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Interactions between hormone and redox signalling pathways in the control of growth and cross tolerance to stress

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ABSTRACT

The ability of plants to respond to a wide range of environmental stresses is highly flexible and finely balanced through the interaction of hormonal plant growth regulators and the redox signalling hub, which integrates information from the environment and cellular metabolism/physiology. Plant hormones produce reactive oxygen species (ROS) as second messengers in signalling cascades that convey information concerning changes in hormone concentrations and/or sensitivity to mediate a whole range of adaptive responses. Cellular redox buffering capacity that is determined largely by the abundance of ascorbate has a profound influence on the threshold at which hormone signalling is triggered and on the interactions between different hormones. Other antioxidants such as glutathione, glutaredoxins and thioredoxins are also central redox regulators of hormone signalling pathways. The complex network of cross-communication between oxidants and antioxidants in the redox signalling hub and the different hormone signalling pathways maximises productivity under stress-free situations and regulates plant growth, development, reproduction, programmed cell death and survival upon exposure to stress. This interactive network confers enormous regulatory potential because it allows plants to adapt to changing and often challenging conditions, while preventing boom or bust scenarios with regard to resources, ensuring that energy is produced and utilised in a safe and efficient manner.

1. Introduction

Cross-tolerance to environmental stresses is a common phenomenon in plants, whereby exposure to one type of stress confers a general increase in resistance to a range of different stresses (Pastori and Foyer, 2002; Suzuki et al., 2012). Cross-tolerance occurs because of synergistic co-activation of non-specific stress-responsive pathways that cross biotic–abiotic stress boundaries (Bostock, 2005). Cross-tolerance phenomena are frequently linked to the enhanced production of reactive oxygen species (ROS) such as H_2O_2, oxidative signalling and the associated regulation of gene expression through the redox signalling hub, as illustrated in Fig. 1. It is widely accepted that H_2O_2 and other ROS are important signalling molecules in abiotic and biotic stress responses, often because they serve as messengers for the activation of defence genes (Foyer and Noctor, 2009, 2012). Tight spatial-temporal control of redox signalling molecules allows different and sometimes diametrically opposed physiological events and generates signal specificity that is integrated with the action of plant hormones such as ethylene (ET), salicylic acid (SA), abscisic acid (ABA) and jasmonates (JA) (Xiong et al., 2002; Glazebrook et al., 2003; Fujita et al., 2006). For example, exposure to the atmospheric pollutant ozone generates ROS in the apoplast of plant cells and initiates an oxidative signalling cascade that shares many signalling and regulatory response components with ROS-mediated responses to biotic and abiotic stresses (Baier et al., 2005). Many plant hormones promote ROS production, often through the activation of NADPH oxidases (Rbohs), or alter redox signalling hormones and so induce

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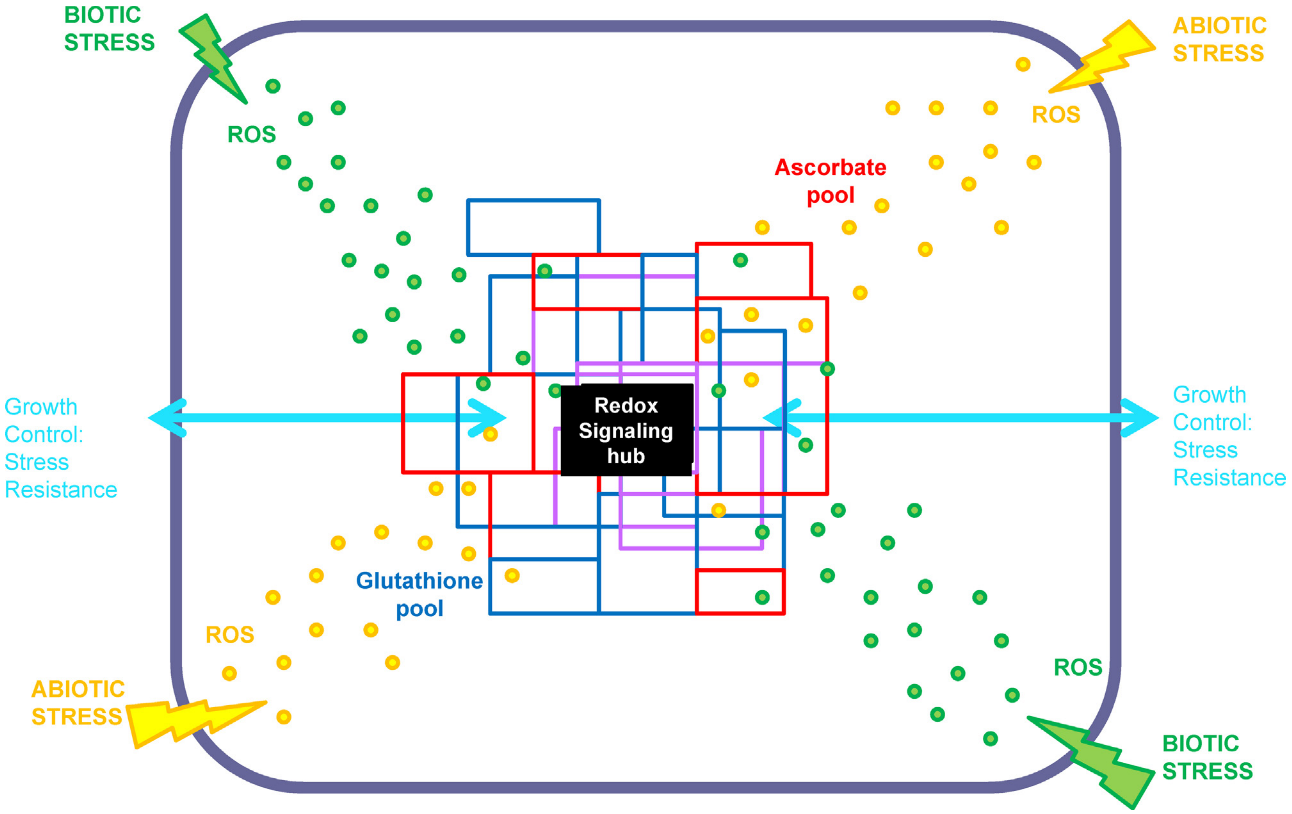

Fig. 1. The redox signalling hub. Reactive oxygen species (ROS).

tolerance to a wide spectrum of stresses (Foyer and Noctor, 2009). Again using the ozone example, ozone fumigation induces ET production (Nakajima et al., 2002) and the activation of abiotic stress responses (Leubner-Metzger et al., 1998), as well as triggering the hypersensitive response (HR) and the induction of programmed cell death, which are intrinsic feature of plant responses to pathogens (Overmeyer et al., 2003). Extensive cross talk is observed between the SA, JA and ET pathways that are induced in response to oxidative stresses such as ozone (Glazebrook et al., 2003) with many points of reciprocal control that can involve neutral, synergistic and antagonistic interactions (Tosti et al., 2006). We discuss the evidence showing that the major plant hormones interact with the cellular redox signalling hub in order to control growth and defence processes in response to environmental stresses.

2. Auxin

Auxin, principally indole-3-acetic acid (IAA) is an essential plant hormone that fulfils numerous roles in plant growth and development including stem elongation, phototropic and gravitropic responses, apical dominance, and lateral and adventitious root formation (Grieneisen et al., 2007; Kleine-Vehn et al., 2008). Like brassinosteroids (BRs) and gibberellins (GAs), auxin promotes cell elongation and controls plant height. BRs and auxin produce ROS as second messengers by activation of NADPH oxidases (Joo et al., 2001; Xia et al., 2009, 2011).

Plant development is regulated by precisely controlled fluctuations in auxin biosynthesis, transport, accumulation, and degradation. The fine-tuning auxin concentrations with local auxin maxima, directional cell-to-cell transport and auxin gradients, together with the differential distribution of the auxin signalling pathways in specific tissues at specific stages of development allow the correct setting of developmental cues in embryogenesis, organogenesis, vascular tissue formation and directional growth in response to environmental stimuli. Auxin transport is controlled by a family of influx facilitators (AUX1, LAX1–LAX3) and two families PIN-FORMED (PIN) and type B ATP binding cassette proteins of efflux carriers. Much attention has focussed on the coordination of the polar sub-cellular localisation of PIN proteins that are responsible for the direction of auxin fluxes (Friml, 2010). The auxin model is considered to be a paradigm for cellular signal transduction pathways (Teale et al., 2008). Moreover, the dynamic interplay between auxin signalling pathways and redox signalling pathways (Fig. 2) permits flexible regulation that is highly responsive of cell metabolism (Pasternak et al., 2005; Tognetti et al., 2012).

The balance between oxidative (ROS) and reductive (antioxidant) signals regulates auxin biology at multiple levels from biosynthesis, conjugation/oxidation, and transport to signal transduction (Gazarian et al., 1998; Cosio and Dunand, 2009; Chen and Xiong, 2009; Tognetti et al., 2010). For example, ROS function as downstream components in auxin-mediated signal transduction to control gravitropism responses in roots (Joo et al., 2001). Genes encoding antioxidant enzymes are among primary auxin-response genes, suggesting a role for auxin in plant stress and defence responses (Abel and Theologis, 1996; Tyburski et al., 2009; George et al., 2010). Changes in auxin distribution and ROS metabolism precede transcriptional regulation (Joo et al., 2001; Pasternak et al., 2005).

To date, relatively little information is available on the complex interplay between ROS and auxin signalling. However, there is evidence in support of a dynamic dialogue and reciprocal dependence between redox (ROS-antioxidant) signalling and the prioritisation of polar auxin transport and signalling. Polar auxin transport, which enables cells to establish local auxin concentrations, is a key feature of auxin homeostasis that is actively controlled by PIN auxin efflux carrier family. The expression of at least some of the PIN