



Research article

Ecophysiological constraints of *Aster tripolium* under extreme thermal events impacts: Merging biophysical, biochemical and genetic insights



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ABSTRACT

Cold and heat waves are phenomenon that occurs in higher frequency and intensity due to global climate changes. Commonly cultivated crop species are crucially affected by extreme weather events, and therefore alternative crops – such as halophytes – gain in agricultural interest. While halophytes are potentially able to cope with temperature extremes on the long term exposure, effects of temporary events such as cold and heat waves are not yet described. In order to unveil the effects of these altered thermal environments, *Aster tripolium* plants were subjected to cold (9/5 °C) and heat (42/38 °C) waves regimes during 3 days and its photochemical and biochemical traits evaluated. In the potential cash crop *A. tripolium* cold waves induced the gene expression of dehydrins in order to counteract desiccation and thus to prevent oxidative stress. Regulatory proteins on the RNA maturation level (Maturase K) were highly expressed. Heat stress induced the gene expression of the cysteine protease gene; most likely to degrade misfolded proteins temporary. Both thermal treatments decreased the photosynthetic efficiency and capacity, driven by a loss in the connectivity between PSII antennae. Nevertheless the light absorption capacity was unaffected due to an increased RC closure net rate. Cold wave-treated individuals showed a decrease in the carotenoid pigmentation, except auroxanthin. In cold wave treated individuals the overall peroxidase activity was significantly increased. Data suggest that exposure to both, cold and heat wave treatment decreased the ecophysiological capacity of *A. tripolium*.

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1. Introduction

Wetlands deliver a wide range of ecosystem services on the global scale (Costanza et al., 1997) including nutrient cycling, primary production, habitats for wildlife, and shoreline stabilization. Wetlands are inhabited by halophytes that are able to persist to adverse environmental constraints. Some of these plant species are considered as alternative cash crop, because they combine tolerance mechanism with high productivity (Ventura and Sagi, 2013).

The world population is expected to reach 9.1 billion by 2050, and global food production needs to increase by 70% in order to match the growing demand (FAO, 2011). Simultaneously, impacts of global climate change reduce land fertility at a rate higher than the adaptation ability of agricultural practices (IPCC, 2014). In addition, climate change imposes increasing physiological constraints such

as drought, salinization and an increasing number as well as intensity of extreme thermal phenomenon (Setter and Waters, 2003). The recent IPCC WG2 5th Assessment Report (IPCC, 2014), points out an increasing global air temperature, and to a further increase in the frequency and duration of extreme heat events. While cold waves might decrease in frequency they appear to be gain in intensity (IPCC, 2014). Recently the Mediterranean countries have been affected by both heat and cold waves with higher frequency (Niu et al., 2014). Extreme thermal events are defined by the World Meteorological Organization (WMO) as an increase or decrease in the average temperature of 5 consecutive days by 5 °C, referring to the average temperature between the years 1961–1990. In 2003 and 2005, southern Europe was affected by severe heat and cold waves, respectively. The majority of conventional agricultural species are affected by climatic extremes, leading to high losses in years with high frequency of heat and cold waves (FAO, 2011).

Halophytes are adapted to adverse environmental factors such as flooding (Duarte et al., 2014a), high salinity (Duarte et al., 2013a) and pollution (Duarte et al., 2013b). The sustainable use of

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halophytes in adverse environments has acquired an increasing interest from the scientific community (Pasternak, 1990). Halophytes with an agricultural potential called cash crop halophytes, comprise about 2500 species worldwide (Lieth et al., 1999; Lieth and Mochtchenko, 2002). A promising potential cash crop halophyte is *Aster tripolium*, with possible applications for human alimentation, as forage, as an ornamental plant (Lieth and Mochtchenko, 2002), or as nutraceutical. It has already been cultivated in pilot schemes in the Netherlands, in Belgium, Portugal and Pakistan. However, information on the physiological responses to extreme adverse climatic conditions such as heat and cold waves is limited. In the context of predicted increases in extreme thermal events (IPCC, 2014), this study should contribute to the discussion of applicability aspects of cash-crop halophytes in a climatic changing world. *A. tripolium* L. (sea aster) is a biennial to short-lived perennial halophyte commonly found in the coastal areas and sometimes in the inland salt marshes of north-western Europe (Clapham et al., 1942).

Abiotic stressors trigger same bottlenecks in the plant metabolism, because key metabolic pathways are affected. Reduction of the photosynthesis activity during cold and heat waves has been observed, although the effects of heat waves on the growth parameters are also dependent on seasonal characteristics, such as the water and nutrient availability, or priming events during earlier experienced stress (De Boeck et al., 2010; Larcher, 2003). Plant temperature sensing seems to be more dependent on the cooling rate (dT/dt) than on the ambient temperature level (Plieth et al., 1999). Thus, cold and heat waves could affect plant metabolism stronger than continuous temperature extremes. For example, the abundance of heat shock proteins in *Physcomitrella patens* was significantly reduced, when the growth temperature was higher (Saidi et al., 2010). Heat stress causes degradation of proteins and membranes (Larcher, 2003). A cold stress induced decrease of the membrane fluidity is discussed as a sensed factor in the plant response to temperature changes, affecting Ca^{2+} channels and triggering an increased Ca^{2+} influx (Monroy and Dhindsa, 1995). Significant influx of Ca^{2+} during cold, heat and drought stress is involved in the stress signalling transduction (Örvar et al., 2000). An altered cellular redox state might be sensed by an imbalanced proportion of absorbed light energy and its metabolic consumption (Emsminger et al., 2006). Reduced availability of oxidized electron acceptors in the electron transport chain then trigger an uncontrolled formation of reactive oxygen species (ROS). Stress levels are further enhanced by accompanying other stresses. Both, extreme cold or heat events often occur in combination with drought or light stress (Larcher, 2003). Although stress-signalling pathways are cross-talking (Mahajan and Tuteja, 2006), the stress response on the gene expression level is very specific (Beck et al., 2007). While approximately 30% of the gene expression patterns changes during cold, salinity and drought stress, only less than 5% of these transcriptional changes overlap between the different stressors in *Arabidopsis thaliana* (Kreps et al., 2002). Stress induced genes can be classified into the functional response (maintenance and protection of metabolic processes) and the regulatory response (signal transduction and transcription factors) (Zhang et al., 2004). Increased abundance of dehydrins during cold stress has been reported in different vascular plants (Nylander et al., 2001; Ohno et al., 2003; Lee et al., 2005). Dehydrins are chaperon-like proteins that maintain protein stability during dehydration, and they are the only strongly induced protein class during cold stress (Schreiber et al., 1986; Nylander et al., 2001; Close, 1996; Kawamura and Uemura, 2003).

The present study aims to describe the effects of temporary temperature extremes on the ecophysiological response of *A. tripolium*, with a special emphasis on its primary production here evaluated throughout its photobiological traits. This approach is

intrinsically connected with the biochemical mechanisms occurring under stress conditions, and thus the expression of some specific genes was also investigated in order to have a more clear view of the thermal stress response mechanisms in this potential cash crop halophyte.

2. Material and methods

2.1. Experimental setup

A. tripolium seeds were collected during November 2013 at Tagus estuary salt marshes (Alcochete, 38°45'38.78"N, 8°56'7.37"W) and dried in a desiccator for 7 days to remove any humidity. Seeds were germinated in petri dishes with moistened filter paper inside a FitoScope 130 RGBIR (Photon System Instruments, Czech Republic) in dim light ($<20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, 16 h light/8 h dark; day temperature $20 \pm 0.5 \text{ }^\circ\text{C}$, night temperature $18 \pm 0.5 \text{ }^\circ\text{C}$). After two months, the plants were transferred to pots with acid-washed sand and perlite (1:1) and replaced inside the chamber for another 2 months in order to increase the biomass. Plants were irrigated with $\frac{1}{4}$ Hoagland solution. The chamber was programmed with a sinusoidal function simulating sunrise and sunset and with a maximum temperature and light intensity at noon to simulate a natural light environment (RGB 1:1:1, Maximum PAR $300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, 16/8 h day/night rhythm; day temperature $20 \pm 0.5 \text{ }^\circ\text{C}$, night temperature $18 \pm 0.5 \text{ }^\circ\text{C}$). After this period plants were separated into 3 groups ($N = 5$) and subjected to different thermal treatments (day/night): control ($20/18 \text{ }^\circ\text{C}$), cold wave ($9/5 \text{ }^\circ\text{C}$) and heat wave ($42/38 \text{ }^\circ\text{C}$). Temperature rises and falls with dawn and sunset was also performed gradually according to a sinusoidal function. Heat and cold waves simulation were performed according to the records of air temperature for the Tagus estuary from the 2003 heat wave and the 2005 cold wave (www.snirh.pt). All experiments lasted for 3 days after which plants were harvested.

2.2. RNA extraction, reverse transcription, and quantitative PCR

RNA was extracted from leaves with the TRIzol protocol (Chomczynski, 1993). RNA purity and concentration was estimated with a NanoDrop (NanoDrop Technologies, Wilmington, DE; <http://www.nanodrop.com>). One unit of DNase (Thermo Scientific) per μg RNA was incubated in a final concentration of 2 mM MgCl for 30 min at $37 \text{ }^\circ\text{C}$, which was then denatured for 15 min at $70 \text{ }^\circ\text{C}$. Approximately one μg of RNA was incubated with 50 pmol random nonamer primer for 5 min at $70 \text{ }^\circ\text{C}$, and rapidly cooled down on ice to induce primer annealing. 200 Units of moloney murine leukaemia virus reverse transcriptase (<http://www.promega.com>), and 1 mM dNTPs were added to the buffer (provided by the manufacturer). Linearity of the cDNA synthesis was controlled with dilutions on the RNA level. cDNA synthesis in the absence of reverse transcriptase was used to estimate DNA contamination. Quantitative PCR was performed with SYBR green fluorescence (Platinum SYBR Green qPCR Mix, Invitrogen, <http://www.invitrogen.com>) detection using an ABI PRISM 7000 cycler (Applied Biosystems; <http://www.appliedbiosystems.com>). The oligo-nucleotide (<http://www.thermoscientific.com>) concentration was 200 mM, and MgCl concentration was 3 mM. The final reaction volume was 20 μl . Details about the used primer are indicated in Table 1. A dilution series of *A. tripolium* cDNA pool was used to quantify the transcript abundance in the samples. Amplification fragments were verified by melting temperature, and on a 1.5% Agarose gel (not shown). Transcript abundance was standardized on the relative gene expression of ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (rbcl).

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