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Review

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O-linked β-*N*-acetylglucosamine modification and its biological functions

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Abstract The covalent attachment of *O*-linked β-*N*-acetylglucosamine (*O*-GlcNAc) to Ser/Thr residues of proteins acts as not only a posttranslational modification but also a nutritional sensor in nucleus and cytoplasm, which directly regulates the expression of genes and multiple crucial signal transduction pathways. Dynamic *O*-GlcNAcylation at Ser/Thr residues is catalyzed by two key enzymes, *O*-GlcNAc transferase (OGT) and *O*-GlcNAcase, which are responsible for addition and removal of the *O*-GlcNAc modification, respectively. *O*-GlcNAc modification plays important roles in cellular signaling in animals, especially in human diseases. Two orthologs of OGT in plants, SECRET AGENT and SPINDLY, have been reported to be involved in diverse plant processes. However, compared with the functional mechanisms revealed in animals, the consequences of protein *O*-GlcNAc modification in plants is largely unknown, and the relationship between *O*-GlcNAcylation and cellular processes needs to be explored. In this review, we summarized the recent advances on *O*-GlcNAc modification and its biological functions in animals and plants, and prospect of more special functions of *O*-GlcNAc will be revealed in plants.

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1 Introduction

O-GlcNAc is a widespread dynamic posttranslational modification on Ser/Thr residues of cytoplasmic and nuclear proteins in higher eukaryotes [1]. Differing from the "classical" protein glycosylation modifications which bear glycosyl side chains in endoplasmic reticulum or Golgi apparatus, *O*-GlcNAc modification occurs in a single *N*-acetylglucosamine moiety and *O*-GlcNAcylated proteins locate in cytosol, nucleus and mitochondria [2, 3]. The donor substrate of *O*-GlcNAc modification, UDP-GlcNAc, is synthesized as the final product by hexosamine biosynthesis pathway (HBP) [4] (Fig. 1). The addition and removal of the sugar moiety are catalyzed by two highly conserved enzymes, *O*-GlcNAc transferase (OGT) and OGA (*O*-GlcNAcase) [5, 6]. OGT is a unique glycosyltransferase in metazoans containing three alternative splicing isoforms: ncOGT (the nucleocytoplasmic isoform), mOGT (the mitochondrial isoform) and sOGT (the short 78-kDa isoform). OGT contains a tandem tetratricopeptide repeat (TPR) domain at N-terminal and a catalytic domain at C-terminal [4]. TPR domains play roles in protein–protein interaction and the formation of OGT trimerization. In particular, TPR domain mediates substrate specificity, and different TPR combinations result in diverse proteins interacting with OGT [7, 8]. OGA also contains two domains, a hexosaminidase domain at N-terminal and a histone acetyltransferase domain at C-terminal [7], which can acetylate histones [4, 9, 10]. OGA-L (102 KD) and OGA-S (76 KD) are two isoforms of OGA with identical N-terminal domains but different C-terminus. OGA-S is a truncated

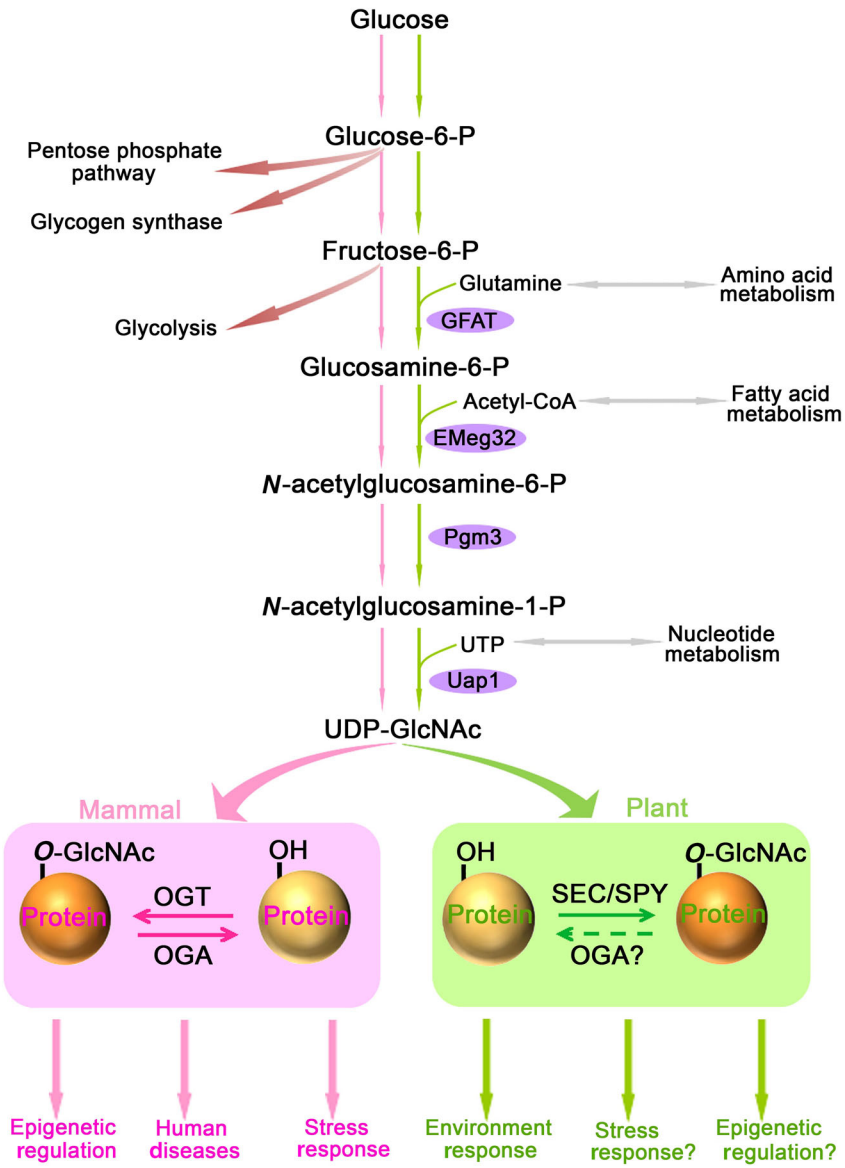

Fig. 1 Hexosamine biosynthetic pathway and cellular response of *O*-GlcNAc signaling in mammals and plants

splice version of OGA and exhibits lower enzyme activity in vitro [11]. In addition, OGT acts as a component of histone deacetylase complexes (HDAC) playing an opposite role with OGA in transcription regulation [10, 12]. In mammalian cells, *O*-GlcNAcylation plays an important role in many signaling pathway such as insulin signaling, degradation of protein by proteasome [13], osteoblast function [14], as well as the cellular stress response [13].

Since the discovery of protein *O*-GlcNAc modification, considerable research works were focused on mechanisms of *O*-GlcNAc signaling in animals. In plants, two orthologs of OGT, SPINDLY (SPY) and SECRET AGENT (SEC), were identified and shown to play important roles in growth and development in *Arabidopsis* [6, 15, 16]. However, *O*-GlcNAc signaling-related functional mechanisms and even *O*-GlcNAcylated proteins are poorly understood in plants. In this review, we summarize the functional characterization of *O*-GlcNAc in animals and recent advances on *O*-GlcNAc signaling in plants.

2 Functional characterization of *O*-GlcNAc in animals

2.1 Cross talk between *O*-GlcNAcylation and other posttranslational modification

O-GlcNAcylation has been reported to interplay with other posttranslational modifications, for example