

The INDITTO2 Transposon Regulates Gene Expression to Enable Rice Adaptation to Abiotic Stress

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ABSTRACT

Plants need to adapt to the constantly changing environment, including reacting to frequent biotic and abiotic stresses. It is necessary to understand the mechanisms by which these adaptations to stress are regulated, which can greatly increase the survival rate and biomass of plants in stress conditions. Transposons have become the subject of intensive research because they are known to be involved in the adaptation to various unfavorable environments. In this short commentary, we focus on the INDITTO2 transposon, which is involved in the regulation of drought stress in plants.

INTRODUCTION

Transposons are DNA fragments scattered throughout the genome known from different organisms. The DNA fragments can be replicated and moved autonomously to other places in the genome through the action of specific transposases. Transposons have recently become an intense area of study, because they are known to be involved in a wide range of activities, including shifts in the activity of gene promoters^[1,2], plant responses to drought stress^[3], genome diversity^[4], plant morphogenesis^[5-8] as well as encoding transposases^[9,10].

Transposons can be divided into two main categories namely retrotransposons and DNA transposons. Depending on whether they encode proteins required by transposons, they can be further divided into autonomous transposons and non-autonomous transposons^[11]. In 1951, the Ac-DS (Activator-Dissociation) transposon system in maize was discovered, and it is the first time that the concept of transposons appeared in the biological literature^[12]. The AC-DS is a non-autonomous DNA transposon^[12]. Ac can transpose autonomously, and is an autonomous transposable element, however, Ds can transpose only by relying on AC. Subsequently, similar transposable elements have been found in the genomes of various other plants, including the mPing DNA transposon in rice^[13], the CCICR reverse transposon in cotton, and the Tnt1 reverse transposon in tobacco^[14].

ABOUT THE STUDY

Miniature Inverted-repeat Transposable Elements (MITEs) are a group of non-autonomous transposable elements found in a number of organisms, including plants. They are found commonly throughout the rice genome with high copy numbers. The position at which transposons are inserted in the genome can affect the regulation of expression of certain genes. In *Arabidopsis thaliana*, the promoter of arginine decarboxylase ADC1 contains a MITE transposon that can bind to many transcription factors. Due to the presence of this transposon, the expression pattern is different from that of its homologous gene ADC2^[15]. In the floral organs of rice, the expression of catalase-related genes is closely related to the Tourist C element at the 5' end of transposon^[16]. In wild barley, the MITE transposon inserted into the promoter of Hsdr4 confers a degree of tolerance to dehydration stress on the plant^[17]. Transposons inserted into introns or untranslated regions of genes are sometimes able to influence the transcription or post-transcriptional processing and translation of genes, and may also influence the tissue specificity and developmental stage of gene expression. The Hbr element inserted into the untranslated region of the maize resistance-related gene hm, was able to

affect mRNA stability, thereby inactivating the gene ^[18]. Furthermore, a transposon-like element inserted into the 3' untranslated region of wheat MATE1B enhanced the expression of the MATE1B gene in the root tip, increased the secretion of citric acid, and ultimately improved wheat tolerance to aluminum ^[19].

MITEs transposon can be divided into different families based on the structural differences between Terminal Inverted Repeats (TIR) and Targetsite Duplication (TSD), and which in rice include the Tourist (TSD: TAA/TTA) and Stowaway (TSD: TA) families. The Tourist transposable elements, including a non-autonomous DNA transposon named INDITTO, have also been found in the genomes of rice, barley, sorghum and maize ^[20-22]. A Tourist transposon inserted into the untranslated 3' terminal region of wheat HSP16.9-3A promoted the transcription of the gene and thus improved the heat resistance of wheat ^[23]. In maize and teosinte, Tourist elements bind to the proximal promoter site of auxin-binding protein 1, and form polymers in maize genomes ^[24-26]. In this paper, we will highlight the INDITTO2 transposon and discuss the mechanisms by which it is able to respond to drought-stressed environments.

DISCUSSION

Recently, we analyzed the sequence of the DEEPER ROOTING 1 (DRO1) gene promoter in a paddy rice landrace Acuce grown in the Yuanyang Hani's terraced fields, Yunnan Province. We found that there are 266 more nucleotides in the DRO1 promoter of Acuce than in that of rice varieties Nipponbare. We analysed this sequence and found that it shared 93.2% identity with the INDITTO transposon, which is a non-autonomous DNA transposon belonging to the Tourist superfamily ^[17] and named INDITTO2 transposon ^[27]. Sequence analysis showed that the INDITTO2 transposon contains an Auxin Response Element (ARE) as well as multiple transcriptional binding sites. We hypothesized that INDITTO2 would interact with auxin to regulate plant growth and development. We constructed different expression vectors to study the role of the INDITTO2 transposon in the auxin-mediated regulation of DRO1 transcription. In the promoter region of DRO1, there are three ARE elements, as well as the ARE in the transposon of INDITTO2 ^[27], all of which respond to auxin ^[28]. A series of experiments showed that under auxin treatment, the three AREs in promoter of DRO1 and the ARE of the INDITTO2 transposon showed different auxin response patterns and therefore were able to regulate DRO1 transcription differently ^[27]. These results indicate that the functional differences in the AREs may cause the DRO1 gene in rice to exhibit different levels of transcription in response to drought stress.

There is no INDITTO2 transposon in the DRO1 promoter of the rice variety Nipponbare, however, we created a transgenic variety in which we cloned an INDITTO2 transposon into the Nipponbare genome ^[27]. Nipponbare normally has low drought avoidance, which is related to low expression of DRO1 and insensitivity to auxin. However, in the transgenic Nipponbare into which we inserted the whole INDITTO2 transposon, the plants show drought avoidance and up-regulated DRO1 expression levels ^[27]. These results suggest that rice varieties with an INDITTO2 transposon in the DRO1 gene promoter can show improved drought avoidance and better adaptations to drought stress. However, when we subjected the rice varieties Kasalath and Xiao hua nuo, both of which contain complete INDITTO2 transposons in their DRO1 gene promoters, to drought stress and auxin treatment, we found that these rice varieties did not show the same drought performance as Acuce ^[27]. We conclude that the INDITTO2 transposon has promoter activity and can regulate the transcription of DRO1 gene through an auxin mediated mechanism, and confer a degree of drought-avoidance to rice, however, this effect varies with the different genetic backgrounds of different rice varieties. Transposons are involved in numerous aspects of plant growth and development, including potato tuber skin color ^[29], rapeseed vernalization, rice glume development and maize latitudinal adaptation ^[30] and their molecular regulatory mechanisms need further study.

CONCLUSION

We found that rice drought avoidance can be enhanced through INDITTO2 transposon-mediated promoter activity and was conveyed through auxin-dependent transcriptional regulation of the DRO1 gene. However, the mechanism by which the INDITTO2 transposon confers drought avoidance on the rice is as yet unknown. Because INDITTO2 and its homologues increase the genetic diversity of the rice varieties, and may enable them to adapt to different environmental stresses, it is necessary to elucidate the detailed regulation mechanism, and a better understanding of the molecular mechanisms by which these genetic elements improve plant fitness in response to different abiotic stresses will enhance crop resistance and yields in stress conditions.

CONFLICTS OF INTEREST

Authors declare no conflicts of interest.

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