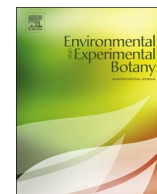




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Linking jasmonates with pigment accumulation and photoprotection in a high-mountain endemic plant, *Saxifraga longifolia*

Alba Cotado, Maren Müller, Melanie Morales, Sergi Munné-Bosch*

Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Faculty of Biology, Avinguda Diagonal 643, 08028 Barcelona, Spain

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ABSTRACT

Jasmonates are widely found in the plant kingdom and play a key role in both plant biotic and abiotic defense and plant development. Jasmonates activity under abiotic stress conditions have been extensively investigated in model plants, but little is known about the bioactive forms and their functions in non-model species, particularly in plants growing in their natural environment. Here, we performed a jasmonate profiling approach to unravel changes in the specific jasmonate signature of leaves as a function of environmental conditions, including the measurement of both free and conjugated forms of jasmonates by UHPLC–MS/MS, during the summer and autumn in *Saxifraga longifolia* plants growing in their natural habitat in the Pyrenees. We evaluated the climatological factors governing specific jasmonate signatures and the correlation between jasmonate accumulation and leaf morphology, PSII efficiency and pigment accumulation, including anthocyanins, chlorophylls and carotenoids. The results showed a jasmonate profiling characterized by an accumulation of free jasmonic acid and its precursor, 12-oxo-phytodienoic acid, with the amino acid conjugated forms being much less abundant. Among amino acid conjugates, jasmonoyl-isoleucine, jasmonoyl-valine and jasmonoyl-phenylalanine were the most abundant forms. Contents of 12-oxo-phytodienoic acid decreased, while those of free jasmonic acid increased during summer drought stress events. The five amino acid conjugated forms did respond similarly to environmental changes with progressive decreases from summer to autumn, but irrespective of drought events. Endogenous contents of free jasmonic acid correlated positively with those of anthocyanins. Furthermore, exogenous jasmonate applications on leaves increased anthocyanin contents, thus confirming a link between jasmonates and anthocyanin accumulation in *S. longifolia* plants.

1. Introduction

Jasmonates (JAs) have been recognized as being signals in plant responses to most of biotic and abiotic stress factors (Santino et al., 2013). When plants detect a stress, they must rapidly act to respond to the new external conditions, activating a variety of specific biochemical pathways depending on the plant species, type of stress, and duration and severity of stress. Jasmonic acid (JA) biosynthesis can be induced by a range of abiotic stresses, including osmotic stress (Ismail et al., 2015), drought (Riemann et al., 2015) and low temperatures (Sharma and Laxmi, 2016). JA is derived from linolenic acid via the octadecanoid pathway, thus leading to the formation of the JA precursor, 12-oxo-phytodienoic acid (OPDA, Conconi et al., 1996; Heitz et al., 2016). JA can be further enzymatically modified into different derivatives such as methyl jasmonate (MeJA), which is volatile (Wasternack and Hause, 2013), or amino acid conjugates by the action of specific jasmonoyl-synthases (Yan et al., 2016). JA conjugates include several forms, which are predominantly present in different plant species and tissues,

possibly having multiple functions. For instance, recent studies have shown that in *Arabidopsis thaliana*, the most bioactive JAs in response to stress is the jasmonoyl-isoleucine (JA-Ile, Fonseca et al., 2009). Jasmonoyl-tyrosine (JA-Tyr) has been shown to predominate in *Vicia faba* flowers, maybe representing a storage form (Kramell et al., 2005), while in *Arabidopsis thaliana*, JA-Tyr interferes with indole-3-acetic acid signalling (Staswick et al., 2017). Jasmonoyl-phenylalanine (JA-Phe) accumulates in *A. thaliana* leaves after wounding (Widemann et al., 2015) and induces accumulation of phytoalexins in *Oryza sativa* (Tamogami et al., 1997). Furthermore, the free JA form has been shown to induce anthocyanin accumulation during abiotic stress in several plant species (Shan et al., 2009). Under high light and drought conditions, JA triggers anthocyanin biosynthesis in a phytochrome A-dependent signalling pathway (Li et al., 2014). Although these examples illustrate the wide variety of possible functions of various JAs forms in different plant species, information is not yet available on how specific JAs signatures respond to the unveiling climatic conditions and modulate anthocyanin accumulation and the extent of photoprotection in

* Corresponding author.

E-mail address: smunne@ub.edu (S. Munné-Bosch).<https://doi.org/10.1016/j.envexpbot.2017.12.018>

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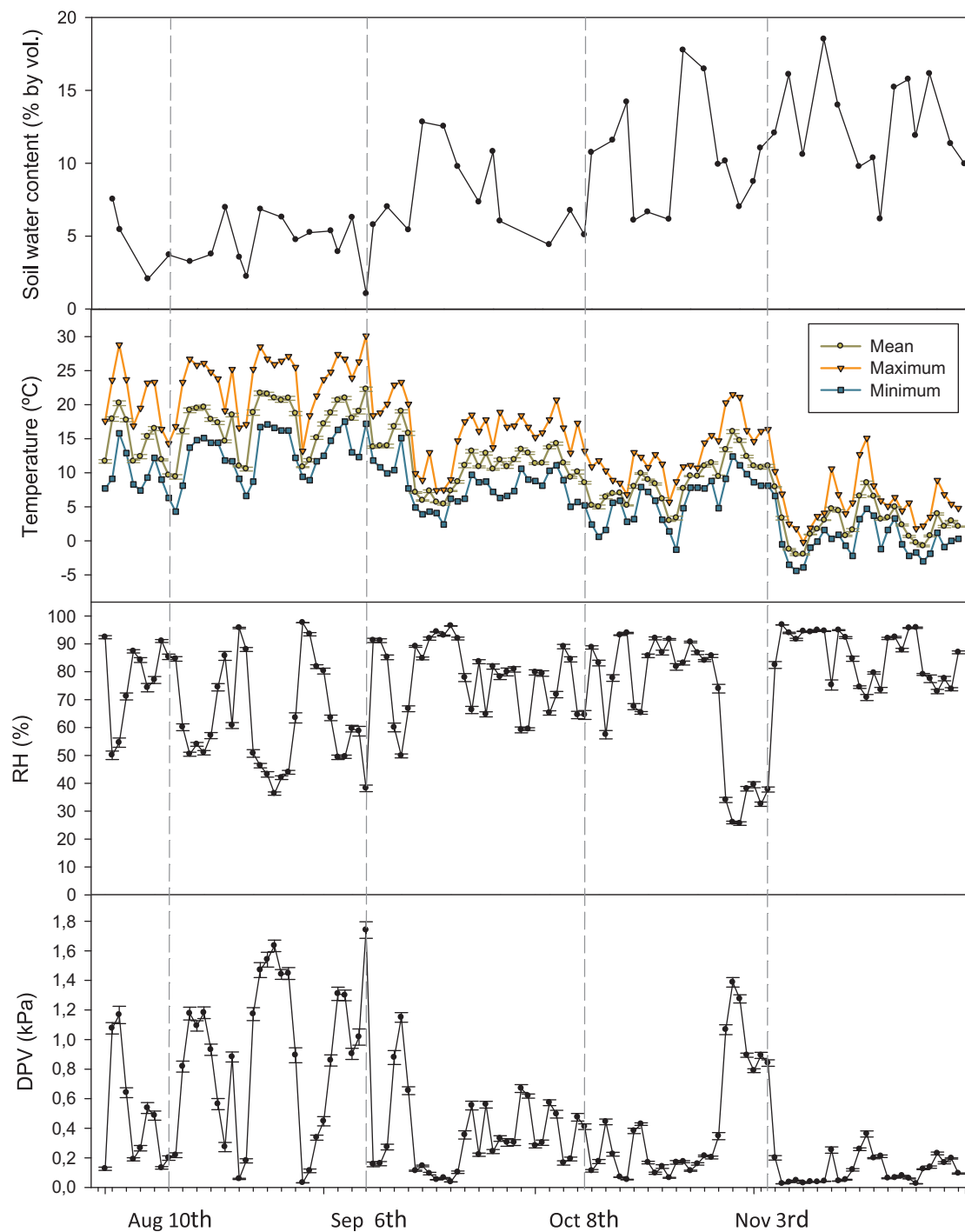


Fig. 1. Climatological conditions in the study area during the experiments. Soil water content (SWC; %, by vol.) was taken from a public database (<http://cp34-bec.cmima.csic.es/data/data-access/>). Mean, maximum and minimum air temperature ($^{\circ}\text{C}$) and mean air relative humidity (RH) were taken from the nearest meteorological station (Port du Somport, 1945 m a.s.l.). Vapour pressure deficit of sampling days (VPD) was calculated from temperature and relative humidity data. Dash grey lines indicate the sampling days during August, September, October and November.

high-mountain plants.

Photoprotection mechanisms are essential in high-mountain plants, where high solar irradiance may coincide with either low temperatures during the autumn and winter, or high temperatures during the summer, particularly in the frame of climate change (Adam and Murthy, 2014). Extreme temperatures combined with high solar irradiance induce a stress response, consequently chlorophyll biosynthesis is affected and changes in light-harvesting complexes occur, shifting from pigment-protein complexes efficient in light harvesting and energy transfer to complexes prepared for energy quenching (Ensminger

et al., 2006). Extreme temperatures in the presence of light specifically induces genes encoding reactive oxygen species (ROS)-scavenging enzymes, antioxidant molecules like phenylpropanoids (flavonoids and anthocyanins) and/or photosynthesis-related carotenoids (Soitamo et al., 2008). Carotenoids are photosynthetic pigments that, beyond their key role in light-harvesting, play a key role in photoprotection, avoiding the formation of the singlet oxygen, one of the most reactive ROS, which is formed in photosystems under unfavourable conditions (Yamamoto and Bassi, 1996). Furthermore, drought and heat events are more and more frequent in the frame of global change in high-mountain

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