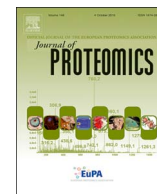




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## Review

## Proteomic approaches to uncover the flooding and drought stress response mechanisms in soybean

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## ABSTRACT

Soybean is the important crop with abundant protein, vegetable oil, and several phytochemicals. With such predominant values, soybean is cultivated with a long history. However, flooding and drought stresses exert deleterious effects on soybean growth. The present review summarizes the morphological changes and affected events in soybean exposed to such extreme-water conditions. Sensitive organ in stressed soybean at different-developmental stages is presented based on protein profiles. Protein quality control and calcium homeostasis in the endoplasmic reticulum are discussed in soybean under both stresses. In addition, the way of calcium homeostasis in mediating protein folding and energy metabolism is addressed. Finally, stress response to flooding and drought is systematically demonstrated. This review concludes the recent findings of plant response to flooding and drought stresses in soybean employed proteomic approaches.

**Biological significance:** Soybean is considered as traditional-health food because of nutritional elements and pharmacological values. Flooding and drought exert deleterious effects to soybean growth. Proteomic approaches have been employed to elucidate stress response in soybean exposed to flooding and drought stresses. In this review, stress response is presented on organ-specific manner in the early-stage plant and soybean seedling exposed to combined stresses. The endoplasmic reticulum (ER) stress is induced by both stresses; and stress-response in the ER is addressed in the root tip of early-stage soybean. Moreover, calcium-response processes in stressed plant are described in the ER and in the cytosol. Additionally, stress-dependent response was discussed in flooded and drought-stressed plant. This review depicts stress response in the sensitive organ of stressed soybean and forms the basis to develop molecular markers related to plant defense under flooding and drought stresses.

## 1. Introduction

Soybean is an important food crop containing abundant protein and vegetable oil [1]. Soybean is unique among crops, because it supplies protein equal in quality to that of animal sources [2]. Soybean is advantageous for biodiesel producing, which is converted from vegetable oil, because it is produced without or nearly zero nitrogen [3]. In addition, soybean is rich in phytochemicals such as isoflavones and phenolic compounds [4], which contributed to reducing the risk of heart/cardiovascular diseases, osteoporosis, and cancer [5]. Furthermore, it is possible for soybean to step into symbiosis with rhizobia to provide nitrogen for plant growth and development [6]. These findings document several aspects of soybean, including nutritional elements, biodiesel production, pharmacological values, and symbiosis potential.

Soybean production is affected by abiotic constraints, including weather-related phenomena, soil-nutrient availability, salinity, and

photoperiod [2]. Annual global losses in crop production due to flooding are comparable to those caused by drought [7]. Flooding is composed of several underlying changes such as oxygen, carbon dioxide, reactive oxygen species (ROS), and phytotoxins inside plants and from environment [8]. Due to restricted gas exchange, deficit of energy/carbohydrate and accumulation of volatile ethylene occurred by flooding [9]. Drought poses as another constraint for plant growth and terrestrial ecosystem productivity [10]. Drought induced meristematic cells, reduced cell division [11], and limited cell elongation/expansion growth [12]. These findings indicate that flooding and drought are complex abiotic stressors affecting plant growth.

A series of findings were obtained in soybean with different exposure time to flooding and drought stresses using proteomic techniques (Fig. 1). With flooding duration, a plethora of biological processes underwent, including signal transduction, hormone regulation, transcriptional control, glucose degradation, sucrose accumulation,

Abbreviations: ER, endoplasmic reticulum; HSP, heat shock protein; PDI, protein disulfide isomerase; ROS, reactive oxygen species; SAM, S-adenosylmethionine

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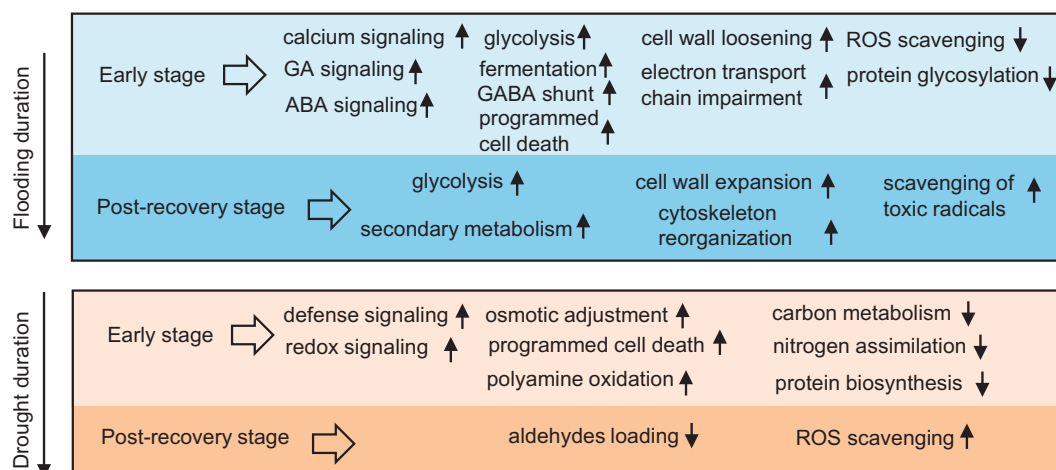


Fig. 1. Overview of cellular processes induced by flooding and drought in soybean. Cellular events in soybean exposed to flooding and drought were explored using proteomic approaches. The up- and down-arrows indicate the activated and suppressed metabolisms, respectively, induced by stress condition. Abbreviations are as follows: ABA, abscisic acid; GA, gibberellic acid; and GABA, gamma-aminobutyric acid.

alcoholic fermentation, mitochondrial impairment, proteasome-mediated proteolysis, and cell wall loosening [13]. Signal transduction of calcium [14] and hormone regulation of abscisic acid [15] as well as gibberellic acid [16] were activated by flooding. Moreover, fermentation [17] as well as gamma-aminobutyric acid shunt [18] were induced in flooded soybean. As reported, lignification [19] and electron transport chains [18] were altered; however, ROS scavenging [19] and protein glycosylation [20] were suppressed. Regarding post-flooding recovery, scavenging of toxic radicals [21], ATP generation/secondary metabolism [22], and cell wall metabolism/cytoskeleton reorganization [23] were responsible for recovery. These findings indicate that different strategies might be utilized in soybean under flooding conditions and during post-flooding recovery stage.

Enormous progress has been made in drought-stressed soybean employed proteomic approaches (Fig. 1). Osmotic adjustment, defense signaling, and programmed cell death were involved in drought adaptation [24]. In drought-stressed soybean, increased S-adenosylmethionine (SAM) synthetases played roles in redox signaling and polyamine oxidation [25]; however, decreased methionine synthase impaired seedling growth [26]. Moreover, carbon metabolism, nitrogen assimilation, and protein biosynthesis responded to drought in soybean nodules [27]. Additionally, peroxidase and aldehyde dehydrogenase took part in post-drought recovery by scavenging toxic ROS and reducing load of harmful aldehydes [28]. These studies indicate a variety of biological processes are in response to drought and such findings form the molecular basis of stress response in soybean. In respect to both stresses, signaling transduction plays roles in stressed plant and ROS scavenging participates in post-stress recovery.

Stress response displays on organ-specific manner, which provides detail information of cellular processes for plant growth and development [29]. Organelle protein profiles not only provide fundamental information of stress response, but also refine the knowledge of signaling pathways [30,31]. In the current review, findings from organ-specific and stage-dependent proteomic studies of flooded and drought-stressed soybean were presented. Subcellular proteomics of endoplasmic reticulum (ER) was summarized. In addition, the ER function and affected-cellular processes were bridged with calcium homeostasis in soybean. Stress response in soybean was addressed in respect to flooding or drought.

## 2. Morphological, biochemical, and physiological changes of soybean under flooding and drought stresses

Flooding and drought are adverse environmental conditions; and

they inhibit soybean growth at both the early stage [25,32] and the seedling stage [26,33]. In early-stage soybean, dry weight of plant was reduced after 1-day exposure to combined stresses [32]; however, length of root including hypocotyl was decreased or increased in flooded or drought-stressed plant [25]. Regarding soybean seedling, flooding and drought significantly suppressed weight of plant and length of root including hypocotyl [26,33]. These results describe the stress effects on soybean growth and differ the changes of plant morphology such as length of root including hypocotyl in response to flooding and drought.

Furthermore, biochemical and physiological processes are illuminated in flooded and drought-stressed soybean beyond the morphological changes. A tight control over carbon metabolism to meet the required energy demand for alleviating stress impacts was exhibited in soybean, irrespective of the kind and severity of extreme-water conditions [34]. Reduction in net photosynthesis was induced by both stresses; however, starch granules and abscisic acid/stomatal conductance were responsible for flooding and drought, respectively [35]. Additionally, stress-response events were investigated in soybean employing proteomic analyses, in which flooding and drought stresses were concurrently conducted. Protein synthesis was suppressed in soybean exposed to combined stresses [20,25]; however, redox signaling and polyamine oxidation were differentially controlled via SAM synthetases [25]. Calcium homeostasis was the mediator for ER stress and it modified carbon metabolism through the regulation of pyruvate decarboxylase in soybean under combined stresses [32]. These results represent the affected events in stressed plant and shed light on the stress specificity underlying the difference in soybean morphology caused by flooding and drought stresses.

A plethora of processes were deciphered in flooded and drought-stressed soybean employing proteomic techniques (Fig. 1). Moreover, other approaches such as reversal genetic, biochemical, and metabolic analyses are employed to determine the highlighted events in response to flooding and drought. For example, activated fermentation was critical for flooding tolerance and alcohol dehydrogenase was key fermentative enzyme [36]. The effects of alcohol dehydrogenase were further validated by overexpression [37] and by biochemical analyses including *in situ* hybridization [38], Western blot [38], as well as enzyme assay [39]. Scavenging of ROS differed in soybean exposed to combined stresses; and it was determined by the changes of ascorbate peroxidase via Western blot, enzyme activity, and biophoton emission [40]. In addition, gamma-aminobutyric acid shunt occurred in stressed soybean [18] and increased accumulation of gamma-aminobutyric acid were examined through metabolomic approaches [41,42]. These results

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