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Review of Research Advances in CDF Transcription Factor

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Abstract: *CDFs are a class of plant-specific transcription factors. The N-terminal region of CDF proteins contains a C2-C2 zinc finger domain composed of a conserved 51-residue structure. Three conserved sequences at their C-terminal end contribute to functional diversity. Studies have demonstrated that CDF genes exhibit circadian rhythm regulation, with expression modulated by photoperiod, and play critical roles in multiple plant growth and developmental processes as well as stress response mechanisms. This review summarizes the structural characteristics of CDF transcription factors and their functions in flowering, growth development, carbon-nitrogen metabolism, and abiotic stress responses.*

Keywords: *CDF transcription factor; Flowering; Growth and development; abiotic stress*

1. Structure of *CDF* Transcription Factors

The *CDF* (*C2-C2* zinc finger DNA binding with one finger) gene family is a plant-specific *DOF* class of transcription factors. The N-terminal of its protein contains a *C2-C2* zinc finger structure composed of 51 conserved residues, which can specifically bind to the AAAG/CTTT sequence in the promoter of target genes[1]. Any mutation in this sequence will lead to the loss of binding ability. This single zinc finger domain contains four absolutely conserved *Cys* residues that covalently bind to Zn^{2+}, which is crucial for maintaining protein activity. Treatment with divalent ion chelators or substitution of *Cys* residues will cause it to become inactive. The C-terminal of the *CDF* transcription factor has three conserved sequences composed of 21, 22, and 33 amino acids respectively, which are the key regions for interaction with the C-terminal *KELCH* repeat domain of F-BOX proteins *FKF1* and *LKP2*. This feature exists in the homologous proteins of various plants such as Jatropha curcas, Brachypodium distachyon, and potato, but its specific biological function still needs further study[3].

2. Biological Functions of CDF Transcription Factors

The N-terminus of *CDF* proteins contains a *C2-C2* zinc finger, which consists of a conserved 51-residue domain and represents a common characteristic of the *DOF* family[2]. In addition, *CDF* proteins possess three conserved sequences at their C-terminus, which contribute to their functional diversity. *CDF* proteins are capable not only of protein–protein interactions but also of binding to most plant-specific promoters to regulate their expression. Numerous studies have demonstrated that *CDF* transcription factors participate in a variety of biological processes during plant growth and development, and play crucial roles in photoperiod-responsive flowering regulation, growth and development, carbon and nitrogen metabolism, as well as tolerance to abiotic stresses[4].

2.1. The effect of CDF transcription factors on flowering

Flowering, a key transition from vegetative to reproductive growth in plants, is regulated by environmental and genetic factors, and *CDF* transcription factors mediate this process by responding to internal and external stimuli.In Arabidopsis thaliana, *AtCDFs* repress flowering: *AtCDF1* binds to CO and FT promoters to inhibit their transcription, while the *GI-FKF1* complex relieves this inhibition under long-day conditions to promote flowering[5].*CD*F regulation is species-specific: tomato S*lCDF1*-

5 expression is photoperiod-dependent, and *SlCDF3* overexpression delays Arabidopsis long-day flowering; rice *OsDof12* (*AtCD*F homolog) is circadian-regulated, with its overexpression promoting long-day early flowering, whereas *OsDof4* overexpression's effect depends on day length.Jatropha curcas Jc*Dof1* and *JcDof3* show circadian oscillation and light quality responsiveness, with *JcDof3* interacting with F-box proteins[6]; poplar *PttCDFs* are functionally conserved with *AtCDFs*, and pear *PbDof9.2* heterologous expression inhibits *FT* activity to delay Arabidopsis flowering.Rapeseed *BnCDF1* overexpression delays Arabidopsis flowering, while *PheDOF12-1* overexpression promotes early flowering; alfalfa *MtCDFd1-1* delays vernalization-dependent flowering by inhibiting *MtFTa1* via a CO-independent pathway distinct from Arabidopsis. The molecular mechanism of *CDF*-regulated flowering remains unclear in most plants[7].

2.2. The effects of CDF transcription factors on growth and development

As endogenous circadian rhythm genes, *CDF* (cycling dof factor) transcription factors play important regulatory roles in plant growth and development[8]. In Arabidopsis thaliana, *AtCDF4* promotes root columella stem cell differentiation; *AtCDF1* and *AtCDF5* facilitate hypocotyl elongation under short-day conditions; *AtCDF2* forms a complex with PIF4 to regulate *YUCCA8* expression and promote hypocotyl elongation, while *AtCDF4* overexpression impairs cotyledon vein development[9]. In Oryza sativa, overexpression of *OsDof12,* a homologous gene of *AtCDF*, causes abnormal plant height, leaf and panicle traits, participating in plant architecture formation[10]. In Solanum tuberosum, *StCDF1* interacts with day-length regulating proteins to control earliness and tuber formation; *GI-FKF1* degrades *StCDF1*, and its functional loss delays tuber signal transduction[11]. In summary, *CDF* transcription factors are crucial for plant growth and development.

2.3. The Effects of CDF Transcription Factors on Carbon and Nitrogen Metabolism

Carbon and nitrogen metabolism are core processes determining plant biomass and quality[12]; excessive fertilization in current agriculture causes environmental issues, making breeding high-nitrogen-use-efficiency crops imperative[13].

Besides regulating flowering and stress resistance, *CDF* transcription factors are involved in carbon and nitrogen metabolism: *SlCDF3* overexpression in Arabidopsis enhances nitrogen use efficiency and sucrose/amino acid accumulation via nitrate nitrogen response[14]; *SlCDF4* overexpression in tomato improves fruit yield, quality and carbon-nitrogen compound content by regulating invertase activity and source-sink relationship; *CsCDF1* in Camellia sinensis shows circadian expression and is up-regulated in different tissues after nitrogen resupply post nitrogen starvation[15].

In conclusion, *CDF* transcription factors play a pivotal role in carbon and nitrogen metabolism, which synergistically regulate plant growth, development, crop yield and quality.

2.4. Induction of Stress-Responsive Gene Expression and Endogenous Hormone Balance by CDF Transcription Factors

The mutated *cdf3-1* gene sensitizes Arabidopsis thaliana to drought and low-temperature stresses, while its overexpression unexpectedly enhances plant resistance to osmotic stress. *AtCDF3* regulates the expression of abiotic stress-responsive genes (e.g., *CBFs*[16], *DREB2A*[17], *ZAT12*[18]) under extreme temperatures, drought, and osmotic stress. Similarly, Brassica napus *BnCDF1* (a homolog of Arabidopsis *CDF1*) positively regulates cold resistance by modulating genes like *CBF1*, *CBF2, COR15A*, and *RD29A*. *AtCDF1-5*[19] expression in Arabidopsis changes under various abiotic stresses, and tomato *SlCDF1-5* act as transcriptional regulators in salinity/drought responses and flowering control, with distinct root/shoot expression patterns under different stresses[20]. Heterologous overexpression of tomato *SlCDF1* and *SlCDF3* in Arabidopsis enhances salt and drought tolerance by inducing stress-responsive genes (e.g., *COR15*[21], *RD29A*[22], *ERD10*[23]), and *SlCDF3* overexpression in tomatoes upregulates *PIF1* and *MYB44* to improve salt tolerance[24]. In summary, *CDF* proteins directly or indirectly regulate abiotic stress-responsive gene expression upon receiving external stress signals.

CDF transcription factors also accumulate stress hormones (information transmission mediators) to respond to adverse stresses[25]. Key hormones regulating plant abiotic stress resistance include ABA, ET, JA, SA, and GA. *AtCDF3* overexpression in tomatoes increases active GA content; under salt stress, IAA and GA decrease while ABA increases, ensuring yield and quality[26]. *SlCDF4* in tomatoes positively regulates the gibberellin signaling pathway by modulating gibberellin biosynthesis, and its overexpression increases fruit/peel gibberellin content[27]. *CDF* proteins enhance stress tolerance mainly by binding to cis-acting elements in upstream promoters of key hormone synthesis genes, regulating endogenous hormone balance and improving plant adaptability[28].

2.5. Accumulation of Osmotic Adjustment Substances and Maintenance of Carbon/Nitrogen Balance by CDF Transcription Factors

Many abiotic stresses can lead to a decrease in plant photosynthetic rate, resulting in carbon assimilation disorders and water deficit[29]. In crops, *CDF* proteins enhance plant stress resistance by regulating the synthesis of a series of osmotic adjustment substances such as proline and soluble sugars[30]. Overexpression of Arabidopsis thaliana *AtCDF3* gene in tomato increases the contents of active ABA and GA1 in plants, ensuring the yield and quality of tomato under salt stress[31-35], while accumulating sugars and amino acids related to improved stress tolerance and nitrogen assimilation, such as sucrose, glucose, L-leucine, L-asparagine, L-glutamine, *GABA*, and L-proline, which is consistent with the previously reported function of maize *ZmDOF1* in resisting abiotic stresses[36]. The proline content of *BnCDF1* under cold stress is 1.5 times that of wild-type Arabidopsis thaliana[37]. *CDF* proteins regulate plant carbon/nitrogen balance by inducing the anabolism of related enzymes in glycolysis and the tricarboxylic acid cycle, synthesize a series of osmotic adjustment substances such as proline and soluble sugars, and enhance plant stress resistance.

3. Conclusions and Future Perspectives

CDFs are a class of plant-specific transcription factor genes that play important roles in plant flowering. Specifically, they play a key role in the floral transition by inhibiting the expression of flowering activator genes such as CO and FT. During growth and development, plants often suffer from abiotic stresses, among which drought, high salt, and high temperature are the main ones, which can seriously affect plant growth, geographical distribution, and even crop yield and quality. Studies have found that the content of *CDF* proteins increases rapidly under cold damage, high temperature, and salt-alkali stresses. They enhance plant stress resistance by inducing the expression of abiotic stress-responsive genes, synthesizing endogenous hormones that respond to stresses, establishing a new balance of sugar and nitrogen metabolism, and accumulating osmotic adjustment substances such as proline. *CDF* proteins play important roles in plant transcriptional regulation, which is of great significance for understanding plant growth and development and solving problems in production practice. According to the characteristics of *CDF* proteins responding to photoperiod signals, the controllability of photoperiod in protected cultivation can be used to precisely regulate the flowering and maturity time of protected vegetables, which can effectively avoid extreme weather and ensure their yield and quality. However, at present, research on the *CDF* family is mainly focused on model plants and annual plants, such as Arabidopsis thaliana, Oryza sativa, Solanum lycopersicum, Glycine max, and Zea mays. It is believed that with the development of genomics and bioinformatics, the mechanisms by which *CDF* proteins participate in the growth and development of various plants and exert their roles in abiotic stresses will become clear.

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