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Mini Review

# Candidates of Cullin-Ring Ligases for Amelioration of Stress Tolerance in Plants

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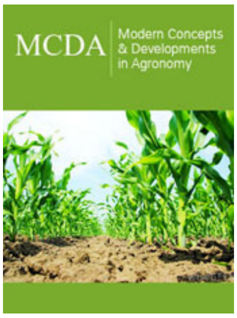

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## Abstract

Advancements in molecular biology techniques such as the use of genetic and genome editing methods have resulted in the development of crop plants with improved productivity under the conditions of stressful environments or limited resource availability. However, the first step towards the development of tailored-made crop varieties is the identification of potential candidate genes for manipulation. Once these genes are identified, their expression can be altered either by silencing or activation using these molecular approaches followed by the studies on phenotypic and physiological consequences of the plant related to yield. Protein ubiquitination is a post-translational process which degrades the proteins that are not needed for cellular functions. Owing to the diversity of protein components of Cullin-RING ligases (CRLs), they can be explored for activities, particular stress-regulation, other than their house-keeping functions. In this mini review, we briefly provide a discussion on the genes that encode members of CRLs which are considered to be the potential targets for stress amelioration and enhancement of plant productivity.

**Keywords:** E3-ligase; Cullins; Crop improvement; Genes

## Introduction

Protein ubiquitination is a post-translational mechanism, aims at maintaining protein equilibrium by degrading those proteins that are more than what is required for the normal functioning of the eukaryotic cells. Ubiquitin, a ubiquitously distributed protein (hence the name ubiquitin) ferries the target protein through a cascade of three enzymes; an ubiquitin-activating enzyme (E1), ubiquitin-conjugating (E2) and ubiquitin-Ligase (E3). E3 ligases mainly control the specificity of the ubiquitination process. If the protein ubiquitination fails to regulate the protein turn over, it could result in the development of a disease in animals and lethal or perturbed phenotypes in plants. Thus, an imbalance in protein levels is associated with infections and diseases.

### Cullins in developmental and stress regulation

There are one or two E1 enzymes, dozens of E2s and hundreds of E3 enzymes in eukaryotes and Cullin-RING ligases (CRLs) form the largest E3 family consisting of many subunits [1]. One of the essential components of CRLs is Cullins, present as Cullin 1, Cullin 3a/3b and Cullin 4 with each one of them acting as a scaffold to bring the E2 enzymes either directly or via adaptor proteins such as S-Phase kinase-associated protein (SKP) [2]. Cullins are a group of hydrophobic proteins implicated in the scaffolding of Ubiquitin E3-ligases. They are characterized on the basis of their homology domains, which consist of 200 amino acids with a bundle of 4 helical domains, a winged-helix domain followed by α and β domains. The size of the Cullin proteins ranges from 85kDa to 100kDa [3]. The genome of *Saccharomyces cerevisiae* encodes three Cullin proteins (Cul1, Cul3, and Cul8) and humans have eight Cullins (Cul1, Cul2, Cul3, Cul4A, Cul4B, Cul5, Cul7 and the closely related p53-associated parkin-like cytoplasmic protein, ParC. The Arabidopsis genome contains five Cullin protein-encoding genes (Cul1, Cul2, Cul3A, Cul4, and ANAPHASE PROMOTING COMPLEX2, APC2 [4]).

The involvement of Cullins in abiotic stress responses emanated from our study on activation tagging of rice which resulted in the identification of Cullin-4 as one of the genes responsible for improved water-use efficiency [5]. Based on these findings, we further performed an elaborate study on the biotic and abiotic stress-responsive roles of *Cullins* and found that some of them became significantly up-regulated, indicating that these genes form important candidates for ameliorating stress tolerance which, however, requires further exploration [6]. The role of Cullins in cell cycle regulation was first identified in nematodes [7]. A Cullin homolog of yeast, cdc53 has been reported for its role in Ubiquitin-mediated proteolysis of cell cycle regulators [8]. Arabidopsis Cul1 mutants exhibited embryonic lethality [9], whereas a point mutation in AtCul1 has revealed its role in jasmonate response [10]. Similarly, AtCul3a and AtCul3b proteins in Arabidopsis bind to RBX1 with their C-terminal region and these Cul3 based CRLs are essential for embryo development [11].

## Other components of E3-ligases

The necrotrophic pathogen infection or pest attack initiates a jasmonic acid pathway to pursue the defense response in plants. Arabidopsis COI1 (Coronatine-insensitive 1) is an F-box protein that regulates jasmonic acid-dependent defense pathways. COI1 negatively regulates the repressor of JA transduction [12]. Jasmonate Zim domain (JAZ), a repressor of jasmonic acid signaling is the target of Skp1/Cullin/F-boxCOI1 (SCF) E3 ligase protein degradation complex [13]. After infection, the increase in the level of JA enhances the interaction of JAZ repressor with SCF-COI complex, which leads to transcriptional activation of JA-responsive genes. Rice coi1 mutants were found to be highly susceptible to the pathogen infection and insect attack. A similar mutation in JAZ protein increased the herbivore susceptibility [14,15].

Protein ubiquitination pathway has also been a major target to develop metal tolerant plants [16]. Rice transgenic plants overexpressing OsHIR1, encoding an E3 ligase, exhibited tolerance to toxic levels of heavy metals [17]. AtHOS1 protein encodes an E3 ligase that mediates the degradation of a master 97 regulatory protein, ICE1 (Inducer of CBF Expression), thus associates the role of E3 ligases in response to extreme temperatures as well [18]. Overexpression of genes involved in protein ubiquitination does not always enhance tolerance. For example, silencing of OsDSG1 encoding an E3 ligase resulted in drought and salt-tolerant transgenic rice plants, indicating that some of the genes of this complex act as negative regulators also. Although many reports have shown the overexpression or silencing of E3 ligase components resulting in enhanced tolerance to abiotic stresses, the stress regulatory roles of Cullins have not been elaborated in great detail. The stress-regulatory role of Cullins can be exploited further by the functional characterization of the selected stress-responsive Cullin genes through genetic or genome engineering methods, which might help in augmenting productivity of crop plants under stressful environments.

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