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Adaptation to Water Stress in Soybean: Morphology to Genetics

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Abstract

Soybean (*Glycine max* L.) is the most important legume and oilseed crop. As a leguminous crop, it plays an irreplaceable role towards the sustainable agricultural system with biological nitrogen fixation. However, its production can be dramatically decreased by the occurrence of water stress. Water stress including drought and flooding induces the morpho-physiological and biochemical changes at different growth stages, which negatively affects the adaptability and yield of soybean. Genetic diversity that ensures productivity in challenging environment exists within germplasm, their wild relatives and species that are adapted to the water stress. The discovery of gene mapping, QTLs associated with root traits, slow canopy wilting, nitrogen fixation and flooding tolerance have accomplished significant progress in breeding programs. Identification of drought-responsive genes and transcription factors such as *WRKY*, *DREBs*, *ERFs*, *ZIP*, *ZFP*, *MYB* and *NAC* are valuable to ameliorate the water stress in soybean. Understanding the genetic mechanism using transcriptomic and proteomic approaches would be the ultimate choice for mitigating the water stress. Integration of well-designed soybean breeding program coupled with omic techniques would pave the way for developing drought and flooding resilient soybean cultivars.

Keywords: soybean, drought, flooding, stress tolerance, quantitative trait locus, genomics, genetic diversity

1. Introduction

Soybean is an important leguminous crop in the world, providing an essential source of protein to human diet, feed for live-stock and as bio-diesel for industry [1, 2]. Soybean seeds consist of 40% protein, 20% oil, 35% carbohydrate and ~5% ash [3]. As compared to other oilseed crops, soybean collectively occupies around 6% of the world's land under cultivation [4].

Due to the rapid rise in the commercial value of soybean in an international market, the total area under soybean cultivation has been increasing from last three decades. Soybean is an important cash crop with a total production of over 313.05 million metric tons in 2015–2016 (USDA data). During this year, the USA has been the world's leading producer of soybean representing 35% of the world production, followed by Brazil with 31%, Argentina with 17%, China with 4%, India with 3%, Paraguay with 3% and Canada with 2% (USDA data).

Water stress including drought and flooding is considered as a major threat, limiting growth and yield of plants [5, 6]. Drought is caused by insufficient rainfall or irrigation which results in soil drying, whereas, in flooding, water exists in soil solution causing water logging and submergence. In response to drought and flooding stress, 40–60% yield losses have been reported in soybean [7, 8]. High temperature, low humidity in atmosphere and water deficiency are the main causes of drought [9, 10]. Drought stress affects germination rate and early seedling growth of the plant [11, 12]. Under water deficit conditions, a significant reduction in germination, hypocotyl length, root and shoot fresh and dry weight were observed whereas the root length is increased [13]. It also affects the carbon assimilation and phenology of the plant [10]. Prolonged drought stress at different growth stages has profound effect on soybean growth and yield [14].

To counteract the adverse effects of drought, the soybean plant adopts three mechanisms i.e. escape, tolerance, and avoidance [15]. In the escape mechanism, the plant completes its life cycle before the onset of drought. Normally, the plants complete their life cycle very quickly and produce few seeds. For instance, early planting of soybean helps to avoid drought, and is largely practiced in the USA—planting in March to April affords escape from water stress [16, 17]. Drought avoidance is performed by maintaining high water potential, grow deeper in soil, stomatal control of transpiration rate, and by reduction of water loss from tissues. The tolerance mechanism includes low tissue water potential, maintenance of turgor through osmotic adjustments [18, 19].

Flooding ranks second after drought, causing yield reduction in soybean [20, 21]. Flooding stress can be categorized as waterlogging or submergence. In waterlogging stress, root goes under water while shoots remains above ground, whereas, during submergence, plant is completely immersed in water saturated soil. As plants are aerobic, hypoxia (insufficient oxygen) or anoxia (complete absence of oxygen) causes losses in crop production. Soybean is more sensitive to flooding stress resulting in yield decline by reducing photosynthesis nitrogen fixation and biomass accumulation. Flooding stress can happen during any growing stage, especially in the seed germination and vegetative stages leads to substantial decrease of soybean grain yield [22] (**Table 1**). In addition, flooding stress hampers yield production during vegetative (17–43%) and reproductive stage (50–56%) [41].

For mitigating the negative impact of flooding stress, plants use a number of strategies for their survival, mainly escape and quiescence strategies [42, 43]. In escape strategy, morphological (aerenchyma development, shoot elongation and adventitious root formation) and anatomical alterations allow the plant to exchange gas between cells and atmosphere. The Quiescence strategy suppresses morphological changes to save energy and resources and retard plant growth. This strategy depends on anaerobic energy production [42, 44].

Growth stage	Experimental material	Indicator	Ref.
Under drought stress			
Germination	4 Bulgarian lines & one USA variety	Germination, shoot and root length, fresh and dry weight	[23]
Germination	L17, M9, Clark, M7, Hobbit and Williams	Root and shoot length, germination rate and percentage of germination	[24]
Second trifoliate leaves	Jindou 21 (C12), Mengjin 1 (W05) and Union (C08)	Gas exchange, water relation parameters, total chlorophyll, proline contents of leaves, root xylem pH, plant growth and root traits	[25]
Third trifoliate leaf (V3)	A5409RG, Jackson and Prima 2000	Root architecture, shoot parameters	[26]
Flowering and pod-filling stage	Habit, L17 and M17	Leaf relative water content, chemical osmolytes and chlorophyll content	[27]
V4, R1 and R3 growth stages.	Eight soybean cultivars	Highest number of node/plant, number of pod/main stem, pod/sub stem and pod/plant	[28]
Reproductive stage (R6–R7)	41 soybean accessions	increases in metaxylem number	[29, 30]
Adult	PI578477A, PI088444, PI458020	Yield, root architecture	[31]
Adult	BARI Soybean 5, BARI Soybean 6, Shohag and BD2331	relative performance (RP), tolerance (TOL), drought susceptibility index (DSI)	[32]
Under flooding stress			
Seedlings stage	Soybean	Secondary aerenchyma formation	[33]
Seedling stage	11 soybean genotypes	Primary/adventitious roots and root nodules, stem and leaf biomass	[34] [35]
Vegetative and flowering stage	Taekwang and Asoagari	Root morphological traits, adventitious roots and Photosynthesis	[36]
Cotyledon-stage seedlings	92 Soybean Lines	Root architecture	[37]
Flowering stage	Cultivars Fundacep 53 RR and BRS Macota	Fermentative metabolism and carbohydrate contents in roots and nodules	[38]
Flowering stage	Five soybean cultivars	Nodule number, nodule dry weight, chlorophyll content, carbon exchange rate, dry matter accumulation and nitrogen content	[39]
Seedling stage	162 soybean accessions	Root development	[40]

Table 1. A list of drought- and flooding-related parameters at different growth stages of soybean.

Understanding the genetic base for water stress tolerance in diverse soybean is a fundamental issue that contributes for the genetic improvement. This chapter will present the research progress about the situation of soybean tolerance to water stress at germination, seedling and adult plant stages. It also includes the current knowledge about QTL mapping, gene discovery and ‘omic’ technologies relevant to drought and flooding tolerance that will be helpful to understand drought and flooding-tolerance mechanisms in soybean.

2. Genetic diversity of water stress tolerance in soybean

2.1. Different response of soybean to water stress

2.1.1. Morphological performance

Drought induces morphological changes in plants, enabling them to sense and rapidly adapt to the stress. Root-related traits are crucial in maintaining crop yield in soybean [45]. Drought alters the root system architecture (root depth, root angle and root branching density) [27]. For instance, root architecture was characterized in field under normal and water deficit conditions using three soybean cultivars (Jackson, Prima 2000 and A5409RG). As a result, Prima 2000 (drought-tolerant cultivar) has an intermediate root phenotype with a root angle of 40–60°, while a shallow root phenotype along with root angle of <40° has been observed in drought-sensitive cultivar A5409RG [27].

Depth of rooting system influenced by the elongation of taproot also plays an important role for plant survival under water deficit [27, 46]. An increase in number of root tips, root length, root surface area and root volume was observed under water limited conditions. Several studies have proposed that roots having large xylem number, diameters, lateral root systems with more root hairs are indicators of drought tolerance [31, 47, 48]. Jackson is considered as drought escaping cultivar with long and deep roots into the soil permitting better water uptake compared with drought-sensitive cultivars [27, 49]. Under water-limited conditions, Plant Introduction (PI) 578477A and 088444 exhibited higher yield due to higher lateral root number in clay soil [50]. It was reported that deeper region of soil has high root density under seasonal drought as compared to dry surface of soil [51]. In addition, total root length/ plant weight, dry root weight/plant weight and root volume/plant weight were positively correlated with drought tolerance [52]. Therefore, studying the relationship between root traits and drought is helpful to develop drought-resistant cultivar.

Root-to-shoot ratio is also a good indicator to allocate the resources between different plant components. The water-limited environment increases the root-to-shoot ratio. For example, in soybean, root-to-shoot ratio increased by 13% indicates the flow of biomass towards roots [53]. The drought-tolerant soybean genotype (C12) showed a higher root-to-shoot ratio than the susceptible genotype (C08) under restricted soil water with application of exogenous ABA. To cope with drought stress, leaf morphology also plays an important role. Under water-limited conditions, plants reduce their leaf area by closing stomata. Due to water scarcity, reduction in soybean plant leaf area has been reported [54]. In contrast, drought-tolerant soybean cultivar exhibited a greater leaf area rather than less-tolerant cultivar under hydric stress condition [55].

Aerenchyma formation is a major indicator that facilitates gas exchange between aerial and submerged plant parts (shoots and/or roots) to avoid flooding stress [56, 57]. Flooding stress induces two kinds of aerenchyma i.e. primary (cortical) [58] and secondary (white and spongy tissues) [33]. A number of aquatic plants develop cortical aerenchymatous tissue by cell disintegration (lysigenous aerenchyma) and cell separation (schizogenous aerenchyma) [59]. In rice, barley, maize and wheat, lysigenous aerenchyma is induced by flooding [60, 61]. In some

species, especially in soybean, secondary aerenchyma having a spongy parenchyma cell layer develops through cell division of phellogen [44, 62]. Secondary aerenchyma is morphologically and anatomically different from cortical aerenchyma (lysigenous and schizogenous aerenchyma) [33]. Waterlogging stimulated the formation of aerenchyma and adventitious roots in soybean plants facilitating transport of oxygen from shoot to root [62–64]. Under waterlogging condition, adventitious roots are formed in several flooded plants including soybean [61, 62, 65]. However, adventitious roots are absent in soybean seedlings under complete submergence [66]. Under flooding conditions, secondary aerenchyma consisting of white and spongy tissues develops within a few weeks in stems, roots and root nodules of soybean [33]. Aerenchyma formations initiated by ethylene, Ca^{2+} , and ROS signalling through a programmed cell death process are involved in aerenchyma development [60, 67].

Rapid shoot elongation is another escape mechanism for adaptation in waterlogging stress [68]. It has been reported that lower stem of soybean having hypertrophic lenticels helps oxygen entry into the aerenchyma [64]. Flooding also causes a significant reduction in leaf number, leaf area, canopy height and dry weight at maturity in soybean crops.

2.1.2. *Physiological and biochemical response under drought stress*

Stress-responsive mechanisms have been studied at the physiological and biochemical level in soybean under drought and flooding stress. To optimize the use of water under water deficit conditions, stomatal control is considered as major physiological indicator. For instance, in soybean, stomatal conductance decreased by 42% in drought-stressed leaves rather than normal leaves [69]. Owing to dehydration, MG/BR46 (drought tolerant soybean variety) showed faster decline in stomatal conductance as compared to BR16 (drought-susceptible variety) (65 versus 50% reduction) [55]. In same study, prolonged drought stress (45 days) exhibited no profound impact on stomatal conductance of BR16 while it had reached 79% in the MG/BR46. Several studies have provided strong evidence that drought-tolerant soybean genotypes (C12 and W05) exhibited a higher reduction in stomatal conductance rather than the susceptible one (C08) [25]. In soybean, ABA is involved in the reduction of stomatal conductance and photosynthesis. For instance, after imposition of exogenous application of ABA under soil drying, leaf stomatal conductance of soybean tolerant genotype C12 declined than the susceptible one (C08).

Maintenance of cell turgidity and water-use efficiency are important indicators to cope with drought stress [26]. Soybean introduction line PI 416937 is an excellent example of drought tolerance by limiting transpiration rate and maintaining a lower osmotic potential. An increase in WUE was observed in drought-tolerant genotype (C12) by regulating stomatal closure during the entire period of water deficiency [25, 52]. The maintenance of cell turgidity under water-limited conditions may be achieved by adjusting the osmotic potential in response to the accumulation of proline, sucrose, soluble carbohydrates, glycine betaine and other solutes [70]. The accumulation of solutes under water deficit condition is known as osmotic adjustment. Some authors have reported higher proline content in drought-tolerant crop species such as bean [71]. In soybean, water stress exhibited significant increase in proline contents in drought tolerance as well as susceptible genotype, but tolerant genotypes recovered to pre-stress levels more quickly after rehydration [25].

The production of ROS, such as superoxide radical (O_2^-), hydroxyl radical (OH^\cdot) and hydrogen peroxide (H_2O_2), is one of the biochemical responses causing damage to DNA, proteins and lipids [72] under drought stress. The toxicity of ROS may be limited by antioxidant enzymatic (superoxide dismutase, catalase, and glutathione peroxidase) and non-enzymatic scavengers [73, 74]. For instance, drought stress increased activities of some antioxidant enzymes (catalase, glutathione reductase and superoxide dismutase) in soybean varieties which were positively correlated to seed yield [75].

Under flooding stress, plant undergoes different physiological and biochemical adaptations. For instance, in soybean, a significant reduction in photosynthetic activity and stomatal conductance was observed in Essex and Forrest within 48 h of flooding at vegetative and reproductive growth stages. Waterlogging also decreases biological nitrogen fixation, as nodules need adequate oxygen to maintain nitrogenase activity for aerobic respiration and contributing adenosine triphosphate [41]. As a consequence of flooding stress, a reduction in root hydraulic conductivity has also been reported [76]. Several studies have provided the correlation between stomatal conductance and carbon fixation. In flooded plants, photosynthetic activities were reduced by restricting CO_2 due to stomatal closure [77, 78]. Furthermore, due to the higher concentration of CO_2 assimilation in flooded soil, biomass and soybean root elongation eventually repressed [79].

Tamang et al. [66] reported that submergence stimulates starch degradation, soluble carbohydrates and ATP in cotyledons and hypocotyls of soybean seedlings. Extensive submergence degrades the chlorophyll contents in aerial parts of several terrestrial plants [80, 81]. However, under submergence, abundance of chlorophyll *a* and *b* remained nearly constant in soybean [66]. The decrease in photosynthetic activity with long-term flooding may be triggered by the reduction in chlorophyll, transpiration and ribulose-1,5-biphosphate (RuBP) carboxylase activity. These combined effects against flooding declined the crop growth, net assimilation and leaf expansion of plants. Blocking of hypertrophic lenticels at the base of stem restricted O_2 transport into the roots resulting in reduction of plant growth under hypoxic conditions [82]. Flooding stress causes higher production of ROS resulting in oxidative damage to proteins related to photosynthetic apparatus [83]. As a result, the scavenging activity is overpassed under flooding stress.

2.2. Parameters for measuring the tolerance degree of water stress

2.2.1. Parameters related to seed tolerance

Seeds need a suitable condition to have a good germination. The germination rate and percentage of different cultivars were affected by levels of drought stress. In soybean, drought stress simulated by polyethylene glycol PEG-6000 significantly reduced seed germination percentage (**Table 1**). An increase in the PEG concentration reduced root growth by two to three times for different genotypes. Seed weight and seed size, and seed weight distribution are key indicators to evaluate the genotypic response to drought stress [84, 85]. A positive correlation between 100-seed weight per plant and seed yield were reported in soybean under water limited conditions. For instance, Habit (soybean drought-tolerant cultivar) exhibited higher 100-seed weight and seed yield under drought stress [29, 86]. Water deficit conditions lead to a significant reduction in seed weight and seed size. It also had little effect on seed shape as

shrunk and wrinkled, and hard seeds were produced in soybean [84, 85, 87]. Same study pointed out 30–40% reduction in proportion of seed having diameter > 4.8 mm. In contrast, the ratio of seeds of diameter < 3.2 mm was increased by 3–15% [85].

Germination is a complex process that consists of several metabolic events. Numerous studies reported that negative correlation exists between germination percentage and flooding stress [88, 89]. Seeds are usually germinated under optimum conditions within 1 or 2 days. But, seed germination is delayed due to the quick absorption of water, collapse of seed structure, and outflow of internal seed contents under flooding stress. When seeds were flooded for 3 days after imbibition, germination percentage was drastically dropped out and seed injury was observed [90]. Flooding causes mechanical damage on the soybean seeds and prohibits germination. Seed coat and seed weight are fundamental factors to evaluate a positive effect on seed flooding tolerance. For example, germination rate (GR) and normal seedling rate (NS) was higher in pigmented varieties as compared to yellow varieties of soybean (**Table 1**). These parameters (GR and NS) were negatively correlated with seed weight (SW) in the combined population [91]. Therefore, pigmented seed coat and small seed weight could be key parameters in response to seed-flooding tolerance.

2.2.2. *Parameters related to vegetative tissues*

Root length, shoot length and leaf area are considered as major determinants to evaluate drought response during vegetative stage. A positive relationship exists between root traits and resistance to drought [52, 92]. At seedling stage, drought stress affects leaf expansion rate, leaf water potential, relative water content of leaves (%RWC) and relative growth. The degradation of chlorophyll contents of soybean leaves was correlated with the different levels of drought stress [75]. Water deficit stress also decreased the number of nodes and intermodal length while the reduction in inter-nodal length depends upon the duration of drought stress. For example, drought stress showed no profound impact on number of internodes in drought tolerant soybean cultivar (C12), whereas drought-susceptible cultivar (C08) showed higher number of internode [93].

Essential traits, root length and shoot length are also important indicators in response to flooding stress. The insufficient allocation of water, minerals, nutrients, and hormones led to root and shoot damage [94]. The first symptom usually appears in soybean is wilting of leaves in response to flooding. Soybean shoot growth under flooded conditions is significantly decreased due to inability of the root system regarding water transport, hormones, nutrients and assimilates [95, 96]. Flooding tolerance in soybean is strongly correlated to root surface area, root length and dry weight [97]. It has been reported that root tips are extremely sensitive to flooding in soybean and pea seedlings [98–100]. Under complete submergence, soybean root growth is absolutely repressed due to the death of root tips.

2.2.3. *Parameters related to adult plants*

In soybean, pod number per plant, seed number per pod and 100-seed weight are major determinants of yield under water stress [101], and these yield components are the important sink for assimilates at reproductive stages [102]. Drought stress especially during flowering (R1)

and pod-filling stages reduces soybean yield [30] (**Table 1**). Under water deficit conditions, an increase in rate of abortion has been reported during early pod-filling stage in soybean [54, 103]. Soybean yield is also affected by the occurrence of drought stress during seed filling (R6) period [93]. Water stress at flowering stage decreased the pod number and seed number resulting in yield loss [104]. Kobraei et al. [29] conducted experiment on eight soybean cultivars to assess yield under normal and drought conditions. This study pointed out that drought reduced the yield components resulting in yield loss. In addition, more yield loss was observed during R1 stage as compared to R6 stage [104].

One of the major traits conferring tolerance to waterlogging is yield and production of good quality seeds [105]. A significant decline in pod number, pods per node, branch number, and seed size was observed following 7 days of flooding at different vegetative and regenerative development stages [106]. Sullivan et al. [107] confirmed reduction in pod number and plant height at early vegetative growth stages. Soybean crops flooded with excessive water at early flowering stage showed severe chlorosis and stunting growth [108]. Schöffel et al. [109] showed a decreased number of pods per plant at the reproductive stage (R4) in pot trials. A field experiment was conducted in flooded soil and obtained yield reduction from 20–39% in the different soybean cultivars when subjected during the R5 stage. During flooding, a significant reduction in soybean yield was observed at R5 stage as compared to the R2 stage [110].

2.3. Genetic variation of tolerance to water stress

2.3.1. Cultivated soybean

Considerable genetic variation in seed yield was observed in soybean genotypes under drought stress. A total of 50 soybean genotypes were screened under rain-fed condition in Bangladesh. Among them, genotypes BARI Soybean 5, BARI Soybean 6, Shohag and BD2331 were identified as drought-tolerant genotypes [32]. In another study, response of eight cultivars of soybean (Clark, Hobbit, Pershing, Williams, Hood, DPX, M7 and M9) was investigated in Iran. Williams cultivar was predicted as drought-tolerant, having highest number of nodes and pods/plant in normal and water deficit conditions [29]. Genetically and geographically, diverse soybean germplasm lines i.e. from Korea (PI085355, PI339984, PI407778A, PI407973A, PI423841, PI424460, PI424608A, PI603170, PI458020), China (PI088444, PI567398, PI567561, PI594410, PI578477A), Japan (PI243548, PI417092, PI507066) were screened to examine root response under water deficit condition in clay and sandy soil. Plant Introduction PI578477A, PI088444 (high lateral root number in clay soil) and PI458020 (thick lateral roots in sandy soil) were found to have higher yield under water-limited conditions [50]. Brazilian cultivars BR-4 and Ocepar 4 were considered as drought-tolerant [111]. Several cultivated germplasm lines (*Glycine max*) including Williams, Jackson, Prima 2000, Jindou 21(C12), PI416937, PI 427136, PI 408105A, PI 471938, PI 424088, PI 081041, N04-9646, DT51 and R02-1325 have promising performance under water deficit conditions and can be used in breeding program [25, 27, 112, 113].

Genetic variation in soybean germplasm was observed in response to flooding tolerance to overcome yield loss. Elite lines conserve genomic regions that can inhibit extensive yield losses during flooding stress. An experiment was conducted to determine genetic variations

using 21 soybean varieties for flooding tolerance in both screen-house and field tests. Three soybean germplasm, Nam Vang from Cambodia, VND2 from China and ATF15-1 from Australia were identified as most flood-tolerant varieties which survived better, grew taller, produced more pods/plants and heavier seed weight as compared to sensitive varieties [114]. A total of 192 soybean germplasm lines were screened for flooding tolerance at seedling stage. Among them, Jangbaegkong, Danbaegkong, Sowonkongkong, Socheong2 and Suwon269 were identified as donor line for flooding tolerance, whereas Shillog, T201, T181, NTS1116 and HP-963 exposed flooding sensitivity [115]. Several cultivated germplasm lines (*Glycine max*) including PI 408105A, PI 561271, PI 567343, PI 407184, PI603910C, PI 567394B, PI 567651, Archer and Misuzudaiz have been identified as a source of potential source for flooding tolerance [112].

2.3.2. Wild soybean

Wild soybean (*Glycine soja*), is a valuable genetic resource for the tolerance to water stress by reintroducing alleles. Wild soybean PI 483463 (*G. soja*) had favourable donor alleles for root angle, while PI 468917 predicted to contribute to slow wilting. Hence, it can be used for development of drought-resistant soybean cultivars [112, 116]. In another study, the wild parent, PI 407162 had favourable alleles for fibrous roots, thus enhancing the soybean ability to survive under drought stress. These studies suggested that it is possible to enhance genetic variation in cultivated soybean by introducing alleles from wild soybeans [117]. For flooding, different wild soybean accessions, PI 467162, PI 479751, PI 407229, PI 597459C, PI 424082, PI 378699A, PI 424107A, PI 366124, PI 378699A were identified, which showed tremendous waterlogging tolerance than *G. max* [112]. Therefore, wild populations can offer useful in breeding program for improving drought and flooding resistance of soybean.

3. Genetic regulation mechanisms for tolerance to water stress

3.1. Drought tolerance

3.1.1. Genetic and QTL structure of morpho-physiological performance

The application of QTL helps in identification of chromosomal regions, detecting phenotypic variation associated with drought-resistance traits and to determine the desirable alleles at these QLs for marker-assisted breeding. Progress towards the identification of drought-related QTLs is needed [118], only a few QTLs have been reported for drought (Table 2). Du et al. [128] identified 19 QTLs associated with seed yield under normal and water-limited conditions and 10 QTLs associated with drought susceptibility index (DSI) in soybean. To develop drought-tolerant varieties, the role of secondary traits associated with yield stability has been accelerated. In crops, under water deficit condition, several secondary traits i.e. early seedling vigor [129], canopy wilting [119, 130], root system architecture (RSA) [117, 131, 132], canopy temperature depression [133], carbon isotope discrimination [134, 135], alterations in photosynthesis [136, 137], and nitrogen fixation [138–141] have been reported.

In soybean, RSAs, slow canopy wilting and biological nitrogen fixation are promising secondary traits under drought [112]. Under water deficit conditions, a simulation analysis model depicted that slow wilting can improve soybean yield >75% while nitrogen fixation up to 85% [142]. In soybean, less information is available on QTL mapping of drought-associated traits and yield [128, 143], fibrous roots [144] and water-use efficiency (WUE) [123, 125, 126] under water-limited conditions. Several studies have been conducted on QTL mapping for RSA traits in major cereals crops with little information in leguminous crops, especially soybean [145–147]. Five QTLs were identified on chromosomes 1, 3, 4, 8, and 20 related with fibrous rooting systems in RIL population of soybean derived from a cross between Benning (low fibrous root) and PI 416937 (extensive fibrous root) [144]. These QTLs were detected by using 240 F6 derived recombinant inbred lines (RILs) under rain-fed conditions for 2 years (2001 and 2009). The parent PI 416937 (extensive fibrous root system) contributed favourable alleles for four QTLs, while one QTL had donor alleles from Benning. Moreover, a total of four QTLs related with root surface area and distribution (based on root length and thickness) were identified in an inter-specific mapping population (*Glycine max* × *Glycine soja*). Two QTLs on Chr 6 had favourable donor alleles from the wild parent, PI 407162 (*G. soja*) with R² value of >10%. As a result, plants enhanced their ability to form fibrous roots. Manavalan et al. [148] identified one QTL cluster associated with root length and lateral root number in 251 BC2F5 backcross inbred lines through linkage mapping with favourable alleles from Dunbar (**Table 2**).

Slow canopy wilting is a key factor to screen soybean germplasm under water-limited conditions [121]. A total of 13 QTLs associated with slow wilting were detected using five bi-parental populations under water-limited conditions, with phenotypic variation (R² 0.04–0.29). Eleven out of 13 QTLs had favourable alleles from PI 416937 and Jackson [119–121]. The major QTL associated with slow wilting was mapped on LG K with 17% phenotypic variation [122]. To validate QTL data from different mapping population on same linkage map, ‘Meta-QTL analysis’ has been proposed [149, 150]. In soybean, Meta-QTL analysis was used to refine the confidence interval of eight QTLs using mapping results from five bi-parental population. However, these QTLs are complex, unstable and quantitative nature, so breeders find difficulties to utilize them [151]. Considering this problem, confirmation of QTL should be performed by using more advanced progeny or near isogenic lines (BC_nF₂).

Studies on QTL mapping associated with biological-nitrogen fixation are very few in plants including soybean. Three QTLs for nodule number (LGs B1, E) were identified using the composite interval mapping and explained 13% phenotypic variation [152]. Two QTLs for shoot ureide were detected on Chrs. 9 and 19, and two QTLs associated with shoot nitrogen concentration were mapped on Chrs. 13 and 17 under water stress. These QTLs explained phenotypic variation ranging from 0.11 to 0.31 (**Table 2**) [127]. Jackson contributed favourable alleles for shoot ureide concentration on Gm 19 and Gm 13 while other two on Gm 09 and Gm17 have favourable alleles from KS4895. Under well-watered conditions, a number of QTLs associated with shoot ureide and nitrogen concentrations were reported. However, not a single QTL was detected under both conditions (stress and control) illustrating that soybean shows diverse mechanisms for regulation of N₂-fixation under well-watered and drought conditions [127].

Trait	QTL	Chro.	Marker	R ²	Population	Ref.
Canopy wilting	<i>Gm02-1</i>	2	ss107913715	0.06–0.12	KJ, BP	[119]
	<i>Gm02-2</i>	2	ss107912946/satt296	0.06–0.18	AP	[119, 120]
	<i>Gm02-3</i>	2	Satt296	0.06–0.19	BP, AP	[119]
	<i>qSW-Gm04</i>	4	Satt646	0.09	BP	[120]
	<i>Gm05</i>	5	ss107913925/satt276	0.04–0.16	KJ	[119, 120]
	<i>Gm08</i>	8	Satt177	0.05–0.15	KJ, KN	[119, 121]
Leaf wilting	<i>Gm09</i>	9	Sat044	0.17	Jackson × KS4895	[122]
Canopy wilting	<i>Gm11</i>	11	ss107913507	0.14–0.39	KJ, KP, AP	[119]
	<i>qSW-Gm12</i>	12	Satt302	0.27	BP	[120]
	<i>Gm13</i>	13	Satt362	0.16	KJ	[121]
	<i>Gm14</i>	14	ss107913401	0.08–0.12	KJ, AP	[119, 121]
	<i>qSW-Gm17/ Gm17-1</i>	17	ss107929993	0.06–0.22	KJ, AP, BP	[119–121]
	<i>Gm17-2</i>	17	ss107913610	0.09–0.10	KJ, KP	[119]
	<i>qSW-Gm19</i>	19	ss107924069	0.11–0.29	KJ, KP, BP	[119]
Yield	<i>Gm06</i>	6	Satt205-satt489	0.7	Minsoy × Noir 1	[123]
Yield and wilting	<i>Gm13</i>	13	Sat_375	–	Hutcheson × PI471938,	[124]
	<i>Gm13-1</i>	13	Sat_074	–		
	<i>Gm17</i>	17	Satt226	–		
Water use efficiency	<i>Gm19</i>	19	A489H	0.14	S-100 × Tokyo	[125]
	–	–	A063-1	0.8		
	<i>Gm18</i>	18	B031-1	8.5	Young × PI416937	[126]
	<i>Gm12</i>	12	A089-1	8.7		
	<i>Gm16</i>	16	cr497-1	13.2		
	<i>Gm16</i>	16	K375-1	7.5		
	<i>Gm4</i>	4	A063-1	5		
Nitrogen fixation (shoot ureide)	<i>Gm09</i>	9	BARC-060299-16,598	0.16	KS4895 × Jackson	[127]
	<i>Gm19</i>	19	Satt561	0.18		
	<i>Gm13</i>	13	BARC-014657-01608	0.24		
	<i>Gm17</i>	17	BARC-057467-14,765	0.12		

KJ = KS4895 × Jackson; BP = Benning × PI 416937; AP = A5959 × PI 416937; KP = KS4895 × PI 424140; KN = Kefeng1 × Nannong1138-2.

Table 2. A list of reported QTLs in soybean associated with drought tolerance.

3.1.2. Identification of important genes for drought tolerance

Drought stress-responsive genes are categorized as effectors and regulatory genes [153]. Effectors include gene encoding protein such as LEA proteins, osmolyte biosynthesis (osmotin), aquaporins, chaperons, antioxidants and enzymes involved in different metabolic pathway. Regulatory genes encoding product such as receptors, calmodulin-binding proteins, kinases, phosphatases and transcription factors are involved in signal transduction and gene expression [153]. A number of plant TFs such as ethylene-responsive factor, WRKY, MYB, basic leucine zipper domain (bZIP) and NAC are involved in ABA signalling under drought stress, while dehydration responsible element binding (DREB) protein, are involved in ABA-independent pathway [154–156]. Major families of TF genes expressed in response to drought stress in plants are summarized in **Table 3**.

In the soybean genome, 5035 TFs models were identified based on in-silico annotation [170]. Among all TFs, the WRKY transcription factor is the largest family in plants. A total of 233 WRKY members have been identified in soybean (<http://planttfdb.cbi.pku.edu.cn/family.php?fam=WRKY>) [171]. Identification of two WRKY genes (GmWRKY21 and GmWRKY54) and their role in enhancing tolerance to drought, salt and cold has been studied in *Arabidopsis* [156]. Moreover, the involvement of GmWRKY27 has been characterized under drought and salt stress. Overexpression of GmWRKY27 RNAi and GmWRKY27 in soybeans results in increased tolerance and hypersensitivity to drought and salt stress, respectively. In the same study, the association of GmWRKY27 with GmMYB174 was observed, which binds to neighbouring cis-elements

Gene family	Gene	Studied plant	Ref.
R2R3-MYB transcription factor	GmMYB84	Soybean	[157]
	GmMYBJ1	Arabidopsis	[158]
bZIP transcription factor	GmFDL19	Soybean	[159]
	GmbZIP1	Arabidopsis	[160]
DREB transcription factor	GmDREB2	Tobacco	[161]
AP2/ERF transcription factor	GmDREB2A;2	Soybean	[162]
AP2/ERF transcription factor	GmERF3	Tobacco	[163]
AP2/ERF transcription factor	GmERF4	Tobacco	[164]
WRKY family	GmWRKY54	Arabidopsis	[156]
WRKY family	GsWRKY20	Arabidopsis	[165]
NAC family	GmNAC20	Soybean	[166]
Homeodomainleucine zipper (HD-Zip) proteins	Multiple HD-Zip genes	Soybean	[167]
C ₂ H ₂ -type Zinc finger protein	GmZFP3	Arabidopsis	[168]
Trihelix transcription factors	GmGT-2B b	Arabidopsis	[169]
	GmGT-2A	Arabidopsis	

Table 3. Major families of TF genes expressed in response to drought stress in plants.

in GmNAC29 promoter and suppressed gene expression of GmNAC29 led to increased tolerance to abiotic stress [172]. In soybean, novel candidates of WRKY genes were detected, which provided the unique function of WRKY transcription factors under water deficit conditions [173].

Another gene family, Homeodomain-leucine zipper (HD-Zip) comprised of 140 HD-Zip genes (<http://plantfdb.cbi.pku.edu.cn/family.php?fam=HD-ZIP>) were detected under drought and salt stress. Out of 140, 59 are coding genes while 20 paralogous genes exhibited differential expression under drought and saline environment [174]. In soybean, overexpression of GmDREB3 also enhances drought tolerance in response to accumulation of proline [175].

3.2. Flooding tolerance

3.2.1. QTL mapping

In recent years, the advent of molecular marker technologies has opened up new opportunities for QTL analyses, fine mapping and cloning of genes for water stress tolerance. The genetic basis of drought and flooding tolerance has been studied by evaluating different component traits in drought and flood-tolerant soybean. Both drought and flooding tolerance are quantitatively inherited and controlled by several genetic loci. Consequently, a large number of QTLs related to flooding tolerance are summarized in **Table 4**.

The analysis of quantitative trait loci (QTLs) for water-logging tolerance in soybean is usually challenging. However, several studies have been done on QTLs associated to flooding tolerance, focused on injury score and tolerance index in soybean [91, 176–179, 182]. For instance, a single QTL located on Chr. 18 (Sat_064) was identified using 208 lines of two recombinant inbred (RI) populations, for soybean growth and grain yields under water-logging conditions [176].

Trait	QTL	Chro.	Marker	Population	Ref.
Grain yield	<i>Gm18</i>	18	Sat_064	Archer × Minsoy, Archer × Noir I	[176]
Injury score, tolerance index	<i>Gm5</i> , <i>Gm13</i>	5, 13	Satt385, Satt269	A5403 × Archer, P9641 × Archer	[177]
Flooding tolerance	<i>ft1</i>	6	Satt100	Misuzudaizu × Gong 503	[178]
Seed germination	<i>Sft1</i> , <i>Sft2</i>	12, 8	Sat_175, Satt 187	Peking × Tamahomare	[91]
	<i>Sft3</i> , <i>Sft4</i>	4, 2	Satt 338, Sat_279		
Flooding toleranceand/or resistance to <i>P. sojae</i>	<i>FTS-13</i>	13	Sct_033, BARC-024569-4982	PI 408105A × S99-2281	[179]
	<i>FTS-11</i>	11	BARC-016279-02316		
Joint waterlogging tolerance index	<i>Wt1</i> , <i>wt2</i>	19	Satt229-Satt527 Satt527-Sat_286	Su88-M21 × Xinyixiaoheidou	[180]
Root length development/ Root surface area	<i>Qhti-12-1</i>	12	Satt052-Satt302	Iyodaizu × Tachinagaha	[181]

Table 4. A summary of QTL mapping studies for flood tolerance traits in soybean.

The results indicated that the Sat_064 QTL is unique in response to flooding. The Sat_064 QTL was further confirmed in a southern cultivar Archer using near-isogenic lines (NILs) [183]. In addition, two flooding-tolerance QTLs on Chr. 5 (Satt385) and Chr.13 (Satt269) were identified associated with water-logging tolerance through partial linkage mapping and bulk-segregation analysis using two populations [177]. Seven loci were detected associated with yield in response to flooding in a mapping population between Misuzudaizu and Moshidou Gong 503. Among them, only a large and stable QTL, *ft1* tightly linked with flowering was reproducible with high LOD score in 2 years, 2012 and 2013 (15.41 and 7.57) [178].

In another experiment, four QTLs, *Sft1*, *Sft2*, *Sft3* and *Sft4* associated with seed-flooding tolerance, during germinating stage, were detected using population derived from cross between a tolerant 'Peking' (black seed coat) × susceptible cultivar 'Tamahomare' (yellow seed coat). Among these QTLs, *Sft1* located on Chr.12 had great effect on germination rate, whereas *sft2* mapped on Chr. 8 had contribution in seed coat pigmentation [91]. Two QTLs, *FTS-11* and *FTS-13* were mapped on Chr. 11 and Chr.13, respectively, using F_7 recombinant inbred lines (RILs) at an early reproductive stage. These QTLs were also related with flooding yield index and flooding injury score. The major QTL *FTS-13*, with phenotypic variation 18.3% was detected in multiple locations and years [179]. Recently, QTLs for root surface area development (RSAD) and root length development (RLD) on Chr. 12 (between markers Satt052 and Satt302) were identified in relation to hypoxia tolerance using F8:9 RILs derived from a cross between Iyodaizu and Tachinagaha in soybean. For the validation of these major and stable QTLs, NILs with the QTL region were developed derived from Iyodaizu [181].

3.2.2. Transcriptome analysis of soybean under water stress

Transcript abundance analysis is vital functional genomics tools to examine flooding responsive mechanisms and identify genes responsible for flooding tolerance. Recently, genome-wide changes associated with gene-expression are investigated through microarray chip analysis, RNA-seq approach and high-coverage gene expression profiling analysis for better understanding the transcriptional response in relation to flooding stress in soybean (**Table 5**). Transcripts were examined in the root tip, including the hypocotyl of soybean, using high-coverage gene expression profiling analysis; 5831 out of 29,388 were significantly altered under water stress. Genes relevant to ethylene biosynthesis, alcoholic fermentation and cell wall relaxation are promptly up-regulated in response to flooding. Defence-related genes, haemoglobin, and Kunitz trypsin protease inhibitor and acid phosphatase are responsible for flooding [184].

In another study, soybean microarray chip-based transcriptomics technique was used to comprehend the molecular response under flooding. In soybean roots including hypocotyl, more than 6000 flooding-responsive genes were identified. The results revealed that genes associated with glycolysis, photosynthesis, amino acid synthesis (Ser-Gly-Cys group), transcriptional regulation of transcription, degradation of ubiquitin-mediated protein, and cell death were expressively up-regulated, whereas genes relevant to cell organization, secondary metabolism, cell wall synthesis, transport of metabolite and chromatin structure were considerably down-regulated. Furthermore, up-regulation of flooding-responsive genes encoding small proteins plays key roles in acclimation to flooding [185]. It has been reported that a total of 2724 and

Stress	Tissues	Platform	DEG*/proteins characterized	Ref
Flooding	Root and hypocotyl	High coverage expression profiling	97 genes and 34 proteins	[184]
Flooding	Roots including hypocotyl	Soybean microarray chip	More than 6000 genes	[185]
Drought & flooding	Leaf tissue	Illumina Genome Analyzer (San Diego, CA) platform	2724 genes for drought and 3498 genes for flooding, 289 Transcription Factors	[186]
Flooding stress	Root tips, root with hypocotyl and cotyledons	RNA sequencing-based transcriptomic analysis	31 genes	[187]
Drought & flooding	Leaf, hypocotyl, and root	Gel-free/label-free proteomic technique	17 proteins	[188]
Drought & flooding	Roots	Gel-free proteomic technique	97 proteins in response to flooding and 48 proteins for drought	[189]
Drought & flooding	Root tip	Gel-free/label-free proteomic analysis	Three S-adenosylmethionine synthetases (SAMs) proteins	[190]
Flooding	Root and cotyledon	Nano spray LTQ XL Orbitrap mass spectrometry (MS)	146 proteins	[191]
Flooding & drought	Roots	Gel-free proteomic technique	97 proteins to flooding, 48 for drought	[189]

*Differentially Expressed Gene.

Table 5. Soybean transcriptome and proteome studies under flooding and drought stress.

3498 genes were differentially expressed in response to drought and flooding stress, respectively, which contain 289 TFs demonstrating ethylene response factors (ERFs), basic helix-loop helix (bHLH), WRKY amino acid motif (WRKY), myeloblastosis (MYB) and no apical meristem (NAC) are involved in stress tolerance mechanism [186].

RNA-seq based transcriptomic analysis resulted in detection of 729 and 255 genes in the flooding-tolerant line and ABA-treated soybean, respectively, which were significantly changed under stress condition. Transcript profiles also revealed that a total of 31 genes included 12 genes involved in the regulation of RNA and protein metabolism were commonly altered between the flooding-tolerant line and ABA-treated soybean under flooding stress [187]. On the basis of the above findings, it can be concluded that transcript profiles can be helpful as an adaptive mechanism for soybean survival under water stress.

3.2.3. Proteomics techniques for identification of water stress-responsive mechanisms

Different proteomics techniques i.e. mass spectroscopy (MS)-based (for identification of a number of environmental stress-responsive proteins), two-dimensional (2D) gel-based (for visual illustration of the proteins) and SDS gel or gel free-based (for detection of the largest number of proteins) are extensively used under water stress (Table 5). The available genomic information in soybean genome database helps to identify water stress-responsive mechanism. Distinct

changes in the soybean proteome during water stress lead to different defence mechanisms. Several studies evidently revealed that some proteins regulating sucrose accumulation, glucose degradation, cell wall relaxing, signal transduction and alcohol fermentation were altered under flooding stress [192, 193]. Flooding stress reduced the differential regulation of proteins involved in maintaining the structure of cell and protein folding [99]. Moreover, the application of exogenous calcium on flooded soybeans up-regulated the lipid metabolism, signalling-related proteins, glycolysis-related proteins and fermentation in roots [189]. A reduction in calcium oxalate crystals was found in cotyledon under flooding [188].

Wang et al. identified three *S*-adenosylmethionine synthetases (SAMs) proteins using gel-free proteomic analysis under water stress in soybean. The SAMs action declined at early-stage flooding but increased in hypocotyls and roots under water deficit. The results recommended that SAMs were involved in response to water stress and it might affect ethylene biosynthesis in soybean. The action of SAMs was different in hypocotyls, root tips and roots under water stress. The down-regulation of *SAMs 1* and *SAMs 2* were observed in roots under drought and flooding. Moreover, up-regulation of ACC synthase was examined under drought, whereas the expression was down-regulated in root tips under flooding. However, ACC oxidase was increased under both stresses. These findings indicate that SAMs have key role in ethylene biosynthesis in soybean [194]. A quantitative proteomics study has been conducted for the better understanding of flooding responsive mechanisms using flooding-tolerant mutant and abscisic acid (ABA)-treated soybean. A total of 146 proteins were usually altered at the early stage of flooding. Proteins related to protein synthesis such as nascent polypeptide-related complex and chaperonin 20, and RNA regulation-associated proteins were up-regulated both at protein and mRNA expression. However, these identified proteins at early stage of flooding were not meaningfully altered. This study suggested that proteins associated with protein synthesis and RNA regulation can influence in triggering tolerance to flooding stress [195]. Therefore, proteomic approaches can be used to understand the response mechanism to drought and flooding stress at the initial stage of soybean growth.

4. Improvement of soybean tolerance to drought and flooding stress

4.1. Breeding objectives and progress of conventional breeding

The objective of soybean breeding programs is to develop cultivars with enhanced yield (more pods/plant, more seeds/pod, 100-seed weight), seed composition (high protein and oil contents), shattering resistance and tolerance to abiotic and biotic stress. Many important agronomic traits (qualitative or simply inherited) are incorporated into commercial cultivar through conventional breeding. As drought and flooding are complex quantitative traits, breeders face difficulties to improve these traits through conventional breeding. Moreover, conventional breeding is tedious, labour extensive, requires a considerable time (8–9 years) and a large amount of space for evaluation. For example, in China, Jindou 21 is an excellent example of drought-tolerant cultivar developed through selective breeding. Initially, Lin Xian White (higher drought tolerance, low yield soybean cultivar) was crossed with Jindou 2 (drought tolerant and high yield).

After six generations, the resulting drought line was selected and further crossed with jindou14. Finally, Jindou 21 was developed after 7 years of selection in arid region of western Shanxi and depicted increased yield under water stress [196]. Xu et al. also identified 463 Chinese strains having high level of drought tolerance through breeding. These strains could be used as a potential source for enhancing drought resistance in soybean [197]. Development of RILs population for flooding tolerance is a long and tedious process. For example, in soybean, to develop F7 population by crossing S992281 X PI4081051 (high yield, flooding tolerant) via single-seed descent method requires 7 years. Hence, conventional breeding approach is less useful [179].

4.2. QTL mapping and marker-assisted selection

To deal with complex nature of drought and flooding, marker-assisted selection to identify QTL can be used as a promising approach. Time consuming phenotypic characterization of large population to get an effective QTL is a major challenge to improve agronomic traits associated with drought and flooding tolerance. If molecular markers are closely linked to the target QTL, it would be possible to transfer character into commercial cultivar through marker-assisted breeding. Marker-assisted selection can be effectively used in soybean having high linkage disequilibrium (low recombinant frequency) [198]. For example, four QTLs associated with root morphology were detected by using 629 SSR markers, indicating that fibrous roots QTL may be related with drought tolerance and seed yield in soybean [144]. In another study, three QTLs for flooding tolerance were detected using 360 SSR markers in soybean. Among three QTLs, one major QTL exhibited large impact on flooding tolerance environments [178].

4.3. Genetic engineering

Genetic engineering in the twenty-first century is a perquisite tool in cell and molecular biology that will provide additional approaches for genetic modification by overexpression or gene silencing, protein sub-cellular localization, transposon mutagenesis and promoter characterization for permitting the development of novel and genetically diverse genotypes. These techniques have become profound strategies in soybean breeding which provide unique chances to modify the genetic makeup of soybean. Recent advancement in genetic mapping and the identification of new drought and flooding stress-responsive genes from various organisms allow researchers to modify plants using several genetic strategies. Genetic transformation in soybean was first reported in 1988 [199, 200], but the stable transformation of soybeans is still a challenging task. Several studies reported on soybean transformation by *Agrobacterium*-mediated transformation and particle bombardment methods [201, 202]. Both approaches have been used successfully for genetic transformation of soybean. The success is mainly dependent on the efficient delivery of transforming DNA and the recovery of transgenic lines from a transformed cell. Transgenic soybean expressing GMFDL19 gene enhanced tolerance towards drought stress [159].

4.4. Other new breeding techniques

Over the past 20 years, several new breeding techniques have been developed and are being implemented to facilitate breeding for the crop improvement. New breeding techniques (NBTs) give the ability to accurately modify DNA by editing DNA and genes on or off. Gene

or genome editing including CRISPR/Cas9 is a broad category that offers an inexpensive, quick and easy technique to manipulate DNA and lessen the time and effort as compared to traditional breeding. Now-a-days, researchers are working on CRISPR/Cas9-edited versions to improve the different crops such as soybeans, rice, corn, canola and wheat with new traits like drought and flooding resistance and higher yields. Recently, various new plant breeding techniques such as zinc finger nuclease (ZFN) technology, acetate-mediated approach, oligonucleotide-directed mutagenesis (ODM), RNA-dependent DNA methylation (RdDM), cisgenesis, intragenesis, grafting (on GM rootstock) and reverse breeding allow the faster and more efficient improvement of crop varieties.

4.5. Agronomic practices to mitigate the effects of water stress

Agronomic practices can be mitigated the adverse effects of drought and flooding stresses by adopting various strategies. Seed priming is an effective and pragmatic technique to mitigate drought in which seeds are moderately hydrated. In this technique, germination rate, germination percentage and germination uniformity of primed seed increased [11, 203]. This approach has been useful to counteract the effects of drought stress in a range of crop species. Foliar application of plant growth regulators is another technique for improving growth against drought stress. Exogenously applied abscisic acid, uniconazole and brassinolide increased yields both under well-watered and drought conditions in soybean. Plant growth regulator treatments meaningfully increased water potential and chlorophyll contents under water stress conditions [204]. Traditional irrigation system causes >50% loss of irrigated water because of uncovered and unlined ditches. Therefore, a well-managed pipe system is required to avoid losses from traditional irrigation system as it can enhance the conveyance efficiency >90% [205]. Mulching involving covering of soil by using straw or plastic sheets, is another best strategy to retain moisture in soil. For instance, in China, soybean yield increased up to 23.4 and 50.6% by using mulching along with hole sowing and row sowing, respectively [206].

Several management practices have been tried to overcome completely or partially flooding injuries. Flooding induces nitrogen deficiencies resulting in a significant decrease in the uptake of nitrogen. As a result, yellowing of leaves occurred following 2–3 days of flooding. It has been reported that the application of nitrogen fertilizer i.e. polymer-coated urea (PCU) is effective to reduce nitrogen loss and recover flood damage in corn. It also helps to overcome oxygen deficiency in response to flooding stress preferentially [207]. Hypoxia also reduces the capacity of plant to absorb potassium (K). K plays a vital role in alleviating both biotic and abiotic stresses [208]. Indeed, K⁺ ions are involved in detoxification of ammonium and ammonia [209], promoting photosynthesis which helps plant recovery and nutrient uptake. Foliar and soil applications oxygen-containing fertilizers lessen the drastic effects of flooding stress [210]. For example, under flooding, oxygen-containing fertilizers considerably retained chlorophyll content and biomass in Italian basil [211].

Under flooding stress, 1-aminocyclopropane-1-carboxylate (ACC) synthase enzyme along with several stress proteins were synthesized [212]. The stressed plant consequently produces more ACC in their roots. In roots, ACC cannot be converted into ethylene due to insufficient oxygen. This ACC transferred from roots to shoots converting ACC to ethylene (sufficient oxygen environment) in shoots [213]. In soybean, phytohormone indole acetic acid (IAA)

prompts the production of ethylene which prevents the inhibitory effects of high IAA on root growth [214]. Elevation in ethylene production by waterlogged plants results in wilting, necrosis, chlorosis and reduced biomass yield. The application of ACC deaminase-producing plant growth-promoting rhizobacteria (PGPR) can protect plants from these damages [215, 216]. PGPR produce ACC deaminase, which converts ACC into α -ketobutyrate and ammonia, thus reducing the levels of ethylene under water stress conditions. A combination of PGPRs, along with arbuscular mycorrhizal (AM) fungi, including ACC deaminase-producing bacteria, *Pseudomonas*, *Azospirillum*, *Rhizobium* and *Bradyrhizobium*, could be a novel step in the alleviation of flooding-impacted plants.

5. Conclusions

Water stress has become major abiotic limitation factor on soybean production under warming climate. To combat drought and flooding stress, there is need to explore the resilient genetic resources and their utilization in breeding program. With the advancement in transcriptomics, proteomics, metabolomics, structural genomics and epigenetics, the production of soybean can be enhanced under water stress by integrating all disciplines. Recent advances in breeding system and agronomic practices will offer an opportunity for significant and predictable incremental improvements in soybean under water stress.

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