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Effects of temperature and watering regime on growth, gas exchange and abscisic acid content of canola (*Brassica napus*) seedlings

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ABSTRACT

Global climate change, including global warming, will likely reduce soil moisture in many parts of the world. Few studies have examined the combined effects of temperature and watering regime on plant growth and physiological parameters, on time-course basis in early developmental stages. We grew canola (*Brassica napus* L. cv. 45H72) plants under lower (22/18 °C) and higher (28/24 °C) temperature regimes in controlled-environment chambers. One half of the plants were watered to field capacity and the other half at wilting point. In three separate experiments, we determined growth, gas exchange and endogenous abscisic acid (ABA) content in 1-week-old seedlings grown for another 1, 5 or 10 days under the above-mentioned conditions. Higher temperature decreased stem height, leaf area, leaf area ratio (LAR) and water-use efficiency (WUE), but increased specific leaf weight (SLW), leaf weight ratio (LWR) and transpiration (*E*). Water stress reduced stem height, leaf number, leaf area, dry matter of individual organs and whole plant, LAR, net CO_2 assimilation, *E* and WUE, but increased SLW and LWR. Overall, plant growth, dry matter, shoot:root weight ratio and ABA content increased with exposure duration, especially by day 10. However, higher temperature inhibited water stress-induced increases in ABA content. Interaction between watering regime and exposure duration was significant for all parameters of growth and dry matter as well as for LWR, WUE and ABA. No significant interaction was found between temperature and watering regime, between temperature and exposure duration, or among temperature, watering regime and exposure duration for any of the measured parameters. This study revealed that water stress strongly, but higher temperature to a lesser extent, affected canola seedlings, leading to reduced growth and dry matter, and the negative effects increased with time.

1. Introduction

Global warming, due to increased concentration of carbon dioxide and other greenhouse gases in the atmosphere by natural means and anthropogenic activities (Cox et al., 2000; Solomon et al., 2007), is likely to increase the surface air temperature in the coming decade from the existing records (Smith et al., 2007). Environmental conditions associated with global warming can have profound impacts on plant growth, development and yield (Qaderi and Reid, 2009). Effects of global warming on crops depend on the current geographic location of a crop, and will generally be detrimental in warmer climates, but may be beneficial in cooler climates that limit plant growth and yield (Pritchard and Amthor, 2005). It has been shown that moderately high temperatures can adversely affect crop growth and yield (Wardlaw and Wrigley, 1994; Stone, 2001).

Higher air temperatures can enhance plant metabolism and development (Larcher, 2003; Qaderi and Reid, 2009). Crop responses to higher temperatures depend on crop developmental stage and the character of temperature increase (Porter and Gawith, 1999). Higher than ideal temperatures decrease photosynthesis, but increase transpiration and stomatal conductance, and in turn, reduce plant biomass (Jones, 1992; Nobel, 2009; Qaderi and Reid, 2009). Plants under higher temperatures usually produce smaller leaves and extensive root systems to increase water uptake from soil but decrease water loss from leaves (Gliessman, 1998).

Due to global warming, there will likely be shifts in precipitation patterns and increased soil water deficits in many parts of the world (Solomon et al., 2007). In some areas, reduced soil moisture, due to warming (Rounsevell et al., 1999) or the absence of precipitation (Takahara and Akashi, 2006), negatively affects plants, particularly leaf growth, and in turn, photosynthesis (Pritchard and Amthor, 2005). Water stress influences transpiration, stomatal conductance, protein synthesis and metabolite accumulation of plants,

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and significantly reduces plant productivity. Plants can acclimate to water stress by morphological and biochemical changes, in non-severe cases, but they are damaged and lose parts, in severe cases (see Qaderi and Reid, 2009).

Abscisic acid (ABA) has been shown to be involved in plant responses to adverse environmental stimuli, including high temperature and water stress (Nilsen and Orcutt, 1996; Dodd and Davies, 2004; Gupta, 2005). ABA regulates a number of physiological processes in plants (Swamy and Smith, 1999) and plays an important role in plant adaptation to water stress, as it balances transpiration by affecting stomatal conductance (Dodd and Davies, 2004) and triggering stomatal closure (Gupta, 2005; Lambers et al., 2008). Plant ABA content can rise in response to both temperature (Daie and Campbell, 1981; Nilsen and Orcutt, 1996) and water stress (Nilsen and Orcutt, 1996). However, reduced ABA contents under higher temperatures have also been reported (see Hartung et al., 1988 and references therein).

Earlier studies have considered the combined effects of temperature and water stress on plants (Nicolas et al., 1984; Wardlaw, 2002; Shah and Paulsen, 2003; Xu and Zhou, 2006). However, we found no studies that have dealt with the interactive effects of these factors on plants during vegetative stage in a time-course manner. Previously we have reported that higher temperature reduces the inducing effects of water stress on ABA for the 18-day-old canola plants, 10 days following the treatment (Qaderi et al., 2006). However, ABA content, at various times after the imposition of the stress, needed to be quantified and the relationship between this phytohormone and plant growth and physiological properties required to be explored in more depth. As reported earlier, the pattern of increase of ABA concentration changes with water stress duration (Gupta, 2005), which, in turn, can affect growth and physiological parameters. We, therefore, were interested in determining the interactive effects of temperature and watering regime on canola (*Brassica napus*) seedlings at different times following the start of the environmental stress, and the role of ABA on such interaction at three stages during vegetative growth.

We hypothesised that higher temperature and water stress will negatively affect canola growth and physiology and the adverse effects of these factors increase with exposure duration. The objectives of this study were to investigate (i) whether there are changes in growth and physiological properties of *B. napus* in response to temperatures and watering regimes at various plant developmental stages, and (ii) whether higher temperature counteracts the water stress effects on ABA in similar patterns at all developmental stages. Findings from this study should shed light on the interactive effects of temperature and watering regime during earlier growth stages of plants and the hormonal involvement in such interactions.

2. Materials and methods

2.1. Plant material and growth conditions

Seeds of canola (*Brassica napus* L. cv. 45H72, Pioneer Hi-Bred Ltd., Chatham, ON, Canada) plants were soaked in water overnight, for improved germination synchronization, and then planted in four 36-cell plant starter (Agri-Growth International Inc., Edmonton, AB, Canada) containing a mixture of peat moss, Perlite, Vermiculite and Terragreen (2:1:1:0.25, v/v/v/v) and pellets of slow releasing fertiliser (N-P-K, 14-14-14). To produce enough seedlings of uniform size, two seeds were sown in each cell, and thinned to one, four days after emergence. Also, undersized seedlings were replaced with larger ones, and trays containing the cell paks were placed in two controlled-environment growth chambers (Model PGR15, Conviron, Controlled Environments Ltd., Winnipeg, MB, Canada) with temperature regime of 22 °C day and 18 °C night, and relative humidity (RH) of ~55%. A mix of cool white fluorescent tubes (Philips F72T12/CW/VHO, Philips Lighting Company, Somerset, NJ, USA) and incandescent lamps (Philips 60W, Philips Electronics Ltd., Markham, ON, Canada) was used to provide light on a 16 h photoperiod. Photosynthetically active radiation (PAR), measured with a quantum LI-185B radiometer/photometer (LI-COR, Inc., Lincoln, NE, USA), was 600 μmol m^{-2} s^{-1} at the shoot apex. Distance between plants and light was adjusted to keep the irradiance fairly constant. One week after seedling emergence, two trays were placed under lower temperature (22 °C day/18 °C night) and two trays under higher temperature (28 °C day/24 °C night) in two Conviron growth chambers, with similar RH, PAR and photoperiod to the initial conditions (see above). Under each temperature regime, plants from one tray were watered to field capacity (well watered) and those from the other tray at wilting point (water stressed). Plants that were grown under lower temperature and received water to field capacity were considered as controls. From each treatment, after 1, 5 and 10 days, plants were used for the measurement of growth, gas exchange and ABA content. Experiments were conducted three times under the same conditions of temperature and watering regimes in controlled-environment growth chambers at the University of Calgary.

2.2. Determination of growth and dry matter

First, plant height was measured for all plants from each treatment on each harvesting date. Then, three samples were taken, from each treatment, to determine leaf number, area and weight, and stem and root weights as well as total above- and below-ground biomass. Leaf area was measured with an area meter (Delta-T Devices Ltd., Cambridge, UK). Leaf weight was determined using an electrobalance (Model H51, Sartorius GmbH, Goettingen, Germany). Leaf, stem and root dry weights (dw) were obtained by drying the samples at 60 °C for 72 h in an Isotemp oven (200 Series Model 255G, Fisher Scientific Ltd., Nepean, ON, Canada) and reweighing. Growth indices were calculated as following: specific leaf weight [SLW ($g\,m^{-2}$) = leaf dry wt:leaf area], leaf weight ratio [LWR = leaf dry wt:plant dry wt], leaf area ratio [LAR ($cm^2\,g^{-1}$) = leaf area:plant dry wt], and shoot:root weight ratio [SRR = shoot dry wt:root dry wt].

2.3. Measurement of gas exchange

Gas exchange was measured with an infra-red gas analyzer (IRGA, CI-310 Portable Photosynthesis System, CID, Inc., Camas, WA, USA) between 11:00 and 15:00 h. Prior to measurements, the IRGA was calibrated with a known CO_2 concentration. Net CO_2 assimilation (A_N, μmol CO_2 m^{-2} s^{-1}) and transpiration (E, mmol H_2O m^{-2} s^{-1}) were determined, using three fully expanded leaves from each treatment, at 600 μmol m^{-2} s^{-1} PAR and relevant temperature for each growth condition. A_N and E values were obtained on the basis of total leaf area within the leaf chamber of IRGA. Photosynthetic water-use efficiency (WUE, μmol CO_2 mmol H_2O^{-1}) was calculated by dividing A_N by E (Lambers et al., 2008).

2.4. Quantification of ABA

For the determination of ABA content, from each treatment fresh leaf tissue was collected, immediately frozen in liquid N_2, and then freeze-dried (Freezemobile 12EL, Virtis, Gardiner, NY, USA). Each sample (~0.5 g dw) was ground and extracted with 80% methanol, using 200 ng of [$^2H_6$] ABA as internal standard.