

# Leaf photosynthesis, plant growth, and carbohydrate accumulation of tomato under different photoperiods and diurnal temperature differences



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## ABSTRACT

Effects of continuous lighting (CL) with or without a diurnal temperature difference (DIF) on leaf photosynthesis, plant growth and development, and carbohydrate accumulation were investigated with tomato. Plants were grown for four weeks under a photoperiod of 12 h d<sup>-1</sup> or CL of 24 h d<sup>-1</sup>, each combined with a DIF of 10 or 0 °C. Measurements included: leaf net photosynthetic rates, the maximal quantum efficiency of PSII, growth analysis, and quantification of leaf carbohydrates. Severe and moderate CL-induced injury was found on leaves grown under CL with a DIF of 0 and 10 °C, respectively, while it was not observed for plants under 12 h d<sup>-1</sup> photoperiod. On the other hand, the apparent severity of the CL-induced injury was not necessarily correlated with leaf net photosynthetic rates. At the initial treatment phase, CL reduced the light-limited photosynthesis while zero DIF reduced the light-saturated photosynthesis, suggesting that CL and zero DIF independently affected different processes in leaf photosynthetic metabolism. Thereafter, CL and zero DIF additively reduced both the light-limited and -saturated photosynthesis. Net photosynthetic rate of leaves under the respective growth conditions were also lowered under CL and/or zero DIF. Such reductions of leaf photosynthesis were reflected in dry matter production at the whole-plant level through decreases in net assimilation rate. Analysis of leaf carbohydrate contents revealed that apparent severity of the CL-induced injury was associated with the diurnal turnover of soluble sugars, suggesting it to be a factor possibly causing the injury.

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## 1. Introduction

Crop productivity is often limited by a shortage of light during a prolonged series of cloudy days, especially in winter. In greenhouse crop production, supplemental assimilation lighting using artificial light sources can be employed, which extends the photoperiod per day and compensates for an insufficient amount of light for photosynthesis in the daytime. On the other hand, excessively long photoperiods such as continuous lighting (CL) to create a 24 h d<sup>-1</sup> photoperiod are known to cause visible mottled chlorosis-like physiological disorders, referred to as CL-induced injury (Valez-Ramirez et al., 2011), which appears in the intervein areas on the

leaves of some crop species (Arthur et al., 1930; Nilwik, 1981; Tibbitts et al., 1990; Vlahos, 1990; Warrington and Norton, 1991; Murage et al., 1996). Tomato is one of the species that is most susceptible to long photoperiods (Hillman, 1956), and the injury is observed in plants grown under photoperiods longer than 20 h d<sup>-1</sup> for several weeks (Demers et al., 1998). Plant growth and yields under CL are lower than those under a 14-h photoperiod, associated with the occurrence of injury (Demers et al., 1998). The growth and yield reductions are reportedly associated with decreases in leaf photosynthetic rate, chlorophyll (Chl) content and the activity of sucrose phosphate synthase (for a review, see Demers and Gosselin, 2002). Although there have been numerous intensive studies of CL-induced injury to date (for a review, see Valez-Ramirez et al., 2011), the detailed mechanism for the reduction of leaf photosynthesis and plant growth associated with the occurrence of CL-induced injury is not fully understood. It has been suggested that the occurrence of CL-induced injury is related to excess carbohydrate (sugars and/or starch) accumulation (for a review, see Valez-Ramirez et al., 2011), although it is still unclear whether there is a direct causal

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relationship between the extent of carbohydrate accumulation and CL-induced injury.

On the other hand, CL-induced injury is not observed in tomato under CL when a diurnal temperature difference (DIF) of 30/17 °C exists for 16/8 h or 8/16 h (Hillman, 1956). A similar result was also reported in tomato (Ohshima et al., 2005) and other crop species including eggplant (Murage et al., 1997) and potato (Tibbitts et al., 1990; Cao and Tibbitts, 1992; Cushman et al., 1995). The combination of CL with a DIF may thus be a good experimental system that enhances our understanding of the mechanism of CL-induced injury and its relation to leaf photosynthesis. To the best of our knowledge, there has been no research on the interactive effect of photoperiod and DIF on leaf photosynthesis of crops except for work done by Rowell et al. (1999) in peanut plants. They reported that the CO<sub>2</sub>-response curve of the leaf photosynthetic rate measured at a relatively low (250–500 μmol m<sup>-2</sup> s<sup>-1</sup>) photosynthetic photon flux density (PPFD) in plants grown under CL with a DIF of 28/22 °C and 28/28 °C for 12/12 h did not significantly differ. Nevertheless, they did not explore detailed photosynthetic characteristics. Further experiments focusing on the interaction of CL and DIF on leaf gas exchange are required. We have recently reported a preliminary result of our work on the relationship between gas-exchange characteristics *in vivo* and the amounts of some biochemical components of photosynthesis *in vitro* in tomato leaves grown under different photoperiods and DIFs (Matsuda et al., 2012). The result showed, however, that the difference in leaf gas-exchange rate was not explained by the differences in Chl, ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) or the nitrogen content.

It has been pointed out by many researchers that photosynthesis at the single-leaf level cannot solely account for dry matter production or growth at the whole-plant level (Stitt and Schulze, 1994; Lawlor, 1995; Poorter and Nagel, 2000). Therefore, investigating only leaf photosynthesis would not provide enough information for us to understand the mechanism of the reduction of dry matter production at the whole-plant level due to CL and its recovery by a DIF. Plant growth is often evaluated through the growth analysis (Poorter and Garnier, 1996) using the relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA). It is not well known how the interaction of photoperiod and DIF affects growth and development, especially how leaf photosynthesis and the morphological aspects contribute to plant dry matter production under CL with or without a DIF. More research focusing on the leaf- and plant-level responses and the relationship between them is needed.

The objectives of this work were to understand the responses of leaf photosynthesis and plant growth and development to CL with or without a DIF. We grew tomato plants for four weeks under a photoperiod of 12 h d<sup>-1</sup> or CL, each condition combined with a DIF of 10 or 0 °C. A treatment with differences in PPFD and temperature between daytime and nighttime was considered as the control, and treatments with either a constant PPFD or a constant temperature throughout the day, or both, were compared with the control. Gas-exchange rates of leaves were measured under the light-limiting and light-saturating conditions as well as under the respective growth conditions. The maximum quantum efficiency of photosystem II (PSII) was also determined to assess the damage done to photosynthesis. At the whole-plant level, the growth analysis was carried out to clarify how the leaf gas-exchange characteristics and morphology as affected by photoperiod and DIF during cultivation were related to plant growth. In addition, sugar and starch contents in leaves were quantified and their turnover during nighttime were calculated to find the relationship between carbohydrate accumulation or turnover and the severity of CL-induced injury.

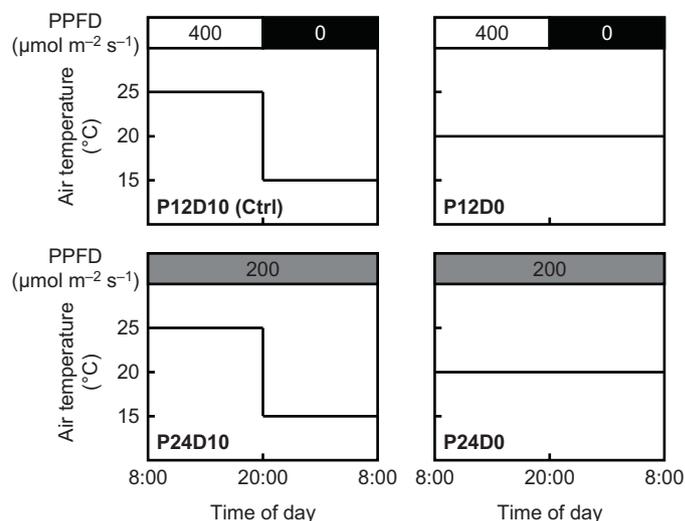


Fig. 1. Schematic diagram of diurnal changes in photosynthetic photon flux density (PPFD) and air temperature for the treatments.

## 2. Materials and methods

### 2.1. Plant material and growth conditions

Tomato (*Solanum lycopersicum* 'Momotaro Fight', Takii Co., Ltd., Kyoto, Japan) seeds were sown into plug trays filled with a commercial substrate (Best Mix No. 3, Nippon Rockwool Co., Tokyo, Japan), germinated, and grown in a temperature-controlled room equipped with fluorescent tubes (FLR110H-N/A/100, Toshiba Lighting & Technology Co., Kanagawa, Japan). The room was maintained at 150 μmol m<sup>-2</sup> s<sup>-1</sup> PPFD at the plant level, under a 12 h d<sup>-1</sup> photoperiod, with 25/20 °C day/night temperatures. The trays were subirrigated once daily with tap water before germination and with a nutrient solution (Otsuka House Solution Recipe A, Otsuka AgriTechno Co., Ltd., Tokyo, Japan) adjusted to an electrical conductivity of 1.3 dSm<sup>-1</sup> after germination. On 21 d after seeding (21 DAS), each seedling was transplanted to a 1.2-L plastic pot filled with the same substrate and transferred to a temperature-controlled growth chamber equipped with fluorescent tubes (FPL55EX-N, Iwasaki Electric Co. Ltd., Tokyo, Japan) to impose treatments described below.

### 2.2. Treatments

Four treatments imposed on 21 DAS consisted of the combination of two photoperiods of 12 h d<sup>-1</sup> (P12) and 24 h d<sup>-1</sup> (P24) and two DIFs of 10 °C (25/15 °C, D10) and 0 °C (20/20 °C, D0) for a 12/12 h day/night cycle (Fig. 1). A photoperiod of 12 h d<sup>-1</sup> was selected because no negative effects of the photoperiod itself on tomato plants were reported so far. In the present study, 8:00–20:00 and 20:00–8:00 were defined as daytime and nighttime, respectively. P12D10 was the control. The PPFD was adjusted with shade cloths and was set at 400 and 200 μmol m<sup>-2</sup> s<sup>-1</sup> at the plant level for the P12 and P24 treatments, respectively. The daily mean PPFD (200 μmol m<sup>-2</sup> s<sup>-1</sup>) and temperature (20 °C) were thus identical irrespective of treatment. Fresh air was supplied into the chambers using air pumps in order to keep them at a CO<sub>2</sub> concentration close to the atmospheric level. The plants were supplied, depending on their growth, with 50–400 mL of the nutrient solution as described above, once daily or every other day.

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