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Signaling events in plants: Stress factors in combination change the picture

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ABSTRACT

Being sessile organisms, plants are constantly exposed to various kinds of environmental stimuli. To survive under unfavorable environmental conditions they have evolved strategies to allow a balance between growth, reproduction and survival. In this review article, we first focus on two major abiotic stress factors, drought and heat, and briefly summarize the current knowledge on signal transduction pathways involved in plant responses to these stresses. In nature it is unlikely that plants are exposed to abiotic or biotic stresses in isolation. Hence, multiple stress situations are more likely to occur including heat, drought, salinity and pathogen attack. Since in many cases stress responses are antagonistic, predictions of molecular responses to multiple stresses based on single stress data is difficult or even impossible. Only recently, researchers started to study multiple-stress interactions and discovered for instance that plant responses to a combination of heat and drought differ from those to both single stresses. Moreover, abiotic stress applications are likely to influence plant-pathogen interactions and vice versa. Here, we discuss various aspects of multiple stress applications published within the last few years and pronounce the importance to study biotic and abiotic stress combinations in order to predict plant responses to future climate changes.

1. Introduction

According to independently calculated climate change models, annual distribution of precipitation will change considerably and average temperatures will increase. These changes are likely to reduce plant growth and yield worldwide (Ahuja et al., 2010; Lobell et al., 2011; Mir et al., 2012; Sreenivasulu et al., 2007). Due to their sessile life style, plants are constantly confronted with biotic and abiotic stresses and are forced to efficiently balance growth, reproduction and defense under these adverse conditions (Bechtold et al., 2010; Smith and Stitt, 2007; Tian et al., 2003). Under stress conditions less energy and nutrients are allocated to growth processes and more is invested in defense responses. To allow reproduction, early flowering and an uncoupling of biomass accumulation and flowering time will be promoted under stress conditions to allow limited seed production even under adverse conditions (see Fig. 1).

This requires a fine tuning of nutrient and energy allocation between growth/reproduction and defense associated processes by complex signaling networks integrating incoming developmental and environmental signals (Cramer et al., 2011; Krasensky and Jonak, 2012). Here the interplay between two protein kinase signaling complexes, target of rapamycin (TOR)-1 and sucrose non-fermenting-1-related protein kinase (SnRK1), may serve as an important interface to provide a balance between metabolic and stress signaling pathways (Hey et al., 2010). Activation of SnRK1 will slow down growth processes and stimulate stress responses by activating i.e. abscisic acid (ABA) response element binding proteins (AREBPs). On the contrary, TOR-1 activation serves as a signal for high nutritional status and will support growth processes. Hence, the balance between TOR-1 and SnRK1 signaling will have a significant impact on assimilate allocation and physiological processes underlying growth and defense responses (Lastdrager et al., 2014). Since several distinct environmental stimuli can affect plant development in combination, a large number of stress responsive signal transduction pathways have to be integrated to adapt resource allocation between defense, growth and reproduction in the most efficient way (Fig. 2).

These include phytohormonal (i.e. ABA, ethylene, jasmonic acid (JA), salicylic acid (SA)) (Fragniere et al., 2011; Kim et al., 2010; Licausi et al., 2013; De Geyter et al., 2012; Rivas-San Vicente and Plasencia, 2011), ROS (Apel and Hirt, 2004; Baxter et al., 2014), Ca^{2+} (Batistic and Kudla, 2012; Lecourieux et al., 2006; Marti et al., 2013), lipid and metabolite signals (Munnik and Testerink, 2009), changes in redox status (Munne-Bosch and Muller, 2013), which are

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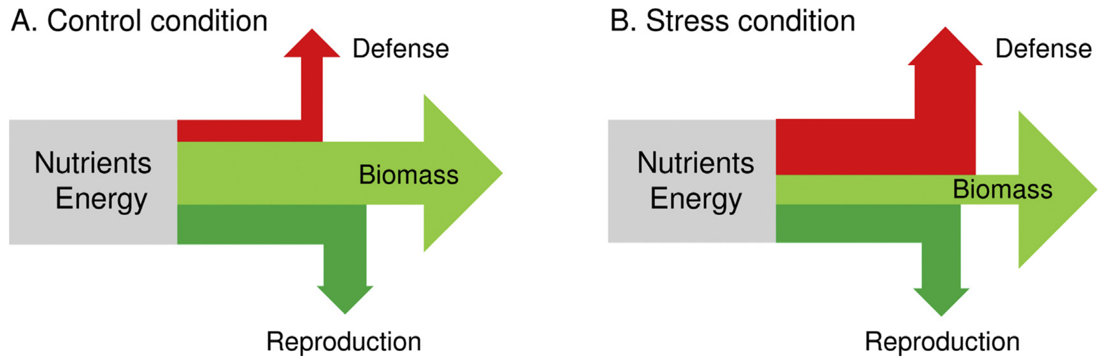

Fig. 1. Energy channeling is shifted from biomass production to defense programs. Under stress conditions nutrients and energy are redirected from biomass production towards defensive processes. Additionally reproduction is accelerated under adverse environmental conditions.

transduced by protein kinase networks and result in cellular adaptations involving altered mRNA accumulation (microRNA, transcription, chromatin structure) (Mazzucotelli et al., 2008; Sunkar et al., 2007), altered protein composition (protein degradation, translation), ion homeostasis (ion channels) (Daszkowska-Golec and Szarejko, 2013) and primary and secondary metabolism (Ramakrishna and Ravishankar, 2011). Phytohormons often magnify the initial signal and trigger a new signaling event either following the same pathway or using further components of other signaling pathways (Huang et al., 2012; Xiong et al., 2002). Protein kinase cascades which are central in stress responses include mitogen-activated protein kinases (MAPKs), Snf1-related kinases (SnRKs) and Ca^{2+}-dependent protein kinase (CPKs) cascades, which initiate a reversible chain of protein phosphorylation events (Zhang et al., 2006). These signal transduction pathways lead to the activation of well-characterized proteins involved in biosynthesis of proteases, transporters, and chaperones as well as osmoprotectants and detoxification enzyme systems. Some plant responses to unfavourable growth conditions are specific, whereas others are general responses providing tolerance to several stress conditions (Huang et al., 2012). More general stress response mechanisms include changes in Ca^{2+} signaling (Pan et al., 2012; Reddy et al., 2011), and induction of antioxidant defense pathways against reactive oxygen species (ROS) (Apel and Hirt, 2004). ROS signaling under abiotic stress conditions has already been reviewed in detail and will not be part of this review (Atkinson and Urwin, 2012; Reguera et al., 2012). In general, it is assumed that stress sensing acts at multidimensional levels integrating several sensing mechanisms in specific stress conditions.

2. Single stress situations

2.1. Drought stress

In many agricultural areas worldwide water deficit significantly limits plant growth and productivity. Therefore, improved water use efficiency is an important trait in plant breeding. The main effect of drought stress is the loss of cell water, primarily through the stomata on the leaf surface and subsequently a decrease of cell osmotic potential. It is estimated that more than 95% water loss occurs via transpiration through stomatal pores. To cope with drought stress, plants close their stomata to guarantee tolerable cell turgor and to continue cellular metabolism. As stomata closure reduces the photosynthetic rate, plants must constantly adjust stomatal conductance to allow sufficient CO_2 uptake and to avoid unnecessary water loss during stress. Therefore, plants must permanently sense water deficit. Amongst the regulators of plant sensing and responses to drought stress the phytohormone ABA is supposed to play a crucial role in stress signaling at different levels, namely transcriptional changes and stomatal closure (Cramer et al., 2011; Shinozaki and Yamaguchi-Shinozaki, 2007; Sreenivasulu et al., 2012). ABA signals can be perceived by different cellular receptors. In the literature, evidence is given for at least three pathways of ABA perception.

The best characterized ABA perception mechanism is represented by the nucleocytoplasmic receptor PYR/PYL/RCARs (Pyrabactin resistance (PYR/PR1-like) also called regulatory component of ABA receptor (RCAR). PYR1 and several PYR1-related homologues of Arabidopsis (PYLs) have been characterized as

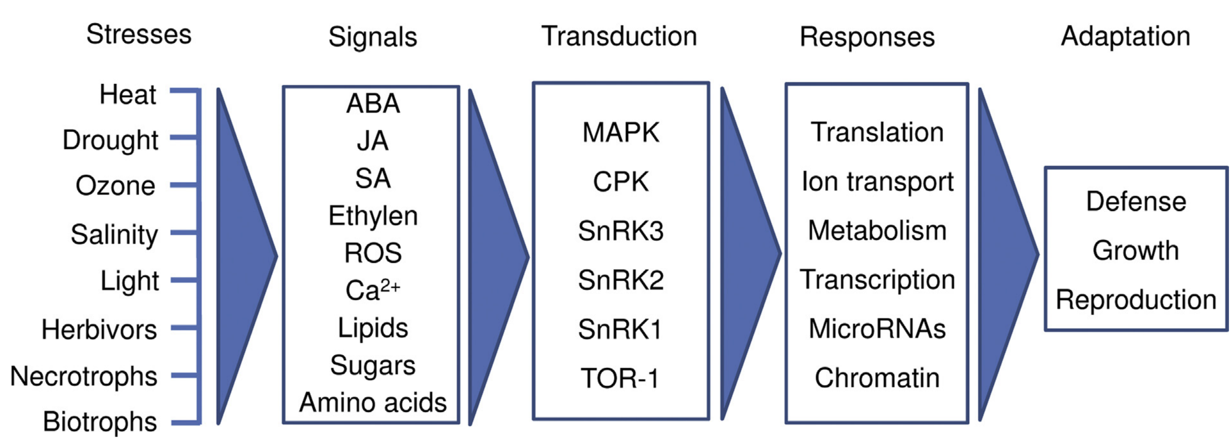

Fig. 2. Crucial events in the signal transduction pathway activated by several biotic and abiotic stress factors. The schematic diagram shows how different stress factors activate different signals, which themselves trigger signal transduction cascades. Different signaling events result in appropriate plant responses leading to adaption processes including defense, growth and reproduction. ABA (abscisic acid); ROS (reactive oxygen species); JA (jasmonic acid); SA (salicylic acid); Ca^{2+} (Calcium); MAPK (mitogen-activated protein kinase); CPK (Ca^{2+}-dependent protein kinases); SnRK (sucrose non-fermenting-1-related protein kinase); TOR-1 (target of rapamycin).