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REVIEW

The IDD Transcription Factors: Their Functions in Plant Development and Environmental Response

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ABSTRACT

INDETERMINATE-DOMAIN proteins (IDDs) are a plant-specific transcription factor family characterized by a conserved ID domain with four zinc finger motifs. Previous studies have demonstrated that IDDs coordinate a diversity of physiological processes and functions in plant growth and development, including floral transition, plant architecture, seed and root development, and hormone signaling. In this review, we especially summarized the latest knowledge on the functions and working models of IDD members in Arabidopsis, rice, and maize, particularly focusing on their role in the regulatory network of biotic and abiotic environmental responses, such as gravity, temperature, water, and pathogens. Understanding these mechanisms underlying the function of IDD proteins in these processes is important for improving crop yields by manipulating their activity. Overall, the review offers valuable insights into the functions and mechanisms of IDD proteins in plants, providing a foundation for further research and potential applications in agriculture.

KEYWORDS

INDETERMINATE DOMAIN; flowering time; root development; shoot gravitropism; plant immunity; hormonal signaling; environmental responses

1 Introduction

Transcription factors (TFs) have played an important role in plant development and response to various environmental changes. Transcription factors recognize and bind to specific DNA sequences (*cis*-acting elements), thus activating or inhibiting the expression of target genes [1]. Cys2His2 (C2H2) zinc-finger structure transcription factors are one of the largest transcription factor families [2]. The plant-specific INDETERMINATE DOMAIN (IDD) family belongs to the subfamily of C2H2 transcription factors and has been identified by its DNA-binding domain, also named the INDETERMINATE (ID) domain [3]. The ID domain includes C2H2 and C2HC zinc-finger domains and is highly conserved at the N-terminal of proteins [4,5] (Fig. 1). Recently, many functions of *IDD* genes have been reported, especially in *Arabidopsis thaliana*, but also in the *Zea mays* (maize) and *Oryza sativa* (rice) [5–8] (Fig. 2). In this paper, we reviewed the recent advances in the biological functions and mechanism of *IDD* gene, especially the roles of IDD in plant development and various environmental response.

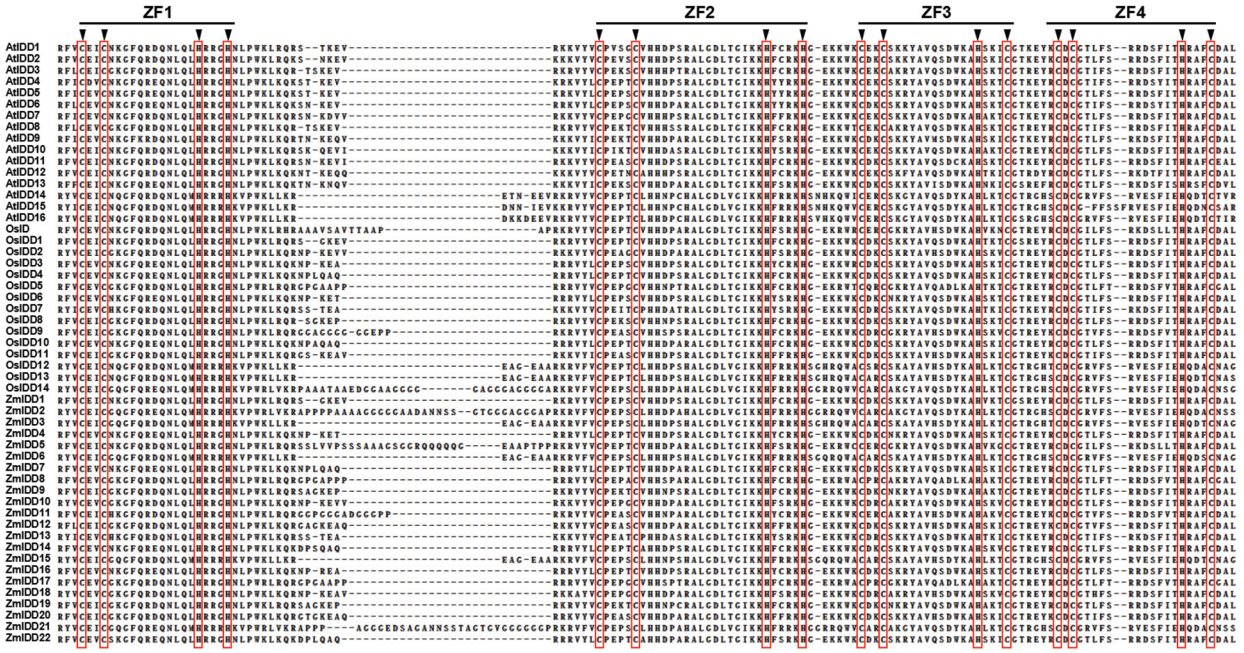

Figure 1: Alignment of *INDETERMINATE DOMAIN* (*IDD*) domains conserved amino acid sequence in different species (adapted from reference [5]), including *Arabidopsis thaliana* (AtIDD), *Oryza sativa* (OsIDD), and *Zea mays* (ZmIDD). ZF1-ZF4 represents the four C2H2-type zinc finger motifs. The arrowheads indicate the conserved cysteine and histidine residues

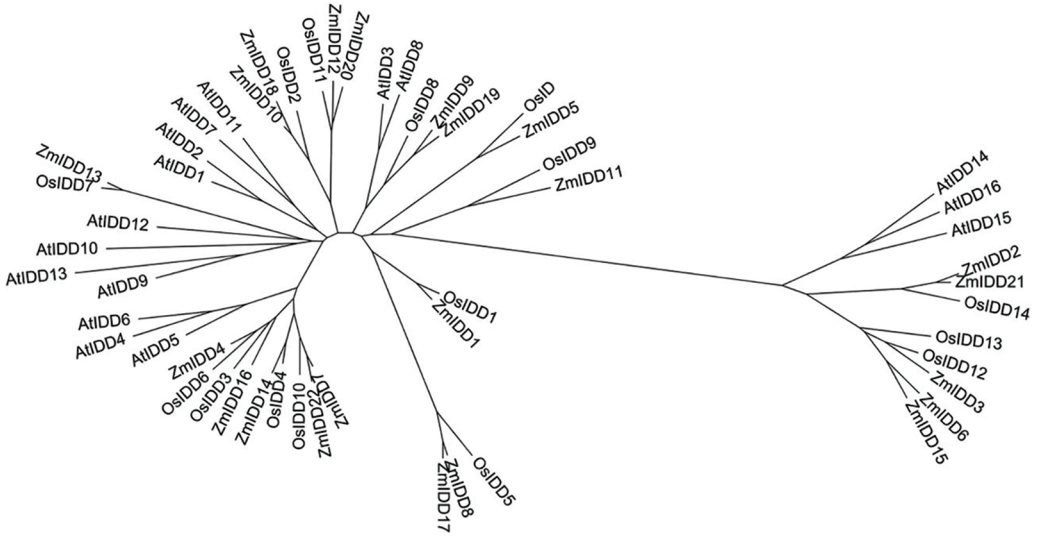

Figure 2: Phylogenetic tree of full-length sequences AtIDD, OsIDD, and ZmIDD proteins. The phylogenetic tree was drawn using the MEGA version 5.1 software

2 Functions in Plant Development

2.1 Control in Flowering Time

The transition from the vegetative stage to the reproductive stage is a key development change in the plant life cycle. The IDD family proteins are highly conserved in angiosperms [4]. Since the first IDD

family gene (*ZmID1*) was isolated from maize and identified as a causal gene for late-flowering [3,9], the functions of this family have been reported on flowering time regulation first. The production of a mobile florigenic (F) signal was proposed to move to the shoot apex, which is controlled by *ZmID1* [10–12]. Further studies showed that *Zea mays CENTRORADIALIS 8* (*ZCN8*) acts as the mobile signal to function downstream of *ZmID1* [13]. It is unclear how *ZmID1* regulates the transcription of the *ZCN8* gene. *ZCN8* is unlikely to be the direct target of ZmID1 because there are no obvious ID1 binding sites in *ZCN8* promoter regions [9]. Thus, *ZmID1* probably regulates the expression of other transcription factors to activate the transcription of *ZCN8* (Fig. 3).

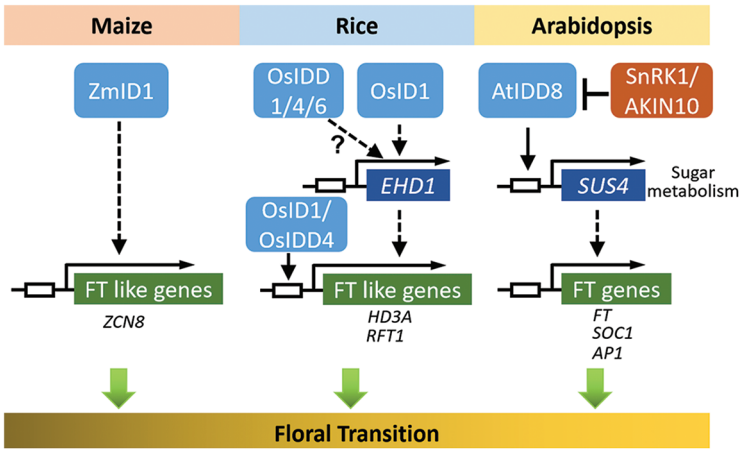

Figure 3: Schematic diagram of IDD members that may have participated in the floral transition of maize, rice, and *Arabidopsis thaliana* (adapted from reference [5]). The white box represents the region of the promoter. OsID1 and OsIDD4 could specially bind to the consensus motif TTTGTC in the promoter regions of *Hd3a* or *RFT1*. AtIDD8 binds directly to the *SUS4* gene promoter containing the conserved CTTTTGTCC motif. The arrows and T-shaped lines represent positive and negative regulation, respectively. Solid arrows indicate direct activation and dashed arrows indicate indirect activation

The IDD transcription factor is also characterized by the regulation of flowering time in rice. Previous studies on rice mutants or natural variants have reported two important ways to participate in the regulation of rice heading date, called the *HD1* (*HEADING DATE 1*)-HD3A (*HEADING DATE 3A*)/*RFT1* (*RICE FLOWERING LOCUS T1*) and *EHD1* (*EARLY HEADING DATE 1*)-*HD3A*/*RFT1* pathways [14]. *INDETERMINATE 1* (*OsID1*)/*EARLY HEADING DATE* (*EHD2*)/*RICE INDETERMINATE1* (*RID1*), a *ZmID1* ortholog, is related to the flowering regulation of rice [15–19]. The OsID1/EHD2/RID1 make a role in the main switch of transition from vegetation to reproduction and may start the activation of florigen genes (including *HD3A* and *RFT1*) by directly binding to their promoters, and then the floral signals are collected to promote floral transition [15–18]. In addition, *id1* results in a non-flowering phenotype, which is restored by the functional gain of *OsIDD1* or *OsIDD6*. Thus, it is likely that the functions of *OsIDD1*, *OsIDD4*, and *OsIDD6* are redundant, and that over-expression of any of these genes could replace *OsID1* to initiate the flowering transition in the absence of *OsID1* [18]. However, *EHD1* is slightly reduced in *idd1* plants, but almost completely repressed in the *id1* mutant, indicating that the *EHD1*-mediated flowering pathway may differ between *id1* and *idd1* mutants. In addition, *OsID1* partly accelerates flowering through negative regulation of rice *OsERF#136* (a repressor of rice flowering), which acts as the repressor of rice flowering and mainly inhibits flowering by the *EHD1*-*HD3A*/*RFT1* pathway [20] (Fig. 3).

Sugar metabolism is likely to be involved in flowering, and IDD proteins are core members of this pathway. Transcriptome and metabolic spectrum of maize *id1* mutant leaves showed that in the pre-flowering stage, transcription of genes encoding polysaccharide metabolizing enzymes increased significantly, and the sucrose output level was low [21]. Sufficient sucrose and starch in the mutant of *id1* revealed that *ZmID1* guided the utilization of carbohydrates in source leaves rather than storage, thus promoting the output of carbohydrates to the shoot apex during flowering [21]. In rice, the overexpression of *OsIDD1*, *OsIDD4/SID1*, and *OsIDD6* rescue the late flowering phenotype of O*sID1*, indicating that the IDDs might have some functional redundancy in sugar metabolism and floral transition [18]. Similarly, IDD members in *Arabidopsis thaliana* also act as transcriptional factors of floral transition by controlling sucrose signal transduction. It has been found that *AtIDD8*/*NUTCRACKER* (*NUC*) can promote the photoperiodic flowering time of plants by binding to the promoter region of downstream *SUCROSE SYNTHASE* (*SUS*) gene directly and up-regulating the gene [22]. Furthermore, SUCROSE NONFERMENTING-1-RELATED PROTEIN KINASE 1 (SnRK1)/AKIN10 interacts with AtIDD8 in the nucleus and phosphorylates AtIDD8 mainly on two serine (Ser) residues. AKIN10-mediated phosphorylation does not influence the DNA-binding properties and subcellular localization of AtIDD8, however, the AtIDD8 activation of transcriptiona was decreased after phosphorylation. In addition, AKIN10 has the function of antagonizing AtIDD8 to control flowering time, which is consistent with the late flowering phenotype of *AKIN10* overexpressed plants and the *idd8-3* mutants. In this signal regulation, AKIN10 signals are integrated into the regulatory network mediated by AtIDD8 directly, which regulates flowering time according to the fluctuation of sugar metabolism, further supporting the regulation of flowering metabolism [23]. To summarize, these findings suggest that *IDD* genes may be involved in the regulation of flowering time through direct or indirect connections with sugar metabolism (Fig. 3).

2.2 Roles in Root Development

An interesting functional analogy is the Arabidopsis IDD proteins in root development. Numerous studies reveal that both epidermal cell and ground tissue characters are formed by IDD proteins. Four IDD proteins, AtIDD3/MAGPIE (MGP), AtIDD8/NUTCRACKER (NUC), AtIDD9/BALDIBIS (BIB), and AtIDD10/JACKDAW (JKD) have overlapping roles in the specification of the cortical cell layer [24–26]. *AtIDD3* and *AtIDD10* regulate root tissue boundaries and asymmetric cell division through mediating SHORT-ROOT (SHR) and SCARECROW (SCR) activity in a transcriptional and protein interaction network [24,27,28]. Moreover, AtIDD10 activates transient expression of the *LUC* reporter gene in protoplasts, and its binding sequence is upstream of the start codon ATG of *SCR* and *AtIDD3*. These results suggest that AtIDD10 acts with *SHR*, *SCR*, and *AtIDD3* to directly regulate the expression of *SCR* and *AtIDD3* [25]. AtIDD10 and its close homolog AtIDD9 modulate SHR movement by enhancing its nuclear retention and cooperating with AtIDD3 and AtIDD8 to activate the formative divisions that pattern the ground tissue into the cortex and endodermis. The normal cell division patterns are operated partly by transcriptional inhibition of *CYCLIND6* (*CYCD6*) [26,29]. Studies showed that AtIDD10 and AtIDD9 restrict *CYCD6* gene expression to the cortex-endois initial/daughter (CEI/CEID) [26]. AtIDD6/BLUEJAY (BLJ) and AtIDD4/IMPERIAL EAGLE (IME), regulate the ground tissue after embryogenesis. Their functions were as the determinants of CEI, which act as effectors of asymmetric cell divisions of the CEID when SHR is activated [30]. *In vivo*, FRET-FLIM results indicate SCR promoted AtIDD10-SHR interaction, and SHR boosted AtIDD10-SCR association, suggesting that SHR, SCR, and AtIDD10 form a ternary complex [31]. Besides SHR and SCR, another transcription factor, SCHIZORIZA (SCZ) was reported to regulate AtIDD10-mediated ground tissue patterning and vasculature formation before emergence at the step of dome-shape primordial [30,32].

Ammonium and nitrate nitrogen are the main sources of nitrogen in the roots of plants, and recent studies have also shown that some IDD members can regulate root growth and development by affecting nitrogen homeostasis. It was reported that *OsIDD10* is involved in regulating ammonium absorption and nitrogen metabolism of roots, which activates the transcription of *Ammonium transporter 1;2* (*AMT1;2*) and *Glutamate dehydrogenase 2* (*GDH2*) by binding to the promoter region of *AMT1;2* and the intron of *GDH2*. Moreover, *OsIDD10* has made significant contributions to the activation of genes participated in N-linked metabolic and cellular responses, for example, genes encoding nitrite reductase, trehalose-6-phosphate (T6P) synthase, and glutamine synthetase 2 [33]. In addition, studies have found that *OsIDD10* can directly activate the transcription of *Calcineurin B-like protein* (*CBL*)*-interacting protein kinase 9* (*CIPK9*) and *CIPK14*, and the expression of *CIPK9* and *CIPK14* was sensitive to exogenous $NH4^+$. At the same time, analysis of the phenotypes of *idd10* mutant and *CIPK9 OX* plants indicated that the overexpressed plant was able to rescue the root growth defects in *idd10* that relied on $NH4^+$.

This suggests that CIPK9 is an $NH4^+$-dependent regulator involved in root growth and seems to act downstream of OsIDD10 [34]. In *Arabidopsis thaliana*, *AtIDD8*-overexpression promoted the primary root growth in both normal and nitrogen-deficient situations. There are AtIDD8-binding sites in the promoter regions of the N-responsive and root-related genes *TGACG SEQUENCE-SPECIFIC BINDING PROTEIN 1* (*TGA1*) and *NITRATE TRANSPORTER 2.4* (*NRT2.4*), and *AtIDD8* can activate and up-regulate their expression under nitrogen deficiency conditions, thereby increasing the number and length of lateral roots [35].

2.3 Seed and Leaf Development

Seed maturation and germination are known to be essential for the production of viable seeds. Heterotopic expression of the Arabidopsis AtIDD1/ENHYDROUS (ENY) gene leads to abnormal seed maturation, and the function of AtIDD2/GAI-ASSOCIATED FACTOR1 (GAF1) in GA homeostasis regulation reveals a role of IDDs in Arabidopsis seed development, such as IDDs have been reported to determining aleurone layers [36,37]. In addition, studies in maize have shown that maize ID transcription factors ZmIDDveg9 (NKD1) and ZmIDD9 (NKD2) are both core regulators of gene expression during endosperm development of maize seeds and can participate in aleurone cell fate regulation and cell differentiation [38–40].

We know that cell proliferation and expansion can lead to leaf growth and formation and that the establishment of leaf polarity is a necessary condition for normal leaf morphogenesis and effective photosynthesis. The Arabidopsis genes *HD-ZIP III* and *KANADI* are typical regulators of leaf abaxial/adaxial patterns, and they play opposite regulatory roles in leaf polarity. Both *AtIDD4* and *AtIDD11*/*WARBLER* promoters have binding sites for HD-ZIP III protein REVOLUTA (REV). In addition, the transcripts of four IDDs (*AtIDD4*, *AtIDD5*, *AtIDD10*, and *AtIDD14*) of the 12 family members measured were downregulated by KAN1, and ChIP-seq results showed that 7 of the Arabidopsis *IDD* gene promoters contained REV binding sites. This suggests that promoter regions of these *IDD* genes are potential targets for REV action [41]. Recently, SHR, IDD, and PIN (PIN-FORMED) family members were reported to play a role in vascular development and ground cell proliferation in rice leaves. Additionally, it was revealed that OsIDD12 and OsIDD13 directly interact with the auxin transporter gene *OsPIN5c* [42].

3 Responses to Diverse Environmental Conditions

The functions of multiple IDD members in plant development have been well-characterized. Increasing shreds of evidence indicate that IDDs also have an impact on a diverse range of responses to biological and abiotic environmental conditions, such as gravity, temperature, water, and pathogens.

3.1 Responses to Abiotic Environmental Factors

Geotropism is a vital factor in plant development, which influences the growth direction of plant organs on the gravity vector [43]. It has been reported that Arabidopsis AtIDD15/SHOOT GRAVITROPISM5 (SGR5) is involved in the gravity perception of the stem. Analysis of the phenotype of the *SGR5* mutant revealed that the deposition rate of starch granules in the mutant was slower than the WT due to the decrease in the total starch accumulation. Moreover, the stem circumnutation movement of *SGR5* was severely weakened, which was manifested by decreased amplitude and periodicity [44,45]. In short, loss of *SGR5* activity affects the accumulation of starch in stem tissues, resulting in reduced sensitivity to gravity and diminished circulation movement in Arabidopsis. Furthermore, our results also indicate that SGR5 belongs to the IDD subfamily classified by *AtIDD14/AtIDD15/AtIDD16* in Arabidopsis, which can co-regulate auxin biosynthesis and transport genes, such as *AtPIN1* and *YUCCA5*. It can also regulate the gravitropic responses and the orientation change of branches and siliques [46]. Similarly, rice OsIDD14/Loose Plant Architecture 1 (LPA1), a homologous gene of Arabidopsis *SGR5*, modulates the sedimentation rate of amyloplasts, tiller, and leaf angles by regulating the adaxial growth of tiller node and lamina joint, thus regulating shoot gravitropism [47]. Taken together, these studies suggest that IDD family transcription factors may coordinate the gravisensing and morphogenesis of aerial organs by acting as intermediates in starch metabolism and hormone signaling.

Several studies have found that the IDD family is also involved in high and low-temperature responses. For example, the role of Arabidopsis *AtIDD14* and *SGR5* in temperature change provides an unexpected gene regulatory mechanism in which the two isoforms produced by alternative splicing play different roles. Interestingly, the AtIDD14α protein gathers under normal temperatures, while the AtIDD14β protein is at low temperatures. Under low temperatures, AtIDD14β can physically interact with AtIDD14α protein, and inhibit their interaction with downstream target genes (for example *Qua-Quine Starch*, *QQS*), thus causing starch degradation to decrease. In short, the self-regulatory circuit of IDD is specifically involved in regulating starch metabolism under cold conditions [48]. There are two splicing variants of the *SGR5* gene in *Arabidopsis thaliana*, a full-size SGR5α and another a truncated SGR5β form that lacks functional ZF motifs [49], and this alternative splicing may be accelerated at high temperatures, leading to high levels of collection of the SGR5β protein. The truncated form of SGR5β may inhibit the function of SGR5α by forming non-functional complex heterodimers. Moreover, SGR5-overexpressing SGR5β plants also showed a reduced response to inflorescence stem geotropism, similar to the *sgr5-1* phenotype in Arabidopsis [49]. In rice, the transcriptional regulator of *CBF1* was isolated using the promoter of *Dehydration-responsive element-binding protein1s* (*DREB1s*)/*C-repeat binding factors* (*CBFs*)/*CBF1*, cold-induced gene, by yeast one-hybrid assay. The results showed that OsIDD3/ROC1 (Regulator of CBF1) can directly bind to *CBF1* promoter. Meantime, *idd3* mutants showed a cold-sensitive phenotype and can inhibit the induction of cold-mediated genes *CBF1* and *CBF3*, showing that *OsIDD3* is a positive factor involved in cold stress response [50]. Recently, our study found that in drought conditions, *idd14-1D*, a gain-of-function mutant, showed reduced water loss rate of leaves and enhanced drought resistance, while a loss-of-function mutant *idd14-1* showed improved water loss rate of leaves and decreased drought tolerance. The expression of *IDD14* also affects the sensitivity to ABA and ABA-mediated stomatal closure. At the same time, we further illustrated that IDD14 can directly interact with ABRE-binding factor 1-4 (ABF1-4) to promote its transcriptional activity, thereby improving drought resistance. Taken together, we suggest that the Arabidopsis IDD14 transcription factor, as a component of the ABA signaling pathway, is involved in positively regulating the drought-stress responses [51]. Overexpression of the *IDD16* gene decreased the stomatal density of the abaxial leaf in Arabidopsis, and ChIP analysis suggested that IDD16 directly combined with the promoter region of the stomatal development gene *SPCH*. Moreover, water use efficiency (WUE) and drought tolerance of Arabidopsis overexpressing IDD16 were significantly increased while leaf transpiration was reduced. In

summary, *AtIDD16* can directly regulate the transcription of the *SPCH* gene as a negative regulator, thereby affecting the initiation of stomatal development and resulting in decreased stomatal density, while *Arabidopsis thaliana* with overexpression of IDD16 shows enhanced drought stress tolerance and WUE [52].

3.2 Responses to Biotic Environmental Factors

The plant immune system is the basis of plant survival, and numerous pieces of evidence support those plants have two immune systems, namely pattern-triggered immunity (PTI) and effector-triggered immunity (ETI) [53]. Research have shown that *AtIDD4* mutations increase resistance to the hemibiotrophic pathogen *Pseudomonas syringae*, and AtIDD4 may be an inhibitor of the underlying immune response and PTI. Comparative transcriptome studies of *idd4* and *IDD4ox* plants, consistent with the whole genome AtIDD4 DNA binding sites studies, identified a target gene responsible for biodefense processes, namely AtIDD4, which interacts with MAP kinase MPK6 and is phosphorylated by the latter at two conserved sites. DNA binding studies of AtIDD4 and AtIDD4 phosphate site mutants treated with FLAGELLIN22 (flg22) show that AtIDD4 has enhanced binding affinity with ID1-containing motif promoters and transcriptional regulation. Additionally, the AtIDD4 chimeric inhibitor (*idd4SRDX*, SRDX, the chimeric repressor gene-silencing technology) expressed in WT increased basal resistance after hemibiotrophic infection, especially after infection with *Botrytis cinerea*. Moreover, high levels of the immune hormones SA and jasmonic acid (JA) in *idd4SRDX* plants suggest that AtIDD4 and other members may form the center of plant immunity, which mediates the defense response and regulation of hormonal pathways [54,55].

As far as we know, the rice sheath blight disease (ShB) seriously affected rice production. It was found that ABI3/VP1-like 1 (RAVL1) participated in the negative regulation of the anti-ShB defense mechanism in rice, while OsIDD3 was positively regulated by RAVL1, and RAVL1 directly bound to the *OsIDD3* promoter region. There was no significant difference in the response of *OsIDD3* mutants to ShB, while *OsIDD3* overexpression plants were more sensitive to ShB [56]. It was found that *OsIDD14*/*LPA1* was almost not expressed in leaves, but the infection of *Rhizoctonia solani* could significantly induce the expression of *OsIDD14* in leaves, and the susceptibility of *lpa1* to *R. solani* was higher than that of wild type and related plants. *OsIDD14* overexpression significantly improved rice resistance to sheath blight disease (ShB) via activating *PIN-FORMED 1a* (*PIN1a*). In addition, the expression of *OsIDD3*, *OsIDD5*, *OsIDD10*, and *OsIDD13* could be changed by infection with *R. solani*, and *OsIDD14* could interact with *OsIDD3* and *OsIDD13*. *OsIDD13 RNAi* plants were susceptible to ShB, while plants that overexpress *OsIDD13* were less susceptible to ShB. *OsIDD3* and *OsIDD13* regulate the transcription of *PIN1a* negatively and positively via binding to the *PIN1a* promoter, respectively. Moreover, OsIDD3, OsIDD13, and OsIDD14 form transcription factor complexes that regulate the expression of the *PIN1a* gene [57,58]. Taken together, these analyses demonstrated that OsIDD3, OsIDD13, and OsIDD14/LPA1 constitute transcriptional regulatory complexes that may influence rice defense against ShB by regulating *PIN1a* and *PIN1b*.

Studies have shown that the absorption of $NH4^+$ ions can promote the resistance of rice to saline-alkaline stress and ShB. *OsIDD10*, which encodes a core TF for $NH4^+$ signaling, causes roots to be sensitive to $NH4^+$ under light conditions but not under dark conditions. OsIDD10 interacted with brassinazole-resistant 1 (BZR1) to activate AMT1;2. When the rice was inoculated with *R. solani*, phytochrome B (PhyB) and OsIDD10 negatively regulated the rice resistance to ShB, while AMT1 and BZR1 were positively regulated. In addition, PhyB has a negative function, and OsIDD10 and AMT1 have a positive regulatory effect on the rice resistance to saline-alkaline stress. Taken together, these findings suggested that PhyB-OsIDD10-AMT1;2 signaling pathway operates the saline-alkaline reaction, while PhyB-BZR1-AMT1;2 pathway controls ShB resistance [59].

4 Functions in Hormone Signal Transduction Pathway

DELLA proteins, such as GIBBERELLIC ACID INSENSITIVE (GAI), REPRESSOR OF GA1-3 1 (RGA1), are transcription factors of the GRAS family in *Arabidopsis thaliana*, which regulate gene expression in response to GA signals. Increasing evidence indicates that IDD family members can act as DNA-binding transcription factors directly or as cofactors of DELLAs indirectly. For example, RGA1 interacts and activates transcription of GA-positive regulator SCARECROW-LIKE3 (SCL3) by interacting with any of the five proteins AtIDD3, AtIDD4, AtIDD5, AtIDD9, and AtIDD10 [60]. More research has revealed that DELLAs and SCL3 regulators play a role as co-regulators, and IDD transcription factors bound to DNA regulate downstream gene expression by balancing SCL3 and DELLA protein levels. Therefore, IDDs family TFs are participated in GA feedback regulation as DNA-binding scaffolds [30,60,61] (Fig. 4a). Additionally, AtIDD2/GAF1 (GAI-ASSOCIATED FACTOR1) and AtIDD1/ENY interact with GAI to regulate the *GA20ox2* gene [37,61–64]. AtIDD2 can also interact with the transcriptional co-suppressor TOPLESS (TPL), for example without the DELLA proteins, AtIDD2-TPL forms complexes that inhibit the transcription of target genes. Recent studies indicated that the GRAS domain of DELLA protein has activation activity, while the GRAS domain of SCL3 has transcriptional repression activity. It was also found that SCL3 represses the activation of AtIDD2-DELLA complex by inhibiting activity rather than by competitively inhibiting AtIDD2-DELLA interaction. In addition, AtIDD2 was found to enhance the repression activity of SCL3 in a manner independent of TPL. In short, SCL3 can form ternary complexes with AtIDD2 and DELLA proteins [65]. Above all, these results provide an important reference for the interpretation of the IDD-DELLA-regulated GA signaling pathway.

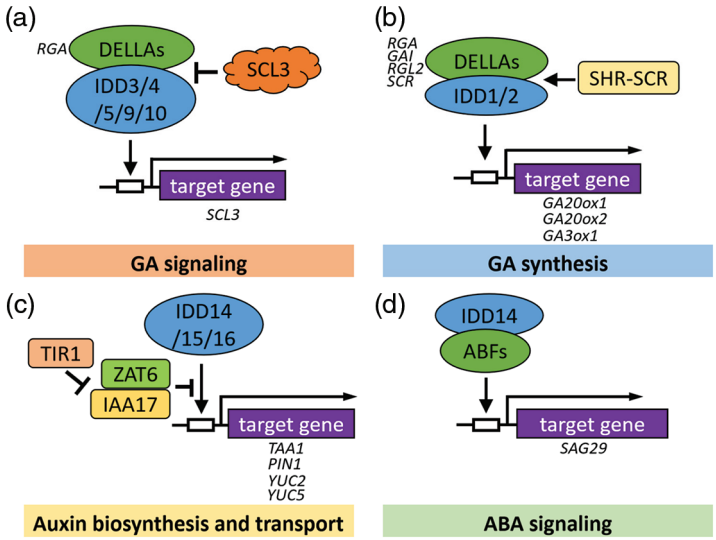

Figure 4: Models of IDDs that might be involved in the hormone signal transduction pathway in Arabidopsis. (a) IDDs participate in the GA signaling pathway. IDD3 protein binds to DNA sequences containing AGACAA as a core motif. (b) IDDs play a role in the GA synthesis process. IDD1 and IDD2/GAF1 proteins bind to DNA sequences containing TTTTGTC or TTTTGT. (c) IDDs coordinate auxin biosynthesis and transport. IDD15 protein binds to DNA sequences containing the TACAAT motif in the promoter. IDD16 could bind to a specific 11 bp DNA consensus motif, TTTGTCG/CT/CT/aT/aT. (d) IDDs mediate the ABA signaling pathway. The white box represents the region of the promoter. The arrows and T-shaped lines represent positive and negative regulation, respectively. Solid arrows indicate direct activation

In addition, it also indicated that AtIDD1 interacted directly with DELLA proteins, which confirmed that AtIDD1 was a component in the hormone signaling pathway during seed maturation [36]. It has recently been summarized that, not only RGA, SHR-SCR also can act as a co-activator of AtIDD2, promoting the expression of *SCR*, *SCL3*, and *AtGA3ox1*, and that these complexes may regulate and coordinate the expression of genes related to root formation [65,66]. Interestingly, in Arabidopsis, AtIDD2 also participates in the GA-dependent flowering pathway by modulating the expression of *FT* and S*UPPRESSOR OF OVEREXPRESSION OF CONSTANS1* (*SOC1*). Under the action of GAs, AtIDD2 forms a transcription suppressor complex and activates the transcription of *FT* and *SOC1* by inhibiting the expression of four flowering suppressor genes, *EARLY FLOWERING3* (*ELF3*), *SHORT VEGETATIVE PHASE* (*SVP*), *TEMPRANILLO1* (*TEM1*), and *TEM2* [64]. Collectively, AtIDD1 and AtIDD2 are involved in seed and root development, and flowering in a GA-dependent manner (Figs. 4a, 4b).

The morphogenesis of plant lateral organs and the establishment of plant structure mainly depend on the spatial accumulation of auxin in the organs, which is determined by the local biosynthesis and polar transportation of auxin. Our previous study showed that the AtIDD14, AtIDD15, and AtIDD16 of the Arabidopsis IDD transcription factor family can activate the gene expression of downstream *TRYPTOPHAN AMINOTRANSFERASE of ARABIDOPSIS1* (*TAA1*), *PINFORMED1* (*PIN1*), and *YUCCA5* (*YUC5*) (YUC5) via directly binds to their promoter regions, thereby promoting the auxin biosynthesis and transportation [46]. Additionally, an investigation showed that the zinc finger of *Arabidopsis thaliana 6* (*ZAT6*) represses the transcription of *IDD15* on the *YUC2* promoter, while *ZAT6* repressed the interaction of *TRANSPORT INHIBITOR RESPONSE 1* (*TIR1*) and *INDOLE-3-ACETIC ACID 17* (*IAA17*) through competitively binding to IAA17. Currently, AtIDD15 and IAA17 interacting with ZAT6 have been found *in vivo*, providing a new perspective to elucidate the ZAT6-mediated auxin signaling pathway [67] (Fig. 4c).

In rice, OsIDD3 expression is widely in different tissues and stages and is transcribed by exogenous auxin. Furthermore, *OsIDD3 OX* is sensitive to polar transporter inhibitor N-1-naphthylphalamic acid (NPA) and auxin. OsIDD3 directly inhibits *PIN1b* expression through binding to the promoter. After inoculation with *R. solani*, *PIN1b RNAi* are more susceptible to ShB infection than WT plants [57,58]. In conclusion, these analyses indicate that OsIDD3 influences resistance to ShB in rice by regulating the auxin transporter *PIN* genes. Additionally, compared with WT, the transcription of brassinosteroid-related genes (D2, D11, and BRI1) decreased in *OsIDD3* repressors, but increased in *OsIDD3* overexpressors. In BRI1 mutant *d61-1*, *OsIDD3* overexpression resulted in decreased OsIDD3 activity. Compared with *OsIDD3* overexpression plants and WT plants, OsIDD3 was less sensitive to ShB, suggesting that OsIDD3 negatively regulates the defense mechanism of rice against ShB via activating the BR pathway [56].

Recently, we demonstrated that Arabidopsis IDD14 interacts with ABF1, ABF2, ABF3, and ABF4 directly, and activates their transcriptional activities, resulting in enhanced drought resistance. We compared the expression levels of three ABA signaling marker genes, *SAG29*, *RAB18*, and *AIL1*, in WT and *IDD14* mutants treated or not with ABA. We found that transcription levels of these ABA-response marker genes were further increased in gain-of-function mutant *idd14-1D* and suppressed in loss-of-function mutant *idd14-1*. These findings indicate that the Arabidopsis IDD14 transcription factor, as a component of the ABA signaling pathway, is related to the ABA pathway and participates in the positive regulation of drought-stress responses [51] (Fig. 4d). Moreover, researchers took advantage of the SRDX to broaden our understanding on the roles of Arabidopsis *AtIDD4* and *IDD* members in plant immunity. Results showed that the growth of *idd4SRDX* lines was impaired and displayed a strong autoimmune phenotype. Through hormone analyses, the results showed that SA and JA accumulate in plants, indicating that IDDs may play role in regulating the metabolism of these hormones [54] (Tables 1–3).

Table 1: Arabidopsis *IDD* genes and their functions in plant development and various environmental responses (adapted from reference [5])

Gene	Phenotype	Function	References
At5g66730 AtIDD1/ ENHYDROUS/ STARLING	*AtIDD1*-overexpression plants showed enhanced starch retention, endosperm-specific fatty acids, and defective mucilage extrusion of mature seeds.	Seed development DELLA interacting protein	[36,37]
At3g50700 AtIDD2/ CARRION CROW/GAF1	*idd2*/*idd1* mutant exhibits reduced GA responsiveness, and overexpression of *AtIDD2* enhances GA responsiveness.	Seed development DELLA interacting protein	[37,62,63]
At1g03840 AtIDD3/ MAGPIE	*MGP RNAi* (*mgp-i*) plants show no phenotype on their own, combination with *jkd-4* homozygotes largely complements the *jkd-4* ground tissue phenotype.	Root development GA signaling DELLA interacting protein	[24–26,30,60]
At2g02080 AtIDD4/ IMPERIAL EAGLE	Overexpression of *AtIDD4* causes downward curled leaves. AtIDD4 coordinates immune responses with plant growth by the regulation of salicylic acid and jasmonic acid homeostasis.	Root development DELLA interacting protein Leaf polarity Plant immunity	[30,41,54,55]
At2g02070 AtIDD5/ RAVEN	*idd5* mutants have deformed chloroplasts and starch granules.	DELLA interacting protein Starch metabolism Leaf polarity	[41,68]
At1g14580 AtIDD6/ BLUEJAY	In *jkd scr* mutants and *blj jkd scr* mutants, expression of ground tissue marker genes decreased, and some *blj jkd scr* mutants roots lacked the entire ground tissue.	Root development	[30,32]
At5g44160 AtIDD8/ NUTCRACKER	*idd8* mutants show delayed flowering phenotype under LD condition. AtIDD8 is an SHR target. Overexpression of *NUC* increases the resistance to N deficiency.	Flowering transition	[22,23,26,30,31,35]
At3g45260 AtIDD9/ BALDIBIS	*bib-i* single mutants, localization of SHR was in nuclear and cytoplasmic in vascular tissue, while it was in the nuclei in the endodermis. Spontaneous cracking of inflorescence stems in transgenic plants expressing a chimeric IDD9 repressor.	Root development Stem integrity	[26,30,69]

(Continued)

Table 1 (continued)

Gene	Phenotype	Function	References
At5g03150 AtIDD10/ JACKDAW	*jkd* mutants result in ectopic divisions and misexpression of SCR in the ground tissue.	Root development	[24–26,28, 30–32,41]
	In *jkd scr* mutants and *blj jkd scr* mutants, expression of ground tissue marker genes decreased, and some *blj jkd scr* mutants roots lacked the entire ground tissue.	DELLA interacting protein Leaf polarity	
At3g13810 AtIDD11/ WARBLER	Unknown.	Leaf polarity	[41]
At1g68130 AtIDD14	*idd14-1* mutant indicates diverse leaf phenotypes. *35S:IDD14α* show retarded growth and downward leaf curling, while *35S:IDD14β* and *idd14-1* mutants were slightly early flowering. IDD14 interacts with ABF to participate in drought stress response through the ABA pathway.	Auxin biosynthesis and transport, starch metabolism under cold stress. Drought stress, leaf polarity	[41,46,48,51]
At2g01940 AtIDD15/SGR5	*idd15-5* enhances angles between inflorescence stem or branches and siliques.	Auxin biosynthesis and transport, starch metabolism under hot stress	[44–46,49,67]
	Loss of *SGR5* regulatory activity affects starch accumulation in shoot tissues and causes decreased sensitivity to gravity and diminished circumnutation movements. Hot stress reduces the gravitropism of inflorescence stems by inducing alternative splicing of SGR5. IDD15 and IAA17 interacted with ZAT6 *in vivo*.	Auxin signaling	
At1g25250 AtIDD16/ FALCON	*IDD16-RNAi* transgenic plants and *idd15-5* mutants have the same phenotype.	Auxin biosynthesis and transport	[46,52]
	The flower organs of the *idd14-1* mutant and IDD16-RNAi plants were enlarged and sterile. IDD16 negatively regulates stomatal initiation via trans-repression of *SPCH*.	Stomatal development and drought stress	

Table 2: Rice (*Oryza sativa*) *IDD* genes and their functions in plant development and various environmental responses (adapted from reference [5])

Gene	Phenotype	Function	References
LOC_Os10g28330 (OsID)/RID1	*id1* results in the never-flowering phenotype, while the gain of function of *OsIDD1*, *OsIDD4*, or *OsIDD6* restores the *rid1* phenotype.	Flowering transition	[15–17,19,20]
	Activation of *EHD1* by *OsID1* is required for the promotion of flowering.		
LOC_Os01g09850 (OsIDD2)	Overexpression of *OsIDD2* showed serious dwarfing with height half of wild-type plants, while *OsIDD 2-RNAi* plants and *idd2* mutants rescued the phenotype. OsIDD2 interacts with SLR1 and may increase the expression of *miR396* in controlling cell proliferation.	Secondary cell wall structure, stem elongation	[70,71]
LOC_Os09g38340 (OsIDD3)/ROC1	*roc1* mutant shows hypersensitivity to chilling stress.	Cold response Plant immunity	[50,56–58]
	Regulate rice defense against sheath blight disease.	BR signaling	
	OsIDD3 binds to the *PIN1a* promoter and negatively regulates *PIN1a* expression.	Auxin transporter	
	OsIDD3 and OsIDD13 interact with LPA1.		
LOC_Os02g45054 (OsIDD4)/SID1	Unknown.	Flowering transition	[18]
(OsIDD6)	Unknown.	Flowering transition	[18]
LOC_Os04g47860 (OsIDD10)	*idd10* mutant roots indicate hypersensitive to exogenous ammonium.	Ammonium uptake and nitrogen metabolism. Plant immunity	[33,34,57,59]
	OsIDD10 binds to CIPK9 directly and its mutation causes sensitivity to ammonium.	Saline–alkaline responses	
LOC_Os08g36390 (OsIDD12)	*Osidd12-3 Osidd13-3* and *Osidd12-4 Osidd13-4* double mutant plants were short, with wide leaves.	Leaf vein formation	[42]
	OsIDD12 and OsIDD13 bound to a conserved motif in intron 3 of *PIN5C*.		
XP_015610838	OsIDD13 bound to the *PIN1a* promoter, positively regulates *PIN1a* expression.	Leaf vein formation	[42,57,59]
(OsIDD13)	OsIDD3 and OsIDD13 interact with LPA1.	Plant immunity Saline–alkaline responses	
LOC_Os03g13400 (OsIDD14)/LPA1	*lpa1* mutant leads to loose plant architecture, and reduces shoot gravitropism.	Shoot gravitropism, plant architecture	[47,57]
		Plant immunity	
		Auxin transporter	

Table 3: Maize (*Zea mays) IDD* genes and their functions in plant development and various environmental responses (adapted from reference [5])

Gene	Phenotype	Function	References
Zm2g011357 (ZmID1)	*id1* mutant did not experienced a healthy transition to flowering and remained in a prolonged vegetative growth.	Flowering transition	[3,9–12]
Zm2g129261	*nkd1* and *nkd2* mutants play a vital role in cell patterning, differentiation, and seed maturation.	Endosperm development	[38–40]
(ZmIDDveg9)/ NKD1 Zm5g884137 (ZmIDD9)/NKD2	In the *Zmnkd1-Ds; Zmnkd2-Ds* mutants, there was no change in vein density and the ratio of rank-1 to rank-2 intermediate veins compared with the wild type.	Leaf development	

5 Conclusions

In plants, transcription factors appear to be susceptible to being influenced as a result of environmental factors and events [1]. IDD proteins are TFs that play a vital role in modulating various developmental processes in plants. These proteins are identified by the presence of a conserved DNA-binding domain known as the IDD domain [3,5]. The majority of these transcription factors have been studied in Arabidopsis, including seed and root development (Table 1) [24–30,36,37,62,63]. However, some functions of IDDs have been reported in other plants, such as rice and maize (Tables 2, 3). They are involved in root development, flowering, sugar homeostasis, starch metabolism, drought/hot/cold-stress signaling, plant immunity, GA signaling and biosynthesis, plant architecture, shoot gravitropism, auxin biosynthesis and transport, and ammonium uptake (Tables 1–3, Figs. 3, 4). In fact, IDDs are reported in almost all aspects of plant development and growth. Studies have indicated that IDD proteins are participated in the development of the integument, which is the outermost layer of cells that protect the plant from external stresses. Mutations in IDD genes can lead to abnormal development of the integument, resulting in reduced seed production and quality [36–39]. In particular, IDD proteins also play a critical role in abiotic stress tolerance in plants. They regulate the expression of stress-responsive genes and help plants adapt to adverse environmental factors such as drought, salinity, and extreme temperatures [49–52,59]. Recent studies have identified several molecular mechanisms that regulate the activity of IDD proteins, including post-translational modifications, protein-protein interactions, and epigenetic regulation [7,39,66,72]. Understanding these mechanisms is essential for developing strategies to manipulate IDD protein function and improve crop yields. In conclusion, IDD proteins have a crucial impact on plant development and stress responses, making them potential targets for crop improvement. Further research is needed to fully elucidate the functions and mechanisms of IDD proteins in plants and develop strategies to enhance their activity for agricultural applications.

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