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Research article

Foliar application of methyl jasmonate induced physio-hormonal changes in *Pisum sativum* under diverse temperature regimes

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A B S T R A C T

Global climate change brings with it unwarranted shifts in both abiotic (heat stress, cold stress, wind, precipitation) and biotic (pathogens, pests) environmental factors, thus posing a threat to agricultural productivity across the world. In plants, lodging due to storms or herbivory causes wounding stress and consequently enhances endogenous jasmonates. In response, the plant growth is arrested as plant defense is prioritized. We pre-treated pea plants with elevated methyl jasmonate (MeJA) levels i.e. 50 μM, 100 μM and 200 μM under controlled growth chamber conditions. The pre-treated plants were then kept at 40 °C (heat stress—HS), 4 °C (cold stress—CS) and 20 °C (optimum/control temperature—OT) for 72 h. The effect of such treatments on plant growth attributes, photosynthesis, stomatal conductance, cell death rate, and regulation of endogenous hormones were observed. Elevated MeJA application hindered plant growth attributes under HS, CS and OT conditions. Moreover, elevated MeJA levels lowered the rate of photosynthesis and stomatal conductance, induced stomatal closure, caused higher cells mortality in leaves under HS, CS, and OT conditions. Endogenous ABA contents significantly declined in all MeJA treatments under HS and OT, but increased under CS conditions. Exogenous MeJA enhanced endogenous jasmonic acid contents of pea plants, but altered endogenous salicylic acid contents under varying temperatures. Current study shows that higher concentrations of exogenous MeJA strengthen plant defense mechanism by hindering plant growth under stress conditions.

1. Introduction

Harsh regional climatic conditions resulting from global climate change have severely affected agriculture worldwide. These changes include either shifts toward higher or lower temperatures or larger seasonal variations. Deviations in temperature from the optimum constitute heat and cold stress conditions (Su et al., 2014; Wang et al., 2015). As plants are sessile organisms and, therefore, cannot escape local environmental changes, a thorough understanding of how plants sense and respond to abiotic stressors is needed (Ruelland and Zachowski, 2010). Both heat and cold stress can arrest plant growth and development, damaging crop production and quality (Ruelland and Zachowski, 2010; Su et al., 2014).

The estimated 1.8–2.5 °C increase that occurred in the middle of the last century has been found to negatively affect agriculture. Simulations of current and future anthropogenic activity predict that average global air temperature will further increase by 1–4.5 °C, at rate of 0.2 °C per decade, by the end of the 21st century, which may reduce global crop yields (IPCC, 2007; Rienth et al., 2014; Sgobba et al., 2015). Although increase of 2–6 °C has dramatic effects on growth (hypocotyls elongation) and flowering time depending on the light conditions (Thines et al., 2014; Bours et al., 2015). However, even brief exposures of tropical or temperate crops to high temperatures (40 °C) at sensitive life stages can bring about irreparable agricultural losses (Sgobba et al., 2015; Wang et al., 2015). Heat stress negatively influences the physiological functions of plants, affecting cellular homeostasis, plant-soil-water relations, photosynthesis, and respiration; causing cell membrane injury and leaf chlorosis and necrosis; and lowering plant biomass and yield (Su et al., 2014). For example, even mild heat stress at the grain-filling stage of wheat, maize, and rice can significantly reduce the yield component (Djanaguiraman et al., 2014; Su et al., 2014; Wang et al., 2015). The

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effects of heat stress differ according to growth stage: high temperatures reduce coleoptile lengths at germination; shorten internode length, increase tiller number, induce premature senescence, and reduce biomass at the vegetative stage; and decrease grain number and plant weight at the grain-filling stage (Djanaguiraman et al., 2014; Sgobba et al., 2015). These events are further accompanied by anatomical alterations, revealed by reductions in cell size, stomatal closure, increased stomatal density, altered trichome numbers, and enlarged xylem vessels in roots and shoots (Chen et al., 2014; Djanaguiraman et al., 2014; Rienth et al., 2014). Crops respond differently to changes in day and night temperatures (Djanaguiraman et al., 2014; Rienth et al., 2014).

Plant growth and development are also affected by cold stress, which may cause chilling injury (0–15 °C) or freezing injury (below 0 °C), both of which significantly reduce crop productivity and quality (Kosova et al., 2012; Baxter, 2014; Luo et al., 2014). Chill-sensitive crops include many economically important temperate- and arid-zone crops, such as cotton, soybean, maize, lima bean, rice, tomato, cucumber, pepper, and eggplant (Thakur et al., 2010; Bhandari and Nayyar, 2014; Thalhammer et al., 2014; Wu et al., 2014). These crops are unable to survive in cold temperatures and the development of cold-resistant cultivars has been suggested (Thakur et al., 2010). During the reproductive stage, cold stress reduces yields by affecting flower organs, inducing pollen sterility, pollen tube distortion, ovule abortion, or flower abscission, and thereby preventing the fruit from developing (Thakur et al., 2010; Sharma and Nayyar, 2014). Cold stress interrupts normal plant growth at the physiological, morphological, cellular, and genetic levels (Thakur et al., 2010; Wu et al., 2014). The combined effects of cold stress—over-production of reactive oxygen species, disintegration, or inactivation of cellular enzymes, and membrane damage—can damage plant tissues and ultimately lead to plant death (Thalhammer et al., 2014).

Climate change may also affect plant growth indirectly by increasing insect herbivory (DeLucia et al., 2012; Su et al., 2014; Svobodová et al., 2014). Warmer climates may increase the number of insect generations per year, increasing the demand for foliage due to increased population numbers (DeLucia et al., 2012; Svobodová et al., 2014). Insect damage is compounded by the decreased nutritional value of foliage caused by climate change. When foliage is low in nutrients, insects will eat consume more of it to meet metabolic demands (DeLucia et al., 2012).

To survive in a rapidly changing environment, plants will need to recruit hormones from their arsenals for defense and growth (DeLucia et al., 2012). Hormones are small organic compounds usually present in very low concentrations at sites of origin or in distant tissues (Santner and Estelle, 2009; Almeida Trapp et al., 2014). Major plant hormones include growth-promoting cytokinins, gibberellic acid (GA), and auxin (IAA), as well as stress-mediating abscisic acid (ABA), ethylene, jasmonic acid (JA), and salicylic acid (SA) (Santner and Estelle, 2009; Hossain et al., 2011; Almeida Trapp et al., 2014). Among these phytohormones, octadecanoid-pathway-derived jasmonic acid and its relevant metabolites, collectively known as jasmonates, mediate stress responses and other aspects of plant growth and development via diverse physiological and biochemical processes (Santner and Estelle, 2009). Mechanical wounding, insect herbivory, and other abiotic and biotic stresses induce the production of JA, high levels of which protect the plant from further damage and allow recovery (Santner and Estelle, 2009). However, this beneficial effect is often offset by a cost, such as slowed growth (Kazan and Manners, 2012; Yang et al., 2012). The responsible mechanism in slowed growth is the antagonistic behavior of JA and GA. In response to JA mediated defense, DELLA and JAZ protein degraded, but in a resting stage JAZ and DELLA interaction cause to titrate out some of the DELLA protein and PIF is released to promote growth. The activation of JA signaling pathway just cause degradation of JAZ protein, make more DELLA protein available for interaction and repression with PIF TF and therefore inhibition of growth (Yang et al., 2012; Huot et al., 2014). There is a very strong correlation between JA in plant stress responses. The initial attack of herbivores is immediately responded by rising endogenous JA level within few minutes. Compounds released in insect oral secretion further stimulate the JA biosynthesis. Similarly JA induces resistance against necrotrophic pathogens, chewing herbivores and some phloem feeding insects (Wasternack and Hause, 2013; Wasternack, 2014). Beside, JA is also a key player in abiotic like drought, salinity and cold stresses, but has negative effect on photosynthesis and growth (Wasternack, 2014). Recently Du et al. (2013) found that endogenous JA is differentially regulated during heat, and cold stress response in monocot plant rice. The endogenous JA level was significantly increased in simultaneous application of cold stress and contrarily down regulated during heat stress (Du et al., 2013; Liu et al., 2015).

Predicted climate scenarios involving more-frequent heat- and cold-stress temperatures suggest an imperative for elucidating the role of jasmonates in response to temperature stress. In addition, two predicted consequences of global climate change, increased herbivory due to larger insect pest populations and more-frequent windstorms, are agents of mechanical or wounding stress and became one of the major cause in crops yield reduction (Svobodová et al., 2014; Zhang and Turner, 2008). It has been reported that wounding stress retard plant growth by reducing cells number via inhibition of mitosis than instead of cell size (Zhang and Turner, 2008). Further to this, JA treated plants show stunted growth, reduced leaf and root size together with increased secondary metabolites biosynthesis (Zhang and Turner, 2008). This highlights the importance of investigating the role of jasmonates in response to wounding stress under diverse temperature conditions.

In this study, pea plant (*Pisum sativum*), a crop widely grown in temperate and subtropical regions, was selected as a model and subjected to temperature-related stress after application of varying concentrations of MeJA. Pea plant was chosen over *Arabidopsis* because it is a food crop and can form the basis for future research on responses of legume crops to physical injury under temperature extremes. Pea is one of the most important legume crops and is widely used as part of the daily diet (Ferraro et al., 2014; Mastromatteo et al., 2015). Pea seeds are a high-quality nutritional source, rich in protein, vitamins, minerals, phenolic compounds, and soluble and insoluble fiber, but low in digestible starch; peas have a low glycemic index (Ferraro et al., 2014). Pea consumption may help prevent chronic health conditions (e.g., diabetes mellitus, coronary heart disease, colon cancer, etc.) by regulating glycemic and gastrointestinal functions and providing antioxidant properties (Mastromatteo et al., 2015; Vaz Patto et al., 2015).

The present study examined the hypothesis that high doses of exogenous MeJA improve plant defense against environmental stressors by inhibiting plant growth. Pea plants were exposed to optimum temperatures, heat-stress, or cold-stress conditions, with or without the exogenous application of various concentrations of MeJA to simulate wounding. Using exogenous MeJA instead of physically wounding the plants ensured uniformity. MeJA concentration was varied to simulate degrees of severity of environmental stresses. Using plants grown in controlled growth chambers, we examined the effects of MeJA on (1) plant growth response; (2) the endogenous stress-related hormones ABA, SA, and JA; (3) anatomical and morphological changes.