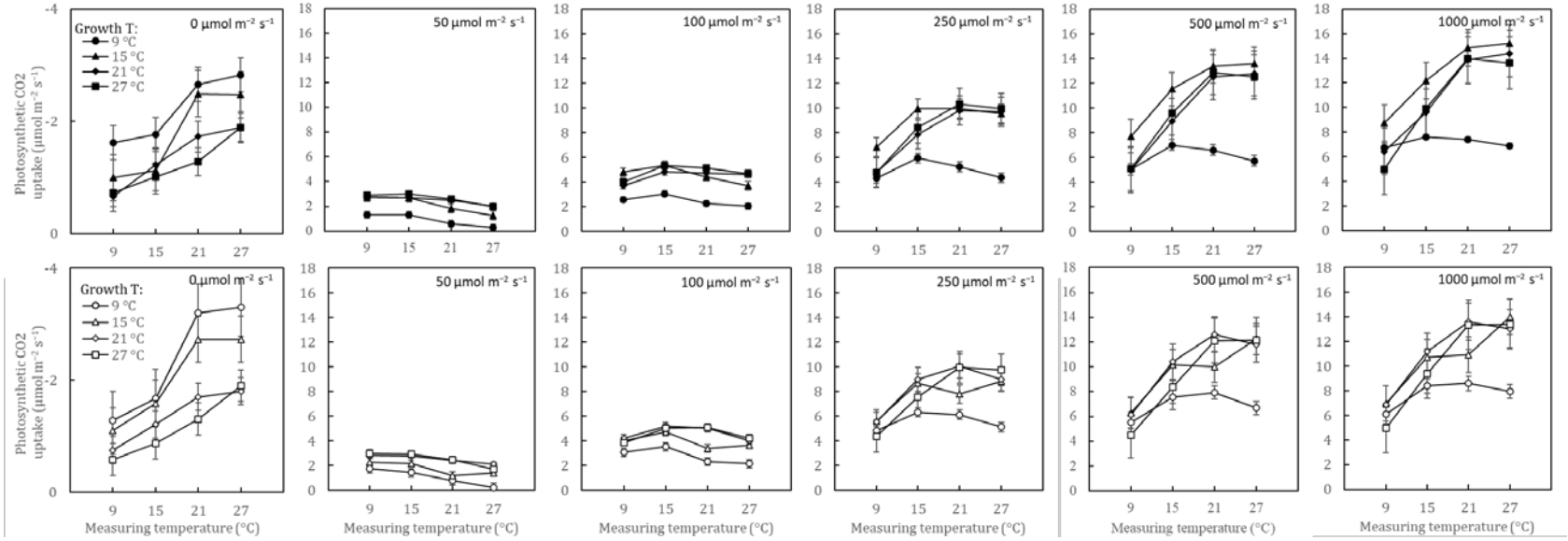

Figure 2. Courses of photosynthetic CO_2-uptake at increasing irradiances from 0 to 1000 µmol, measured at various temperatures in 'Favori' strawberry plants grown at 9, 15, 21 or 27 °C in 10 (SD) or 20 h (LD). Upper and lower panels correspond to plants grown in SD (filled symbols) and in LD (open symbols), respectively. Error bars represent ±standard errors, n=3.

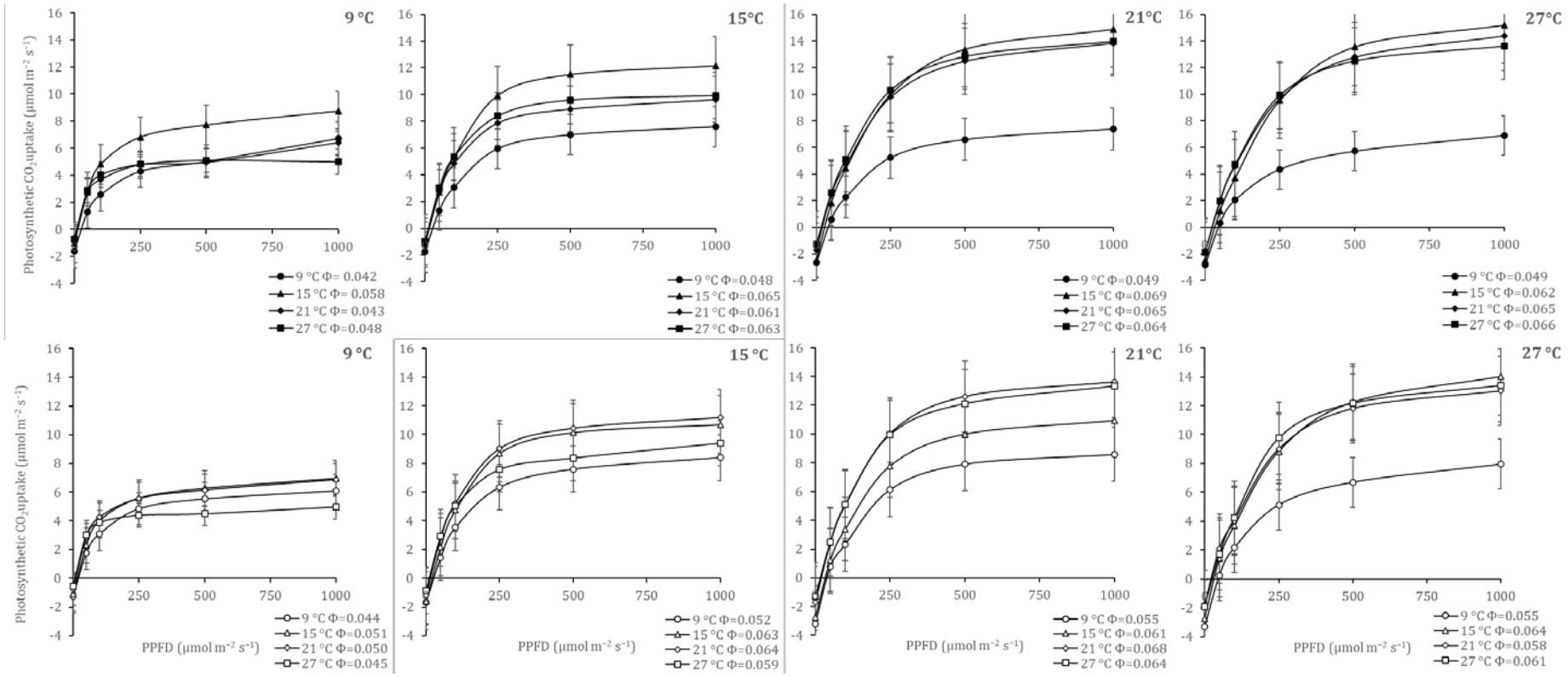

Figure 3. Light response curves for 'Favori' strawberry plants grown at various temperatures and photoperiods (each panel correspond to a given temperature/photoperiod combination), measured at increasing temperatures. Upper panels correspond to plants grown in 10 h (SD, filled symbols), lower panel correspond to plants grown in 20 h (LD, open symbols) photoperiod. Vertical bars on each point represent ±standard errors, n=3.