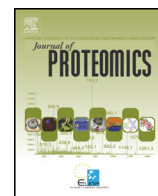




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Comprehensive analysis of response and tolerant mechanisms in early-stage soybean at initial-flooding stress

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ABSTRACT

Soybean is one of the most cultivated crops in the world; however, it is very sensitive to flooding stress, which markedly reduces its growth and yield. Morphological and biochemical changes such as an increase of fresh weight and a decrease of ATP content happen in early-stage soybean at initial-flooding stress, indicating that soybean responses to flooding stress are keys for its survival and seedling growth. Phosphoproteomics and nuclear proteomics are useful tools to detect protein-phosphorylation status and to identify transcriptional factors. In the review, the effect of flooding on soybean response to initial flooding stress is discussed based on recent results of proteomic, phosphoproteomic, nuclear proteomic, and nuclear phosphoproteomic studies. In addition, soybean survival under flooding stress, which is defined as tolerance mechanism, is discussed with the results of comprehensive analysis in flooding-tolerant mutant line and abscisic acid-treated soybean.

Biological Significance: Soybean is one of the most cultivated crops in the world; however, it is very sensitive to flooding stress, especially soybean responses to initial flooding stress is key for its survival and seedling growth. Recently, proteomic techniques are applied to investigate the response and tolerant mechanisms of soybean at initial flooding condition. In this review, the progress in proteomic, phosphoproteomic, nuclear proteomic, and nuclear phosphoproteomic studies about the initial-flooding response mechanism in early-stage soybean is presented. In addition, the tolerant mechanism in soybean is discussed with the results of comprehensive analysis in flooding-tolerant mutant line and abscisic acid-treated soybean. Through this review, the key proteins and genes involved in initial flooding response and tolerance at early stage soybean are summarized and they contribute greatly to uncover response and tolerance mechanism at early stage under stressful environmental conditions in soybean.

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1. Introduction

Flooding is a complex stress that imposes many constraints to plant growth [1]. The severe constraint is starvation of oxygen and carbon dioxide, which is caused by extremely slow rates of diffusion in water compared to those in air [2]. The exchange of gas such as oxygen between the atmosphere and the plant tissue is reduced by flooding [3]. The limitation of oxygen availability in flooded soil causes hypoxic and anoxia conditions in root [4]. Respiration of root system, which provides substantial reduction in energy status, is inhibited by hypoxic and anoxia conditions [5]. The capacity for ATP production and energy

transformation through mitochondrial oxidative phosphorylation was restricted by lower oxygen concentration in flooded plants [6]. Furthermore, flooding leads to change in soil chemical characteristics including soil acidification and redox potential [7], which limits the availability of soil nutrients and causes the accumulation of phytotoxins [8]. These results indicate that plant growth is suppressed under flooding stress through decreasing energy/nutrients supply and accumulating toxic metabolites.

Soybean, which is one of the major agricultural crops, is particularly sensitive to flooding stress [9]. The plant growth and grain yield are markedly reduced in flooded soil [9]. When soybean was treated with flooding at the vegetative growth stage or the reproductive stage, grain yield and quality were reduced compared to untreated soybean [10]. In addition, secondary aerenchyma is formed and worked as an oxygen pathway under flooded conditions [11]. In soybean, flooding stress impaired plant growth by inhibiting root elongation and reducing hypocotyl pigmentation [12]. In root tip of soybean, ubiquitin-mediated

Abbreviations: LC, liquid chromatography; MS, mass spectrometry; ROS, reactive oxygen species; ABA, abscisic acid; QTL, quantitative trait loci.

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proteolysis was activated [13], and cell death was detected under flooding stress [14]. These findings suggest that flooding causes damage to soybean at early stage of growth.

Root tip is comprised of actively dividing cells that develop into primary and lateral roots [15], which plays great roles during water and nutrient uptake [16]. In soybean, root tip is characterized by an open meristem and quiescent center, which is located below the meristem and is mainly composed of a pool of stem cells that are important for root development [17]. Proteomic analysis indicated that root tip is the most sensitive organ to flooding stress compared to root, hypocotyl, and cotyledon [18]. The root tip plays key roles in the development of root structure and responses to environmental stresses, particularly flooding [19]. Based on the above reasons, the study of soybean-root tip is necessary to provide insight into plant responses to flooding stress.

Post-translational modifications such as phosphorylation, acetylation, and glycosylation contribute to plant responses to biotic and abiotic stresses [20]. Phosphorylation is one of the most studied post-translational modifications and a common signaling event occurred upon plant exposure to stresses [21]. Approximately one-third of all eukaryotic proteins are modified by phosphorylation [22]. Phosphorylation leads to changes of protein structure, which directly regulates protein activity and induces interacting partners or subcellular localization [23]. In the present review, the initial (3 h)-response mechanism in early-stage (2- or 3-day-old) soybean under flooding stress is explored based on recent proteomic, phosphoproteomic, and nuclear proteomic studies. In addition, the initial-flooding tolerant mechanism in early-stage soybean is discussed using the results from proteomic and transcriptomic studies.

2. Characterization of initial-response mechanism in early-stage soybean under flooding stress

Proteomic techniques have been applied up to now to understand the underlying mechanisms of soybean responses to flooding stress [19,24–28]. Reactive oxygen species [ROS] scavengers such as ascorbate peroxidase, were decreased in soybean under flooding stress [28], indicating that the ability to remove ROS in soybean was reduced by flooding stress. Proteins involved in glycolysis/fermentation such as enolase and alcohol dehydrogenase were increased under flooding stress [19], indicating that anaerobic respiration was activated to provide necessary energy in soybean. Cell wall loosening and synthesis-related proteins were increased and decreased, respectively, under flooding stress [25], suggesting that cell wall was damaged in soybean by flooding stress. The results of these proteomic studies could be used to explain the mechanism in soybean responses to flooding stress during the early stage of growth. However, the mechanism in soybean how to sense and transduce flooding signal is still not clear. To better understand this mechanism, proteomic study at initial flooding stress is needed in soybean.

2.1. Response mechanism in soybean at initial-flooding stress

Abiotic stress response in plant is divided into 3 different stages including an alarm, acclimation, and resistance phases [29]. In soybean, although many flooding responsive mechanisms have been identified in early stage [27], the flooding response mechanism at initial stage has not been characterized completely. To identify initial flooding responsive proteins and explore mechanism underlying soybean response to initial flooding stress, proteomic study was performed [30]. Proteins related to amino acid metabolism, glycolysis, tricarboxylic acid cycle, hormone metabolism, stress, and protein synthesis, were identified with time course manner under flooding stress [30]. Among them, alcohol dehydrogenases and calreticulin were clearly increased; however, ATP-citrate lyase and xylosidase were decreased at initial flooding stress (Fig. 1) [30].

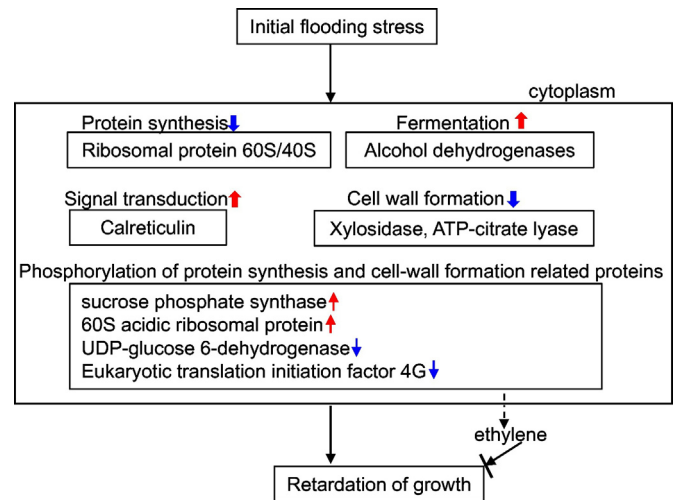


Fig. 1. The model of cellular responses affected by initial flooding stress in soybean root tip. The solid line means clarified points and dotted line means speculative aspects. The upward red arrows mean increased/up-regulated and downward blue arrows mean decreased/down-regulated proteins or processes.

Oxygen was markedly reduced under flooding condition, and plants have to adapt to low oxygen status through increasing anaerobic energy production [1]. Alcohol fermentation is a major pathway for anaerobic energy production, and alcohol dehydrogenase works as a key enzyme for fermentation [31]. In soybean, alcohol dehydrogenase was rapidly activated at initial flooding stress [30], indicating that anaerobic metabolism was quickly triggered by initial flooding stress. On the other hand, calreticulin has a key role in endoplasmic reticulum, which works as a molecular chaperone to newly synthesized unfolded proteins or glycoproteins and regulates the calcium homeostasis in the endoplasmic reticulum lumen [32]. In *Arabidopsis*, calreticulin was involved in regulating plant defense against biotrophic pathogens and pathogen invasion [33,34]. Based on these findings, initial flooding stress might activate fermentation and calcium-related signal transduction pathways through increasing abundances of alcohol dehydrogenase and calreticulin in soybean.

Xylosidase plays an important role in xylem remodeling during the process of cell wall maturation [35]. During germination of *Lupinus albus* seeds, xylosidase involved in protecting the spermosphere environment and acted as a first defense against pathogens [36]. ATP-citrate lyase catalyzes the formation of acetyl-CoA/oxaloacetate from citrate/CoA with the concomitant hydrolysis of ATP [37]. In *Arabidopsis*, ATP-citrate lyase was required for the normal growth and development [38]. Taken together, these findings suggest that cell wall formation and the ability of defense against pathogens in soybean might be suppressed by decreasing xylosidase and ATP-citrate lyase at initial flooding stress.

2.2. Response mechanism with phosphorylation in soybean at initial-flooding stress

To understand the role of phosphorylation at the initial stages of flooding stress in soybean, the phosphorylation status of differentially changed proteins in flooding-stressed plants was analyzed [39]. Phosphoproteins related to ribosomal, cell wall, and protein synthesis was significantly changed during the early stage of flooding stress [39]. Among them, sucrose phosphate synthase and 60S acidic ribosomal protein were phosphorylated; however, UDP-glucose 6-dehydrogenase and eukaryotic translation initiation factor 4G were dephosphorylated (Fig. 1) [39]. It is suggested that phosphorylation affects protein synthesis and cell wall formation in soybean under flooding stress.

Previous proteomic research indicated that flooding mainly affects protein synthesis in the endoplasmic reticulum of soybean root tip

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