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REVIEW

The role of gibberellin signalling in plant responses to abiotic stress

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ABSTRACT

Plant hormones are small molecules that regulate plant growth and development, as well as responses to changing environmental conditions. By modifying the production, distribution or signal transduction of these hormones, plants are able to regulate and coordinate both growth and/or stress tolerance to promote survival or escape from environmental stress. A central role for the gibberellin (GA) class of growth hormones in the response to abiotic stress is becoming increasingly evident. Reduction of GA levels and signalling has been shown to contribute to plant growth restriction on exposure to several stresses, including cold, salt and osmotic stress. Conversely, increased GA biosynthesis and signalling promote growth in plant escape responses to shading and submergence. In several cases, GA signalling has also been linked to stress tolerance. The transcriptional regulation of GA metabolism appears to be a major point of regulation of the GA pathway, while emerging evidence for interaction of the GA-signalling molecule DELLA with components of the signalling pathway for the stress hormone jasmonic acid suggests additional mechanisms by which GA signalling may integrate multiple hormone signalling pathways in the response to stress. Here, we review the evidence for the role of GA in these processes, and the regulation of the GA signalling pathway on exposure to abiotic stress. The potential mechanisms by which GA signalling modulates stress tolerance are also discussed.

KEY WORDS: Gibberellin, DELLA, Abiotic stress, Growth, Stress tolerance

Introduction

Plant development is regulated and coordinated through the action of several classes of small molecules (plant hormones), which may act either close to or remote from their sites of synthesis to mediate genetically programmed developmental changes or responses to environmental stimuli (Davies, 2010). Through the action of these molecules, plants are able to modify their physiology and biochemistry in rapid response to changes in their environment, a critical requirement for their survival as sessile organisms. Hormones thus have an important role in the plant's response to abiotic stress, such as drought, shading, flooding or low temperature, from which the plant may attempt to escape by outgrowing the stress, e.g. shade avoidance (Franklin, 2008) and in some cases flooding (Bailey-Serres and Voesenek, 2010), or, more commonly, may result in reduced growth in order that the plant can focus its resources on withstanding the stress (Skirycz and Inzé, 2010). Thus such stresses often elicit changes to the production, distribution or signal transduction of growth hormones as well as stress hormones, which may promote specific protective mechanisms. For example, reduced water availability, which is first perceived by the roots, results in closure of the leaf stomata and the resulting reduction in transpiration, at least in part through the action of the stress hormone abscisic acid (ABA) (Wilkinson and Davies, 2002). This and other hormones have been suggested to act as signals to communicate the stress between roots and shoots (Jackson, 1997), although the speed of the response may be too rapid for a chemical signal and the true inter-organ stimulus may be hydraulic, which promotes ABA biosynthesis within the leaves (Christmann et al., 2007).

Early indications that stress tolerance was sensitive to the hormonal status of the plant came from applications of chemical growth retardants, a common agronomic practice used to control stature of many crop species and which has been shown in numerous studies to enhance drought tolerance (Halevy and Kessler, 1963). A primary mode of action of these chemicals is through inhibition of the biosynthesis of gibberellins (GAs) (Rademacher, 2000), and indeed application of GAs to retardant-treated plants and to GA-deficient mutants reverses their enhanced stress tolerance as well as their dwarf growth habit (Gilley and Fletcher, 1998; Vettakkorumakankav et al., 1999). The relationship between GA status and tolerance to drying soil is illustrated in Fig. 1, which compares mutant lines of the model plant species *Arabidopsis thaliana* displaying different degrees of GA deficiency or over-accumulation. As classical growth hormones, the GAs are prime targets for stress-induced growth modulation and there is increasing evidence for the involvement of GA signalling in either growth suppression or promotion, depending on the response to a particular abiotic stress. This article reviews the evidence and addresses the mechanisms by which stress modifies GA signalling and the much less clear issue of how reduced GA signalling results in enhanced stress tolerance.

GA biosynthesis and signal transduction

The GAs are a large group of tetracyclic diterpenoid carboxylic acids, of which a very small number function as growth hormones in higher plants, the predominant bioactive forms being GA_1 and GA_4 (Sponsel and Hedden, 2004). They act throughout the plant life cycle to stimulate growth of most organs through enhanced cell division and cell elongation, and also to promote developmental phase transitions, including those between seed dormancy and germination, juvenile and adult growth phases, and vegetative and reproductive development. Although GA action is necessary for normal growth and development, seedlings lacking the capacity to synthesise or perceive GAs will undergo limited development, including even the transition to flowering under certain light conditions (Griffiths et al., 2006; Koornneef and van der Veen, 1980; Ueguchi-Tanaka et al., 2005). The GA signalling pathway comprises the biosynthesis of the active hormones, their perception, signal transduction and inactivation, each of which is subject to regulation by environmental signals, including abiotic stress (Fig. 2). GAs are biosynthesised from *trans*-geranylgeranyl diphosphate,

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Genotype:	WT	*35S:GA20ox*	*ga20ox1/2*	*ga2ox*	*ga3ox1/2*	*ga20ox1/2/3*
GA status:	Normal	High	Reduced	High	Reduced	Very low

Fig. 1. Drought tolerance of gibberellin (GA) metabolism mutants of *Arabidopsis thaliana*. Watering ceased after 15 days and plants were grown for a further 10 days. The genotypes are: wild type (WT; Col-0); *35S:GA20ox* (high GA content due to overexpression of *AtGA20ox1*, a rate-limiting enzyme); *ga20ox1/2* (GA content reduced through knockout of *AtGA20ox1* and *AtGA20ox2*, two of the five *AtGA20ox* genes); *ga2ox* (elevated GA content through knockout of five *AtGA2ox* genes); *ga3ox1/2* (reduced GA content through knockout of *AtGA3ox1 AtGA3ox2*, two of the four *AtGA3ox* genes); and *ga20ox1/2/3* (very low GA content through loss of three *AtGA20ox* genes).

formed in plastids via the methylerythritol phosphate pathway (Kasahara et al., 2002), through the sequential action of two plastid-localised terpene cyclases, followed by oxidation on the endoplasmic reticulum by cytochrome P450 monooxygenases and then by soluble 2-oxoglutarate-dependent dioxygenases (reviewed by Hedden and Thomas, 2012; Yamaguchi, 2008). The dioxygenases comprise small families of GA 20-oxidase (GA20ox) and GA 3-oxidase (GA3ox) isozymes, while a third class of dioxygenases, the GA 2-oxidases (GA2ox), produce inactive products and function to enable GA turnover. Most evidence points to the genes encoding the dioxygenases as the main sites of regulation of the GA biosynthetic pathway by developmental and environmental signals, the *GA2ox* genes being particularly responsive to abiotic stress. Expression of certain paralogues within the *GA20ox*, *GA3ox* and *GA2ox* gene families is regulated by GA action, the biosynthetic genes being downregulated, while *GA2ox* expression is upregulated, providing a mechanism for GA homeostasis (O'Neill et al., 2010; Thomas et al., 1999; Weston et al., 2008).

The details of how GAs are perceived and the early events in signal transduction have accumulated in the last few years and are beginning to explain in molecular terms the pleiotropic action of GA in plant development (reviewed by Davière et al., 2008; Schwechheimer, 2011; Sun, 2011; Ueguchi-Tanaka and Matsuoka, 2010). It was known for some time that GA action resulted in the degradation of a group of transcriptional regulators known as DELLA proteins that form a subgroup of the GRAS family of proteins. DELLA proteins are named for a conserved domain within the N terminus that is unique to this subgroup and is necessary for GA-induced degradation. Binding of GA to its soluble, nuclear receptor, GID1, causes a conformational change in the protein that promotes its association with the N-terminal domain of the DELLA protein, enabling, in turn, interaction with an SCF ubiquitin ligase, such that the DELLA is ubiquitinated, and thus targeted for degradation via the 26S proteasome. Although DELLA proteins act as growth repressors, they may activate or suppress gene expression. However, there is no evidence that they bind directly to gene promoters, but rather act in association with transcription factors, the complex sometimes acting as a transcriptional activator (Hirano et al., 2012), or as an inhibitor through sequestration (de Lucas et al., 2008; Feng et al., 2008). Several DELLA-interacting proteins have been shown to be components of other hormone signalling pathways, providing a mechanism for GA signalling to interact with these pathways (Bai et al., 2012; Gallego-Bartolomé et al., 2012; Hou et al., 2010).

GA in growth and stress responses to abiotic stress

Growth restriction in response to abiotic stress

A significant breakthrough in our understanding of the role of GA in regulating plant growth in response to stress came from the observation that growth restraint on exposure to several forms of abiotic stress is at least in part mediated by DELLA proteins (Achard et al., 2006; Achard et al., 2008a; Magome et al., 2008). In *A. thaliana* seedlings, exposure to salinity triggered a reduction in endogenous bioactive GAs (Achard et al., 2006; Magome et al., 2008), which coincided with DELLA accumulation (Achard et al., 2006). Consistent with this, the growth of wild-type *A. thaliana* seedlings was inhibited by salt stress, whilst in a quadruple-*della* mutant, stress responses including reduction in primary root growth and rate of leaf production, and delayed flowering time were attenuated (Achard et al., 2006). Furthermore, a link between DELLA function and survival of salt stress has been identified (Achard et al., 2006; Achard et al., 2008b; Magome et al., 2004). Lines with reduced GA content or signalling, such as the GA-deficient biosynthetic mutant *ga1-3*, showed enhanced survival of severe salt stress, with the quadruple-*della* mutant more susceptible (Achard et al., 2006). Importantly, analysis of growth parameters and salt tolerance in a range of *della* mutants indicated a strong correlation between plant height, time to flowering transition and susceptibility to severe salt stress, suggesting that DELLA proteins may restrain growth and enhance stress tolerance through a common mechanism (Achard et al., 2008b). Similar to responses to salt stress, exposure of *A. thaliana* seedlings to cold stress also triggers a reduction in bioactive GA, promotes DELLA accumulation and results in DELLA-mediated growth restriction (Achard et al., 2008a). Again, DELLA function contributed to stress tolerance, with *della* mutants showing reduced survival of freezing. In both cases, the upregulation of specific *GA2ox* genes by dehydration-responsive element binding protein (DREB1)/C-repeat binding factor (CBF) (DREB1/CBF) family transcription factors appears to contribute to

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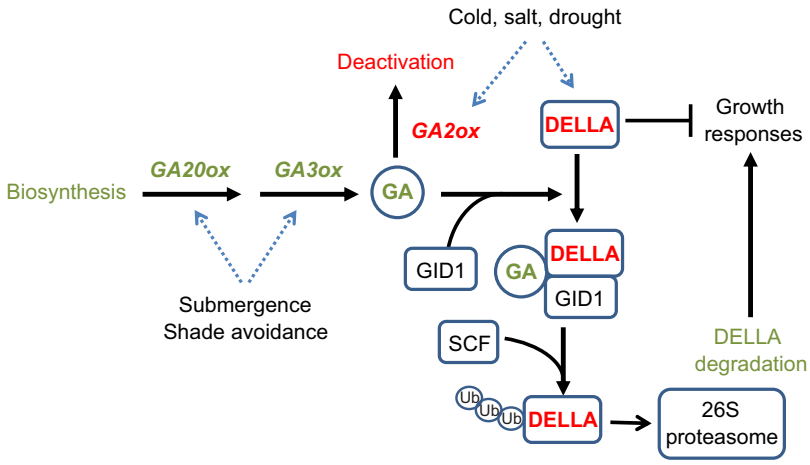

Fig. 2. Summary of the GA biosynthesis and signal transduction pathways showing points of intervention by abiotic stress. Escape mechanisms involving growth promotion act to enhance GA biosynthesis through upregulation of specific paralogues of the dioxygenase genes *GA20ox* and *GA3ox*. Growth inhibition occurs predominantly via upregulation of specific GA-deactivating *GA2ox* genes and in some cases DELLA genes. Attenuation of GA concentration allows stabilisation of the DELLA growth suppressors, which would otherwise be degraded by the 26S proteasome via interaction with the GA receptor GID1 and SCF ubiquitin E3 ligase-mediated ubiquitination. Normal arrows denote a positive, while the T-bar indicates a negative (inhibitory) relationship. The blue dotted arrows indicate points of intervention by environmental stress factors. Ub, ubiquitin.

the observed reduction in bioactive GA, and subsequent downstream responses (Achard et al., 2008a; Magome et al., 2008).

Response to submergence

The involvement of GA signalling in mediating growth and stress responses to abiotic stress is supported by current models of survival strategies employed by rice varieties adapted to escape or tolerate flooding (Bailey-Serres and Voesenek, 2010). Varieties adapted to environments in which shallow, long-lived floods are common employ an 'escape' strategy, in which submergence triggers rapid internode elongation. This response allows the shoot to out-grow the flood waters. Internode elongation is triggered by upregulation of the ethylene response factor (ERF) domain proteins *SNORKEL1* and *SNORKEL2* in response to ethylene accumulation (Hattori et al., 2009), which directly or indirectly leads to increases in bioactive GA levels. In contrast, the *Sub1* locus controls the quiescence strategy of rice varieties that are adapted to short-lived, deep floods (Xu et al., 2006). Upon submergence, rice plants carrying the *Sub1A* gene will not activate an escape response (Fukao and Bailey-Serres, 2008a). Instead, shoot elongation is restricted and carbohydrate resources are conserved for utilisation in re-growth when the flood recedes (Fukao et al., 2006; Xu et al., 2006). This restriction of elongation growth is associated with increased levels of the rice DELLA protein SLENDER LIKE-1 (SLR1) and the negative regulator of GA signalling SLR1-LIKE 1 (SLRL1), both of which decline in response to submergence in varieties without *Sub1A* (Bailey-Serres and Voesenek, 2010; Fukao and Bailey-Serres, 2008b). The presence of *Sub1A* is also associated with a dramatic increase in tolerance to submergence, with both leaf viability and recovery of leaf production significantly improved in *Sub1A* lines (Fukao et al., 2006). GA is also thought to be involved in a related escape response, in which certain flood-tolerant species such as *Rumex palustris* undergo leaf hyponasty (bending upwards) on submergence because of differential growth of the petiole, followed by elongation of the petiole and leaf blade (reviewed in Polko et al., 2011).

Shade avoidance

Another escape strategy involving increased growth is the shade avoidance response in which, in order to avoid the risk of shading, plants alter their morphology when the presence of close neighbours is detected, in large part because of associated changes in the light spectrum and intensity (Smith, 1982). The responses include increased growth of the hypocotyl and stem, as well as leaf hyponasty and petiole extension, and involve the action of multiple hormones, including auxin, ethylene, brassinosteriods and GA (Keuskamp et al., 2010b; Stamm and Kumar, 2010). Because of strong absorption of red light by chlorophyll, the presence of surrounding vegetation is indicated by a decrease in the ratio of red to far-red light, which is detected by the photoreceptor phytochrome B (PhyB). A second photoreceptor, cryptochrome, detects a reduction in the intensity of blue light. For the leaf responses in *A. thaliana*, it has been suggested that the photoreceptors signal via separate pathways that converge on the bHLH transcription factors PHYTOCHROME INTERACTING FACTOR 4 (PIF4) and PIF5 (Keller et al., 2011). The PhyB-mediated shade avoidance response requires GA signalling (Djakovic-Petrovic et al., 2007) and involves altered auxin biosynthesis (Tao et al., 2008) and distribution (Keuskamp et al., 2010a). The action of ethylene in shade avoidance appears to be closely linked to that of auxin and is, at least in part, independent of the GA pathway (Pierik et al., 2009). The phytochromes are photoreversible between the P_r and P_{fr} forms, the latter predominating in red light and functioning as a protein kinase (Rockwell et al., 2006). As illustrated in Fig. 3, the PIF transcription factors are inactivated through phosphorylation by PhyB in its P_{fr} form, whereas under far-red light, PhyB is converted to its inactive P_f form and the PIFs remain active. PIF4 is also a target for GA signalling through interaction with DELLA proteins, which block its transcriptional activity (de Lucas et al., 2008; Feng et al., 2008). Thus by destabilising DELLAs, GA signalling promotes PIF4 function. Under far-red light, GA biosynthesis is enhanced by strong upregulation of *GA20ox* expression, as shown in petioles of *A. thaliana* (Hisamatsu et al., 2005) and *R. palustris* (Pierik et al., 2011), with a slight increase in *GA3ox* expression also detected in the latter. The mechanism for this regulation is currently unknown, but it is potentially mediated by auxin, which has been shown to stimulate GA biosynthetic gene expression in other contexts (Frigerio et al., 2006; O'Neill et al., 2010).

Response to mild osmotic stress

Our understanding of the role of GA in growth restriction triggered by abiotic stress has recently been advanced by a number of studies focusing on the response of *A. thaliana* seedlings to mild osmotic stress (Claeys et al., 2012; Skirycz et al., 2011; Skirycz et al., 2010). Seedlings were exposed to a low concentration of the solute mannitol, which resulted in a 50% reduction in final leaf size as a result of effects on both cell proliferation and cell expansion (Skirycz et al., 2011; Skirycz et al., 2010). A precise analysis of cellular growth dynamics allowed the sampling of leaves at points where they were exclusively composed of proliferating, expanding

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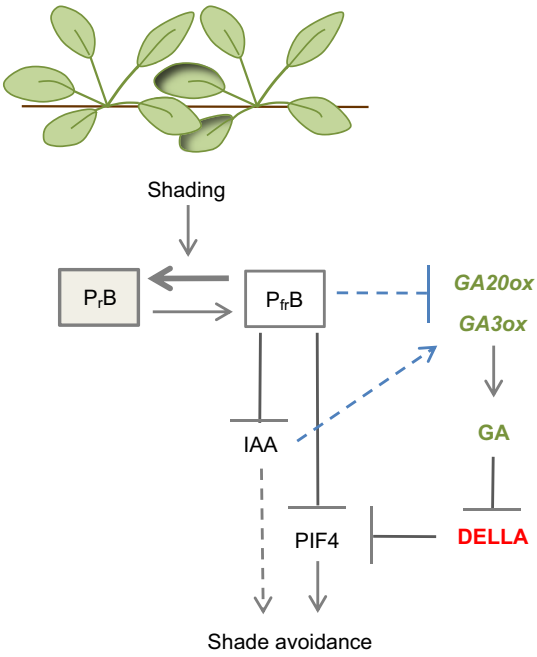

Fig. 3. Phytochrome B-mediated signalling and the involvement of GA in the shade avoidance response. A low red/far-red light ratio converts the active P_{fr} form to inactive P_r (indicated by the thick grey arrow), allowing the gene activation function of PIF4. This light regime also promotes GA biosynthesis through transcriptional activation of *GA20ox* and *GA3ox* genes, resulting in degradation of DELLA proteins, which otherwise inhibit PIF4 function by sequestration. The mechanism for the transcriptional activation is uncertain but it may be mediated by auxin (IAA), whose synthesis and distribution is promoted by far-red light. Normal arrows and T-bars indicate positive and negative interactions, respectively. Blue arrows denote transcriptional activation. Dashed arrows indicate unclear or indirect relationships.

or mature cells (Skirycz et al., 2010). Comparison of the transcriptional profiles for each leaf stage with publicly available data on transcriptional responses to hormone treatments suggested that ABA-mediated responses were associated with expanding and mature cells, with some classical ABA-mediated responses, differentially expressed exclusively in mature cells. In both proliferating and expanding cells, ethylene signalling and DELLA target genes were over-represented, with changes associated with cell walls (such as xyloglucan transferases and expansins) occurring predominantly in expanding cells. This apparent developmental separation of hormone-mediated responses to osmotic stress suggests that ethylene and GA may play predominant roles in regulating cell proliferation and expansion, whilst ABA regulates responses mainly in mature tissues (Skirycz et al., 2010). In addition, the rapid nature of the cellular response to mild osmotic stress has led to speculation that hormone signals are imported from other tissues, rather than synthesised *de novo* (Verelst et al., 2010).

Further investigation into growth arrest by mild osmotic stress revealed that effects on cell proliferation were associated with a rapid, but reversible arrest of the cell cycle until 48 h post-transfer, at which point mitotic exit was triggered. Proliferating cells responded to the stress with the rapid induction of ethylene-related transcripts, and an increase in levels of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid was later detected in shoots. Two mutants with impaired ethylene sensitivity showed a reduced effect of mannitol on cell number and leaf area, supporting ethylene-mediated regulation of reversible cell-cycle arrest (Skirycz et al., 2011). However, the early onset of endoreduplication and cellular differentiation did not appear to be affected (Skirycz et al., 2011). Consistent with the predicted role for ethylene and GA in proliferating cells (Skirycz et al., 2010) differential expression of GA metabolism genes and DELLA-regulated transcripts as well as accumulation of RGA was observed in proliferating cells of mannitol-treated seedlings by 24 h post-transfer (Claeys et al., 2012; Skirycz et al., 2011). Early onset of endoreduplication triggered by mannitol was found to be abolished in several mutant lines with altered GA metabolism or signalling, including lines with increased (*quintuple ga2ox*) and reduced (*ga3ox1-3*) endogenous GA, or increased GA signalling (*rga28*, *gai-2*) (Claeys et al., 2012). This implies that the response is disrupted by both positive and negative effects on DELLA function. Together, these results suggest that ethylene and GA signalling contribute to regulation of the cell cycle and endoreduplication, respectively, in proliferating cells of *A. thaliana* exposed to mild osmotic stress (Claeys et al., 2012; Skirycz et al., 2011). The ethylene and GA-mediated responses are likely linked by the action of the ERF transcription factor ERF6 (Dubois et al., 2013). Understanding how this model of developmentally separated hormone-mediated responses (Claeys et al., 2012; Skirycz and Inzé, 2010) can be integrated with the role of DELLA as a point of convergence of multiple hormone signalling pathways in the response to abiotic stress (Achard et al., 2006; Fukao and Bailey-Serres, 2008a) is an important challenge for future work.

Response to soil drying

Soil moisture deficit is a major constraint to crop yields that is predicted to become more serious in some regions, including southern Europe, as a result of climate change (Dai, 2011; Lobell and Gourdji, 2012). Soil drying exposes plants to multiple abiotic stresses, the relative contributions of which will depend on the nature of the soil and the extent of drying (Chapman et al., 2011; Mittler, 2006). As soils dry, they become mechanically strong and more resistant to root growth (Gao et al., 2012), while water and nutrients become less accessible to the roots (Passioura, 1991). The relationship between these factors is complex and their effects on plant development may be difficult to separate (Bengough et al., 2011; Whalley et al., 2008). In moderately dry soil, mechanical impedance is likely to be a major factor limiting root growth; in contrast, under water deficit in the absence of mechanical stress, plants maintain or increase root growth (Leach et al., 2011; Saucedo et al., 2012). Soil-borne abiotic stress typically impacts shoot growth, with reductions in leaf elongation reported for plants growing under water (Leach et al., 2011; Liu et al., 2003) or in nitrogen-deficient environments (Kavanová et al., 2008). Leaf growth is also inhibited by strong soils, with reported reductions in both cell size and number (Beemster and Masle, 1996). Increased mechanical impedance over a relatively narrow range of matric potentials was also shown to decrease tiller production in wheat, under field conditions (Atwell, 1990) and in sand culture experiments (Whalley et al., 2006). However, it is unclear how soil strength is sensed and the mechanism through which it influences shoot growth and development is unknown (Young et al., 1997). Furthermore, there is no consensus on the relative importance of root impedance in comparison with the other stress factors.

There has been relatively little published on the influence of water deficit on GA metabolism, although osmotic stress, which is often used as a proxy for drought, was reported to reduce GA content in maize leaves (Wang et al., 2008). The meta-analysis illustrated in Fig. 4B and the work discussed above indicates that drought and

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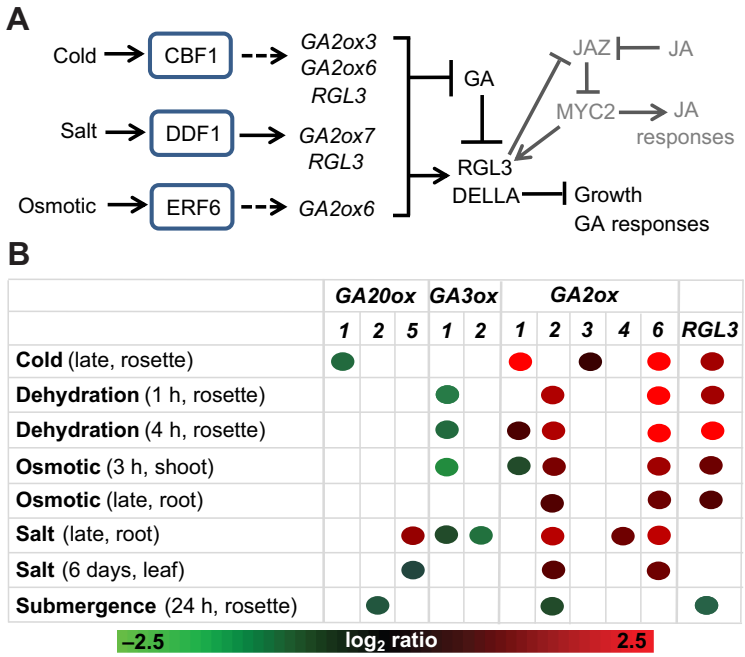

Fig. 4. Summary of transcriptional regulation of genes involved in GA metabolism and signalling under abiotic stress conditions. (A) Upregulation of *GA2ox* and *RGL3* transcripts by AP2/ERF family transcription factors leads to a reduction in bioactive GA and GA signalling under abiotic stress conditions. A possible interaction with jasmonic acid signalling is indicated in grey. Dashed arrows indicate indirect regulation or unknown relationship. T-bars indicate inhibition or a negative relationship. (B) Transcriptional responses of GA biosynthesis and deactivation genes as well as *RGL3* on exposure to the abiotic stress indicated. Data were extracted from Genevestigator v3 (Hruz et al., 2008), applying a fold-change cut-off of 1.5 and a *P*-value of 0.05. Empty cells indicate no significant change. Genes that showed a significant change in at least one of the selected experiments are shown. Data shown are from: Genevestigator experiment ID AT-00120 (Kilian et al., 2007); AT-00419 (Mizoguchi et al., 2010); AT-00520 (Kinoshita et al., 2012); AT-00403 (Chan et al., 2012); and AT-00560 (Lee et al., 2011).

osmotic stress in *A. thaliana* result in changes in gene expression that would be expected to reduce GA content. However, in a study on the effects of drought on the transcriptome of wild accessions of emmer, it was reported that this treatment was associated with a decrease in *GA2ox* expression in the roots, with the most drought-sensitive accessions showing the largest response (Krugman et al., 2011). This is consistent with the maintenance of root growth under water deficit, allowing a redistribution of growth between roots and shoot.

Evidence for root-derived signals as mediators of the leaf stunting caused by soil compaction was obtained from work with barley (Hussain et al., 1999a). While a temporary elevation of ABA concentration in the xylem sap when roots encountered compacted soil could be associated with reduced stomatal conductance, the effect on growth could not be assigned directly to ABA, and work with tomato indicated a possible role for ethylene (Hussain et al., 1999b). Recent work has indicated that GA signalling may also be involved in this phenomenon (Coelho Filho et al., 2013). Wheat seedlings were grown in soil columns in which mechanical impedance was increased by application of weights without altering water or nutrient availability. Reduced leaf elongation in the strong soil was rescued by applying GA to the sand, with lines growing in strong soil responding more to the applied GA than those in the weaker soil. Furthermore, *Rht* semi-dwarf lines with reduced GA sensitivity gave a weaker growth reduction response to the strong soil. These results are consistent with a lower GA concentration in the leaf, which has been confirmed by direct measurement (D. P. A. Lloyd, S. P. Vaughan, W. R. Whalley, P.H. and A.L.P., unpublished). Because shoots are not thought to be dependent on roots for their supply of GA (Kaneko et al., 2003), it seems unlikely that root-derived GA is the signal regulating leaf elongation, and GA metabolism in the leaf may be responding to other root signals. In the experiments described by Coelho Filho et al. (Coelho Filho et al., 2013), the observation that applied GA exacerbated the negative effect of soil strength on root elongation and tiller number did not support a role for GA signalling in these effects.

GA signalling and stress tolerance

Many of the studies linking DELLA function to restricted growth under abiotic stress also showed a positive effect on stress tolerance (Achard et al., 2006; Achard et al., 2008b; Fukao and Bailey-Serres, 2008b; Magome et al., 2004). As noted above, analysis of a range of *della* mutants in *A. thaliana* indicated that DELLA function and associated growth restraint under non-stressed conditions correlated well with reduced susceptibility to severe salt stress, suggesting that a common regulatory mechanism might mediate both responses (Achard et al., 2008b). Investigation of DELLA-mediated transcriptional regulation in *A. thaliana* implicated control of the antioxidant system as an important DELLA-mediated response to stress (Achard et al., 2008b). DELLA activity was found to restrain the accumulation of reactive oxygen species (ROS), which are known to accumulate in salt-treated plants, as well as under a range of other biotic and abiotic stresses. At high levels, ROS trigger plant cell death, a response that is also delayed by DELLA (Achard et al., 2008b). In rice, a similar link between maintained levels of SLR1 and reduced levels of oxidative stress was reported for Sub1A lines exposed to drought and to dehydration following flooding (Fukao et al., 2011). As ROS also appear to be involved in controlling GA-mediated root growth, it was suggested that they may link DELLA-mediated growth and stress tolerance effects (Achard et al., 2008b).

In *A. thaliana*, the level of DELLA-mediated growth restraint under unstressed conditions appears to be linked to survival of stress (Achard et al., 2008b), while DELLA accumulation is linked to growth restriction on exposure to abiotic stress (Achard et al., 2006; Claeys et al., 2012; Fukao and Bailey-Serres, 2008b; Magome et al., 2008). Cell proliferation is known to be regulated by DELLA (Achard et al., 2009; Ubeda-Tomás et al., 2009), and DELLA accumulation triggers mitotic exit on exposure to mild osmotic stress (Claeys et al., 2012). However, under those conditions, an observed reduction in cell number in wild-type plants was also seen in *A. thaliana* lines with reduced DELLA activity (although the early onset of endoreduplication was abolished) (Claeys et al., 2012). This, together with data suggesting that DELLA targeted different cell cycle regulators under osmotic stress to those reported

previously (Achard et al., 2009; Claeys et al., 2012), may indicate a distinction between the role of DELLA in stressed and non-stressed conditions. The relative contributions of the effects of DELLA on growth rate under unstressed conditions and DELLA-mediated growth restriction activated on exposure to abiotic stress to the stress tolerance attributed to DELLA (Achard et al., 2006; Achard et al., 2008a; Magome et al., 2004) are still poorly understood, and it is possible that the mechanisms by which DELLA acts are different under these conditions.

Regulation of GA metabolism and signalling in the response to abiotic stress

Interaction between GA and other hormone signalling pathways

It has been clear for some time that a major role of GA signalling in the response to abiotic stress is to integrate information from a number of other hormone signalling pathways (Achard et al., 2006). The classical stress hormones ABA and ethylene appear to be closely integrated with GA signalling in a number of systems. In *A. thaliana*, inhibition of root growth in seedlings treated with ABA was associated with the accumulation of DELLA proteins, and was reduced (though not abolished) in the quadruple-*della* mutant (Achard et al., 2006). The ABA-mediated accumulation of DELLA could not be replicated in the severe GA biosynthesis mutant *ga1-3*, even after treatment with a low concentration of GA to reduce DELLA levels, suggesting that DELLA accumulation was related to a reduction in bioactive GA levels, rather than a direct effect on DELLA stability (Zentella et al., 2007). DELLA accumulation in response to ABA was not observed in the ABA-receptor mutant *abi1-1* (Achard et al., 2006; Leung et al., 1997). These results suggest that ABA-mediated growth restriction is at least partially DELLA-dependent, and requires ABI1 signalling. The role of DELLA in stress responses controlled by other hormone signalling pathways was investigated further by assessing salt tolerance in a *ctr1*, *gai-t6*, *rga-24* mutant. The *ctr1* mutant shows enhanced survival of severe salt stress, because of the constitutive activation of ethylene responses (Achard et al., 2006; Ju et al., 2012; Kieber et al., 1993). This salt tolerance was significantly reduced in the *ctr1*, *gai-t6*, *rga-24* mutant, suggesting that, as with ABA, ethylene signalling is at least partly integrated with GA signalling at the level of DELLA function (Achard et al., 2006).

In submerged rice, the passive accumulation of ethylene in flooded tissue is believed to be the primary signal triggering the GA-mediated growth responses (Jackson, 2008). The accumulation of ethylene also triggers ABA catabolism, probably by increased ABA 8′-hydroxylase activity. This occurs independently of *Sub1A*, but may be required for the observed strong upregulation of *Sub1A* on submergence (Fukao and Bailey-Serres, 2008b). Transcriptional profiling suggests that *Sub1A*, an ERF subfamily protein, regulates a large number of transcripts in hormone signalling pathways, including those mediated by ABA, ethylene, cytokinin and GA (Jung et al., 2010). Interestingly, maintained expression of a *GA2ox* transcript in *Sub1A* lines (compared with a control line) on submergence suggests regulation of GA deactivation as a mechanism by which *Sub1A* could restrain the accumulation of bioactive GA, and thus maintain levels of SLR1 (Jung et al., 2010). In addition to promoting tolerance to submergence, *Sub1A* also promotes tolerance of dehydration and drought stress (Fukao et al., 2011). On de-submergence (which triggers dehydration), and after withholding water, *Sub1A* lines maintained a higher leaf relative water content, showed reduced ROS accumulation and oxidative stress, and recovered their growth more effectively on re-watering. This enhanced tolerance was associated with increased responsiveness to ABA, and enhanced expression of both ABA-dependent and ABA-independent drought-responsive transcripts (Jung et al., 2010). Enhanced ABA-responsiveness is consistent with the reduced GA responsiveness also mediated by *Sub1A* (Fukao and Bailey-Serres, 2008b; Fukao et al., 2011), although it is not yet clear whether this response is dependent on SLR1.

As in deep-water rice, the leaf hyponastic response to submergence in *R. palustris* is initiated by the accumulation of ethylene. Differential growth of the petiole is proposed to involve a redistribution of the auxin IAA (indole-3-acetic acid) transported from the leaf blade (Cox et al., 2006). Ethylene induces a reduction in the concentration of ABA in the petiole followed by an increase in GA production, which is associated with enhanced *GA3ox* expression (Benschop et al., 2006). The relatively slow promotion of GA biosynthesis is possibly a consequence of the reduced concentration of ABA, the action of which was shown to suppress GA biosynthesis through downregulation of *GA20ox* and *GA3ox* expression (Benschop et al., 2006).

Regulation of GA metabolism and signalling during abiotic stress

Information on the signalling networks by which GA metabolism and signal transduction are regulated by abiotic stress is emerging (summarised in Fig. 4A). The identification of Sub1A as a member of the ERF subfamily of transcription factors (Xu et al., 2006) is consistent with evidence from *A. thaliana* suggesting a central role for APETALA2/ERF (AP2/ERF) family transcription factors in regulating GA metabolism in response to abiotic stress (Achard et al., 2008a; Dubois et al., 2013; Magome et al., 2004; Magome et al., 2008). Two transcription factors of the DREB1/CBF family, a subfamily of the AP2/ERF group, have been found to regulate GA deactivation in response to salt and cold stress in *A. thaliana* (Achard et al., 2008a; Magome et al., 2004; Magome et al., 2008). The GA-deficient phenotype of the activation-tagged *dwarf and delayed flowering-1* (*ddf1*) line led to the elucidation of the role of the DDF1 transcription factor in directly promoting the expression of *AtGA2ox7* on exposure to salt stress (Magome et al., 2008). Analysis of the *ga2ox7-1* mutant revealed a small increase in primary root length compared with wild-type seedlings exposed to salt stress, indicating that activation of *GA2ox7* contributes to this growth restriction, although there was no difference in tolerance to salt stress in *ga2ox7-1* or in a loss-of-function *ddf1* line. DREB1B/CBF1 was found to regulate expression of *AtGA2ox3* and *AtGA2ox6* in response to cold stress (Achard et al., 2008a). This regulation is believed to contribute to the observed reduction in bioactive GA on exposure to cold stress, and subsequent DELLA-mediated root growth restriction and freezing tolerance (Achard et al., 2008a). Regulation of GA metabolism does not appear to be limited to the DREB1/CBF subfamily, as the ERF subfamily transcription factor ERF6 has been implicated in control of *GA2ox6* in response to mild osmotic stress (Dubois et al., 2013). Interestingly, in these cases a number of other *GA2ox* genes were also found to be differentially expressed in response to abiotic stress (Achard et al., 2008a; Magome et al., 2008), further supporting that regulation of GA deactivation is an important point of control in the reduction of bioactive GA levels in response to stress and that different members of this gene family are differentially regulated depending on the stress encountered, and potentially the plant organ or developmental stage affected. A meta-analysis of transcriptional changes to *A. thaliana* GA metabolism and signalling genes in response to abiotic stress is summarised in Fig. 4B. This confirms the general hypothesis that abiotic stress reduces GA content through upregulation of *GA2ox* genes, while in some cases there is also downregulation of the biosynthetic *GA20ox* and/or *GA3ox*

genes. Of the five *A. thaliana DELLA* genes, only *RGL3* is upregulated by stress at the transcript level, while all DELLA paralogues should be stabilised by the low GA environment.

Regulation of expression or activity of transcription factors that modulate expression of GA metabolism genes could represent one mechanism by which GA signalling is integrated into the wider stress response network. Expression of most of the DREB1/CBF transcription factors is considered to be ABA-independent, with the precise mechanisms by which transcription is induced still unclear (reviewed by Mizoi et al., 2012). Data suggesting that the *A. thaliana* EIN3 protein, a transcription factor that regulates ethylene-dependent responses, binds directly to, and negatively regulates expression of, *DREB1/CBF* transcription factors, indicates a potential mechanism for integration (Shi et al., 2012).

GA signalling integrates developmental and environmental signals

The rapidly expanding information on the mechanism of DELLA signalling is providing important insight into how DELLA may function as an integrator of signals from multiple hormone pathways in the response to stress (Hou et al., 2010; Wild et al., 2012; Yang et al., 2012; Zhu et al., 2011). For example, the plant hormone jasmonic acid (JA) triggers both resistance to necrotrophic pathogens and growth inhibition, via interaction with DELLA signalling (Navarro et al., 2008; Yang et al., 2012). Direct interaction between DELLA and JA ZIM-domain (JAZ) proteins, repressors of JA signalling that are degraded by the 26S proteasome in the presence of active forms of JA, provides competition for binding of JAZ proteins to the MYC2 transcription factor, one of a number of transcription factors regulating JA-dependent transcriptional responses (Boter et al., 2004; Hou et al., 2010). Furthermore, JAZ proteins compete with growth-promoting PIF transcription factors for binding to DELLA (Yang et al., 2012). As such, the DELLA–JAZ interaction modulates both JA- and DELLA-mediated responses (Hou et al., 2010; Yang et al., 2012). JA signalling is also believed to inhibit growth via effects on DELLA levels (Yang et al., 2012). Importantly, the DELLA gene *RGL3* is transcriptionally upregulated by JA signalling and its promoter was shown to be a direct target of MYC2 (Wild et al., 2012). Analysis of interactions between RGL3 and JAZ repressors indicated that RGL3 physically interacts with both JAZ1 and JAZ8, the latter of which is relatively resistant to JA-mediated degradation (Shyu et al., 2012; Wild et al., 2012). As such, the current model of the role of RGL3 suggests that release of MYC2 from sequestration by JA-degradable JAZ1 in the presence of JA triggers the induction of RGL3 by MYC2. RGL3 then potentiates JA signalling by binding the non-JA degradable forms of JAZ (JAZ8), further promoting MYC2-dependent JA responses (Wild et al., 2012). The level of bioactive GA in the plant determines the level of DELLA degradation, and thus the level of potentiation of the JA responses, providing a mechanism by which the two hormone signalling pathways can be linked. Similar physical interaction between JAZ repressors and the EIN3/EIL1 transcription factors in ethylene signalling suggest that this mechanism is conserved between other hormone signalling pathways (Zhu et al., 2011). The role of RGL3 in this interaction is particularly interesting, given the induction of *RGL3* expression by cold (Achard et al., 2006), high salinity (Magome et al., 2008) and drought (E.H.C., S.G.T., A.L.P. and P.H., unpublished). GA signalling has also been linked to regulation of ABA biosynthesis in the response to abiotic stress, via the putative early DELLA target gene *XERICO* (Zentella et al., 2007), which is induced by DELLA and believed to inhibit or repress a negative regulator of ABA biosynthesis (Ko et al., 2006; Zentella et al., 2007). Together, these data suggest a number of mechanisms by which GA signalling could integrate signals from multiple hormone signalling pathways in order to coordinate responses to abiotic stress in plants.

Conclusions

Evidence is accumulating that suppression of GA signalling is a general response to abiotic stress, with transcriptional upregulation of *GA2ox* genes, encoding GA-inactivating enzymes, and in *A. thaliana*, of the DELLA gene *RGL3*, which encodes a growth suppressor, demonstrated in studies of different stresses. While in some cases it has been shown that the genes are direct targets of stress-induced AP2/ERF-type transcription factors, understanding of the signalling networks linking stress to expression of these genes is still in its infancy. There is still less understanding of the relationship between GA signalling and stress tolerance, beyond the well-established role of GA as a growth regulator and the finding that it regulates the levels of ROS (Achard et al., 2008b). Furthermore, the action of GA cannot be considered in isolation of the other hormone signals, not least because of the rapidly emerging evidence for interactions between hormone pathways, in many cases mediated by the DELLA proteins. Experimental expedience has meant that stresses have generally been studied in isolation, although this is seldom representative of the true situation. For example, soil drying results in strengthening of the soil, increasing its mechanical resistance to root growth, as well as reducing access to water and nutrients, these individual stresses producing distinct physiological effects. In order to understand plant responses to environmental challenges it is necessary to determine the contributions and influence of the component stress factors, but predicting the outcome from their combination is a considerable task.

A major practical goal in research on abiotic stress has been the identification of ‘key’ genes that might be manipulated to enhance stress tolerance. It has been pointed out in relation to drought tolerance that the common feature of such manipulation has been a reduction in leaf area and therefore transpiration, such that the available water is used more slowly (Lawlor, 2013). This is likely to contribute to the improved drought tolerance resulting from reduced GA signalling, but less leaf area is not usually compatible with maintaining crop yields. Breaking the link between DELLA-mediated stress tolerance and growth restriction could potentially provide a mechanism to retain growth and therefore crop productivity under mild stress. Even if this link cannot be broken, moderating the plant’s growth response to mild stress may allow yields to be maintained without compromising tolerance. However, GA is clearly involved in a broad spectrum of responses to both mild and severe abiotic stress, and a clearer understanding of the role of GA signalling in these responses would be an important step towards understanding and improving plant growth and stress responses under adverse environmental conditions.

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Competing interests

The authors declare no competing financial interests.

Author contributions

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