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Effects of diurnal temperature alternations and light quality on growth, morphogenesis and carbohydrate content of *Cucumis sativus* L.

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ABSTRACT

The effects of the difference (DIF) between day/night temperature (DT/NT) and end-of-day (EOD) light quality on growth, morphology, dry matter (DM) content and carbohydrate status in cucumber (*Cucumis sativus* L.) were examined. Plants were grown under a 12 h high light intensity period and DT/NT of 25/19 °C (positive DIF) or 19/25 °C (negative DIF) in combination with an exposure of 30 min EOD-red (EOD-R) or far-red (EOD-FR) light. A significant interaction between DIF and EOD light quality was found on morphology, DM and carbohydrate content in axial plant organs like stems and petioles, but not in leaf blades and roots. Positive DIF induced taller stems, and higher DM and carbohydrate content than negative DIF when the plants were grown under EOD-R. The stems developed under EOD-FR were tall and accumulated the highest content of DM and carbohydrates and only small differences were found between positive DIF and negative DIF. Under EOD-R a higher content of glucose and fructose was found under positive than negative DIF, while EOD-FR light resulted in a high glucose and fructose content under both positive and negative DIF and thereby equalized the effect of the two temperature treatments. The results show that positive DIF can induce similar responses in elongation growth, DM and carbohydrate accumulation as EOD-FR, and further that phytochrome status interact with the responses to alternating DT and NT.

1. Introduction

Temperature and light climate are important environmental factors that can be altered under greenhouse production in order to substitute the use of growth retardants for controlling plant height. Diurnal temperature alternation is found to regulate plant morphogenesis in many species (reviewed by Myster and Moe, 1995). Day temperature (DT)/night temperature (NT) alternation can be described as the difference (DIF) between DT and NT (DT minus NT) (Erwin et al., 1989). A higher NT than DT is termed negative DIF, while lower NT than DT is referred to as positive DIF. Stem elongation is usually suppressed when plants are grown under negative DIF compared to constant temperature (zero DIF) or positive DIF. Also, a short temporary drop in temperature in the early morning or during the last 2 h of the night has similar effects as negative DIF in some plants. Negative DIF and drop strategies have been successfully used as practical tools to control stem elongation in several horticultural crops (Erwin and Heins, 1995; Myster and Moe, 1995).

Studies have shown that thermoperiodic responses can be modified by light climate, like photoperiod (Grindal, 1997) and light intensity (Myster, 1999; Catley et al., 2002). Also, a distinct interaction between light quality and DIF on stem elongation is demonstrated in several plant species. Continuous day-extension or an end-of-day (EOD) treatment with far-red (FR) light or incandescent light with a low R/FR ratio almost overcame the reduction in stem elongation under negative DIF in *Campanula isophylla* (Moe et al., 1991), *Fuchsia* × *hybrida* (Erwin et al., 1991), *Pisum sativum* (Grindal, 1997), *Arabidopsis thaliana* (Thingnaes et al., 2008) and cucumber (Xiong et al., 2002; Patil et al., 2003; Patil and Moe, 2009). Recently, Patil and Moe (2009) have shown that screening daylight through light quality selective plastic film in combination with negative and positive DIF treatments reduced stem, hypocotyls and internodes lengths in the cucumber plants by 45–50% under plastic films creating a high R/FR ratio of 1.6 compared to the control film with R/FR ratio of 1.1. The physiological mechanisms underlying the interaction between DIF and R/FR light regime is not well understood. However, the phytochrome is assumed to play a central role in control of thermoperiodic elongation growth. Mutant analyses suggest that phytochrome B (PhyB) is required for a maximum effect of daily temperature alternations on stem elongation in *A. thaliana* (Thingnaes et al., 2008) and cucumber (Xiong et al.,

Abbreviations: DIF, difference between day temperature (DT) and night temperature (NT); DM, dry matter; EOD, end-of-day; FR, far-red light; GA, gibberellin; LAR, leaf area ratio; NAR, net assimilation rate; Negative DIF, DT < NT; Positive DIF, DT > NT; R, red light; RGR, relative growth rate; RI_{DIF}, DIF response index = (negative DIF/positive DIF) × 100; WT, wild type.

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2002; Patil et al., 2003; Patil and Moe, 2009). PhyB is known to play a major role in the R:FR ratio signal perception that leads to shade avoidance responses (Smith and Whitelam, 1997).

Light quality, and particularly R and FR light, is also known to strongly influence the dry matter (DM) partitioning and carbohydrate accumulation (Kasperbauer, 1971, 1987; Ranwala et al., 2002). However, limited information is available on the effects of DIF on distribution of DM and carbohydrates in different plant parts. Division and expansion of cells are closely related to the carbon status of the plant and changes in elongation rate are classically associated with changes in carbohydrate concentration (for review see Madore and Lucas, 1995; Pontis et al., 1995). Carbohydrates also regulate a large number of enzymes, including those involved in carbon metabolism (Ho et al., 2001) as well as enzymes in the cell cycle (Riou-Khamlichi et al., 2000).

This study was conducted to further investigate the interaction between DIF and light quality in cucumber. The aim of the present study was to examine how the DIF response is modified by an EOD light condition on the regulation of growth, morphology, DM and carbohydrate distribution of the plant. Cucumber is highly responsive to both DIF and EOD-R and FR light and thus an ideal model species for interaction studies. The plants were grown in a soil-less growing system making it possible to study biomass distribution of whole plants including roots.

2. Materials and methods

2.1. Plant material and growing conditions

Seeds of cucumber were soaked on wet filter paper for one day, and planted in 11 cm diameter plastic pots with 1 vermiculite:1 perlite (v/v) mixture. The seedlings were grown at 20 °C for two days and then transferred to growth chambers where either positive DIF (DT/NT of 25/19 °C) or negative DIF (DT/NT of 19/25 °C) were established. The sensor for air temperature and humidity was placed at the canopy level and the microclimate controlled and recorded by a PRIVA environmental computer. The actual temperature varied ±0.5 °C from the set point temperature. The water vapour deficit was 0.50 kPa with a maximal deviation of ±0.10 kPa. During a 12 h photoperiod the photosynthetic photon flux density (PPFD) was 200 μmol m^{-2} s^{-1} (Li-Cor, Model LI-250, USA) at the top of plants. The light was provided by fluorescent lamps (F96T12/CW/1500, General Electric, USA) and enriched with light from incandescent bulbs (OSRAM, 60W, Norway) to establish a R/FR ratio of 1.7 (Skye Instruments Ltd., 660/730 Radiation Detector and Measuring Unit, UK). A 30 min EOD-R (Philips TLD 36W/15), or FR treatment (0.8 μmol m^{-2} s^{-1}, detected by 660/730 Radiation Detector and Measuring Unit, Skye Instruments Ltd., UK) was given immediately after the 12 h lighting period. The EOD-FR light was supplied by FR fluorescent light tubes, No. 7080 (Sylvania BioSystems, van Lieburg & Kendrick, 1996), wrapped with red (Primary red, No. 106, LEE filters, UK) and green plastic filters (Dark green, No. 124) in order to remove peaks in the blue light region. Spectral distribution of the R and FR light was measured between 450 and 900 nm by a Spectra Wiz spectrometer (Model EPP 2000 Fiberoptic, Stellarnet Inc., Tampa, FL, USA) (Fig. 1). The plants were watered twice a day during the first two weeks of growth and then three times a day until harvest with a complete nutrient solution (EC was 2.0 mS cm^{-1}, and pH ranged from 5.5 to 6.0).

2.2. Growth and morphology analysis

Two weeks after the plants were transferred to the growth chambers, leaf area was measured by an area meter (Li-Cor, Model 3100 area meter, USA), and hypocotyl, stem, petiole and internode length were recorded. Leaf blades, cotyledons, stems, leaf petioles and roots were oven-dried separately at 80 °C for 4 days. Relative growth rate (RGR), net assimilation rate (NAR), leaf area ratio (LAR) were calculated as described by Pearcy et al. (1989). Stem length was defined as the height of the plant from the growth medium line of the pot to the tip of the uppermost shoot. Average internode length was calculated by dividing stem length subtracted the hypocotyl length by leaf number minus one. The growth and morphology experiment was carried out three times with 10–12 plants in each treatment and replicate.

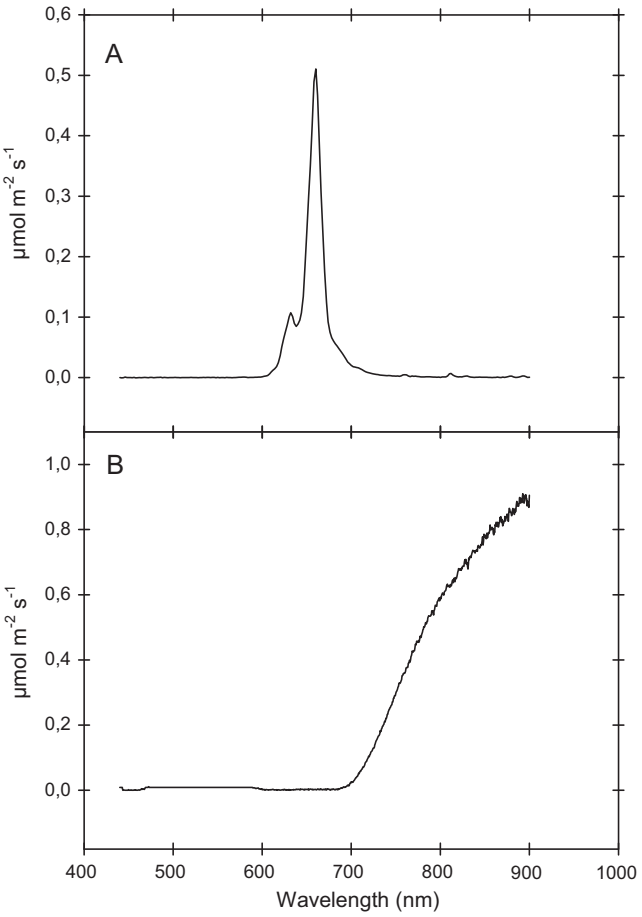

Fig. 1. Spectral distribution of the light sources used during 30 min EOD-R (A) and EOD-FR (B) exposure measured between 450 and 900 nm by a Spectra Wiz spectrometer.

2.3. Carbohydrate measurements

Samples for carbohydrate analysis were collected at the end of the dark period and frozen in liquid nitrogen. The procedures for soluble carbohydrate extraction and analysis were similar to those outlined by Miller and Langhans (1989) with some modifications. Briefly, frozen leaf blades (mixture of mature and immature leaves), stems and roots were homogenised in 70% ethanol and grounded with an agate mortar in liquid nitrogen. The slurry was shaken for 3 h. An aliquot of the extract was dried to remove the ethanol, dissolved in water and cleaned by passing through an ion exchange cartridges (SPE C18, SPE SAX) and a membrane filter. The supernatants were immediately used to analyse for stachyose (tetrasaccharide), raffinose (trisaccharide), sucrose (disaccharide), glucose, galactose, fructose and inositol (monosaccharide) by injecting the sample into a HPLC system (Interface/software D-6000, pump L-6200, autosampler AS-4000, column oven L-5025,