Functional characterization and unraveling the Gene Regulatory Networks (GRNs) of HD-Zip transcription factor HB40 (and HB22) in Arabidopsis thaliana

Dong, S.

Chapter 1.

General introduction

Phytohormone- and transcription factor-regulated growth and development in plants

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Plant growth and development

Growth and development are fundamental characteristics of all living organisms. Plants grow in both height and width throughout their lifespan. Plant growth is defined as size increase through cell division and enlargement, which also includes synthesis of new cellular material and arrangement of subcellular organelles. There are multiple ways to measure plant growth, such as the increase in fresh/dry weight, volume, length, height and surface area. Plant growth is an irreversible change in mass, while development is an irreversible change in tissue and organ structure. In general, plant development is divided into four stages: embryogenesis, juvenile stage, adult vegetative and reproductive stage. All developmental events, from the embryo to the mature plant, occur in a well-ordered manner (Thomas and Ougham, 2017). Fundamental research on plant growth and development has led to many breakthroughs in the past decades. With a better understanding of growth and development in plants, we will ultimately be able to control breeding and cultivation according to our demands. This can include improving crop yield and securing food supply for the increasing world population, enhancing fiber production and identifying new sources of renewable biofuels, bioactive compounds and medicines (Brown, 2016; Małyska and Jacobi, 2018). *Arabidopsis thaliana* was selected as a model plant for scientific research more than thirty years ago (Koornneef and Meinke, 2010). Since then, it has become the most thoroughly studied flowering plant. Significant progress in understanding plant growth and development has been made by investigating the molecular genetics of this simple angiosperm (Provart et al., 2016).

Arabidopsis was originally adopted as a model organism due to its advantages in genetic experiments. This organism has the ability to grow in the lab maintaining a small plant size and a short generation time. Each plant can produce 10,000 to 40,000 seeds though self-fertilization. Moreover, Arabidopsis has a relatively small nuclear genome (around 135 Mbp) for a complex multicellular eukaryote. Its genome sequence was published in 2000 and more than 25,000 genes were annotated (Bevan and Walsh, 2005). In plant research, the Arabidopsis genome is generally used as the standard reference for the sequence alignment of crop genomes (Meinke et al., 1998; Bussemaker et al., 2001).

Taking Arabidopsis as an example, a typical life cycle starts from a seed that germinates and grows into a mature plant (**Figure 1**). Every seed harbors a miniature embryo. During seed development or embryogenesis, the zygote develops into a mature embryo which possesses a shoot apical meristem (SAM) and a root apical meristem (RAM). Further organogenesis is

determined by the action of the SAM and RAM. The meristems are very essential parts of plants, as new tissues and organs are all initiated from meristems, which makes plants able to grow indefinitely over time. The next stage is seedling development or germination, which gives rise to seedlings. In this process, an embryonically-formed hypocotyl pushes through the soil along with the cotyledons. During the vegetative growth stage, leaves initiate from the flanks of the SAM and undergo expansion, morphogenesis and differentiation in a highly flexible process that forms the final leaf shape. Seedlings accumulate biomass and energy for reproductive growth through photosynthesis. After some time, flower buds emerge and plants become mature. The mature plants are composed of primary and secondary roots, rosette and cauline leaves, stems, inflorescences and siliques. Flowers contain stamens (male reproductive organ) and carpels (female reproductive organ) sepals and petals. After pollination, the fertilized egg develops into an embryo inside the seed (Diévart and Clark, 2004).

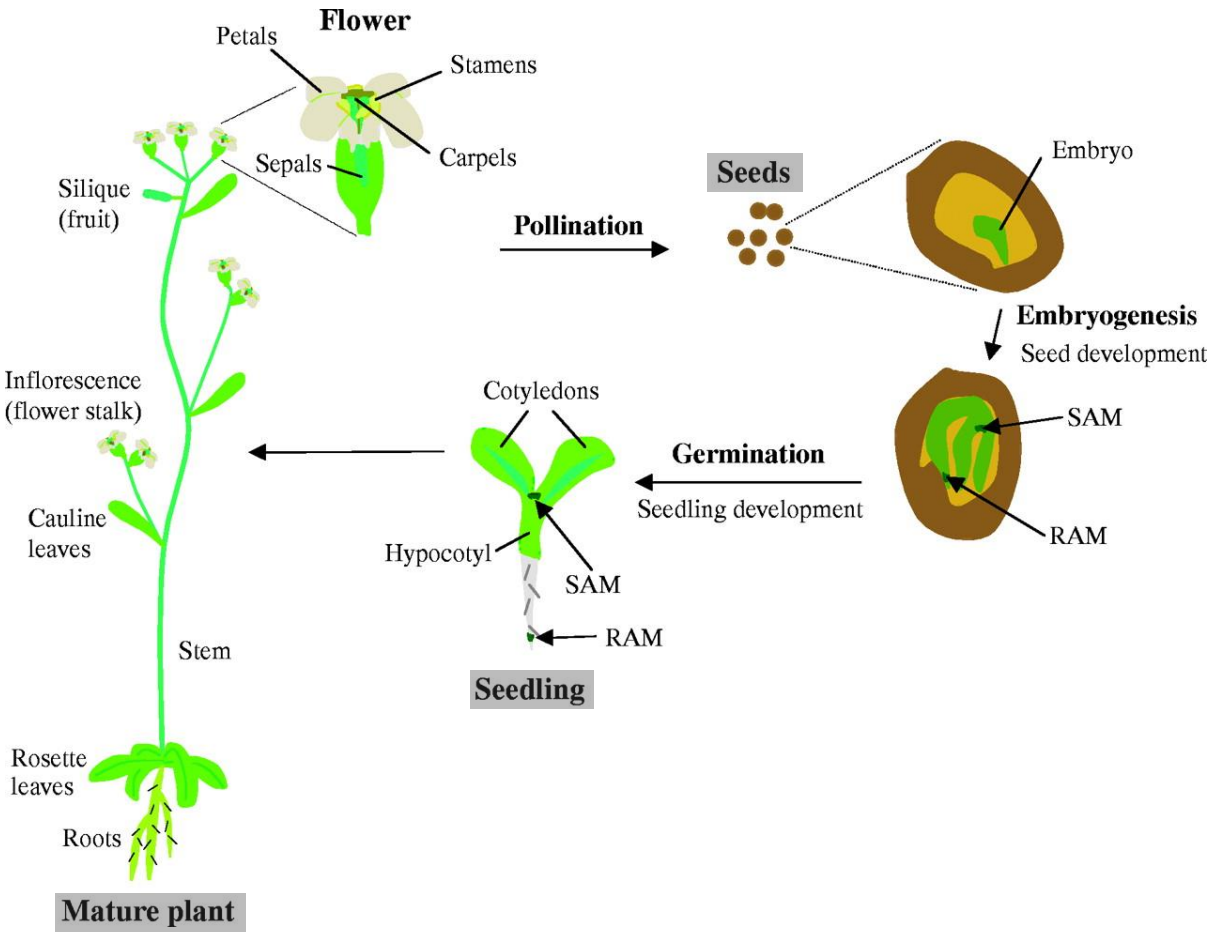

Figure 1. Life cycle of *Arabidopsis thaliana* (modified from Dievart and Clark, 2004). The typical life cycle of Arabidopsis starts from the seed stage. Seeds undergo embryogenesis and germination to

grow into seedlings, which further develop into mature plants. Flowers of mature plants produce seeds after pollination. SAM, shoot apical meristem. RAM, root apical meristem.

Growth and development are complex and dynamic processes which involve environmental and intrinsic stimuli. Environmental factors influencing plant growth/development include, besides others, light, water, temperature and nutrition. Three principal characteristics of light have an effect on plant growth: quantity, quality and duration (or photoperiod) (Singh and Singh, 2015). Temperature affects most biological processes, including photosynthesis, respiration, transpiration, germination and flowering. Temperature also influences the transition from vegetative growth to reproductive growth when combined with day length (Hatfield and Prueger, 2015). Water plays plenty of roles in plants. It is a basic component in photosynthesis and respiration, the solvent for minerals and carbohydrates, and the medium in which most biochemical reactions occurs. Water evaporates from leaf tissue during transpiration, which provides the power to move nutrients through the plant. Moreover, it is responsible for turgor pressure in cells, and turgor is important to maintain cell shape and keep cell growth. Plants need 17 elements for normal growth and development. Except for carbon, hydrogen and oxygen that can be taken from air and water, the other nutrients are found in soil. Nitrogen, potassium, magnesium, calcium, phosphorus and sulfur are defined as macronutrients which are used in relatively large amounts (e.g. 20 g/m^2) by plants. Eight micronutrients or trace elements are chloride, nickel, molybdenum, zinc, boron, copper, manganese and iron that are used in much smaller amounts (e.g. 0.05-2 g/m^2) (Briat et al., 2015; Chrysargyris et al., 2016). Most of these nutrients are dissolved in water; plants absorb them by roots and translocate them through transpiration to other organs. When a plant is under stress, for example because of extreme temperature or low light which leads to reduced photosynthesis, nutrient deficiency may occur (Pregitzer and King, 2005; Yan et al., 2012). Intrinsic factors regulating plant growth/development can be genes, e.g. transcription factors, or chemicals. These chemicals are small, simple chemicals produced naturally by plants to regulate their growth and development, which are also referred to as plant growth regulators or phytohormones (Neumann et al., 2009).

Phytohormonal regulation of plant growth

There are many plant growth factors that affect the function, growth and development of plants. Phytohormones (also known as plant hormones) are one of these essential factors. They are small chemicals that are used by plants for communication, coordination and development

between cells. Plant hormones have been discovered in a variety of species, ranging from algae to higher plants (Tarakhovskaya et al., 2007). They are signal molecules, like animal hormones, that control growth and development in extremely low concentrations. However, phytohormones have a simpler structure in contrast to those of animals and humans. There are no specific or specialized glands in plants that produce phytohormones. Generally, these can be synthesized in any cell of the plant and act on any part of the plant. Phytohormones are involved in numerous aspects of growth and development, such as forming organs like leaves, flowers, stems, and fruits and determining the sex of flowers and the color of fruits and leaves (Miyakawa and Tanokura, 2017). They also play a role in respiration, energy production, plant longevity and death (Umehara et al., 2008). Phytohormones coordinate the plant's body and response to the various endogenous/exogenous signals (Shan et al., 2012). As crucial signaling molecules, the homeostasis of hormone biosynthesis and metabolism is tightly and differentially regulated in different tissues though the development stages (Vert et al., 2005).

Phytohormones are categorized into several classes based on their chemical features. Within each class, they share common physiological effects, but their exact structures differ. There are five major classes of early discovered plant hormones. They are auxin, gibberellin (GA), cytokinin, abscisic acid (ABA) and ethylene (Santner and Estelle, 2009). Auxin, GA and cytokinin are hormones that promote growth, whereas ABA and ethylene act as growth inhibitors. In addition to the five traditionally known classes, brassinosteroid (BR), jasmonic acid (JA), salicylic acid (SA), strigolactone (SL), nitric oxide (NO), polyamine, and peptide were also characterized as new groups of plant hormones in recent decades (Shapiro, 2005; Moschou and Roubelakis-Angelakis, 2013; Takahashi et al., 2018). JA and SA are essential in the plant's response to pathogen attack, and plants use them as long-distance signals to communicate with distant leaves within one plant and even with neighboring plants (Katsir et al., 2008; Rivas-San Vicente and Plasencia, 2011). Except for its role in defense, JA also functions in root growth, seed germination, and the storage of protein in seeds (Browse, 2005). Additionally, SA is also involved in abiotic stress responses, for example, the response to drought, heavy metal and osmotic stress (Verma et al., 2016; Berens et al., 2019). Roles of SL have been shown in shoot branching, leaf senescence, light signaling, as well as the response to phosphate starvation and salt stress (Ha et al., 2014). Plant peptide hormones are small secreted peptides that serve as signaling molecules involved in cell-to-cell communication (Lindsey et al., 2002). For instance, the small peptide CLE25 was identified as a long-distance signal that transduces drought stress sensed by roots to stomata in leaves (Takahashi et al.,

2018). In plants, polyamines are associated with the regulation of senescence, programed cell death and the process of mitosis and meiosis (Moschou and Roubelakis-Angelakis, 2013; Sobieszczuk-Nowicka, 2017). NO acts as a second messenger in hormonal and defense responses that modulate various biological processes, including root development, seed germination, stomatal closure, nitrogen fixation and cell death (Shapiro, 2005).

Gibberellins

Gibberellin (GA) was first discovered in the fungus *Gibberella fujikuroi* by plant pathology field researchers in the 20th century (Yabuta, 1938). GAs are essential growth hormones in plants which are mainly present in the meristems of roots and apical buds, young leaves and embryos. GAs promote plant growth throughout development. For example, they can stimulate stem elongation, delay senescence and break seed dormancy (Hedden and Sponsel, 2015). Mutants with defects in GA biosynthesis exhibit decreased germination and reduced elongation of the hypocotyl, root and stem (Magome et al., 2004; Achard and Genschik, 2009; Rizza et al., 2017). Furthermore, GAs have many commercial uses in agriculture. Farmers use synthetic GAs to increase the size of fruits and enhance seed germination. Moreover, GA also plays an important role in abiotic stress responses, such as the response to cold, salt, drought and osmatic stress (Daviere and Achard, 2013).

In Arabidopsis, GA biosynthesis proteins mainly consist of 14 members (Sun, 2008). In **Table 1**, we list these genes including CPS (*ent*-copalyl diphosphate synthase, or GA1), KS (*ent*-kaurene synthase, or GA2), KO (*ent*-kaurene oxidase, or GA3), KAO (*ent*-kaurenoic acid oxidase), GA20OX (GA 20-oxidase) and GA3OX (GA 3-oxidase) (Martinez-Bello et al., 2015). Nine GA catabolism proteins have been characterized, which includes seven GA2OXs (GA 2-oxidases) and two GAMTs (GA methyltransferases). Shown in **Figure 2**, GA biosynthesis starts from the conversion of GGDP (geranylgeranyl diphosphate) by CPS and KS into *ent*-kaurene in plastids (Helliwell et al., 2001). Subsequently, KO converts *ent*-kaurene to *ent*-kaurenoic acid, followed by an oxidation reaction, which is catalyzed by endoplasmic reticulum (ER)-associated KAO, and GA12 is synthesized as a product (Grennan, 2006). Together with other GA oxidases, GA20OXs produce GA15, GA53, GA15, GA44, GA24, GA19, GA9 and GA20 from GA12 in the cytosol (Serrani et al., 2007; Magome et al., 2013). All these GAs are intermediates in the GA biosynthesis pathway and are not bioactive. The final steps are catalyzed by GA3OXs, and bioactive GAs (GA1 and GA4) are produced (Yamaguchi, 2008).

Table 1. GA-associated genes in *Arabidopsis thaliana*.

Group	LOCUS ID	GENE NAME	FUNCTION
GA biosynthesis	AT4G02780	*CPS* (*GA1*)	*ent*-copalyl diphosphate synthase
	AT1G79460	*KS* (*GA2*)	*ent*-kaurene synthase
	AT5G25900	*KO* (*GA3*)	*ent*-kaurene oxidase
	AT1G05160	*KAO1*	*ent*-kaurenoic acid oxidase
	AT2G32440	*KAO2*	*ent*-kaurenoic acid oxidase
	AT4G25420	*GA20OX1*	GA 20-oxidase
	AT5G51810	*GA20OX2*	GA 20-oxidase
	AT5G07200	*GA20OX3*	GA 20-oxidase
	AT1G60980	*GA20OX4*	GA 20-oxidase
	AT1G44090	*GA20OX5*	GA 20-oxidase
	AT1G15550	*GA3OX1*	GA 3-oxidase
	AT1G80340	*GA3OX2*	GA 3-oxidase
	AT4G21690	*GA3OX3*	GA 3-oxidase
	AT1G80330	*GA3OX4*	GA 3-oxidase
GA catabolism	AT1G78440	*GA2OX1*	GA 2-oxidase
	AT1G30040	*GA2OX2*	GA 2-oxidase
	AT2G34550	*GA2OX3*	GA 2-oxidase
	AT1G47990	*GA2OX4*	GA 2-oxidase
	AT1G02400	*GA2OX6*	GA 2-oxidase
	AT1G50960	*GA2OX7*	GA 2-oxidase
	AT4G21200	*GA2OX8*	GA 2-oxidase
	AT4G26420	*GAMT1*	GA methyltransferase
	AT5G56300	*GAMT2*	GA methyltransferase
GA signaling	AT3G05120	*GID1A*	GA receptor
	AT3G63010	*GID1B*	GA receptor
	AT5G27320	*GID1C*	GA receptor
	AT2G01570	*RGA*	DELLA, GA signaling repressor
	AT1G14920	*GAI*	DELLA, GA signaling repressor
	AT1G66350	*RGL1*	DELLA, GA signaling repressor
	AT3G03450	*RGL2*	DELLA, GA signaling repressor
	AT5G17490	*RGL3*	DELLA, GA signaling repressor
	AT3G11540	*SPY*	OGT, GA signaling repressor
	AT4G24210	*SLY1*	F-box protein
	AT5G48170	*SNE*	F-box protein

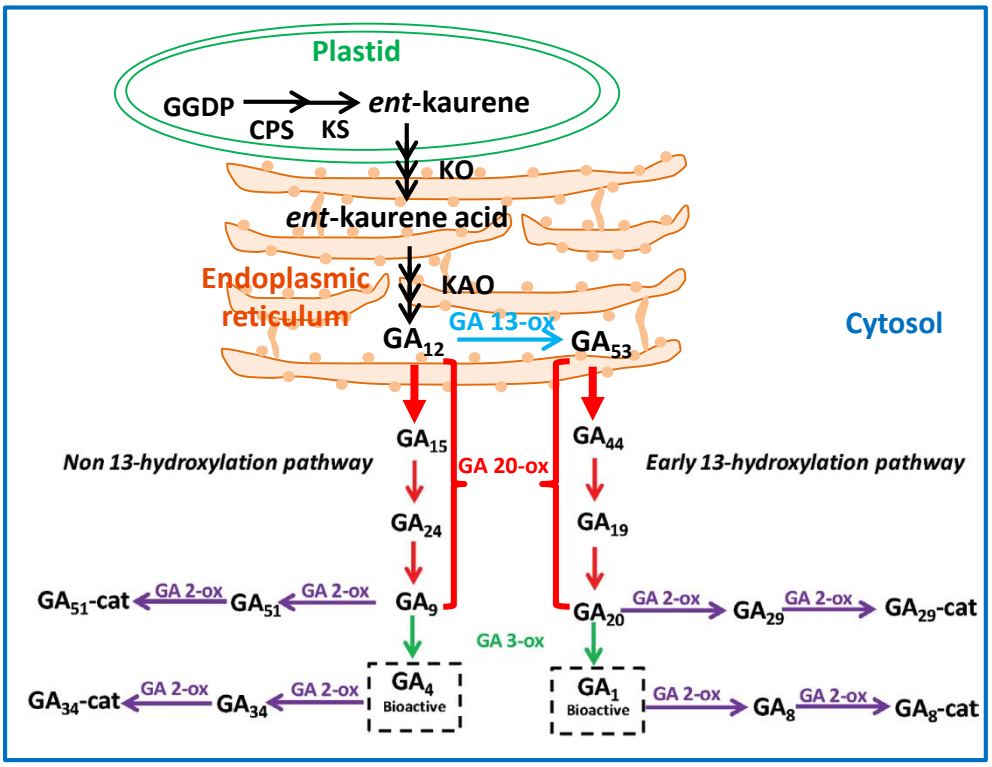

Figure 2. GA biosynthesis and catabolism pathways (modified from Hedden and Thomas, 2012; Martinez-Bello et al., 2015). The GA biosynthesis starts from plastid and yields bioactive GAs (GA1 and GA4) in the cytosol. GA 3-oxidases are key GA biosynthesis enzymes that catalyze the last step of GA biosynthesis. GA 2-oxidases are important GA catabolism enzymes that convert GAs into bio-inactive GAs.

The mechanism of the GA signaling pathway in the model plant Arabidopsis and crops including rice (*Oryza sativa*) and tomato (*Solanum lycopersicum*) has been well elucidated *via* biochemical, genetic and structural analysis (Umehara et al., 2008; Hirano et al., 2010). The GA receptor GID1 (GIBBERELLIN INSENSITIVE DWARF1) is a soluble protein which is similar to hormone-sensitive lipases. Three homologous genes in Arabidopsis called *GID1a*, *GID1b* and *GID1c* have been characterized as functionally redundant GA receptors (Eckardt, 2007). Loss of function of GID partially or completely shuts down GA signaling, and the mutants show severe dwarfing phenotypes (Griffiths et al., 2006). DELLAs are key repressors in GA signaling pathways. The name is based on a short chain of amino acids (D-E-L-L-A) located in the N-terminal region, which is tightly conserved among all plant species (Locascio et al., 2013). As shown in **Figure 3**, DELLAs contain a functional domain and a regulatory domain. The DELLA domain is located at the N-terminus, which binds to GID and acts as a regulatory domain. The GRAS domain interacts with TFs and usually contains the nuclear localization signals (Taiz and Zeiger, 2010). The rice and barley genomes encode

a single DELLA protein, SLENDER1 (SLR1) and Slender1 (Sln1), respectively (Locascio et al., 2013). In contrast, in Arabidopsis there are five DELLA proteins: GAI (GA-insensitive), RGA (repressor of GAI), RGL1, RGL2 and RGL3 (RGA-like) (Eckardt, 2007). In Arabidopsis, each of the three GID1 proteins interacts with each of the five DELLA proteins. Genetic studies indicate that these DELLA proteins have overlapping yet distinct functions in regulating plant growth and development. GAI and RGA are important for GA-induced vegetative growth, floral initiation and stem elongation (Dill and Sun, 2001; Bouton et al., 2002). GA-promoted seed germination is mainly repressed by RGL2, and RGA, RGL1 and RGL2 are involved in flower and fruit development (Cheng et al., 2004; Piskurewicz et al., 2008). There is little evidence for the direct binding of DELLA proteins to DNA, suggesting that they probably regulate target genes by interacting with DNA-binding transcription factors (Locascio et al., 2013). DELLAs regulate specific developmental processes through interaction with many different transcription factors. They sequester DNA-binding transcription factors and prevent them from inducing or repressing the target genes through direct interaction. For instance, Arabidopsis DELLAs interact with bHLH transcription factors PIF3 (PHYTOCHROME INTERACTING FACTOR 3) and PIF paralogs, which prevents PIFs from binding to the promoters of their target genes and results in short hypocotyls in light-grown plants (Li et al., 2016). They can also bind directly to SPL (SQUAMOSA PROMOTER BINDING–LIKE) transcription factors, which explains the mechanism by which GA accelerates flowering (Yu et al., 2012). There are plenty of publications demonstrating that DELLAs are key components in the crosstalk between GA and other phytohormones. They directly interact with the brassinosteroid-dependent BES1 and BZR1 transcription factors (Gallego-Bartolomé et al., 2012). DELLA proteins facilitate the gibberellin–jasmonic acid crosstalk though interaction with MYC2 and JAZs (Hong et al., 2012; Wild et al., 2012). Moreover, DELLAs are involved in feedback regulation of GA metabolism. In general, genes encoding GA biosynthesis enzymes including *GA3OXs* and *GA20OXs* are positively regulated by DELLAs, while *GA2OXs* encoding GA catabolism enzymes are repressed by DELLAs (Cheminant et al., 2011; Gallego-Bartolomé et al., 2011). As growth repressors, DELLA proteins accumulate under stresses like drought, low temperature, salt stress and nutrient deficiency (Achard et al., 2008; Xie et al., 2016; Dubois et al., 2017). DELLAs enhance ROS (reactive oxygen species) scavenging to reduce cell death (Achard et al., 2008). They promote stress-induced anthocyanin biosynthesis, as well as the formation of a JAZ–DELLA–MYBL2 complex (Xie et al., 2016). DELLA proteins thereby increase tolerance to abiotic stresses in plants.

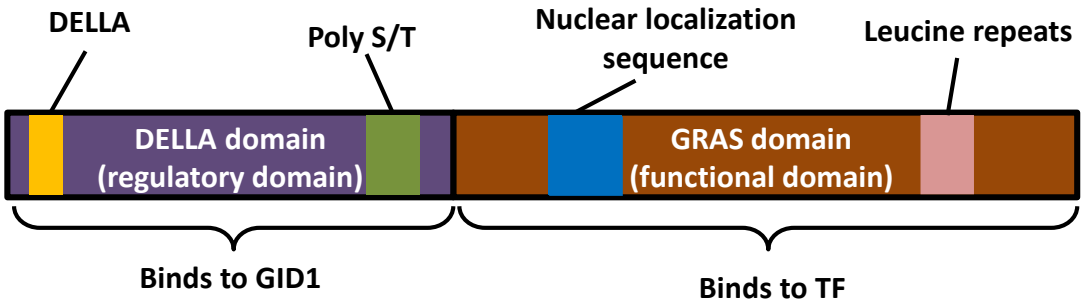

Figure 3. Schematic diagram of the structure of DELLA proteins (modified from Taiz and Zeiger, 2010). DELLA proteins contain two essential domains, the DELLA and GRAS domain. The DELLA domain is responsible for binding to the GA receptor GID. The GRAS domain binds to TFs and represses the transcription of the target genes regulated by these TFs.

As indicated in **Figure 4**, a typical GA signaling model is composed of three steps: first, perception of the GA signal followed by formation of a GA-GID1-DELLA complex; second, proteasome-dependent degradation of DELLAs induced by GA; and finally, releasing the repression of growth and development controlled by DELLAs (Sun, 2010). The GA receptor GID1 contains a pocket structure allowing GA binding. The GID1 protein shows subcellular localization in both the cytosol and nucleus, revealing its role in GA perception and signaling transduction (Ueguchi-Tanaka et al., 2005). The GA response is activated when the GA-GID1 complex translocates to the nucleus and triggers the destruction of the DELLA proteins (Livne and Weiss, 2014). In the presence of bioactive GA, GID1 recognizes and binds to GA molecules (Murase et al., 2008). Subsequently, the GA–GID1–DELLA complex is formed in the nucleus through interaction between GA–GID1 and DELLA domains of DELLA proteins, which leads to the degradation of the DELLA proteins *via* the ubiquitin-proteasome pathway (Ueguchi-Tanaka et al., 2005). GA-GID1 can also decrease DELLA activity by means of a degradation-independent mechanism (Ariizumi et al., 2013). Degradation of the DELLAs relieves the DELLA-mediated growth repression and facilitates GA responses, including cell expansion, stem elongation, dormancy and flowering (Miyazaki et al., 2018). Moreover, DELLAs also play central roles in stress responses (Nir et al., 2017). Under stress conditions, plants consume more resources and energy for survival partially through lowering the activity of the GA signaling pathway by upregulating GA-inactivating genes *GA2OXs* and some *DELLA* genes (Colebrook et al., 2014; Martinez-Bello et al., 2015).

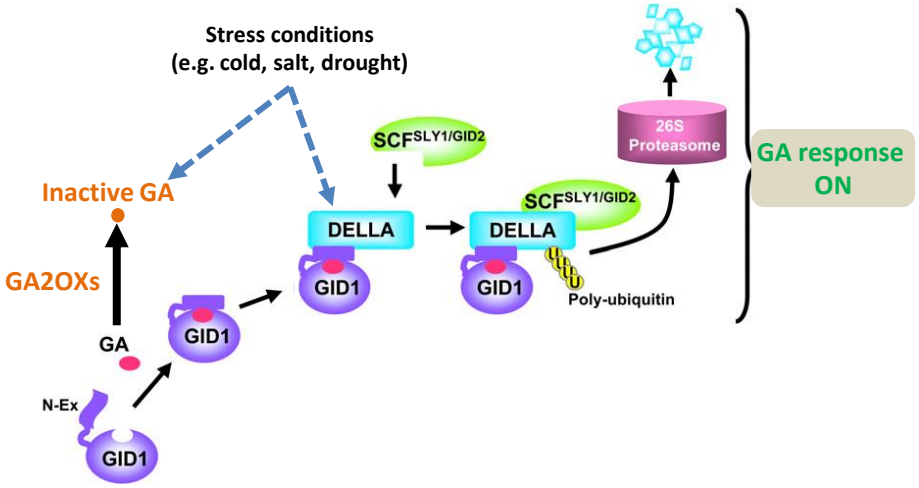

Figure 4. Model of GA signaling in plants (modified from Sun, 2010; Colebrook et al., 2014). The GA receptor GID perceives the GA signal and triggers the degradation of GA signaling repressors DELLAs. Thus, the GA response is activated. Stress conditions promote GA inactivation and an increase of the stability of DELLA proteins.

Brassinosteroids

Brassinosteroids (BRs) are recognized as the sixth class of phytohormones playing essential and diverse roles in plant growth and development (Kutschera and Wang, 2012). Researchers have demonstrated the role of BRs for various developmental processes, including the promotion of cell expansion, vascular differentiation, leaf development and pollen tube formation (Nemhauser et al., 2004; Choe, 2006; Hedden and Sponsel, 2015). BR-mediated growth responses are partially mediated through the regulation of genes involved in cell expansion and division (Shigeta et al., 2011). It has been shown that BRs regulate the reorientation of cortical microtubules in hypocotyl cells of Arabidopsis and the modulation of plasma membrane ion channels to promote cell expansion (Zhang et al., 2005b). Moreover, BRs control plant responses to environmental stresses and immunity (Divi and Krishna, 2010; Wang, 2012). BRs have been shown to confer tolerance to a variety of biotic and abiotic stresses, including drought, salinity, extreme temperatures and heavy metals (Bajguz, 2000; Fariduddin et al., 2009; Fariduddin et al., 2011; Yusuf et al., 2012).

BRs are synthesized using sterols as precursors in plants. The genes encoding BR biosynthetic enzymes have been characterized and reported in many plant species. Cytochrome P450 monooxygenases including DWF4 (DWARF4), CYP90A1/CPD, CYP90C1 and CYP90D1 are important enzymes in BR biosynthesis. DWF4 is a 22α-hydroxylase which catalyzes a rate-limiting step in BR biosynthesis (Kim et al., 2006). CYP90A1/CPD, CYP90C1 and CYP90D1

act as 23α-hydroxylases (Ohnishi et al., 2006). Another enzyme involved in BR biosynthesis is BR6OX, which catalyzes the C-6 oxidation of different 6-deoxo-BRs (Bishop et al., 1999). BR biosynthesis starts from campesterol which goes through oxidation, hydroxylation, dehydrogenation and reduction reactions catalyzed by associated enzymes, and brassinolide is generated as the end product *via* two parallel pathways: the early and late C-6 oxidation pathways (Fujioka and Yokota, 2003; Choe, 2006).

Signaling transduction studies have unraveled the signaling pathway involving BRs. They bind to the extracellular domain of a membrane-associated receptor-like kinase, BRASSINOSTEROID-INSENSITIVE1 (BRI) at the cell surface, to activate the signaling cascade and regulate the transcription of target genes (Nam and Li, 2002; Li, 2005; Wang et al., 2005). In the presence of BRs, BRI1 perceives and binds to the BRs, which activates the kinase activity of BRI1 and its co-receptor, BRI1-associated receptor kinase (BAK1), which leads to the disassociation of the inhibitory protein BRI1 kinase inhibitor (BKI1) and transphosphorylation of the kinase domains of BRI1 and BAK1 (Wang et al., 2002). BRI1 then phosphorylates BRASSINOSTEROID-SIGNALLING KINASE1 (BSK1) and CONSTITUTIVE DIFFERENTIAL GROWTH1 (CDG1), which triggers the phosphorylation of phosphatase BRI1-SUPPRESSOR1 (BSU1) and inactivates the GSK3-like kinase BRASSINOSTEROID INSENSITIVE2 (BIN2). BIN2 acts as a BR signaling inhibitor through phosphorylation and inactivation of two extensively characterized transcription factors mediating the BR signaling pathway, BZR1 Brassinazole-Resistant1 (BZR1) and bri1-EMS-Suppressor 1 (BES1) (Yin et al., 2002). Thus, the presence of BR suppresses BIN2 activity, which leads to dephosphorylation, activation and accumulation of BZR1 and BES1 in the nucleus followed by activating BR response genes, e.g. *RD26*, *WRKY74*, *ANAC059*, *ATHB-2* and *ATMYBL2*, which play diverse roles in growth and stress response (Li et al., 2002; Yu et al., 2011).

The relationship between GA and BR signaling pathways

BR and GA are two important plant growth-promoting hormones, sharing similar functions in a variety of developmental processes throughout the plant lifespan. BR and GA interaction exists in processes including seed germination, flowering, gene expression regulation, cell elongation, and hormone biosynthesis (Depuydt and Hardtke, 2011). The GA-deficient mutant *ga1*and BR-deficient mutant *cpd* were reported to show delayed flowering phenotypes (Sun et al., 1992; Szekeres et al., 1996). Later, another paper reported that the double mutant *cpd ga1*

showed further delayed flowering than the single mutant *cpd*. Moreover, the transgenic line overexpressing GA biosynthetic gene *GA5* and BR biosynthetic gene *DWF4* flowered earlier than the single overexpressor of *GA5*, which implies that BR-promoted flowering is dependent on GA. This study thereby supports a genetic interaction of GA and BR pathways in controlling flowering time in Arabidopsis (Szekeres et al., 1996). Defects in either the GA or BR biosynthesis pathway lead to dwarfism and a decrease in seed yield (Tong and Chu, 2016). Germination of GA-deficient and insensitive mutants could be partially recovered by BR in Arabidopsis, suggesting a possible interaction of GA and BR signaling in regulating seed germination by regulating each other's biosynthesis or response (Steber and McCourt, 2001). Although GA and BR signaling pathways have been considered to largely act on non-overlapping transcriptional responses, the effects of GA and BR can also be additive (Nemhauser et al., 2006). Recent studies reveal more independent roles of GA and BR signaling pathways and direct interactions between them. Microarray data of the GA-deficient mutant *ga1-3* and the BR-insensitive mutant *bri1-116* revealed numerous common genes co-regulated by GA and BR (Bai et al., 2012).

Evidence obtained from genetic, physiological and biochemical analyses imply crosstalk between GA and BR signaling pathways at the molecular level (**Figure 5**). In the presence of BR, active BZR1 and BES1 directly interact with GA signaling repressor DELLA proteins and inhibit their DNA binding without affecting protein stability, and thus BR enhances GA-regulated gene expression by releasing DELLAs' inhibition of their target genes (Gallego-Bartolomé et al., 2012; Li et al., 2012). When GA levels are low or in the absence of GA, DELLAs bind to BZR1 or BES1 and prevent their dephosphorylation by protein phosphatase PP2A, which results in their inactivation. Therefore, the destabilization of DELLAs by GAs enhances BR-regulated cell elongation (Li et al., 2012). Stabilization of DELLAs in the absence of GA or BR leads to the inactivation of target transcription factors, such as bHLH factor PIF4, which promotes dark-induced cell elongation (de Lucas et al., 2008). Moreover, DELLA proteins have been shown in several studies to interact with BZR1 and PIFs, which integrate GA, BR, and light signals to modulate photomorphogenesis *via* transcriptional regulation (Feng et al., 2008). A recent study on rice explored BR-GA crosstalk through multiple analyses ranging from genetic and physiological to hormone quantification. The results indicate that BR regulates cell elongation by adjusting GA metabolism. Endogenous BR targeted D18/GA3ox-2 to enhance GA biosynthesis and promote cell elongation. On the other hand, high exogenous BR levels target GA2ox-3 to inactivate GA and repress cell

elongation. A high concentration of exogenous GA activates the primary BR signaling pathway that facilitates cell elongation. However, endogenous GA inhibits BR biosynthesis and signaling, which forms an inhibitory feedback loop (Tong et al., 2014). Moreover, the GA pathway is just one of the multiple downstream pathways in BR-controlled cell elongation. BR is also involved in the regulation of cell division, microtubule formation and shoot apical meristem development (Yamamuro et al., 2000; Hong et al., 2002). For instance, *brd1* is the most severe BR-deficient mutant, which fails to form microtubules, and exogenous GA treatment does not complement growth defects in severe BR mutants, while the most severe GA-deficient mutant, *d18*, maintains normal microtubule formation (Mori et al., 2002). Application of GA to BR-deficient and BR-insensitive mutants failed to increase hypocotyl elongation, while BR and the dominant gain-of-function *bzr1-1D* mutation was able to promote cell elongation in GA-deficient mutants (Zhu et al., 2013).

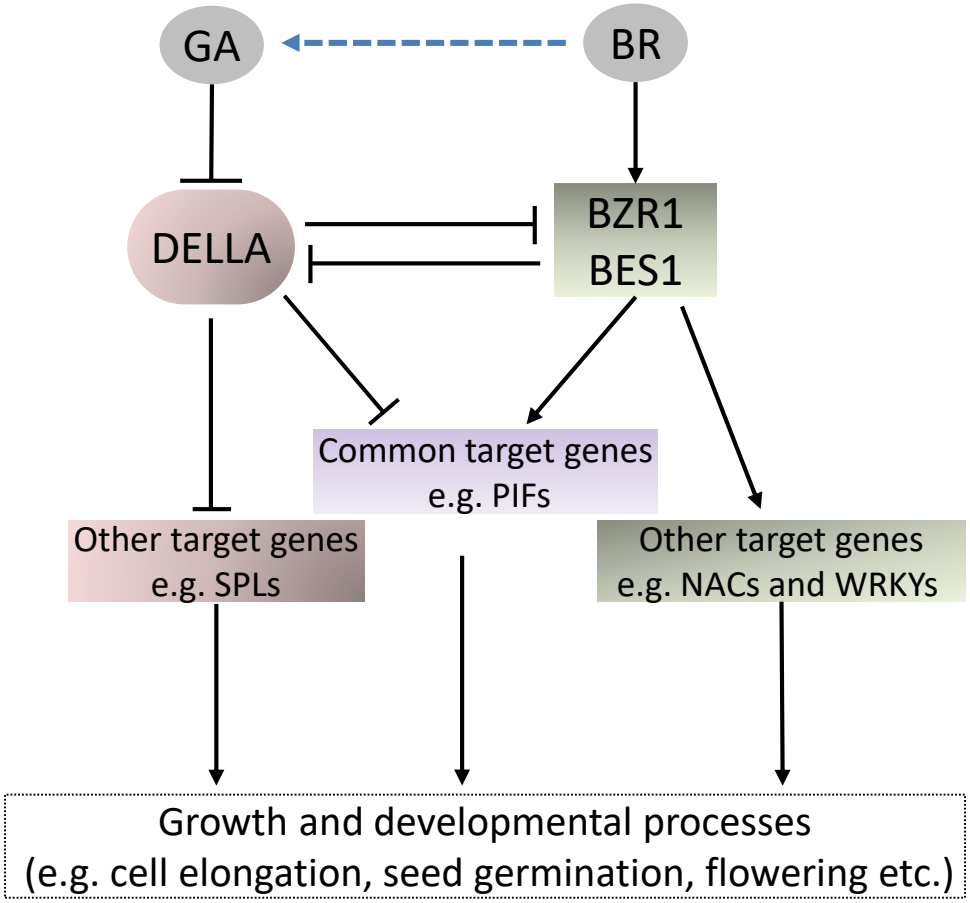

Figure 5. Model of GA-BR crosstalk centering around the interaction of DELLAs and BZR1/BES1. DELLA proteins interact with BZR1/BES1 and inhibit its activity. When GA signaling is activated, DELLAs are degraded by releasing its repression on BZR1/BES1 activity. On the other hand, BR promotes GA biosynthesis and production. Therefore, GA and BR signaling pathways

positively affect each other (Peres et al., 2019). DELLAs and BZR1/BES1 regulate growth and development through common targets and also specific target genes (Li and He, 2013).

Auxins

Auxins were first discovered in the 1920s (Paciorek and Friml, 2006). Typically, auxins promote cell enlargement and elongation. Auxins are responsible for various aspects of plant growth, including embryo and fruit development, organogenesis, differentiation of phloem and xylem, root initiation and patterning, delaying lead senescence and fruit ripening, apical hook formation and apical dominance (Kepinski and Leyser, 2005). It has been well studied how auxins mediate phototropism and geotropism, which allows plants to react to sunlight and gravity, also known as tropistic growth. In many plants, auxins are responsible for establishing the apical meristem and the growth direction of the plant (Estelle, 1996; Feraru et al., 2015). As it was one of the earliest discovered plant hormones, the commercial uses of auxins have expanded widely. Synthetic auxins are used as a weed killer by disrupting the growth cycle of many plants. They can also suppress lateral bud growth when applied to apical buds or stop the growth of unwanted branches on ornamental trees.

The most abundant auxin produced by plants is indole-3-acetic acid (IAA). It is present in plant seed embryos, young leaves and apical bud meristems. Previous studies have established the complete Trp (tryptophan)-dependent auxin biosynthesis pathway, in which Trp is used as a precursor (Zhao, 2010). The first step is catalyzed by the TAA family amino transferases that transfer the amino group from Trp to an alpha ketoacid (e.g. pyruvate) and generate indole-3-pyruvate (IPA). Subsequently, IPA is converted by the YUCCA (YUC) family of flavin monooxygenases to IAA (Zhao et al., 2001; Tao et al., 2008). The major mechanism through which auxin signals are converted into cellular response is *via* transcriptional regulation (Chapman and Estelle, 2009; Salehin et al., 2015). In the response to auxin, hundreds of genes rapidly adjust their expression patterns (Paponov et al., 2008). The key components of auxin signaling are three protein families: the auxin co-receptors F-box TIR1/AFB (TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX PROTEIN), the transcriptional repressors Aux/IAA (Auxin/INDOLE-3-ACETIC ACID) and the ARF (AUXIN RESPONSE FACTOR) transcription factors (Tan et al., 2007). ARF proteins interact with AREs (AUXIN RESPONSE ELEMENTS) in the promoters of auxin-inducible genes, and expression of these genes is repressed by Aux/IAA binding to these promoters. The auxin-mediated interaction between TIR1/AFB and Aux/IAA proteins brings them to SCF-type E3 ubiquitin ligase,

resulting in ubiquitination and degradation of the Aux/IAAs (Gray et al., 2001; Lavy and Estelle, 2016). Thus, repression o auxin-inducible genes by ARF proteins is induced.

Cytokinins

Cytokinins (CKs) are an essential class of phytohormones that are involved in numerous developmental processes, including cell division, cell elongation, morphogenesis, differentiation, senescence, phloem transport, accumulation of salts, flowering and sex expression; they are also important for apical dominance, seed dormancy, and establishing resistance to stress (Werner et al., 2001). CKs are synthesized in both shoots and roots and can undergo long-distance transport (Kamada-Nobusada and Sakakibara, 2009). From roots to shoots, CKs are transported through the xylem, and from shoots to roots through the phloem (Kieber and Schaller, 2018). Naturally occurring CKs are adenine derivatives. There are two classes of CKs which carry either an isoprenoid side chain or an aromatic side chain. CKs with an isoprenoid side chain include isopentenyladenine (iP), *trans*-zeatin (tZ), dihydrozeatin (DZ) and *cis*-zeatin (cZ). The other type of CKs with an aromatic side chain includes benzyladenine (BA), *meta*-topolin (mT) and *ortho*-topolin (oT) (Hwang and Sakakibara, 2006). Isoprenoid CKs exist more commonly in higher plants than lower plants and are more abundant than aromatic CKs. The biosynthesis pathway of isoprenoid CKs has been studied extensively (Kamada-Nobusada and Sakakibara, 2009). In the biosynthesis pathway of isoprenoid CKs, the first step is catalyzed by adenosine phosphate-isopentenyltransferase (IPT) using hydroxymethylbutenyl diphosphate (HMBDP), adenosine 5'-phosphates (ATP, ADP or AMP) or dimethylallyl diphosphate (DMAPP) as substrates (Sakakibara, 2010). IPT use HMBDP to produce *trans*-zeatin (tZ) nucleotides. On the other hand, iP-nucleotides are generated by IPT when DMAPP is used as a substrate. The iP-nucleotides are subsequently converted to tZ through hydroxylation. There are two cytochrome P450 monooxygenases, CYP735A1 and CYP735A2, which have been characterized in Arabidopsis as catalyzing the reaction (Takei et al., 2004).

The signaling pathway of CKs in plants has not been well demonstrated. The current model relies on phosphorelay signal transduction (Hutchison and Kieber, 2002). CKs are perceived by membrane-localized receptors through binding to histidine kinase CRE1, which induces His-Asp phosphorylation on His-containing phosphotransfer proteins (AHPs). Next, AHPs translocate to the nucleus and activate a family of sequence-specific DNA binding transcription factors (type-B ARRs or auxin response regulators). The activated type-B ARRs then bind to

the regulatory elements within the promoter of type-A ARRs and induce their transcription. Moreover, increased protein levels of type-A ARRs inhibit transcription of type-B ARRs, which forms a negative feedback loop (Hwang and Sakakibara, 2006).

Abscisic acid

Unlike auxin, cytokinin, and GA, abscisic acid (ABA) is an important stress phytohormone. It is particularly vital for stress responses in plants, including responses to drought, high/low temperature, salinity and heavy metal stress (Ng et al., 2014). ABA was originally named after its role in the abscission of flowers and fruits. In addition, the ABA-mediated signaling pathway is also involved in other developmental processes, including establishing bud and seed dormancy, stimulation of stomatal closure, leaf senescence, transpiration and starch hydrolysis (Miyakawa et al., 2013). In vascular plants, a major function of ABA is to induce stomatal closure in response to water loss. Under drought or high temperature conditions, ABA is produced in leaves. Increased ABA levels subsequently lead to stomatal closure, so that water is maintained in the leaves (Milborrow, 2001; Nambara and Marion-Poll, 2005).

Abiotic stresses such as heat, water deficit and salinity induce ABA biosynthesis. Studies on ABA-deficient mutants have largely helped reveal the ABA biosynthesis pathway, and the genes coding ABA biosynthesis enzymes have been well characterized in plants (Schwartz et al., 2003; Siewers et al., 2004). These studies suggest that ABA biosynthesis starts in plastids from the epoxidation of zeaxanthin and antheraxanthin to violaxanthin catalyzed by ZEP (zeaxanthin epoxidase). Violaxanthin subsequently undergoes a set of structural modifications and is converted to 9-*cis*-epoxycarotenoid. Next, NCED (9-*cis*-epoxycarotenoid dioxygenase) cleaves the major epoxycarotenoid 9-*cis*-neoxanthin and produces xanthoxin, a C_{15} intermediate. The conversion of epoxycarotenoid to xanthoxin is considered as the first key step in ABA biosynthesis. Xanthoxin is then exported from plastids to the cytosol and used by SDR (short-chain alcohol dehydrogenase/reductase) as a substrate to yield ABA-aldehyde. The final step of ABA biosynthesis is catalyzed by AAO (ABA aldehyde oxidase), which converts ABA-aldehyde to ABA (Xiong and Zhu, 2003). The model of the ABA signaling pathway has been confirmed by multiple genetic, biochemical and structural studies (Zang et al., 2016; Vishwakarma et al., 2017; Zhang et al., 2017). Key elements of the signaling cascade are ABA receptors, SnRK2s (Snf1-related protein kinases 2) and PP2Cs (type 2C protein phosphatases). ABA receptors were originally referred to as RCAR1-RCAR14 (Regulatory Component of ABA Receptor), or PYR1 (Pyrabactin Resistance 1) and PYL1-PYL13 (PYR1-like 1–13).

Later, they became known as PYLs (Park et al., 2009; Santiago et al., 2009; Nishimura et al., 2010). SnRK2s are positive regulators in ABA signaling. In the absence of ABA or when the ABA level is low, SnRK2s are inhibited by PP2Cs through direct binding, which keeps the ABA response silent. Stress-induced ABA accumulation activates the ABA receptors, PYLs, thereby allowing them to bind to PP2Cs. Thus, the PP2C-SnRK2 complexes dissociate and the inhibition of SnRK2s by PP2Cs is therefore released. Active SnRK2s then phosphorylate different target proteins in different tissues and trigger the downstream signaling cascade by activating the transcription of genes containing ABREs (ABA-responsive elements) in their promoters. As a result, the ABA response is switched on (Ng et al., 2014). For instance, SnRK2s phosphorylate the SLAC1 and KAT1 ion channels in guard cells, which leads to stomatal closure and prevents water loss due to transpiration (Yamazaki et al., 2003; Geiger et al., 2009; Sato et al., 2009).

Coordination of growth in response to environmental stresses

Plants grown in nature or agricultural farms are often confronted with various environmental conditions that are not optimal for plant growth and development. Throughout their life span, they may be exposed to a variety of abiotic stresses such as drought, salinity, shortage of water and nutrients and unstable temperatures, as well as biotic stresses such as an attack by pests, pathogen invasion and herbivore damage. These environmental stresses lead to a series of changes in physiological, biochemical and molecular processes and dramatically affect the yield of crops in agriculture (Verslues et al., 2006). Due to global climate change, crops are exposed more frequently to environmental constraints, including drought, salinity and high temperatures (Munns and Tester, 2008; Rengasamy, 2010; Roy et al., 2014). For instance, the most important crops that provide two-thirds of human caloric intake are wheat (*Triticum aestivum*), rice, maize (*Zea mays*) and soybean (*Glycine max*). Research on the impact of temperature increase on the yield of these staple food crops have indicated that a one degree-Celsius increase in global mean temperature would result in the decrease of global yield of rice by 3.2%, wheat by 6.0%, maize by 7.4%, and soybean by 3.1% (Porter and Gawith, 1999; Ottman et al., 2012; Wheeler and von Braun, 2013; Rosenzweig et al., 2014; Zhao et al., 2016; Zhao et al., 2017).

In confrontation with stresses, plants consume more resources to combat the negative impact of the stress. Therefore, adaptation occurs at the expense of plant growth and causes a reduction in yield (Granier and Tardieu, 1999; Skirycz et al., 2010). The inhibition of growth by stress

may be relieved once the environment becomes stable and suitable. For example, when plants are subjected to water deprivation, the transpiration rate decreases to keep water within the plants, followed by a slower uptake of nutrients from the soil that is driven by transpiration. Subsequently, leaf growth is significantly restrained. If plants are put back into normal conditions with a sufficient water supply, they will reset the stress response and recover growth rapidly (Hsiao and Xu, 2000; Thirumalaikumar et al., 2018). Stressful environments can also induce a quicker transition to reproductive development from vegetative growth, leading to early flowering and altered senescence (Balazadeh et al., 2008; Balazadeh et al., 2010a). These growth alterations enable plants to make the most of the resource supply, which might become limited under extreme stress conditions.

Severe stresses restrain plant growth or even kill plants. Nevertheless, exposure to mild stress helps plants survive when facing the same stress more intensely later. Animals can avoid or escape from harmful environments by moving to other places more suitable for survival. They remember stresses they have been through and use the memory of previous experience to make proper decisions when they face similar conditions (Yehuda, 2002; Wang et al., 2018). Although plants do not have a neurological system like animals, there is an increasing amount of experimental evidence suggesting that over their long period of evolution, plants have successfully developed a molecular memory system that enables them to survive better under stress conditions if previously exposed to the same abiotic stress (Larkindale et al., 2005; Hilker et al., 2015). As sessile organisms, plants indeed rapidly respond and adapt to recurring stresses (Blechert et al., 2007; Charng et al., 2007; Milad et al., 2009; Garfinkel et al., 2014). Stress response and stress memory in higher plants are dynamic and complex processes, which involves massive changes at the DNA, transcript, protein and metabolite levels (Bruce et al., 2007; Balazadeh et al., 2010b; Peyraud et al., 2017; Santamaria et al., 2018; Stahl et al., 2018; Thomas et al., 2018).

It is of great importance for plants to control the distribution of energy supplies between growth and stress adaptation and maintain a balance between growth and stress response in varying environmental conditions. Plenty of publications have demonstrated that dwarfed mutants survive better than non-dwarfed plants in abiotic stress conditions, which is partially due to the lower allocation of resources to growth in the absence of stress (Yang et al., 2011; Colebrook et al., 2014). Modifications of this trade-off in favor of agriculture are of high interest, as both growth and stress responses are essential for crop yield. Transgenic plants with improved stress tolerance without decreasing productivity become attractive for agriculture (Haake et al., 2002;

Sakamoto, 2004; Papdi et al., 2008). Plant breeders are making efforts to combine good traits of growth and stress tolerance together.

Drought response and drought tolerance

Drought is defined as soil and/or atmospheric water deficit. It is among the top causes of agricultural productivity losses globally and often occurs together with high temperature and radiation (Kamanga et al., 2018). Because of increasing aridity and a growing human population, water is becoming a scarcer commodity in the near future. Agriculture is the major user of water resources in many regions of the world. Studies on drought response have been conducted over the last decades to illustrate plant responses to water deficits, including physiological and biochemical processes and plant strategies of controlling water status under drought (Chaves, 1991; Cornic and Massacci, 1996). Progress has also been made on interpreting the correlation between leaf structures, root morphology and stress tolerance (Jackson et al., 2000; Maggio et al., 2001). So far, hundreds of drought responsive genes have been identified, and their functions in adaptation to water deficits or acclimation have been characterized. Many stress-responsive genes participate in cellular adaptive processes, while some of them are only involved in short-term deleterious responses (Chaves et al., 2003; Mun et al., 2017).

Drought stress induces massive changes in plants at the organ, tissue, cell and molecular levels. These changes include alterations in chlorophyll fluorescence, chlorophyll content, photosynthesis efficiency, stomatal conductance, transpiration rate, electrolyte leakage and relative water content in leaves (Batra et al., 2014). Other biochemical and physiological changes include an altered concentration of potassium in leaf tissues and an accumulation of proline, ROS and antioxidants (Kamanga et al., 2018).

Tolerance to water deficit usually involves maintaining turgor under low tissue water potential, osmotic adjustment, the formation of rigid cell walls, or a decrease of cell size (DaCosta and Huang, 2006). Alteration of agronomic traits indeed can aid plant adaptation to drought. The beneficial traits mainly include those that determine plant development and shape, such as, xylem properties, the size and depth of the root, leaf shape, water potential, osmotic adjustment capabilities, stability of the cell membrane and ABA content. These traits are mostly constitutive instead of stress-induced (Passioura, 2002). The drought resistance of plants is sorted into four basic types: drought escape, drought recovery, drought avoidance and drought

tolerance. During the past decades, scientists have investigated the genetic and molecular mechanisms of drought resistance in various crops, and significant progress has been made on the two major mechanisms of drought resistance utilized by plants: drought avoidance and drought tolerance (Yue et al., 2006; Laxa et al., 2019).

Drought avoidance represents the capability of plants to maintain normal and fundamental physiological activities under moderate drought stress conditions by adjusting growth rates or morphological structures to avoid drought stress (Blum, 2005; Luo, 2010). Therefore, drought avoidance is generally characterized by the maintenance of high water potentials when plants are exposed to a water deficit (Mitra, 2001; Luo, 2010). Plants have developed a series of ways to acquire drought avoidance: (1) enhancing the water uptake capacity through increasing rooting density, rooting depth, or the root/shoot ratio, (2) improving the water storage ability of specific organs (Sawidis et al., 2005; Ogburn and Edwards, 2010; Tardieu, 2013), (3) reducing water loss through leaf rolling, rapid stomatal closure, or increasing wax accumulation on the leaf surface (Zhang et al., 2005a; Cameron et al., 2006; Islam et al., 2009) and (4) adjusting the conversion from vegetative growth to reproductive growth to avoid complete abortion at the severe drought stress stage (Luo, 2010).

The term ‘drought tolerance’ refers to the ability to conduct a certain level of physiological processes under drought stress *via* the regulation of metabolic pathways and related genes to reduce or repair stress damages. For instance, a rapid ABA signaling response aids plants in surviving under drought stress. Alternatively, a plant can increase the activity of ROS scavenging enzymes, which reduces damage caused by drought-induced ROS accumulation (Mitra, 2001). In nature, plants may encounter short-term water deficits (hours to days) or long-term drought conditions. In the event of rapid dehydration, plants tend to respond by minimizing water loss or exhibiting metabolic protection against the dehydration damage and co-occurring oxidative stress. In the case of long-term drought stress, plants can either escape water shortage by adjusting planting time, life cycle or growth period to prevent the growing season affected by seasonal or climatic drought or optimizing their resource gain through acclimation responses, which is referred to as ‘drought escape’ (Manavalan et al., 2009). Drought recovery is the capability of plants to resume growth and gain yield (in the case of crops) after exposure to severe drought (Luo, 2010).

Transcription factors

In general, transcription factors (TFs) are proteins regulating the transcription of target genes *via* binding to specific DNA sequences through their DNA-binding domains (DBDs). The binding sites of TFs are usually located in promoters of target genes (Kummerfeld and Teichmann, 2006). However, some regulatory proteins without a DBD are also involved in transcriptional regulation *via* direct interaction with TFs and are also defined as TFs. TFs can function as activators or repressors to activate or repress transcription of downstream target genes. There is a considerable number of TFs in plants. About 6% to 10% of the genes in the plant genomes encode TFs. Genome-wide comparative structural analyses have recognized more than 2,000 genes encoding TFs in Arabidopsis (Guo et al., 2005; Riano-Pachon et al. 2007; Jin et al., 2015), 1,845 in tomato, 3,308 in maize, and 1,611 in rice (Xiong et al., 2005; Jin et al., 2014; Jin et al., 2017). TFs are classified into different families according to conserved sequence motifs and their DNA-binding domains (Riechmann et al., 2000). As shown by the Plant Transcription Factor Database (PlantTFDB), *Arabidopsis thaliana* TFs are grouped into 58 families based on the presence of the DNA-binding domain, auxiliary domain and forbidden domain (Molina and Grotewold, 2005; Palaniswamy et al., 2006; Qu and Zhu, 2006). The largest family is basic/helix-loop-helix (bHLH), which consists of 225 TFs (Toledo-Oritz et al., 2003), and the smallest family is the LEAFY (LYF) family, which includes only one plant-specific protein (William et al., 2004). Other families include the NAC family, which comprises 126 members, heat stress transcription factors (HSFs), which are encoded by 21 loci in Arabidopsis (Kotak et al., 2004) and the MYB family, which contains 125 TFs (Stracke et al., 2001; Kotak et al., 2004; Olsen at al., 2005; Fang et al., 2008).

During the process of growth and development, plant TFs play important roles in sensing and responding to diverse environmental stresses and developmental signals (Liu et al., 2001; Franco-Zorrilla et al., 2014). They control a variety of biological processes and trigger cascades of biochemical reactions in cells (Ramirez and Basu, 2009; Seo and Choi, 2015). Plant cells perceive extracellular (drought, heat, cold, salt, hormones, pathogens, etc.) or intracellular signals and transduce the signals to TFs (Tsuda and Somssich, 2015; Zhao et al., 2015; Guo et al., 2016; Wang et al., 2016; Zong et al., 2016; Mun et al., 2017). Afterwards, TFs regulate the transcription of target genes by binding to specific *cis*-elements (Tian et al., 2018). The target genes might encode TFs or other genes with different physiological and biochemical functions. With the products of target genes, plants respond to various stimuli and adapt to environmental changes (Perez-Rodriguez et al., 2009). Research into NAC and HD-Zip transcription factors

has demonstrated the importance of these two TF families in controlling plant growth and adaption to environmental changes.

NAC transcription factors

The NAC abbreviation is derived from the first letters of three genes that contain a specific domain (the NAC domain): NAM (no apical meristem), ATAF1/2 (Arabidopsis transcription activator factor 1/2) and CUC2 (cup-shaped cotyledon) (Moyano et al., 2018). The NAC transcription factor contains a DNA-binding NAC domain at the N-terminus, which is divided into five typical subdomains (called A, B, C, D and E) and a variable transcriptional regulation C-terminal domain (Tran et al., 2010). NAC transcription factors represent one of the largest plant-specific transcription factor families. The NAC family is distributed among a wide range of land plants (Olsen et al., 2005). They play vital roles in diverse developmental processes, such as senescence, secondary wall synthesis, wood formation and lateral root development (Xie et al., 2000; Zhong et al., 2010; Shao et al., 2015; Kim et al., 2016). For example, NAC family proteins NARS1/NAC2 and NARS2/NAM regulate embryogenesis in Arabidopsis (Kunieda et al., 2008). In tomato, SlNAP2 plays a central role in controlling fruit yield and leaf senescence (Ma et al., 2018). SlNAM2 is involved in the establishment of tomato sepal boundaries and flower whorl (Hendelman et al., 2013). ZmNAC84 affects pollen development by repressing *ZmRbohH* expression in maize (Yang et al., 2018). OsNAC2 acts as a negative regulator of flowering time and plant height by directly regulating the GA biosynthesis pathway in rice. On the other hand, it promotes ABA-induced leaf senescence (Chen et al., 2015; Mao et al., 2017). OsNAC011 is a positive regulator of heading and leaf senescence during the reproductive phase in rice (El Mannai et al., 2017). Additionally, NAC transcription factors show multiple functions in biotic and abiotic stress responses. AtNAC4 promotes pathogen-induced cell death in Arabidopsis (Lee et al., 2017). OsNAC106 increases salt tolerance in rice (Sakuraba et al., 2015). Overexpression of *OsNAC022* improves salt and drought stress tolerance in rice by modulating an ABA-mediated pathway (Hong et al., 2016). Overexpression of *SlNAC35* enhances resistance to bacterial pathogens in transgenic tobacco (Wang et al., 2016). ThNAC13 is an NAC transcription factor from *Tamarix hispida*. Overexpressing *ThNAC13* in Arabidopsis or *Tamarix hispida* improves osmotic stress and salt tolerance (Wang et al., 2017). TaNAC29 enhances salt stress tolerance in wheat through reducing membrane damage and H_2O_2 accumulation by reinforcing the antioxidant system (Xu et al., 2015).

Overexpressing *MlNAC9* from *Miscanthus lutarioriparius* in Arabidopsis plants increases tolerance to drought, salt and cold stress (Zhao et al., 2016).

JUB1 is a central regulator of growth and stress response

NAC transcription factor JUNGBRUNNEN1 (JUB1; AT2G43000) has been characterized as a longevity regulator in Arabidopsis as overexpression of *JUB1* strongly delays senescence (Wu et al., 2012). Although overexpressing *JUB1* in Arabidopsis inhibits growth and development, it dampens intracellular H_2O_2 levels and enhances tolerance to salinity, heat and drought stress (Shahnejat-Bushehri et al., 2012; Wu et al., 2012; Ebrahimian-Motlagh et al., 2017). Thirumalaikumar et al. reported that overexpression of *AtJUB1* (*JUB1*) improves survival of tomato under drought stress (Thirumalaikumar et al., 2018). Another recently published paper has demonstrated that overexpression of *AtJUB1* also increases tolerance to salt in tomato (Alshareef et al., 2019). Results of EMSA (Electrophoretic Mobility Shift Assay), ChIP-qPCR (Chromatin Immunoprecipitation coupled with quantitative PCR) and transcripts level analysis demonstrated that JUB1 directly represses the expression of GA and BR biosynthesis genes. Thus, overexpressing *JUB1* reduces the levels of both growth hormones followed by a stabilization of DELLA proteins, which restrict growth and confer resistance to various abiotic stresses (Achard et al., 2008; Shahnejat-Bushehri et al., 2012).

During the process of leaf senescence, *JUB1* expression increases. Under stress conditions, H_2O_2 is massively produced and the expression level of *JUB1* is increased. JUB1 binds to the NAC binding site in the *DREB2A* promoter, and enhances its expression. As a target of DREB2A, *HsfA3* is upregulated when the expression level of *DREB2A* is increased (Schramm et al., 2008), thus triggering a transcriptional regulation cascade. As indicated in Nishizawa-Yokoi's paper, HsfA3 promotes the expression of *HSP* (*HEAT-SHOCK PROTEIN*) genes in the heat stress response together with HsfA2 (Nishizawa-Yokoi et al., 2011). On the other hand, it also induces expression of ROS scavenging enzymes, which reduces intracellular ROS levels. Therefore, plants overexpressing *JUB1* accumulate less ROS and survive better than wild-type plants. Additionally, JUB1 may increase longevity and enhance stress tolerance through other target genes (**Figure 6**).

In order to determine the upstream TFs regulating *JUB1*, phylogenetic footprinting analysis combined with promoter deletion analysis of the *JUB1* promoter and Y1H assays were performed. Several HD-Zip I TFs were identified as potential upstream regulators of *JUB1*.

Thereafter, *HB22* (AT2G36610) and *HB40* (AT4G36740) were selected for further characterization in this project.

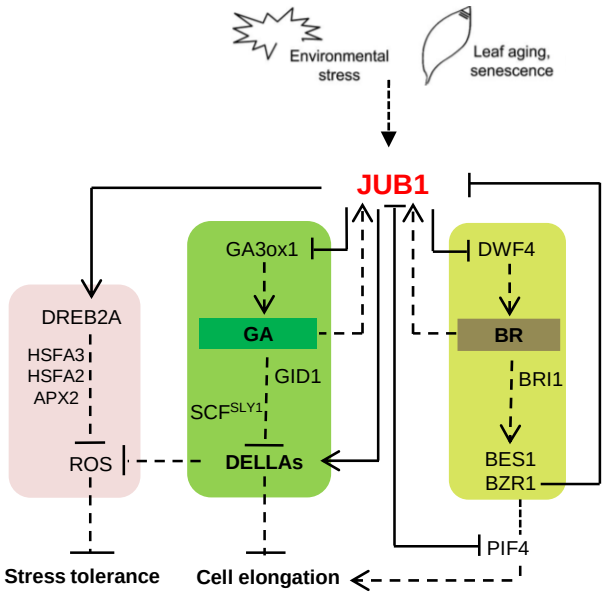

Figure 6. Model of JUB1 functions (modified from Shahnejat-Bushehri et al., 2016). Briefly, JUB1 represses cell elongation *via* inhibition of GA (gibberellin) and BR (brassinosteroid) biosynthesis. It directly and negatively regulates expression of GA and BR biosynthesis genes *GA3ox1* and *DWF4*. JUB1 is also a key stress response gene and central regulator of senescence. Its expression level is induced by environmental stress and during senescence. Under drought stress, *JUB1* expression is activated which promotes transcription of *DREB2A*, which further restricts accumulation of reactive oxygen species. As a result, plants overexpressing *JUB1* show increased tolerance to multiple stresses.

HD-Zip I TFs

Members of the HD-Zip family are characterized by a common region of DNA homeobox (HB) encoding a homeodomain (HD), which is a conserved 60-amino acid motif present in all eukaryotic organisms, and a plant-specific leucine zipper (LZ) domain, termed the HALZ (HB associated leucine zipper), immediately downstream of the HD. The encoded proteins have a molecular mass of ~35 kDa and exhibit a highly conserved HD and a less conserved LZ motif. The HD is responsible for the specific binding to the DNA, and LZ is involved in the formation of hetero- or homo-dimers, which are necessary for binding to DNA (Ariel et al., 2007; Belamkar et al., 2014). HD-Zip proteins have been identified in various plants such as Arabidopsis, rice, tomato, sunflower (*Helianthus annuus*) and *Medicago truncatula* (Manavella et al., 2006; Agalou et al., 2008, Lin et al., 2008; Ariel et al., 2010). Agalou et al. identified 33 HD-Zip genes in rice (*Oryza sativa* L.) and classified them into family I (14 genes), family II (14 genes) and family III (5 genes) (Agalou et al., 2008). There are 51 HD-Zip genes (*SlHZ01-51*) identified and categorized into four classes by their gene and protein structures in

the tomato genome (Zhang et al., 2014). Fifty-seven HD-Zip genes (*MeHDZ01-57*) were identified in the cassava (*Manihot esculenta*) genome (Ding et al., 2017). The soybean (*Glycine max*) HD-Zip family contains 88 members, 59 of which were differentially expressed under salinity and drought stress (Chen et al., 2014). Analysis of the genome sequence of Arabidopsis identified 48 HD-Zip genes, which are divided into four subfamilies (HD-Zip I–IV) according to four distinguishing features: (a) intron/exon patterns of the encoding genes; (b) sequence conservation of the HD-Zip domain determining DNA-binding specificities; (c) the additional conserved motifs outside the HD-Zip domain; and (d) the pathways that they are involved in (Ribone et al., 2015). The Arabidopsis HD-Zip class I subfamily contains 17 members. Through phylogenetic analysis and genome-wide sequence comparison, the 17 members of the HD-Zip I protein family were grouped into six different clades, I to VI. Their specific functions are defined by the presence and the position of conserved sequences (Henriksson et al., 2005; Arce et al., 2011). HD-Zip I TFs are able to form homodimers or heterodimers and recognize the pseudo-palindromic sequence CAAT (A/T) ATTG (Chen et al., 2014). In addition to the HD and LZ domains, HD-Zip class I TFs contain an AHA (aromatic and large hydrophobic residues embedded in an acidic context) motif at the C-terminus that directly interacts with the basal transcriptional machinery and acts as an activation domain (**Figure 7**).

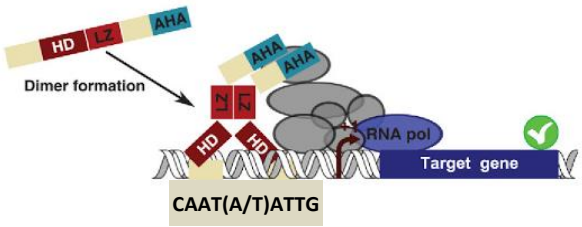

Figure 7. Schematic representation of putative mechanisms of HD-ZIP I TFs function (modified from Capella et al., 2016). HD-Zip class I TFs recognize and bind to target *cis*-elements by forming homo- or heterodimers and then activating transcription through the interaction of the AHA motif with the basal transcription machinery.

Functional studies of HD-Zip I members have demonstrated that they are integrators of intrinsic developmental processes and external signals in the regulation of abiotic and biotic stresses. Their expression is mainly regulated by water deficit, extreme temperatures, osmotic stresses, light conditions and hormones such as ABA and ethylene (Ariel et al., 2010; Harris et al., 2011; Bou-Torrent et al., 2012; Chen et al., 2014; Zhang et al., 2014; Romani et al., 2016; Ding et al., 2017; Sessa et al., 2018). Their role as TFs is related to the developmental activities in response

to environmental conditions, particularly abiotic stresses (**Figure 8**). It is believed that the majority of stress-responsive HD-Zip genes in plants encode members of the HD-Zip class I subfamily. Overexpression of HD-Zip I genes often leads to alterations in the shape and growth of the plant, including the cotyledon, leaf and supporting organs (Aoyama et al., 1995; Hanson et al., 2001), suggesting a role of HD-Zip I proteins in specific growth and/or developmental pathways. *ATHB16* from Arabidopsis is involved in blue-light signaling (Wang et al., 2003). *ATHB51* (*LMI1*) is a meristem identity gene regulating leaf shape and bract formation (Saddic et al., 2006). Moreover, several HD-Zip class I members have been identified and characterized for their roles in regulating drought responses (Henriksson et al., 2005). As a direct target of PHYTOCHROME INTERACTING FACTOR 1 (PIF1), *ATHB1* is known to play a role in regulating hypocotyl elongation (Leivar and Quail, 2011). It has also been shown to be a mediator in leaf cell fate determination (Pierik et al., 2009; Capella et al., 2015). Expression of *ATHB1* is positively regulated by ethylene, and its orthologue in tomato has been shown to directly regulate the expression of the ethylene biosynthesis gene *LeACO1* (Zhong et al., 2003; Lin et al., 2008). *ATHB7* and *ATHB12* are both strongly induced by drought stress and ABA (Arce et al., 2011). ChIP (Chromatin immunoprecipitation) assay and gene expression analyses have demonstrated that *ATHB7* and *ATHB12* negatively regulate ABA signaling by promoting the expression of the PP2C-type phosphatase gene family (PP2C) (Merlot et al., 2001; Saez et al., 2004; Kuhn et al., 2006). Furthermore, it has been shown that ATHB7 and ATHB12 repress the PYRABACTIN RESISTANCE1 (PYR1)/PYR1-LIKE (PYL) gene family, which encodes ABA receptors. Together, these data indicate that ATHB7 and ATHB12 function as negative regulators in the ABA signaling pathway (Miyazono et al., 2009; Park et al., 2009; Valdes et al., 2012). The homolog to *ATHB7* and *ATHB12* in sunflower, *HAHB4*, is also regulated by ABA and drought, as well as by methyl-jasmonic acid (MeJa) or ethylene (ET) and biotic stresses. The ectopic expression of *HAHB4* in Arabidopsis represses biosynthesis of ET and enhances drought tolerance (Manavella et al., 2006). *ATHB13* is positively regulated by low temperature, drought and salinity. Overexpression of *ATHB13* confers increased resistance to cold, drought and broad-spectrum disease (Cabello et al., 2012). ATHB5 positively regulates and promotes the GA-mediated expansion of the epidermis and cortex. It also promotes hypocotyl growth in post-embryonic development (Stamm et al., 2017). A recent work found that the central regulator in axillary buds to restrain constitutive branch outgrowth, BRANCHED1 (BRC1), directly and positively regulates the transcription of *HB21*, *HB40* and *HB53*. These HD-Zip I proteins are necessary and sufficient to enhance the expression of the ABA biosynthesis gene, *NCED3*, which causes suppression of bud development (Gonzalez et

al., 2017). It has been reported that *ATHB6* and its close homolog, *ATHB5*, may act redundantly in restricting auxin signaling during embryogenesis (De Smet et al., 2013). A molecular and genetic analysis has shown that *ATHB52* is positively regulated by the ethylene signal transduction pathway. Moreover, ATHB52 has also been found to directly regulate transcription of *PIN FORMED2* (*PIN2*), which encodes a polar auxin carrier and affects the local polar auxin transport in the root tip followed by inhibition of primary root elongation (Ruzicka et al., 2007; Stepanova et al., 2007; Swarup et al., 2007; Markakis et al., 2012; Miao et al., 2018).

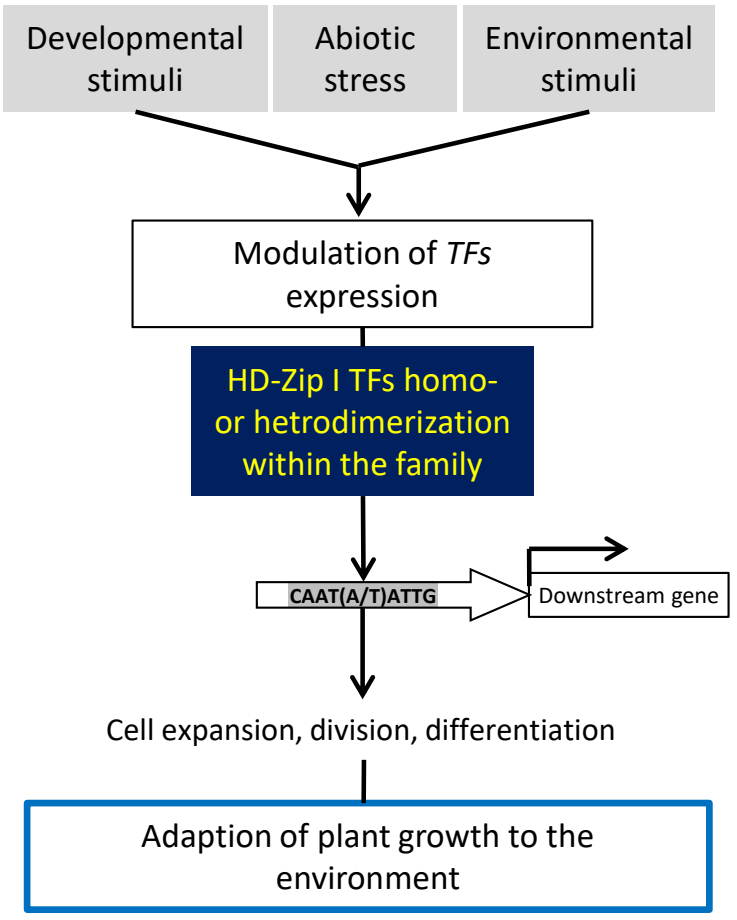

Figure 8. Roles of HD-Zip I TFs (modified from Harris et al., 2011). HD-Zip class I TFs respond to developmental and environmental signals. When their expression is activated by upstream stimuli and TFs, they induce the transcription of downstream target genes by forming hetero- or homodimers and binding to the target DNA sequence, which triggers the cascade of stress response pathways and the adaptation of plants to environmental changes.

Thesis outline

The Arabidopsis NAC transcription factor JUNGBRUNNEN 1 (JUB1) has been previously characterized as a central regulator of longevity and the interplay between gibberellins (GAs)- and brassinosteroids (BRs)-mediated growth and stress responses. By employing a yeast-one-hybrid (Y1H) assay and transcript analysis of transgenic lines, we identified two TFs (HB40 and HB22) from the HD-Zip class I subfamily as potential upstream regulators of *JUB1*. Studies have shown that members of HD-Zip transcription factors play a role in controlling plant growth and development as well as in responses to environmental cues. However, the functions of HB40 and HB22 with respect to the regulation of growth and responses to stresses have not been investigated.

In this thesis, we investigated the growth-related and developmental functions and the gene regulatory networks (GRNs) of HB40, and to a lesser extent HB22, in Arabidopsis. *HB40* expression is strongly induced by drought, similar to that of *JUB1* expression. We also studied the role of HB40 in response to drought stress and identified the biological relevance of the HB40-*JUB1* control unit for the regulation of growth and drought tolerance. The result of our research adds to the understanding of molecular mechanisms underlying growth and contributing to drought tolerance, mediated by the HD-Zip TFs-JUB1 module, and can guide the development of new strategies for improving plant growth and stress responses.

In **Chapter 2**, we analyzed the expression pattern of *HB40* in different tissues and in response to the treatments with GAs and BRs by means of a β-glucuronidase (*GUS*) reporter gene assay and quantitative real-time PCR (qRT-PCR). We characterized the growth and developmental phenotypes of Arabidopsis transgenic lines with altered expression of *HB40* (overexpressors and T-DNA knockout mutant) and showed that HB40 negatively regulates growth, cell elongation, and flowering time, mainly by lowering the levels of bioactive GAs. Our extensive molecular and biochemical studies which included employing technologies such as qRT-PCR, chromatin immunoprecipitation (ChIP), electrophoretic mobility shift (EMSA) and transactivation assays showed that HB40 directly activates the transcription of *JUB1*. Furthermore, we identified genes encoding GA-catabolic enzymes, *GA-2 oxidases* (*GA2OXs*) as direct targets of HB40. Our genetic studies confirmed that indeed HB40 suppresses growth and the levels of bioactive GAs through the regulation of *JUB1* and *GA2OXs*. Finally, we demonstrated the genetic and functional relevance of HB40 and GA signaling components, i.e.

DELLA proteins. We conclude that HB40 as an important regulator of GA homeostasis in Arabidopsis.

In Chapter 3, we show that HB40 plays a positive role in drought tolerance. Overexpression of *HB40* (driven by the CaMV 35S promoter) resulted in enhanced tolerance to drought. Moreover, we demonstrated that HB40-conferred drought tolerance requires JUB1. To uncouple the effects of HB40 on plant growth and drought response, we also generated transgenic Arabidopsis lines expressing *HB40* under the control of the stress-inducible *RD29A* (*RD29A:HB40*) and the guard cell-specific *KST1* (*KST1:HB40*) promoter. The *RD29A:HB40* lines did not show defects in growth and development, but retained the enhanced drought-tolerant phenotype suggesting that the enhanced tolerance phenotype of HB40 is not solely due to its growth retarding effect. However, no significant tolerance to drought was observed in *KST1:HB40* plants, indicating that drought tolerance conferred by HB40 is not due to a function in stomata.

In **Chapter 4**, we investigated the functional redundancy of HB40 and two other members of the HD-Zip class I family, *HB21* and *HB53*, in controlling hypocotyl growth and the regulation of *JUB1* expression. Hypocotyl elongation of an *HB40* single knockout mutant (under dark) was comparable to that of the wild type, while the mutant lacking the three HD-Zips (triple mutant of *HB21, HB40,* and *HB5)* showed significantly longer hypocotyls than the wild type, suggesting these HBs are functionally redundant in controlling hypocotyl growth. EMSA and transactivation assays confirmed that HB21 and HB53 directly and positively regulate *JUB1* expression. No interactions between HB40 and HB21/HB53 were detected in bimolecular fluorescence complementation (BiFC) assays suggesting that these TFs do not form heterodimers and rather act independently and redundantly in the regulation of *JUB1* and hypocotyl growth.

In **Chapter 5**, we analyzed the expression of *HB22* at the cellular level. We generated transgenic lines expressing β-glucuronidase (*GUS*) and *HB22* in fusion with a green fluorescent protein (GFP) under the control of the *HB22* promoter and showed that HB22 is specifically expressed in young leaves and floral primordia of Arabidopsis seedlings. Phenotypic analysis of *HB22* transgenic lines showed that overexpression of *HB22* affected the transition of vegetative growth to reproductive growth. However, a knockout mutant of *HB22* (T-DNA insertion line) did not show any phenotype, likely due to functional redundancy with its closest members within the HD-Zip I family. We analyzed expression levels of *JUB1* and several

meristem identity genes in *HB22* transgenic lines. Our results show that transcript levels of *JUB1*, *CAL* (*CAULIFLOWER*) and *AP1* (*APETALA1*), were upregulated in *HB22OXs*, whereas in the T-DNA mutants they were less expressed compared to wild type. Our data suggest HB22 as a potential regulator of meristem identity in Arabidopsis.

References

Achard, P., and Genschik, P. (2009). Releasing the brakes of plant growth: how GAs shutdown DELLA proteins. J Exp Bot 60, 1085-1092.

Achard, P., Renou, J.-P., Berthomé, R., Harberd, N.P., and Genschik, P. (2008). Plant DELLAs restrain growth and promote survival of adversity by reducing the levels of reactive oxygen species. Curr Bio 18, 656-660.

Agalou, A., Purwantomo, S., Övernäs, E., Johannesson, H., Zhu, X., Estiati, A., de Kam, R.J., Engström, P., Slamet-Loedin, I.H., Zhu, Z., Wang, M., Xiong, L., Meijer, A.H., and Ouwerkerk, P.B.F. (2008). A genome-wide survey of HD-Zip genes in rice and analysis of drought-responsive family members. Plant Mol Bio 66, 87-103.

Alshareef, N.O., Wang, J.Y., Ali, S., Al-Babili, S., Tester, M., and Schmöckel, S.M. (2019). Overexpression of the NAC transcription factor *JUNGBRUNNEN1* (*JUB1*) increases salinity tolerance in tomato. Plant Physiol Biochem 140, 113-121.

Aoyama, T., Dong, C.H., Wu, Y., Carabelli, M., Sessa, G., Ruberti, I., Morelli, G., and Chua, N.H. (1995). Ectopic expression of the Arabidopsis transcriptional activator *Athb-1* alters leaf cell fate in tobacco. Plant Cell 7, 1773–1785.

Arce, A.L., Raineri, J., Capella, M., Cabello, J.V., and Chan, R.L. (2011). Uncharacterized conserved motifs outside the HD-Zip domain in HD-Zip subfamily I transcription factors; a potential source of functional diversity. BMC Plant Biol 11, 42.

Ariel, F., Diet, A., Verdenaud, M., Gruber, V., Frugier, F., Chan, R., and Crespi, M. (2010). Environmental regulation of lateral root emergence in *Medicago truncatula* requires the HD-Zip I transcription factor HB1. Plant Cell 22, 2171-2183.

Ariel, F.D., Manavella, P.A., Dezar, C.A., and Chan, R.L. (2007). The true story of the HD-Zip family. Trends Plant Sci 12, 419-426.

Ariizumi, T., Hauvermale, A.L., Nelson, S.K., Hanada, A., Yamaguchi, S., and Steber, C.M. (2013). Lifting DELLA repression of Arabidopsis seed germination by nonproteolytic gibberellin signaling. Plant Physiol 162, 2125-2139.

Bai, M.Y., Shang, J.X., Oh, E., Fan, M., Bai, Y., Zentella, R., Sun, T.P., and Wang, Z.Y. (2012). Brassinosteroid, gibberellin and phytochrome impinge on a common transcription module in Arabidopsis. Nat Cell Biol 14, 810-817.

Bajguz, A. (2000). Effect of brassinosteroids on nucleic acids and protein content in cultured cells of *Chlorella vulgaris*. Plant Physiol Biochem 38, 209-215.

Balazadeh, S., Riano-Pachon, D.M., and Mueller-Roeber, B. (2008). Transcription factors regulating leaf senescence in *Arabidopsis thaliana*. Plant Biol (Stuttg) 10 Suppl 1, 63-75.

Balazadeh, S., Siddiqui, H., Allu, A.D., Matallana-Ramirez, L.P., Caldana, C., Mehrnia, M., Zanor, M.-I., Köhler, B., and Mueller- Roeber, B. (2010a). A gene regulatory network controlled by the NAC transcription factor ANAC092/AtNAC2/ORE1 during salt-promoted senescence. Plant J 62, 250–264.

Balazadeh, S., Wu, A.H., and Mueller-Roeber, B. (2010b). Salt-triggered expression of the ANAC092-dependent senescence regulon in *Arabidopsis thaliana*. Plant Signal Behav 5, 1–3.

Batra, N.G., Sharma, V., and Kumari, N. (2014). Drought-induced changes in chlorophyll fluorescence, photosynthetic pigments, and thylakoid membrane proteins of *Vigna radiata*. J Plant Interact 9, 712-721.

Belamkar, V., Weeks, N.T., Bharti, A.K., Farmer, A.D., Graham, M.A., and Cannon, S.B. (2014). Comprehensive characterization and RNA-Seq profiling of the HD-Zip transcription factor family in soybean (*Glycine max*) during dehydration and salt stress. BMC Genomics 15, 950.

Berens, M.L., Wolinska, K.W., Spaepen, S., Ziegler, J., Nobori, T., Nair, A., Kruler, V., Winkelmuller, T.M., Wang, Y., Mine, A., Becker, D., Garrido-Oter, R., Schulze-Lefert, P., and Tsuda, K. (2019). Balancing trade-offs between biotic and abiotic stress responses through leaf age-dependent variation in stress hormone cross-talk. Proc Natl Acad Sci U S A 116, 2364-2373.

Bevan, M., and Walsh, S. (2005). The Arabidopsis genome: A foundation for plant research. Genome Res 15, 1632-1642.

Bishop, G.J., Nomura, T., Yokota, T., Harrison, K., Noguchi, T., Fujioka, S., Takatsuto, S., Jones, J.D.G., and Kamiya, Y. (1999). The tomato DWARF enzyme catalyses C-6 oxidation in brassinosteroid biosynthesis. Proc Natl Acad Sci U S A 96, 1761-1766.

Blechert, J., Michael, T., Vriends, N., Margraf, J., and Wilhelm, F.H. (2007). Fear conditioning in posttraumatic stress disorder: evidence for delayed extinction of autonomic, experiential, and behavioural responses. Behav Res Ther 45, 2019-2033.

Blum, A. (2005). Drought resistance, water-use efficiency, and yield potentialare they compatible, dissonant, or mutually exclusive? Aust J Agric Res 56, 1159-1168.

Bouton, S., Leydecker, M.T., Meyer, C., and Truong, H.N. (2002). Role of gibberellins and of the *RGA* and *GAI* genes in controlling nitrate assimilation in *Arabidopsis thaliana*. Plant Physiol Biochem 40, 939-947.

Bou-Torrent, J., Salla-Martret, M., Brandt, R., Musielak, T., Palauqui, J.C., Martinez-Garcia, J.F., and Wenkel, S. (2012). ATHB4 and HAT3, two class II HD-ZIP transcription factors, control leaf development in Arabidopsis. Plant Signal Behav 7, 1382-1387.

Briat, J.F., Dubos, C., and Gaymard, F. (2015). Iron nutrition, biomass production, and plant product quality. Trends Plant Sci 20, 33-40.

Brown, P.J. (2016). Plant breeding: Effective use of genetic diversity. Nat Plants 2, 16154.

Browse, J. (2005). Jasmonate: An oxylipin signal with many roles in plants. In Vitamins & Hormones, G. Litwack, ed (Academic Press), pp. 431-456.

Bruce, T.J.A., Matthes, M.C., Napier, J.A., and Pickett, J.A. (2007). Stressful "memories" of plants: Evidence and possible mechanisms. Plant Sci 173, 603-608.

Bussemaker, H.J., Li, H., and Siggia, E.D. (2001). Regulatory element detection using correlation with expression. Nat Genetics 27, 167-171.

Cabello, J.V., Arce, A.L., and Chan, R.L. (2012). The homologous HD-Zip I transcription factors HaHB1 and AtHB13 confer cold tolerance via the induction of pathogenesis-related and glucanase proteins. Plant J 69, 141-153.

Cameron, K.D., Teece, M.A., and Smart, L.B. (2006). Increased accumulation of cuticular wax and expression of lipid transfer protein in response to periodic drying events in leaves of tree tobacco. Plant Physiol 140, 176-183.

Capella, M., Ribone, P.A., Arce, A.L., and Chan, R.L. (2015). *Arabidopsis thaliana* HomeoBox 1 (AtHB1), a Homedomain-Leucine Zipper I (HD-Zip I) transcription factor, is regulated by PHYTOCHROME-INTERACTING FACTOR 1 to promote hypocotyl elongation. New Phytol 207, 669-682.

Capella, M., Ribone, P.A., Arce, A.L., and Chan, R.L. (2016). Chapter 7 - Homeodomain–Leucine Zipper transcription factors: structural features of these proteins, unique to plants. In plant transcription factors, D.H. Gonzalez, ed (Boston: Academic Press), pp. 113-126.

Chapman, E.J., and Estelle, M. (2009). Mechanism of auxin-regulated gene expression in plants. Annu Rev Genet 43, 265-285.

Charng, Y.Y., Liu, H.C., Liu, N.Y., Chi, W.T., Wang, C.N., Chang, S.H., and Wang, T.T. (2007). A heat-inducible transcription factor, HsfA2, is required for extension of acquired thermotolerance in *Arabidopsis*. Plant Physiol 143, 251-62.

Chaves, M.M. (1991). Effects of water deficits on carbon assimilation. J Exp Bot 42, 1-16.

Chaves, M.M., Maroco, J.P., and Pereira, J.S. (2003). Understanding plant responses to drought–from genes to the whole plant. Funct Plant Biol 30, 239.

Cheminant, S., Wild, M., Bouvier, F., Pelletier, S., Renou, J.P., Erhardt, M., Hayes, S., Terry, M.J., Genschik, P., and Achard, P. (2011). DELLAs regulate chlorophyll and carotenoid biosynthesis to prevent photooxidative damage during seedling deetiolation in Arabidopsis. Plant Cell 23, 1849-1860.

Chen, X., Chen, Z., Zhao, H., Zhao, Y., Cheng, B., and Xiang, Y. (2014). Genome-wide analysis of soybean HD-Zip gene family and expression profiling under salinity and drought treatments. PLoS One 9, e87156.

Chen, X., Lu, S., Wang, Y., Zhang, X., Lv, B., Luo, L., Xi, D., Shen, J., Ma, H., and Ming, F. (2015). *OsNAC2* encoding a NAC transcription factor that affects plant height through mediating the gibberellic acid pathway in rice. Plant J 82, 302-314.

Cheng, H., Qin, L., Lee, S., Fu, X., Richards, D.E., Cao, D., Luo, D., Harberd, N.P., and Peng, J. (2004). Gibberellin regulates *Arabidopsis* floral development via suppression of DELLA protein function. Development 131, 1055-1064.

Choe, S. (2006). Brassinosteroid biosynthesis and inactivation. Physiol Plantarum 126, 539-548.

Chrysargyris, A., Panayiotou, C., and Tzortzakis, N. (2016). Nitrogen and phosphorus levels affected plant growth, essential oil composition and antioxidant status of lavender plant (*Lavandula angustifolia* Mill.). Ind Crop Prod 83, 577-586.

Colebrook, E.H., Thomas, S.G., Phillips, A.L., and Hedden, P. (2014). The role of gibberellin signalling in plant responses to abiotic stress. J Exp Biol 217, 67-75.

Cornic, G., and Massacci, A. (1996). Leaf photosynthesis under drought stress. in photosynthesis and the environment, N.R. Baker, ed (Dordrecht: Springer Netherlands), pp. 347-366.

DaCosta M., and Huang B. (2006). Osmotic adjustment associated with variation in bentgrass tolerance to drought stress. J Amer Soc Hort Sci 131, 338-344.

Daviere, J.M., and Achard, P. (2013). Gibberellin signaling in plants. Development 140, 1147-1151.

Davuluri, R.V., Sun, H., Palaniswamy, S.K., Matthews, N., Molina, C., Kurtz, M., and Grotewold, E. (2003). AGRIS: Arabidopsis gene regulatory information server, an information resource of Arabidopsis *cis*-regulatory elements and transcription factors. BMC Bioinformatics 4, 25.

de Lucas, M., Daviere, J.M., Rodriguez-Falcon, M., Pontin, M., Iglesias-Pedraz, J.M., Lorrain, S., Fankhauser, C., Blazquez, M.A., Titarenko, E., and Prat, S. (2008). A molecular framework for light and gibberellin control of cell elongation. Nature 451, 480.

De Smet, S., Cuypers, A., Vangronsveld, J., and Remans, T. (2015). Gene Networks Involved in Hormonal Control of Root Development in *Arabidopsis thaliana*: A Framework for Studying Its Disturbance by Metal Stress. Int J Mol Sci 16, 19195-19224.

Depuydt, S., and Hardtke, C.S. (2011). Hormone signalling crosstalk in plant growth regulation. Curr Biol 21, R365-R373.

Dievart, A., and Clark, S.E. (2004). LRR-containing receptors regulating plant development and defense. Development 131, 251-261.

Dill, A., and Sun, T. (2001). Synergistic derepression of gibberellin signaling by removing RGA and GAI function in *Arabidopsis thaliana*. Genetics 159, 777-785.

Ding, Z., Fu, L., Yan, Y., Tie, W., Xia, Z., Wang, W., Peng, M., Hu, W., and Zhang, J. (2017). Genome-wide characterization and expression profiling of HD-Zip gene family related to abiotic stress in cassava. PLoS One 12, e0173043.

Divi, U.K., and Krishna, P. (2010). Overexpression of the brassinosteroid biosynthetic gene *AtDWF4* in Arabidopsis seeds overcomes abscisic acid-induced inhibition of germination and increases cold tolerance in transgenic seedlings. J Plant Growth Regul 29, 385-393.

Dubois, M., Claeys, H., Van den Broeck, L., and Inzé, D. (2017). Time of day determines Arabidopsis transcriptome and growth dynamics under mild drought. Plant Cell Environ 40, 180-189.

Ebrahimian-Motlagh, S., Ribone, P.A., Thirumalaikumar, V.P., Allu, A.D., Chan, R.L., Mueller-Roeber, B., and Balazadeh, S. (2017). JUNGBRUNNEN1 confers drought tolerance downstream of the HD-Zip I transcription factor AtHB13. Front Plant Sci 8, 2118.

Eckardt, N.A. (2007). GA perception and signal transduction: molecular interactions of the GA receptor GID1 with GA and the DELLA protein SLR1 in rice. Plant cell 19, 2095-2097.

El Mannai, Y., Akabane, K., Hiratsu, K., Satoh-Nagasawa, N., and Wabiko, H. (2017). The NAC transcription factor gene *OsY37* (*ONAC011*) promotes leaf senescence and accelerates heading time in rice. Int J Mol Sci 18, 2165.

Estelle, M. (1996). Plant tropisms: The ins and outs of auxin. Curr Biol 6, 1589-1591.

Fariduddin, Q., Khanam, S., Hasan, S.A., Ali, B., Hayat, S., and Ahmad, A. (2009). Effect of 28-homobrassinolide on the drought stress-induced changes in photosynthesis and antioxidant system of *Brassica juncea* L. Acta Physiol Plant 31, 889-897.

Fariduddin, Q., Yusuf, M., Chalkoo, S., Hayat, S., and Ahmad, A. (2011). 28-homobrassinolide improves growth and photosynthesis in *Cucumis sativus* L. through an enhanced antioxidant system in the presence of chilling stress. Photosynthetica 49, 55-64.

Feng, S., Martinez, C., Gusmaroli, G., Wang, Y., Zhou, J., Wang, F., Chen, L., Yu, L., Iglesias-Pedraz, J.M., Kircher, S., Schäfer, E., Fu, X., Fan, L.M., and Deng, X.W. (2008). Coordinated regulation of *Arabidopsis thaliana* development by light and gibberellins. Nature 451, 475.

Feraru, M.I., Kleine-Vehn, J., and Feraru, E. (2015). Auxin carrier and signaling dynamics during gravitropic root growth. In plant gravitropism: methods and protocols, E.B. Blancaflor, ed (New York, NY: Springer New York), pp. 71-80.

Franco-Zorrilla, J.M., Lopez-Vidriero, I., Carrasco, J.L., Godoy, M., Vera, P., and Solano, R. (2014). DNA-binding specificities of plant transcription factors and their potential to define target genes. Proc Natl Acad Sci U S A 111, 2367-2372.

Fujioka, S., and Yokota, T. (2003). Biosynthesis and metabolism of brassinosteroids. Annu Rev of Plant Biol 54, 137-164.

Gallego-Bartolome, J., Alabadi, D., and Blazquez, M.A. (2011). DELLA-induced early transcriptional changes during etiolated development in *Arabidopsis thaliana*. PLoS One 6, e23918.

Gallego-Bartolome, J., Minguet, E.G., Grau-Enguix, F., Abbas, M., Locascio, A., Thomas, S.G., Alabadí, D., and Blazquez, M.A. (2012). Molecular mechanism for the interaction between gibberellin and brassinosteroid signaling pathways in Arabidopsis. Proc Natl Acad Sci U S A 109, 13446-13451.

Garfinkel, S.N., Abelson, J.L., King, A.P., Sripada, R.K., Wang, X., Gaines, L.M., and Liberzon, I. (2014). Impaired contextual modulation of memories in PTSD: an fMRI and psychophysiological study of extinction retention and fear renewal. J Neurosci 34, 13435-13443.

Garoosi, G.A., Salter, M.G., Caddick, M.X., and Tomsett, A.B. (2005). Characterization of the ethanol-inducible *alc* gene expression system in tomato. J Exp Bot 56, 1635-1642.

Geiger, D., Scherzer, S., Mumm, P., Stange, A., Marten, I., Bauer, H., Ache, P., Matschi, S., Liese, A., Al-Rasheid, K.A.S., Romeis, T., and Hedrich, R. (2009). Activity of guard cell anion channel SLAC1 is controlled by drought-stress signaling kinase-phosphatase pair. Proc Natl Acad Sci U S A 106, 21425-21430.

Gepstein, S., Sabehi, G., Carp, M.J., Hajouj, T., Nesher, M.F., Yariv, I., Dor, C., and Bassani, M. (2003). Large-scale identification of leaf senescence-associated genes. Plant J 36: 629–642.

Gonzalez-Grandio, E., Pajoro, A., Franco-Zorrilla, J.M., Tarancon, C., Immink, R.G., and Cubas, P. (2017). Abscisic acid signaling is controlled by a BRANCHED1/HD-ZIP I cascade in Arabidopsis axillary buds. Proc Natl Acad Sci U S A 114, E245-E254.

Granier, C., and Tardieu, F. (1999). Water deficit and spatial pattern of leaf development. Variability in responses can be simulated using a simple model of leaf development. Plant Physiol 119, 609-620.

Gray, W.M., Kepinski, S., Rouse, D., Leyser, O., and Estelle, M. (2001). Auxin regulates SCFTIR1-dependent degradation of AUX/IAA proteins. Nature 414, 271-276.

Grennan, A.K. (2006). Gibberellin metabolism enzymes in rice. Plant Physiol 141, 524-526.

Griffiths, J., Murase, K., Rieu, I., Zentella, R., Zhang, Z.L., Powers, S.J., Gong, F., Phillips, A.L., Hedden, P., Sun, T.P., and Thomas, S.G. (2006). Genetic characterization and functional analysis of the GID1 gibberellin receptors in Arabidopsis. Plant cell 18, 3399-3414.

Guo, A., He, K., Liu, D., Bai, S., Gu, X., Wei, L., and Luo, J. (2005). DATF: a database of Arabidopsis transcription factors. Bioinformatics 21, 2568-2569.

Ha, C.V., Leyva-González, M.A., Osakabe, Y., Tran, U.T., Nishiyama, R., Watanabe, Y., Tanaka, M., Seki, M., Yamaguchi, S., Dong, N.V., Yamaguchi-Shinozaki, K., Shinozaki, K., Herrera-Estrella, L., and Tran, L.S. (2014). Positive regulatory role of strigolactone in plant responses to drought and salt stress. Proc Natl Acad Sci U S A 111, 851-856.

Haake, V., Cook, D., Riechmann, J.L., Pineda, O., Thomashow, M.F., and Zhang, J.Z. (2002). Transcription factor CBF4 is a regulator of drought adaptation in Arabidopsis. Plant Physiol 130, 639–48.

Hanson, J., Johannesson, H., and Engström, P. (2001). Sugar-dependent alterations in cotyledon and leaf development in transgenic plants expressing the HDZhdip gene *ATHB13*. Plant Mol Biol 45, 247-262.

Harris, J.C., Hrmova, M., Lopato, S., and Langridge, P. (2011). Modulation of plant growth by HD-Zip class I and II transcription factors in response to environmental stimuli. New Phytol 190, 823-837.

Hatfield, J.L., and Prueger, J.H. (2015). Temperature extremes: effect on plant growth and development. Weather Clim Extreme 10, 4-10.

Hedden, P., and Sponsel, V. (2015). A century of gibberellin research. J of Plant Growth Regul 34, 740-760.

Helliwell, C.A., Chandler, P.M., Poole, A., Dennis, E.S., and Peacock, W.J. (2001). The CYP88A cytochrome P450, *ent*-kaurenoic acid oxidase, catalyzes three steps of the gibberellin biosynthesis pathway. Proc Natl Acad Sci U S A 98, 2065-2070.

Hendelman, A., Stav, R., Zemach, H., and Arazi, T. (2013). The tomato NAC transcription factor SlNAM2 is involved in flower-boundary morphogenesis. J Exp Bot 64, 5497-5507.

Henriksson, E., Olsson, A.S., Johannesson, H., Johansson, H., Hanson, J., Engstrom, P., and Soderman, E. (2005). Homeodomain leucine zipper class I genes in Arabidopsis. Expression patterns and phylogenetic relationships. Plant Physiol 139, 509-518.

Hilker, M., Schwachtje, J., Baier, M., Balazadeh, S., Bäurle, I., Geiselhardt, S., Hincha, D.K., Kunze, R., Mueller-Roeber, B., Rillig, M.C., Rolff, J., Romeis, T., Schmülling, T., Steppuhn, A., van Dongen, J., Whitcomb, S.J., Wurst, S., Zuther, E., and Kopka, J. (2016). Priming and memory of stress responses in organisms lacking a nervous system. Biol Rev 91, 1118-1133.

Hirano, K., Asano, K., Tsuji, H., Kawamura, M., Mori, H., Kitano, H., Ueguchi-Tanaka, M., and Matsuoka, M. (2010). Characterization of the molecular mechanism underlying gibberellin perception complex formation in rice. Plant Cell 22, 2680-2696.

Hong, G.J., Xue, X.Y., Mao, Y.B., Wang, L.J., and Chen, X.Y. (2012). Arabidopsis MYC2 interacts with DELLA proteins in regulating sesquiterpene synthase gene expression. Plant Cell 24, 2635-2648.

Hong, Y., Zhang, H., Huang, L., Li, D., and Song, F. (2016). Overexpression of a stress-responsive NAC transcription factor gene *ONAC022* improves drought and salt tolerance in rice. Front Plant Sci 7, 4-4.

Hong, Z., Ueguchi-Tanaka, M., Shimizu-Sato, S., Inukai, Y., Fujioka, S., Shimada, Y., Takatsuto, S., Agetsuma, M., Yoshida, S., Watanabe, Y., Uozu, S., Kitano, H., Ashikari, M., and Matsuoka, M. (2002). Loss-of-function of a rice brassinosteroid biosynthetic enzyme, C-6 oxidase, prevents the organized arrangement and polar elongation of cells in the leaves and stem. Plant J 32, 495-508.

Hsiao, T.C., and Xu, L.K. (2000). Sensitivity of growth of roots versus leaves to water stress: biophysical analysis and relation to water transport. J Exp Bot 51, 1595-1616.

Hutchison, C.E., and Kieber, J.J. (2002). Cytokinin signaling in Arabidopsis. Plant Cell 14, S47-S59.

Hwang, I., and Sakakibara, H. (2006). Cytokinin biosynthesis and perception. Physiol Plant 126, 528-538.

Islam, M.A., Du, H., Ning, J., Ye, H., and Xiong, L. (2009). Characterization of *Glossy1*-homologous genes in rice involved in leaf wax accumulation and drought resistance. Plant Mol Biol 70, 443-456.

Jackson, R.B., Sperry, J.S., and Dawson, T.E. (2000). Root water uptake and transport: using physiological processes in global predictions. Trends Plant Sci 5, 482-488.

Jin, J., He, K., Tang, X., Li, Z., Lv, L., Zhao, Y., Luo, J., and Gao, G. (2015). An Arabidopsis transcriptional regulatory map reveals distinct functional and evolutionary features of novel transcription factors. Mol Biol Evol 32, 1767-1773.

Jin, J., Tian, F., Yang, D.C., Meng, Y.Q., Kong, L., Luo, J., and Gao, G. (2016). PlantTFDB 4.0: toward a central hub for transcription factors and regulatory interactions in plants. Nucl Acids Res 45, D1040-D1045.

Jin, J., Zhang, H., Kong, L., Gao, G., and Luo, J. (2013). PlantTFDB 3.0: a portal for the functional and evolutionary study of plant transcription factors. Nucl Acids Res 42, D1182-D1187.

Kamada-Nobusada, T., and Sakakibara, H. (2009). Molecular basis for cytokinin biosynthesis. Phytochemistry 70, 444-449.

Kamanga, R.M., Mbega, E., Ndakidemi, P. (2018). Drought tolerance mechanisms in plants: physiological responses associated with water deficit stress in *Solanum lycopersicum*. Adv Crop Sci Tech 6, 362.

Kamranfar, I., Xue, G.P., Tohge, T., Sedaghatmehr, M., Fernie, A.R., Balazadeh, S., and Mueller-Roeber, B. (2018). Transcription factor RD26 is a key regulator of metabolic reprogramming during dark-induced senescence. New Phytol 218, 1543-1557.

Katsir, L., Chung, H.S., Koo, A.J.K., and Howe, G.A. (2008). Jasmonate signaling: a conserved mechanism of hormone sensing. Curr Opin Plant Biol 11, 428-435.

Kepinski, S., and Leyser, O. (2005). Plant development: auxin in loops. Curr Biol 15, R208-R210.

Kieber, J.J., and Schaller, G.E. (2018). Cytokinin signaling in plant development. Development 145, dev149344.

Kim, H.B., Kwon, M., Ryu, H., Fujioka, S., Takatsuto, S., Yoshida, S., An, C.S., Lee, I., Hwang, I., and Choe, S. (2006). The regulation of *DWARF4* expression is likely a critical mechanism in maintaining the homeostasis of bioactive brassinosteroids in Arabidopsis. Plant Physiol 140, 548-557.

Kim, H.J., Nam, H.G., and Lim, P.O. (2016). Regulatory network of NAC transcription factors in leaf senescence. Curr Opin Plant Biol 33, 48-56.

Koornneef, M., and Meinke, D. (2010). The development of Arabidopsis as a model plant. Plant J 61, 909-921.

Kotak, S., Port, M., Ganguli, A., Bicker, F., and Von Koskull-Döring, P. (2004). Characterization of C-terminal domains of Arabidopsis heat stress transcription factors (Hsfs) and identification of a new signature combination of plant class A Hsfs with AHA and NES motifs essential for activator function and intracellular localization. Plant J 39, 98-112.

Kuhn, J.M., Boisson-Dernier, A., Dizon, M.B., Maktabi, M.H., and Schroeder, J.I. (2006). The protein phosphatase *AtPP2CA* negatively regulates abscisic acid signal transduction in Arabidopsis, and effects of *abh1* on *AtPP2CA* mRNA. Plant Physiol 140, 127-139.

Kummerfeld, S.K., and Teichmann, S.A. (2006). DBD: a transcription factor prediction database. Nucl Acids Res 34, D74-D81.

Kunieda, T., Mitsuda, N., Ohme-Takagi, M., Takeda, S., Aida, M., Tasaka, M., Kondo, M., Nishimura, M., and Hara-Nishimura, I. (2008). NAC family proteins NARS1/NAC2 and NARS2/NAM in the outer integument regulate embryogenesis in *Arabidopsis*. Plant Cell 20, 2631-2642.

Kutschera, U., and Wang, Z.Y. (2012). Brassinosteroid action in flowering plants: a Darwinian perspective. J Exp Bot 63, 3511-3522.

Larkindale, J., Hall, J.D., Knight, M.R., and Vierling, E. (2005). Heat stress phenotypes of *Arabidopsis* mutants implicate multiple signaling pathways in the acquisition of thermotolerance. Plant Physiol. 138: 882–97.

Lavy, M., and Estelle, M. (2016). Mechanisms of auxin signaling. Development (Cambridge, England) 143, 3226-3229.

Laxa, M., Liebthal, M., Telman, W., Chibani, K., and Dietz, K.J. (2019). The role of the plant antioxidant system in drought tolerance. Antioxidants (Basel) 8, 94.

Lee, M.-H., Jeon, H.S., Kim, H.G., and Park, O.K. (2017). An Arabidopsis NAC transcription factor NAC4 promotes pathogen-induced cell death under negative regulation by microRNA164. New Phytol 214, 343-360.

Leivar, P., and Quail, P.H. (2011). PIFs: pivotal components in a cellular signaling hub. Trends Plant Sci 16, 19-28.

Li, J. (2005). Brassinosteroid signaling: from receptor kinases to transcription factors. Curr Opin Plant Biol 8, 526-531.

Li, J., Wen, J., Lease, K.A., Doke, J.T., Tax, F.E., and Walker, J.C. (2002). BAK1, an Arabidopsis LRR receptor-like protein kinase, interacts with BRI1 and modulates brassinosteroid signaling. Cell 110, 213-222.

Li, K., Yu, R., Fan, L.M., Wei, N., Chen, H., and Deng, X.W. (2016). DELLA-mediated PIF degradation contributes to coordination of light and gibberellin signalling in Arabidopsis. Nat Commun 7, 11868.

Li, Q.F., and He, J.X. (2013). Mechanisms of signaling crosstalk between brassinosteroids and gibberellins. Plant Signal Behav 8, e24686.

Li, Q.F., Wang, C., Jiang, L., Li, S., Sun, S.S.M., and He, J.X. (2012). An interaction between BZR1 and DELLAs mediates direct signaling crosstalk between brassinosteroids and gibberellins in *Arabidopsis*. Sci Signal 5, ra72.

Lin, Z., Hong, Y., Yin, M., Li, C., Zhang, K., and Grierson, D. (2008). A tomato HD-Zip homeobox protein, LeHB-1, plays an important role in floral organogenesis and ripening. Plant J 55, 301-310.

Lindsey, K., Casson, S., and Chilley, P. (2002). Peptides: new signalling molecules in plants. Trends Plant Sci 7, 78-83.

Liu, Q., Zhang, G., and Chen, S. (2001). Structure and regulatory function of plant transcription factors. Chinese Sci Bull 46, 271-278.

Livne, S., and Weiss, D. (2014). Cytosolic activity of the gibberellin receptor GIBBERELLIN INSENSITIVE DWARF1A. Plant Cell Physiol 55, 1727-1733.

Locascio, A., Blazquez, M.A., and Alabadi, D. (2013). Genomic analysis of DELLA protein activity. Plant Cell Physiol 54, 1229-1237.

Luo, L.J. (2010). Breeding for water-saving and drought-resistance rice (WDR) in China. J Exp Bot 61, 3509-3517.

Ma, X., Zhang, Y., Tureckova, V., Xue, G.P., Fernie, A.R., Mueller-Roeber, B., and Balazadeh, S. (2018). The NAC transcription factor SlNAP2 regulates leaf senescence and fruit yield in tomato. Plant Physiol 177, 1286-1302.

Maggio, A., Hasegawa, P.M., Bressan, R.A., Consiglio, M.F., and Joly, R.J. (2001). Review: Unravelling the functional relationship between root anatomy and stress tolerance. Funct Plant Biol 28, 999-1004.

Magome, H., Nomura, T., Hanada, A., Takeda-Kamiya, N., Ohnishi, T., Shinma, Y., Katsumata, T., Kawaide, H., Kamiya, Y., and Yamaguchi, S. (2013). CYP714B1 and CYP714B2 encode gibberellin 13-oxidases that reduce gibberellin activity in rice. Proc Natl Acad Sci U S A 110, 1947-1952.

Magome, H., Yamaguchi, S., Hanada, A., Kamiya, Y., and Oda, K. (2004). *dwarf and delayed-flowering 1*, a novel Arabidopsis mutant deficient in gibberellin biosynthesis because of overexpression of a putative AP2 transcription factor. Plant J 37, 720-729.

Małyska, A., and Jacobi, J. (2018). Plant breeding as the cornerstone of a sustainable bioeconomy. N Biotechnol 40, 129-132.

Manavalan, L.P., Guttikonda, S.K., Phan Tran, L.S., and Nguyen, H.T. (2009). Physiological and molecular approaches to improve drought resistance in soybean. Plant Cell Physiol 50, 1260-1276.

Manavella, P.A., Arce, A.L., Dezar, C.A., Bitton, F., Renou, J.P., Crespi, M., and Chan, R.L. (2006). Cross-talk between ethylene and drought signalling pathways is mediated by the sunflower Hahb-4 transcription factor. Plant J 48, 125-137.

Mao, C., Lu, S., Lv, B., Zhang, B., Shen, J., He, J., Luo, L., Xi, D., Chen, X., and Ming, F. (2017). A rice NAC transcription factor promotes leaf senescence via ABA biosynthesis. Plant Physiol 174, 1747-1763.

Markakis, M.N., De Cnodder, T., Lewandowski, M., Simon, D., Boron, A., Balcerowicz, D., Doubbo, T., Taconnat, L., Renou, J.P., Höfte, H., Verbelen, J.P., and Vissenberg, K. (2012). Identification of genes involved in the ACC-mediated control of root cell elongation in *Arabidopsis thaliana*. BMC Plant Biol 12, 208.

Martinez-Bello, L., Moritz, T., and Lopez-Diaz, I. (2015). Silencing C19-GA 2-oxidases induces parthenocarpic development and inhibits lateral branching in tomato plants. J Exp Bot 66, 5897-5910.

Meinke, D.W., Cherry, J.M., Dean, C., Rounsley, S.D., and Koornneef, M. (1998). *Arabidopsis thaliana*: a model plant for genome analysis. Science 282, 662-682.

Merlot, S., Gosti, F., Guerrier, D., Vavasseur, A., and Giraudat, J. (2001). The ABI1 and ABI2 protein phosphatases 2C act in a negative feedback regulatory loop of the abscisic acid signalling pathway. Plant J 25, 295-303.

Miao, Z.Q., Zhao, P.X., Mao, J.L., Yu, L.H., Yuan, Y., Tang, H., Liu, Z.B., and Xiang, C.B. (2018). HOMEOBOX PROTEIN52 mediates the crosstalk between ethylene and auxin signaling during primary root elongation by modulating auxin transport-related gene expression. Plant Cell 30, 2761-2778.

Milad, M.R., Pitman, R.K., Ellis, C.B., Gold, A.L., Shin, L.M., Lasko, N.B., Zeidan, M.A., Handwerger, K., Orr, S.P., and Rauch, S.L. (2009). Neurobiological basis of failure to recall extinction memory in posttraumatic stress disorder. Biol Psychiatry 66, 1075-1082.

Milborrow, B.V. (2001). The pathway of biosynthesis of abscisic acid in vascular plants: a review of the present state of knowledge of ABA biosynthesis. J Exp Bot 52, 1145-1164.

Mitra, J. (2001). Genetics and genetic improvement of drought resistance in crop plants. Curr Sci 80, 758-763.

Miyakawa, T., and Tanokura, M. (2017). Structural basis for the regulation of phytohormone receptors. Biosci Biotechnol Biochem 81, 1261-1273.

Miyakawa, T., Fujita, Y., Yamaguchi-Shinozaki, K., and Tanokura, M. (2013). Structure and function of abscisic acid receptors. Trends in Plant Science 18, 259-266.

Miyazaki, S., Tomita, K., Yamane, H., Kobayashi, M., Asami, T., and Nakajima, M. (2018). Characterization of a helminthosporic acid analog that is a selective agonist of gibberellin receptor. Bioorg Med Chem Lett 28, 2465-2470.

Miyazono, K., Miyakawa, T., Sawano, Y., Kubota, K., Kang, H.J., Asano, A., Miyauchi, Y., Takahashi, M., Zhi, Y., Fujita, Y., Yoshida, T., Kodaira, K.-S., Yamaguchi-Shinozaki, K., and Tanokura, M. (2009). Structural basis of abscisic acid signalling. Nature 462, 609.

Molina, C., and Grotewold, E. (2005) Genome wide analysis of Arabidopsis core promoter. BMC Genomics, 6:25

Mori, M., Nomura, T., Ooka, H., Ishizaka, M., Yokota, T., Sugimoto, K., Okabe, K., Kajiwara, H., Satoh, K., Yamamoto, K., Hirochika, H., and Kikuchi, S. (2002). Isolation and Characterization of a Rice Dwarf Mutant with a Defect in Brassinosteroid Biosynthesis. Plant Physiol 130, 1152-1161.

Moschou, P.N., and Roubelakis-Angelakis, K.A. (2013). Polyamines and programmed cell death. J Exp Bot 65, 1285-1296.

Moyano, E., Martinez-Rivas, F.J., Blanco-Portales, R., Molina-Hidalgo, F.J., Ric-Varas, P., Matas-Arroyo, A.J., Caballero, J.L., Muñoz-Blanco, J., and Rodríguez-Franco, A. (2018). Genome-wide analysis of the NAC transcription factor family and their expression during the development and ripening of the *Fragaria* × *ananassa* fruits. PLoS One 13, e0196953.

Mun, B.G., Lee, S.U., Park, E.J., Kim, H.H., Hussain, A., Imran, Q.M., Lee, I.J., and Yun, B.W. (2017). Analysis of transcription factors among differentially expressed genes induced by drought stress in *Populus davidiana*. 3 Biotech 7, 209.

Munns, R., and Tester, M. (2008). Mechanisms of salinity tolerance. Ann Rev Plant Biol 59, 651-681.

Murase, K., Hirano, Y., Sun, T.P., and Hakoshima, T. (2008). Gibberellin-induced DELLA recognition by the gibberellin receptor GID1. Nature 456, 459.

Nam, K.H., and Li, J. (2002). BRI1/BAK1, a receptor kinase pair mediating brassinosteroid signaling. Cell 110, 203-212.

Nambara, E., and Marion-Poll, A. (2005). Abscisic acid biosynthesis and catabolism. Ann Rev Plant Biol 56, 165-185.

Nemhauser, J.L., Hong, F., and Chory, J. (2006). Different plant hormones regulate similar processes through largely nonoverlapping transcriptional responses. Cell 126, 467-475.

Nemhauser, J.L., Mockler, T.C., and Chory, J. (2004). Interdependency of brassinosteroid and auxin signaling in Arabidopsis. PLoS Biol 2, e258.

Neumann, K.H., Imani, J., and Kumar, A. (2009). Phytohormones and growth regulators. In plant cell and tissue culture - A tool in biotechnology: basics and application (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 227-233.

Ng, L.M., Melcher, K., Teh, B.T., and Xu, H.E. (2014). Abscisic acid perception and signaling: structural mechanisms and applications. Acta Pharmacol Sin 35, 567.

Nir, I., Shohat, H., Panizel, I., Olszewski, N., Aharoni, A., and Weiss, D. (2017). The tomato DELLA protein PROCERA acts in guard cells to promote stomatal closure. Plant Cell 29, 3186-3197.

Nishimura, N., Sarkeshik, A., Nito, K., Park, S.Y., Wang, A., Carvalho, P.C., Lee, S., Caddell, D.F., Cutler, S.R., Chory, J., Yates, J.R., and Schroeder, J.I. (2010). PYR/PYL/RCAR family members are major in-vivo ABI1 protein phosphatase 2C-interacting proteins in Arabidopsis. Plant J 61, 290-299.

Nishizawa-Yokoi, A., Nosaka, R., Hayashi, H., Tainaka, H., Maruta, T., Tamoi, M., Ikeda, M., Ohme-Takagi, M., Yoshimura, K., Yabuta, Y., and Shigeoka, S. (2011). HsfA1d and HsfA1e involved in the transcriptional regulation of HsfA2 function as key regulators for the Hsf signaling network in response to environmental stress. Plant Cell Physiol 52, 933-945.

Ogburn, R.M., and Edwards, E.J. (2010). Chapter 4 - The ecological water-use strategies of succulent plants. In advances in botanical research, Kader, J.C. and Delseny, M. eds (Academic Press), pp. 179-225.

Ohnishi, T., Nomura, T., Watanabe, B., Ohta, D., Yokota, T., Miyagawa, H., Sakata, K., and Mizutani, M. (2006). Tomato cytochrome P450 CYP734A7 functions in brassinosteroid catabolism. Phytochemistry 67, 1895-1906.

Olsen, A.N., Ernst, H.A., Leggio, L.L., and Skriver, K. (2005). NAC transcription factors: structurally distinct, functionally diverse. Trends Plant Sci 10, 79-87.

O'Malley, R.C., Huang, S.C., Song, L., Lewsey, M.G., Bartlett, A., Nery, J.R., Galli, M., Gallavotti, A., and Ecker, J.R. (2016). Cistrome and epicistrome features shape the regulatory DNA landscape. Cell 165, 1280-1292.

Ottman, M. J., Kimball, B. A., White, J. W., & Wall, G. W. (2012). Wheat growth response to increased temperature from varied planting dates and supplemental infrared heating. Agron J 104(1), 7-16.

Paciorek, T., and Friml, J. (2006). Auxin signaling. J Cell Sci 119, 1199-1202.

Palaniswamy, S.K., James, S., Sun, H., Lamb, R.S., Davuluri, R.V., and Grotewold, E. (2006). AGRIS and AtRegNet. a platform to link cis-regulatory elements and transcription factors into regulatory networks. Plant Physiol 140, 818-829.

Papdi, C., Abraham, E., Joseph, M.P., Popescu, C., Koncz, C., and Szabados, L. (2008). Functional identification of *Arabidopsis* stress regulatory genes using the controlled cDNA overexpression system. Plant Physiol 147: 528-42.

Paponov, I.A., Paponov, M., Teale, W., Menges, M., Chakrabortee, S., Murray, J.A.H., and Palme, K. (2008). Comprehensive transcriptome analysis of auxin responses in Arabidopsis. Mol Plant 1, 321-337.

Park, S.Y., Fung, P., Nishimura, N., Jensen, D.R., Fujii, H., Zhao, Y., Lumba, S., Santiago, J., Rodrigues, A., Chow, T.F., Alfred, S.E., Bonetta, D., Finkelstein, R., Provart, N.J., Desveaux, D., Rodriguez, P.L., McCourt, P., Zhu, J.K., Schroeder, J.I., Volkman, B.F., and Cutler, S.R. (2009). Abscisic acid inhibits type 2C protein phosphatases via the PYR/PYL family of START proteins. Science 324, 1068-1071.

Passioura, J.B. (2002). Review: Environmental biology and crop improvement. Funct Plant Biol 29, 537-546.

Pencik, A., Rolcik, J., Novak, O., Magnus, V., Bartak, P., Buchtik, R., Salopek-Sondi, B., and Strnad, M. (2009). Isolation of novel indole-3-acetic acid conjugates by immunoaffinity extraction. Talanta 80, 651-655.

Peres, A., Soares, J.S., Tavares, R.G., Righetto, G., Zullo, M.A.T., Mandava, N.B., and Menossi, M. (2019). Brassinosteroids, the sixth class of phytohormones: a molecular view from the discovery to hormonal interactions in plant development and stress adaptation. Int J Mol Sci 20.

Perez-Rodriguez, P., Riano-Pachon, D.M., Correa, L.G., Rensing, S.A., Kersten, B., and Mueller-Roeber, B. (2010). PlnTFDB: updated content and new features of the plant transcription factor database. Nucl Acids Res 38, D822-827.

Peyraud, R., Dubiella, U., Barbacci, A., Genin, S., Raffaele, S., and Roby, D. (2017). Advances on plant-pathogen interactions from molecular toward systems biology perspectives. Plant J 90, 720-737.

Pierik, R., Djakovic-Petrovic, T., Keuskamp, D.H., de Wit, M., and Voesenek, L.A.C.J. (2009). Auxin and ethylene regulate elongation responses to neighbor proximity signals independent of gibberellin and DELLA proteins in Arabidopsis. Plant Physiol 149, 1701-1712.

Piskurewicz, U., Jikumaru, Y., Kinoshita, N., Nambara, E., Kamiya, Y., and Lopez-Molina, L. (2008). The gibberellic acid signaling repressor RGL2 inhibits Arabidopsis seed germination by stimulating abscisic acid synthesis and ABI5 activity. Plant Cell 20, 2729-2745.

Porter, J.R., and Gawith, M. (1999). Temperatures and the growth and development of wheat: a review. Eur J Agron 10, 23-36.

Pregitzer, K.S., and King, J.S. (2005). Effects of soil temperature on nutrient uptake. In Nutrient acquisition by plants: An ecological perspective, H. BassiriRad, ed (Berlin, Heidelberg: Springer Berlin Heidelberg), pp. 277-310.

Provart, N.J., Alonso, J., Assmann, S.M., Bergmann, D., Brady, S.M., Brkljacic, J., Browse, J., Chapple, C., Colot, V., Cutler, S., Dangl, J., Ehrhardt, D., Friesner, J.D., Frommer, W.B., Grotewold, E., Meyerowitz, E., Nemhauser, J., Nordborg, M., Pikaard, C., Shanklin, J., Somerville, C., Stitt, M., Torii, K.U., Waese, J., Wagner, D., and McCourt, P. (2016). 50 years of Arabidopsis research: highlights and future directions. New Phytol 209, 921-944.

Qu, L.J., and Zhu, Y.X. (2006). Transcription factor families in Arabidopsis: major progress and outstanding issues for future research. Curr Opin Plant Biol 9, 544-549.

Ramirez, S.R., and Basu, C. (2009). Comparative analyses of plant transcription factor databases. Curr Genomics 10, 10-17.

Rengasamy, P. (2010). Soil processes affecting crop production in salt-affected soils. Funct Plant Biol 37, 613-620.

Riano-Pachon , D.M. , Ruzicic , S. , Dreyer , I. and Mueller-Roeber , B. (2007). PlnTFDB: an integrative plant transcription factor database. BMC Bioinformatics 8, 42.

Ribone, P.A., Capella, M., and Chan, R.L. (2015). Functional characterization of the homeodomain leucine zipper I transcription factor AtHB13 reveals a crucial role in Arabidopsis development. J Exp Bot 66, 5929-5943.

Riechmann, J.L., Heard, J., Martin, G., Reuber, L., Jiang , C.-Z., Keddie, J., Adam, L., Pineda, O., Ratcliffe, O.J., Samaha, R.R., Creelman, R., Pilgrim, M., Broun, P., Zhang, J.Z., Ghandehari, D., Sherman, B.K., and Yu, G. (2000). *Arabidopsis* transcription factors: genome-wide comparative analysis among eukaryotes. Science 290, 2105-2110.

Rivas-San Vicente, M., and Plasencia, J. (2011). Salicylic acid beyond defence: its role in plant growth and development. J Exp Bot 62, 3321-3338.

Rizza, A., Walia, A., Lanquar, V., Frommer, W.B., and Jones, A.M. (2017). In vivo gibberellin gradients visualized in rapidly elongating tissues. Nat Plants 3, 803-813.

Romani, F., Ribone, P.A., Capella, M., Miguel, V.N., and Chan, R.L. (2016). A matter of quantity: common features in the drought response of transgenic plants overexpressing HD-Zip I transcription factors. Plant Sci 251, 139-154.

Rosenzweig, C., Elliott, J., Deryng, D., Ruane, A.C., Müller, C., Arneth, A., Boote, K.J., Folberth, C., Glotter, M., Khabarov, N., Neumann, K., Piontek, F., Pugh, T.A.M., Schmid, E., Stehfest, E., Yang, H., and Jones, J.W. (2014). Assessing agricultural risks of climate change in the 21st century in a global gridded crop model intercomparison. Proc Natl Acad Sci U S A 111, 3268-3273.

Roy, S.J., Negrao, S., and Tester, M. (2014). Salt resistant crop plants. Curr Opin Biotechnol 26, 115-124.

Ruzicka, K., Ljung, K., Vanneste, S., Podhorská, R., Beeckman, T., Friml, J., and Benkova, E. (2007). Ethylene regulates root growth through effects on auxin biosynthesis and transport-dependent auxin distribution. Plant Cell 19, 2197-2212.

Saddic, L.A., Huvermann, B., Bezhani, S., Su, Y., Winter, C.M., Kwon, C.S., Collum, R.P., and Wagner, D. (2006). The LEAFY target LMI1 is a meristem identity regulator and acts together with LEAFY to regulate expression of *CAULIFLOWER*. Development 133, 1673-1682.

Saez, A., Rodrigues, A., Santiago, J., Rubio, S., and Rodriguez, P.L. (2008). HAB1-SWI3B interaction reveals a link between abscisic acid signaling and putative SWI/SNF chromatin-remodeling complexes in Arabidopsis. Plant Cell 20, 2972-2988.

Sakakibara, H. (2010). Cytokinin biosynthesis and metabolism. In plant hormones: biosynthesis, signal transduction, action!, Davies, P.J. ed (Dordrecht: Springer Netherlands), pp. 95-114.

Sakamoto, H. (2004). *Arabidopsis* Cys2/His2-Type Zinc-Finger proteins function as transcription repressors under drought, cold, and high-salinity stress conditions. Plant Physiol. 136, 2734–2746.

Sakuraba, Y., Piao, W., Lim, J.H., Han, S.H., Kim, Y.S., An, G., and Paek, N.C. (2015). Rice ONAC106 inhibits leaf senescence and increases salt tolerance and tiller angle. Plant Cell Physiol 56, 2325-2339.

Salehin, M., Bagchi, R., and Estelle, M. (2015). SCFTIR1/AFB-based auxin perception: mechanism and role in plant growth and development. Plant Cell 27, 9-19.

Santamaria, M.E., Arnaiz, A., Gonzalez-Melendi, P., Martinez, M., and Diaz, I. (2018). Plant perception and short-term responses to phytophagous insects and mites. Int J Mol Sci 19, 1356.

Santiago, J., Rodrigues, A., Saez, A., Rubio, S., Antoni, R., Dupeux, F., Park, S.-Y., Márquez, J.A., Cutler, S.R., and Rodriguez, P.L. (2009). Modulation of drought resistance by the abscisic acid receptor PYL5 through inhibition of clade A PP2Cs. Plant J 60, 575-588.

Santner, A., and Estelle, M. (2009). Recent advances and emerging trends in plant hormone signalling. Nature 459, 1071.

Sato, A., Sato, Y., Fukao, Y., Fujiwara, M., Umezawa, T., Shinozaki, K., Hibi, T., Taniguchi, M., Miyake, H., Goto, Derek B., and Uozumi, N. (2009). Threonine at position 306 of the KAT1 potassium channel is essential for channel activity and is a target site for ABA-activated SnRK2/OST1/SnRK2.6 protein kinase. Biochem J 424, 439-448.

Sawidis, T., Kalyva, S., and Delivopoulos, S. (2005). The root-tuber anatomy of *Asphodelus aestivus*. Flora 200, 332-338.

Schramm, F., Larkindale, J., Kiehlmann, E., Ganguli, A., Englich, G., Vierling, E., and von Koskull-Do¨ ring, P. (2008). A cascade of transcription factor DREB2A and heat stress transcription factor HsfA3 regulates the heat stress response of Arabidopsis. Plant J. 53, 264–274.

Schwartz, S.H., Qin, X., and Zeevaart, J.A.D. (2003). Elucidation of the indirect pathway of abscisic acid biosynthesis by mutants, genes, and enzymes. Plant Physiol 131, 1591-1601.

Seo, E., Choi, D., and Choi. (2015). Functional studies of transcription factors involved in plant defenses in the genomics era. Brief Funct Genomics 14, 260-267.

Serrani, J.C., Sanjuán, R., Ruiz-Rivero, O., Fos, M., and García-Martínez, J.L. (2007). Gibberellin regulation of fruit set and growth in tomato. Plant Physiol 145, 246-257.

Sessa, G., Carabelli, M., Possenti, M., Morelli, G., and Ruberti, I. (2018). Multiple links between HD-Zip proteins and hormone networks. Int J Mol Sci 19.

Shahnejat-Bushehri, S., Mueller-Roeber, B., and Balazadeh, S. (2012). Arabidopsis NAC transcription factor JUNGBRUNNEN1 affects thermomemory-associated genes and enhances heat stress tolerance in primed and unprimed conditions. Plant Signal Behav 7, 1518-1521.

Shahnejat-Bushehri, S., Nobmann, B., Devi Allu, A., and Balazadeh, S. (2016). JUB1 suppresses Pseudomonas syringae-induced defense responses through accumulation of DELLA proteins. Plant Signal Behav 11, e1181245.

Shahnejat-Bushehri, S., Tarkowska, D., Sakuraba, Y., and Balazadeh, S. (2016). Arabidopsis NAC transcription factor JUB1 regulates GA/BR metabolism and signalling. Nat Plants 2, 16013.

Shan, X., Yan, J., and Xie, D. (2012). Comparison of phytohormone signaling mechanisms. Curr Opin Plant Biol 15, 84-91.

Shao, H., Wang, H., and Tang, X. (2015). NAC transcription factors in plant multiple abiotic stress responses: progress and prospects. Front Plant Sci 6, 902-902.

Shapiro, A.D. (2005). Nitric oxide signaling in plants. In vitamins & hormones, Litwack, G. ed (Academic Press), pp. 339-398.

Shigeta, T., Yasuda, D., Mori, T., Yoshimitsu, Y., Nakamura, Y., Yoshida, S., Asami, T., Okamoto, S., and Matsuo, T. (2011). Characterization of brassinosteroid-regulated proteins in a nuclear-enriched fraction of Arabidopsis suspension-cultured cells. Plant Physiol Biochem 49, 985-995.

Siewers, V., Smedsgaard, J., and Tudzynski, P. (2004). The P450 monooxygenase bcaba1 is essential for abscisic acid biosynthesis in *Botrytis cinerea*. Appl Environ Microbiol 70, 3868-3876.

Singh, S.P., and Singh, P. (2015). Effect of temperature and light on the growth of algae species: A review. Renew Sust Energ Rev 50, 431-444.

Skirycz, A., De Bodt, S., Obata, T., De Clercq, I., Claeys, H., De Rycke, R., Andriankaja, M., Van Aken, O., Van Breusegem, F., Fernie, A.R., and Inze, D. (2010). Developmental stage specificity and the role of mitochondrial metabolism in the response of Arabidopsis leaves to prolonged mild osmotic stress. Plant Physiol. 152, 226-244.

Sobieszczuk-Nowicka, E. (2017). Polyamine catabolism adds fuel to leaf senescence. Amino Acids 49, 49-56.

Stahl, E., Hilfiker, O., and Reymond, P. (2018). Plant-arthropod interactions: who is the winner? Plant J 93, 703-728.

Stamm, P., Topham, A.T., Mukhtar, N.K., Jackson, M.D.B., Tomé, D.F.A., Beynon, J.L., and Bassel, G.W. (2017). The transcription factor ATHB5 affects GA-mediated plasticity in hypocotyl cell growth during seed germination. Plant Physiol 173, 907-917.

Steber, C.M., and McCourt, P. (2001). A role for brassinosteroids in germination in Arabidopsis. Plant Physiol 125, 763-769.

Stepanova, A.N., Yun, J., Likhacheva, A.V., and Alonso, J.M. (2007). Multilevel interactions between ethylene and auxin in *Arabidopsis* Roots. Plant Cell 19, 2169-2185.

Stracke, R., Werber, M., and Weisshaar, B. (2001). The R2R3-MYB gene family in *Arabidopsis thaliana*. Curr Opin Plant Biol 4, 447-456.

Sun, T., Goodman, H.M., and Ausubel, F.M. (1992). Cloning the Arabidopsis *GA1* locus by genomic subtraction. Plant Cell 4, 119-128.

Sun, T.P. (2008). Gibberellin metabolism, perception and signaling pathways in Arabidopsis. Arabidopsis Book 6, e0103.

Sun, T.P. (2010). Gibberellin-GID1-DELLA: a pivotal regulatory module for plant growth and development. Plant Physiol 154, 567-570.

Swarup, R., Perry, P.; Hagenbeek, D., Van Der Straeten, D., Beemster, G.T., Sandberg, G., Bhalerao, R., Ljung, K., and Bennett, M.J. (2007). Ethylene upregulates auxin biosynthesis in Arabidopsis seedlings to enhance inhibition of root cell elongation. Plant Cell 19, 2186–2196.

Szekeres, M., Németh, K., Koncz-Kalman, Z., Mathur, J., Kauschmann, A., Altmann, T., Redei, G.P., Nagy, F., Schell, J., and Koncz, C. (1996). Brassinosteroids rescue the deficiency of CYP90, a Cytochrome P450, controlling cell elongation and de-etiolation in Arabidopsis. Cell 85, 171-182.

Taiz, L. and Zeiger, E. (2010). Plant Physiology. 5th Edition, Sinauer Associates Inc., Sunderland, 782 p.

Takahashi, F., Suzuki, T., Osakabe, Y., Betsuyaku, S., Kondo, Y., Dohmae, N., Fukuda, H., Yamaguchi-Shinozaki, K., and Shinozaki, K. (2018). A small peptide modulates stomatal control via abscisic acid in long-distance signalling. Nature 556, 235-238.

Takei, K., Yamaya, T., and Sakakibara, H. (2004). Arabidopsis *CYP735A1* and *CYP735A2* encode cytokinin hydroxylases that catalyze the biosynthesis of *trans*-zeatin. J Biol Chem 279, 41866-41872.

Tan, X., Calderon-Villalobos, L.I.A., Sharon, M., Zheng, C., Robinson, C.V., Estelle, M., and Zheng, N. (2007). Mechanism of auxin perception by the TIR1 ubiquitin ligase. Nature 446, 640.

Tao, Y., Ferrer, J.L., Ljung, K., Pojer, F., Hong, F., Long, J.A., Li, L., Moreno, J.E., Bowman, M.E., Ivans, L.J., Cheng, Y., Lim, J., Zhao, Y., Ballare, C.L., Sandberg, G., Noel, J.P., and Chory, J. (2008). Rapid synthesis of auxin via a new tryptophan-dependent pathway is required for shade avoidance in plants. Cell 133, 164-176.

Tarakhovskaya, E.R., Maslov, Y.I., and Shishova, M.F. (2007). Phytohormones in algae. Russ J Plant Physl 54, 163-170.

Tardieu, F. (2013). Plant response to environmental conditions: assessing potential production, water demand, and negative effects of water deficit. Front Physiol 4.

Thirumalaikumar, V.P., Devkar, V., Mehterov, N., Ali, S., Ozgur, R., Turkan, I., Mueller-Roeber, B., and Balazadeh, S. (2018). NAC transcription factor JUNGBRUNNEN1 enhances drought tolerance in tomato. Plant Biotechnol J 16, 354-366.

Thomas, E.L., and van der Hoorn, R.A.L. (2018). Ten prominent host proteases in plant-pathogen interactions. Int J Mol Sci 19, 639.

Thomas, H., and Ougham, H. (2017). On plant growth and form. New Phytol 216, 337-338.

Tian, F., Yang, D.C., Meng, Y.Q., Jin, J., and Gao, G. (2018). Decoding functional regulatory maps via genomic evolutionary footprints in 63 green plants. bioRxiv, 484493.

Toledo-Ortiz, G., Huq, E., and Quail, P.H. (2003). The Arabidopsis basic/helix-loop-helix transcription factor family. Plant Cell 15, 1749-1770.

Tong, H., and Chu, C. (2016). Reply: brassinosteroid regulates gibberellin synthesis to promote cell elongation in rice: critical comments on Ross and Quittenden's letter. Plant Cell 28, 833-835.

Tong, H., Xiao, Y., Liu, D., Gao, S., Liu, L., Yin, Y., Jin, Y., Qian, Q., and Chu, C. (2014). Brassinosteroid regulates cell elongation by modulating gibberellin metabolism in rice. Plant Cell 26, 4376-4393.

Tran, L.S., Nishiyama, R., Yamaguchi-Shinozaki, K., and Shinozaki, K. (2010). Potential utilization of NAC transcription factors to enhance abiotic stress tolerance in plants by biotechnological approach. GM Crops 1, 32-39.

Tsuda, K., and Somssich, I.E. (2015). Transcriptional networks in plant immunity. New Phytol 206, 932-947.

Ueguchi-Tanaka, M., Ashikari, M., Nakajima, M., Itoh, H., Katoh, E., Kobayashi, M., Chow, T.Y., Hsing, Y.I., Kitano, H., Yamaguchi, I., and Matsuoka, M. (2005). *GIBBERELLIN INSENSITIVE DWARF1* encodes a soluble receptor for gibberellin. Nature 437, 693-698.

Umehara, M., Hanada, A., Yoshida, S., Akiyama, K., Arite, T., Takeda-Kamiya, N., Magome, H., Kamiya, Y., Shirasu, K., Yoneyama, K., Kyozuka, J., and Yamaguchi, S. (2008). Inhibition of shoot branching by new terpenoid plant hormones. Nature 455, 195.

Valdes, A.E., Overnas, E., Johansson, H., Rada-Iglesias, A., and Engstrom, P. (2012). The homeodomain-leucine zipper (HD-Zip) class I transcription factors ATHB7 and ATHB12 modulate abscisic acid signalling by regulating protein phosphatase 2C and abscisic acid receptor gene activities. Plant Mol Biol 80, 405–418.

Verma, V., Ravindran, P., and Kumar, P.P. (2016). Plant hormone-mediated regulation of stress responses. BMC Plant Bio 16, 86-86.

Verslues, P.E., Agarwal, M., Katiyar-Agarwal, S., Zhu, J., and Zhu, J.K. (2006). Methods and concepts in quantifying resistance to drought, salt and freezing, abiotic stresses that affect plant water status. Plant J 45: 523–39.

Vert, G., Nemhauser, J.L., Geldner, N., Hong, F., and Chory, J. (2005). Molecular mechanisms of steroid hormone signaling in plants. Annu Rev Cell Dev Biol 21, 177-201.

Vishwakarma, K., Upadhyay, N., Kumar, N., Yadav, G., Singh, J., Mishra, R.K., Kumar, V., Verma, R., Upadhyay, R.G., Pandey, M., and Sharma, S. (2017). Abscisic acid signaling and abiotic stress tolerance in plants: a review on current knowledge and future prospects. Front Plant Sci 8.

Wang, G., Zhang, S., Ma, X., Wang, Y., Kong, F., and Meng, Q. (2016). A stress-associated NAC transcription factor (SlNAC35) from tomato plays a positive role in biotic and abiotic stresses. Physiol Plantarum 158, 45-64.

Wang, H., Wang, H., Shao, H., and Tang, X. (2016). Recent advances in utilizing transcription factors to improve plant abiotic stress tolerance by transgenic technology. Front Plant Sci 7, 67.

Wang, L., Li, Z., Lu, M., and Wang, Y. (2017). ThNAC13, a NAC transcription factor from *Tamarix hispida*, confers salt and osmotic stress tolerance to transgenic *Tamarix* and *Arabidopsis*. Front Plant Sci 8, 635-635.

Wang, S.C., Lin, C.C., Chen, C.C., Tzeng, N.S., and Liu, Y.P. (2018). Effects of oxytocin on fear memory and neuroinflammation in a rodent model of posttraumatic stress disorder. Int J Mol Sci 19.

Wang, X., Goshe, M.B., Soderblom, E.J., Phinney, B.S., Kuchar, J.A., Li, J., Asami, T., Yoshida, S., Huber, S.C., and Clouse, S.D. (2005). Identification and functional analysis of in vivo phosphorylation sites of the Arabidopsis BRASSINOSTEROID-INSENSITIVE1 receptor kinase. Plant Cell 17, 1685-1703.

Wang, Y., Henriksson, E., Soderman, E., Henriksson, K.N., Sundberg, E., and Engstrom, P. (2003). The arabidopsis homeobox gene, *ATHB16*, regulates leaf development and the sensitivity to photoperiod in Arabidopsis. Dev Biol 264, 228-239.

Wang, Z.Y. (2012). Brassinosteroids modulate plant immunity at multiple levels. Proc Natl Acad Sci U S A 109, 7-8.

Wang, Z.Y., Nakano, T., Gendron, J., He, J., Chen, M., Vafeados, D., Yang, Y., Fujioka, S., Yoshida, S., Asami, T., and Chory, J. (2002). Nuclear-localized BZR1 mediates brassinosteroid-induced growth and feedback suppression of brassinosteroid biosynthesis. Dev Cell 2, 505-513.

Werner, T., Motyka, V., Strnad, M., and Schmulling, T. (2001). Regulation of plant growth by cytokinin. Proc Natl Acad Sci U S A 98, 10487-10492.

Wheeler T., and von Braun J. (2013). Climate change impacts on global food security. Science 341, 508–513.

Wild, M., Daviere, J.-M., Cheminant, S., Regnault, T., Baumberger, N., Heintz, D., Baltz, R., Genschik, P., and Achard, P. (2012). The Arabidopsis DELLA RGA-LIKE3 is a direct target of MYC2 and modulates jasmonate signaling responses. Plant Cell 24, 3307-3319.

William D.A., Su Y., Smith M.R., Lu M., Baldwin D.A., Wagner D. (2004). Genomic identification of direct target genes of LEAFY. Proc Natl Acad Sci U S A 10, 101(6):1775-80.

Wu, A., Allu, A.D., Garapati, P., Siddiqui, H., Dortay, H., Zanor, M.I., Asensi-Fabado, M.A., Munne-Bosch, S., Antonio, C., Tohge, T., Fernie, A.R., Kaufmann, K., Xue, G.P., Mueller-Roeber, B., and Balazadeh, S. (2012). JUNGBRUNNEN1, a reactive oxygen species-responsive NAC transcription factor, regulates longevity in Arabidopsis. Plant Cell 24, 482-506.

Xie, Q., Frugis, G., Colgan, D., and Chua, N.H. (2000). Arabidopsis NAC1 transduces auxin signal downstream of TIR1 to promote lateral root development. Genes Dev 14, 3024-3036.

Xie, Y., Tan, H., Ma, Z., and Huang, J. (2016). DELLA proteins promote anthocyanin biosynthesis via sequestering MYBL2 and JAZ suppressors of the MYB/bHLH/WD40 complex in *Arabidopsis thaliana*. Mol Plant 9, 711-721.

Xiong, L., and Zhu, J.K. (2003). Regulation of Abscisic Acid Biosynthesis. Plant Physiol 133, 29-36.

Xiong, Y., Liu, T., Tian, C., Sun, S., Li, J., and Chen, M. (2005). Transcription factors in rice: a genome-wide comparative analysis between monocots and eudicots. Plant Mol Biol 59, 191-203.

Xu, Z., Gongbuzhaxi, Wang, C., Xue, F., Zhang, H., and Ji, W. (2015). Wheat NAC transcription factor TaNAC29 is involved in response to salt stress. Plant Physiol Biochem 96, 356-363.

Yabuta, T. (1938). On the crystal of gibberellin, a substance to promote plant growth. J Agric Chem Soc Japan 14, 1526.

Yamaguchi, S. (2008). Gibberellin Metabolism and its Regulation. Annu Rev Plant Biol 59, 225-251.

Yamamuro, C., Ihara, Y., Wu, X., Noguchi, T., Fujioka, S., Takatsuto, S., Ashikari, M., Kitano, H., and Matsuoka, M. (2000). Loss of function of a rice *brassinosteroid insensitive1* homolog prevents internode elongation and bending of the lamina joint. Plant Cell 12, 1591-1605.

Yamazaki, D., Yoshida, S., Asami, T., and Kuchitsu, K. (2003). Visualization of abscisic acid-perception sites on the plasma membrane of stomatal guard cells. Plant J 35, 129-139.

Yan, Q., Duan, Z., Mao, J., Li, X., and Dong, F. (2012). Effects of root-zone temperature and N, P, and K supplies on nutrient uptake of cucumber (*Cucumis sativus* L.) seedlings in hydroponics. Soil Sci Plant Nutr 58, 707-717.

Yang, Q., Zhang, H., Liu, C., Huang, L., Zhao, L., and Zhang, A. (2018). A NAC transcription factor ZmNAC84 affects pollen development through the repression of zmrbohh expression in maize. J Plant Biol 61, 366-373.

Yang, W., Liu, X.D., Chi, X.J., Wu, C.A., Li, Y.Z., Song, L.L., Liu, X.M., Wang, Y.F., Wang, F.W., Zhang, C., Liu, Y., Zong, J.M., and Li, H.Y. (2011). Dwarf apple MbDREB1 enhances plant tolerance to low temperature, drought, and salt stress via both ABA-dependent and ABA-independent pathways. Planta 233, 219-229

Yehuda, R. (2002). Post-traumatic stress disorder. N Engl J Med 346, 108–114.

Yilmaz, A., Mejia-Guerra, M.K., Kurz, K., Liang, X., Welch, L., and Grotewold, E. (2011). AGRIS: the Arabidopsis Gene Regulatory Information Server, an update. Nucl Acids Res 39, D1118-1122.

Yin, Y., Wang, Z.Y., Mora-Garcia, S., Li, J., Yoshida, S., Asami, T., and Chory, J. (2002). BES1 accumulates in the nucleus in response to brassinosteroids to regulate gene expression and promote stem elongation. Cell 109, 181-191.

Yu, S., Galvao, V.C., Zhang, Y.C., Horrer, D., Zhang, T.Q., Hao, Y.H., Feng, Y.Q., Wang, S., Schmid, M., and Wang, J.W. (2012). Gibberellin regulates the Arabidopsis floral transition through miR156-targeted *SQUAMOSA* promoter binding-like transcription factors. Plant Cell 24, 3320-3332.

Yu, X., Li, L., Zola, J., Aluru, M., Ye, H., Foudree, A., Guo, H., Anderson, S., Aluru, S., Liu, P., Rodermel, S., and Yin, Y. (2011). A brassinosteroid transcriptional network revealed by genome-wide identification of BESI target genes in *Arabidopsis thaliana*. Plant J 65, 634-646.

Yue, B., Xue, W., Xiong, L., Yu, X., Luo, L., Cui, K., Jin, D., Xing, Y., and Zhang, Q. (2006). Genetic basis of drought resistance at reproductive stage in rice: separation of drought tolerance from drought avoidance. Genetics 172, 1213-1228.

Yusuf, M., Fariduddin, Q., and Ahmad, A. (2012). 24-Epibrassinolide modulates growth, nodulation, antioxidant system, and osmolyte in tolerant and sensitive varieties of *Vigna radiata* under different levels of nickel: A shotgun approach. Plant Physiol Biochem 57, 143-153.

Zang, G., Zou, H., Zhang, Y., Xiang, Z., Huang, J., Luo, L., Wang, C., Lei, K., Li, X., Song, D., Din, A.U., and Wang, G. (2016). The *De-Etiolated 1* homolog of Arabidopsis modulates the ABA signaling pathway and ABA biosynthesis in rice. Plant Physiol 171, 1259-1276.

Zhang, G., Lu, T., Miao, W., Sun, L., Tian, M., Wang, J., and Hao, F. (2017). Genome-wide identification of ABA receptor PYL family and expression analysis of PYLs in response to ABA and osmotic stress in *Gossypium*. PeerJ 5, e4126.

Zhang, J.Y., Broeckling, C.D., Blancaflor, E.B., Sledge, M.K., Sumner, L.W., and Wang, Z.Y. (2005a). Overexpression of *WXP1*, a putative *Medicago truncatula* AP2 domain-containing transcription factor gene, increases cuticular wax accumulation and enhances drought tolerance in transgenic alfalfa (*Medicago sativa*). Plant J 42, 689-707.

Zhang, Z., Chen, X., Guan, X., Liu, Y., Chen, H., Wang, T., Mouekouba, L.D., Li, J., and Wang, A. (2014). A genome-wide survey of homeodomain-leucine zipper genes and analysis of cold-responsive HD-Zip I members' expression in tomato. Biosci Biotechnol Biochem 78, 1337-1349.

Zhang, Z., Ramirez, J., Reboutier, D., Brault, M., Trouverie, J., Pennarun, A.M., Amiar, Z., Biligui, B., Galagovsky, L., and Rona, J.P. (2005b). Brassinosteroids regulate plasma membrane anion channels in addition to proton pumps during expansion of *Arabidopsis thaliana* cells. Plant Cell Physiol 46, 1494-1504.

Zhao, C., Lang, Z., and Zhu, J.K. (2015). Cold responsive gene transcription becomes more complex. Trends Plant Sci 20, 466-468.

Zhao, C., Liu, B., Piao, S., Wang, X., Lobell, D.B., Huang, Y., Huang, M., Yao, Y., Bassu, S., Ciais, P., Durand, J.-L., Elliott, J., Ewert, F., Janssens, I.A., Li, T., Lin, E., Liu, Q., Martre, P., Müller, C., Peng, S., Peñuelas, J., Ruane, A.C., Wallach, D., Wang, T., Wu, D., Liu, Z., Zhu, Y., Zhu, Z., and Asseng, S. (2017). Temperature increase reduces global yields of major crops in four independent estimates. Proc Natl Acad Sci U S A 114, 9326-9331.

Zhao, C., Piao, S., Wang, X., Huang, Y., Ciais, P., Elliott, J., Huang, M., Janssens, I.A., Li, T., Lian, X., Liu, Y., Müller, C., Peng, S., Wang, T., Zeng, Z., and Peñuelas, J. (2016). Plausible rice yield losses under future climate warming. Nat Plants 3, 16202.

Zhao, X., Yang, X., Pei, S., He, G., Wang, X., Tang, Q., Jia, C., Lu, Y., Hu, R., and Zhou, G. (2016). The *Miscanthus* NAC transcription factor *MlNAC9* enhances abiotic stress tolerance in transgenic *Arabidopsis*. Gene 586, 158-169.

Zhao, Y. (2010). Auxin biosynthesis and its role in plant development. Anuu rev Plant Biol 61, 49-64.

Zhao, Y., Christensen, S.K., Fankhauser, C., Cashman, J.R., Cohen, J.D., Weigel, D., and Chory, J. (2001). A role for flavin monooxygenase-like enzymes in auxin biosynthesis. Science 291, 306-309.

Zhao, Y., Ma, Q., Jin, X., Peng, X., Liu, J., Deng, L., Yan, H., Sheng, L., Jiang, H., and Cheng, B. (2014). A novel maize homeodomain-leucine zipper (HD-Zip) I gene, *Zmhdz10*, positively regulates drought and salt tolerance in both rice and Arabidopsis. Plant Cell Physiol 55, 1142-1156.

Zhong, G.Y., Zhong, G.V., and Burns, J.K. (2003). Profiling ethylene-regulated gene expression in *Arabidopsis thaliana* by microarray analysis. Plant Mol Biol 53, 117–131.

Zhong, R., Lee, C., and Ye, Z.-H. (2010). Evolutionary conservation of the transcriptional network regulating secondary cell wall biosynthesis. Trends Plant Sci 15, 625-632.

Zhu, J.Y., Sae-Seaw, J., and Wang, Z.Y. (2013). Brassinosteroid signalling. Development (Cambridge, England) 140, 1615-1620.

Zong, W., Tang, N., Yang, J., Peng, L., Ma, S., Xu, Y., Li, G., and Xiong, L. (2016). Feedback regulation of aba signaling and biosynthesis by a bZIP transcription factor targets drought-resistance-related genes. Plant Physiol 171, 2810-2825.

Zuo J., Niu Q.W., and Chua N.H. (2000). An estrogen receptor-based transactivator XVE mediates highly inducible gene expression in transgenic plants. Plant J 24, 265-273.