Chapter 3
Soybean Improvement for Waterlogging Tolerance

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Abstract Flooding is the second most destructive abiotic stress affecting soybean yield worldwide. Waterlogging or flooding causes losses in soybean grain yield mainly due to root damages, reduction in root nodule development, insufficient water and nutrient uptake, chlorosis due to weakened photosynthesis and carbon assimilation, and plant death. Waterlogging tolerance can be observed and measured on the basis of relative germination capability, plant survival rate, foliar damage score, stem elongation rate, differences in leaf chlorosis, coefficient based on yield/dry weight reduction due to waterlogging stress, and yield attributes. Conventional breeding method like pedigree selection leads to development of waterlogging-tolerant varieties, i.e., JS 97-52, NRC 128, etc., in India. Several

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major and minor significant QTLs associated with waterlogging tolerance have been identified worldwide. Availability of high-density genetic maps, EST sequencing and analysis, gene expression analysis, assembling of cDNA and oligo arrays, sequencing and comparison of homologous segments, etc. may further advance the understanding of underlying mechanism of waterlogging tolerance in soybean. Due to advances in genomics and cultural aspects, we will be able to further face the challenges of different kind of abiotic stresses including flooding in soybean cultivation.

Keywords Soybean · Waterlogging · Flooding · Quantitative trait locus · Transcriptomics · Genomics

3.1 Introduction

Soybean is considered a wonder crop due to its exclusive combination of protein and oil, making it suitable to be used as both food and feed. In India, this oilseed contributes in earning through export of de-oiled cake, in addition to a large share in edible oil for domestic consumption (Shrivastava et al. 2014). Besides protein (38–45%) and oil (18–22%), this "miracle bean" contains carbohydrate, ash, nutritional elements, and antioxidants largely beneficial for the human being. Therefore, it is gaining boundless popularity in the food, health, pharmaceutical, and cosmetic industries worldwide (Kumar et al. 2019). Globally, soybean is being grown in an area around 122 million hectares (mha), and average production of this crop is around 336 million tons (mt) annually (USDA, 2020). The major soybean producer countries are Brazil, the USA, China, Argentina, and India (USDA, 2020). In India, soybean is grown in an area of 11.39 million ha (mha) with productivity of 1015 kg/ha in 2019–2020 (Anonymous 2021). The average productivity of soybean in India is only about ~1 t/ha, and one of the primary reasons for it is soil moisture stress at critical growth stages. Waterlogging stress is the second significant destructive abiotic stress after drought in the world as well as in India. The prolonged periods of monsoon rains, excessive irrigation, undulating fields, overflow of rivers, and impermeable soils lead to the development of the waterlogged or excessive moisture conditions in the soybean fields. In the past, this stress has affected various economically important crops worldwide; the annual yield losses in rice, wheat, and maize were reported nearly about 18%, 40%, and 25% respectively, in different regions of the world (Mohanty and Khush 1985; Rathore and Warsi 1998; Collaku and Harrison 2002). Flooding or waterlogging stress causes about 16% annual loss in soybean productivity globally (Ahmed et al. 2013; Boyer 1982). In India, excessive soil moisture or waterlogging caused slaughter in grain yield nearly 18%, mainly in central India (SOPA 2019). In the wake of global climate change, weather simulation models indicated an expected increase in loss of crop production due to flooding in the future (Rosenzweig et al. 2002). The climate change projection scenario for years 2021–2050 also signposted an increase of 11.6% annual rainfall with irregular extreme events in central India (Goswami et al. 2006) which may negatively affect the total soybean production in India.

3.2 Waterlogging Stress and the Tolerance Mechanisms in Soybean

Phenotype is the result of the interaction between the genotype and the environment in which soil moisture plays an important role. Due to global warming, our climate is constantly facing the rising incidence of weather extremities like drought, high temperature, flooding, etc. (Wani et al. 2018; Wani 2018; El-Esawi et al. 2020). Flooding mainly occurs due to extensive rainfall over a period of time and may be classified as waterlogging in which the level of water covers the roots, partial waterlogging in which the root zone is partially submerged, submergence in which the entire plant remains submerged under water, and partial submergence in which some aerial parts remain under water (Sashidharan et al. 2017). Overall, soybean as a crop is sensitive to waterlogging stress; reduction in seed yields is observed in a range of 17–46% during stress at vegetative stages while 50–72% reduction during stress at the reproductive stages (Oosterhuis et al. 1990; Van Toai et al. 2010; Chandra et al. 2020). Waterlogging situations for a short extent of 2 days can bring around 27% yield reduction in soybean (Linkeme et al. 1998). Yield losses due to waterlogging or flooding are mainly because of injuries in the roots, reduction in root nodule development, insufficient water and nutrient uptake, chlorosis due to weakened photosynthesis and carbon assimilation, and plant death due to diseases (Oosterhuis et al. 1990; Sakazono et al. 2014; Ye et al. 2018). The accumulation of carbon dioxide produced during anaerobic respiration is also the main reason for injury to plants. Waterlogging takes significant reduction in photosynthetic activity and stomatal conductance with limited span of 48 h of stress at the vegetative and reproductive stages of the plant. Besides, waterlogging also affects the biological nitrogen fixation as root nodules need oxygen to maintain the adequate nitrogenase enzyme activity and production of adenosine triphosphate (Oosterhuis et al. 1990). Some studies also reported a correlation between stomatal conductance and carbon fixation due to a closure of stomata under waterlogging stress (Jackson and Hall 1987; Malik et al. 2001).

In soybean plants, different physiological and biochemical mechanisms help to mitigate the stress due to excess soil moisture conditions, viz., escape and quiescence approach (Colmer and Voesenek 2009; Van Veen et al. 2013). The gaseous conversation between the tissue and the atmosphere is maintained by some morphological and anatomical changes in escape mechanism. Morphological alterations include the development of aerenchyma and rapid shoot elongation. Under prolonged waterlogged conditions, formation of adventitious roots was observed; they improved gaseous exchange in plants (Bacanamwo and Purcell 1999a, b). However, adventitious roots are not formed under complete submerged conditions (Tamang et al. 2014). These morphological alterations suggest an association with higher tolerance to excess soil moisture conditions. Under quiescence strategy, the morphological changes are suppressed which helps conserve energy and retard the plant's growth. However, this mechanism is dependent on the amount of energy produced during anaerobic respiration (Bailey-Serres and Voesenek 2008; Colmer and Voesenek 2009). The formation of aerenchyma cells and adventitious roots was found better in waterlogging-tolerant lines than susceptible soybean lines (Anonymous 2015; Kim et al. 2015). Ethylene accumulation during anaerobic conditions helps in the formation of aerenchyma and adventitious roots (Alamgir and Uddin 2011), and significant differences in the levels of endogenous hormones like ethylene, ABA, and gibberellic acid were observed in a study (Kim et al. 2015).

Waterlogging reduces the supply of oxygen in root zone; thus, it decreases the availability of oxygen for generation of energy and growth of plant. The diffusion rate of oxygen gas in water is approximately 1/10,000th of air, attributing slow diffusion of oxygen in water as compared to air (Colmer and Pedersen 2008). This reduces the availability of adequate air for the crucial aerobic metabolic processes of the plant roots (Colmer and Pedersen 2008). Oxygen deprivation in roots leads to accrual of reactive oxygen species (ROS), phytotoxic products, inorganic carbon, gaseous plant hormone ethylene, etc. This affects root growth and metabolism processes negatively. At a cellular level, many deleterious consequences are associated with hypoxia and anoxia which include drop in cellular level energy, decline in cytoplasmic pH, accumulation of toxic products and ROS, etc. (Subbaiah and Sachs 2003). Under waterlogged soil condition, roots are the first organ to be affected due to low oxygen concentration; further, new root formation is inhibited, and root decay is promoted in flooded soils. In aboveground plant parts, waterlogging results in chlorosis and senescence of leaves and loss in specific leaf weight, dry matter, relative water content, and membrane stability index in roots and leaves. The impact of damage to cellular and plant metabolic process can be seen in the form of reduced crop yield as wholesome (Sairam et al. 2008; Ahmed et al. 2013; Chandra et al. 2020).

To improve plant growth and survival under waterlogging/flooding-induced hypoxic environment, a series of metabolic and physiological changes are convinced in plants (Horchani et al. 2009). As soon as low O_2 is sensed, energy production through aerobic respiration decreases, and anaerobic energy production metabolism processes activate (Kumutha et al. 2008; Sairam et al. 2008; Zabalza et al. 2009). If there is a lack of oxygen, it will be sensed by final electron acceptor which led to the accumulation of intermediates of Krebs cycle, pyruvate, and NAD(P)+, and thus, ATP levels decline. Enzymes of lactic fermentation and ethanolic fermentation pathways induce to sustain the activity of anaerobic fermentation (Tadege et al. 1999; Zabalza et al. 2009). Plants undertake fermentation processes for ATP production as a rescue mechanism (Drew 1997), which leads to sharp reduction in ATP formation, impairing cellular metabolism and function. Because, fermentation outcomes indecline of cytosolic pH, induction of glycolysis and accumulation of lactate & other products (Geigenberger 2003; Drew 1997). But fermentation is necessary for survival under anaerobic environment. In response to decreased ATP production, many high ATP-demanding cellular processes such as DNA synthesis, rRNA synthesis, protein synthesis, and cell division are reduced to a minimum requirement.

In the root system of soybean under hypoxic conditions, ethanol and lactate content increases in roots and nodules, due to increased activities of alcohol dehydrogenase, pyruvate decarboxylase, and lactate dehydrogenase enzymes. Enrichment in sucrose level in roots and reduction in root nodules have been seen under hypoxia in soybeans (Borella et al. 2014; Chandra et al. 2020). Under flooded sub-ambient O_2 condition, ethylene levels build up in root systems, due to a more production of ethylene and reduction in diffusion of ethylene from root to water, as ethylene diffusion is 1/10th in water as compared to air. The reduced concentration of oxygen and elevated ethylene level induces programmed cell death in the cortex tissue to develop lysigenous aerenchyma to provide an internal pathway for oxygen transmission, and it reduces the number of O_2-consuming cells as tolerance mechanism. Thus, aerenchyma tissues are one of the important adaptive features of plants in waterlogged conditions to avoid anaerobiosis by the roots. Aerenchyma tissues also act as an internal pathway with low resistance for the exchange of different gases between aerobic shoot to the anaerobic root (Colmer and Pedersen 2008). Oxygen leaks out into the roots and surrounding soil through the aerenchyma. This creates oxygenated microenvironment which gives aerobic condition to microorganisms and prevents the development of potentially toxic soil components such as oxides of Fe, Mn, etc. Adventitious roots also act as another tolerance mechanism in soybean; they develop from the submerged part of the stem in waterlogged plants. They grow and develop horizontally closely parallel to the upper water surface so that oxygen can be more available to these roots compared to belowground roots (Sairam et al. 2008). Diffusion of gases between shoot parts and root parts is facilitated through the large airspaces in the adventitious roots as adventitious roots generally contain more aerenchyma as compared to the primary lateral roots (Visser et al. 1997). Evidences about adventitious root formation during flooding were provided by many workers (Bragina et al. 2003; Sairam et al. 2008). Reports have also not only confirmed about increased contribution of the apoplastic bypass to water flow in adventitious roots but also showed reduced dependence of roots on the hypoxia-sensitive aquaporin-mediated water transport in the adventitious roots (Calvo-Polanco et al. 2012). Flooding induces the development of aerenchyma and adventitious roots in soybean, and these developments were more rapid in the waterlogging-tolerant than the waterlogging-sensitive genotype (Valliyodan et al. 2014; Anonymous 2015). A tolerant genotype was able to maintain higher-energy level in terms of root ATP concentration at 7th day of flooding as compared to sensitive genotype (Valliyodan et al. 2014). Stem elongation is also another strategy where plant keeps on trying to maintain its vital organs like reproductive parts in aerobic environments. During flooding stress, stem elongation also have been reported as tolerance mechanism in soybean (Russell and Sachs 1992; Chandra et al. 2020).

Reduced level of oxygen in cells activates several mechanisms subsequently which affects plant growth. Ionic imbalance in light reaction, mitochondrial respiration, and electron transport chain led to the accumulation of free electrons which results in generation of reactive oxygen species (ROS). Increased level of superoxide radical, hydroxyl radical, and hydrogen peroxide leads to oxidative stress in plants (Ito et al. 2007; Rhoads et al. 2006; Goggin and Colmer 2005). As a consequence of ROS accumulation membrane lipids undergoes in peroxidation and thiobarbituric acid reactive substances (TBARS), malonaldehyde adducts etc. develops. In response to the accumulation of reactive oxygen species and other toxic by-products, the antioxidant defense system activates in plants. As tolerance mechanism, antioxidant enzymes such as superoxide dismutase (SOD), peroxidase, ascorbate peroxidase, glutathione reductase, and catalase also increase. Increase in level of antioxidant enzymes scavenges the ROS and provides protection against the ROS-mediated damage in plants. In addition to antioxidant enzymes, other antioxidant compounds, such as glutathione, ascorbate, and β-carotene, also play an important role in the removal of toxic oxygen compounds (Foyer et al. 1991; Hodges et al. 1996; Li et al. 2012a, b; Garcia et al. 2020). ROS also acts as signaling molecule under stress to activate the stress tolerance mechanisms, so concentration of these enzymes in waterlogged genotypes may be correlated to tolerance levels against flooding stress. In cucumber plants, ROS signal mechanisms found to play crucial role in both ethylene production and auxin-induced adventitious root formations (Qi et al. 2019). In another study, it was found that pretreatment of soybean seeds with hydrogen peroxide (H_2O_2) stimulates the waterlogging tolerance in seedlings. H_2O_2 pretreatment resulted in lower cell membrane damages, improved photosynthetic rate, and high dry matter accumulation. The researchers proposed that hydrogen peroxide pretreatment induces the tolerance in soybeans through stress memory (Andrade et al. 2018).

Phytoglobin proteins are found extensively in plants as they have an important role in the metabolism. These proteins are similar to animal hemoglobins, as they bind to oxygen and remove nitric oxide. During hypoxia, produced NO in plant tissues can be converted to oxidized product (NO_3) by oxy-phytoglobin which contribute toward increased homeostasis of cellular redox and energy potentials during hypoxia, which is known as the phytoglobin-NO cycle (Igamberdiev and Hill 2004; Nie et al. 2006). This suggests the potential for Pgbs to improve tolerance to waterlogging stress. In soybean plants, overexpression of GmPgb1 reveals about improvement of photosynthetic rate and lower development of ROS during waterlogging/submergence relative to wild-type plants. This confirms the protective role during conditions of excess moisture/waterlogging/submergence in soybean (Mira et al. 2021). Thus, under waterlogging stress, plant growth and development processes modify in a very complex manner. Mechanism of tolerance varies among the different crops, different varieties of the same crop, and different growth periods of the same genotype and vice versa.

3.3 Phenotyping for Waterlogging Tolerance

Waterlogging tolerance is a mechanism that causes minimum loss of yield in excess soil moisture conditions relative to the maximum in an optimal environment. Again, comparatively, high yield in waterlogged conditions is not typically related to high yield in an optimum environment (VanToai et al. 1994). Phenotyping for waterlogging tolerance can be performed under field as well as under greenhouse conditions in pots. Most commonly used screening criteria are visual rating (Cornelious et al. 2005) and yield (VanToai et al. 1994; Rhine et al. 2010) for characterization of waterlogging tolerance in soybean. Cornelious et al. (2005) rated the soybean plants based on the presence as well severity and frequency of chlorosis symptoms and plant death on a scale of 0–9 where score 0 was given to plants showing no symptom of damage and score 9 was given when 90% of the plants died; now, this scoring method is used worldwide with/without some modifications to identify tolerant soybean plant (Fig. 3.1) (Wu et al. 2017a; Anonymous 2019). Under greenhouse conditions, the waterlogged environment can be developed using plexiglass boxes containing porous membrane with 5 cm of silt loam, and seedlings can be transferred at the vegetative stages, after which waterlogging stress can be provided for phenotyping of tolerance level (Sallam and Scott 1987). Linkeme et al. (1998) evaluated the effect of waterlogging stress at different vegetative and reproductive growth stages in the greenhouse by submerging the pots in water tanks. Similarly, some soybean germplasm lines and an RIL population were evaluated at $V_{2\text{–}3}$ stages in pots in waterlogging structures (cemented structures where waterlogging conditions can be maintained for a specific time) for waterlogging stress and tolerant genotypes were identified at ICAR-IISR, Indore (Fig. 3.2) (Anonymous 2018, 2019).

Different soybean genotypes show variable response to excess soil moisture stress conditions, and considerable genetic variation had been observed in soybean (Srivastava et al. 2014). Response of soybean to excess soil moisture stress is mainly dependent on the growth stage at initiation, duration of stress, and texture of the soil. Tolerance to excess moisture was not found to be uniform in different growth

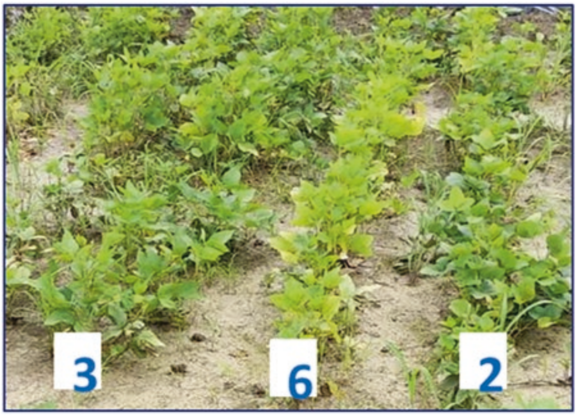

Fig. 3.1 Flooding damage score (FDS) at field-level evaluation after waterlogging stress

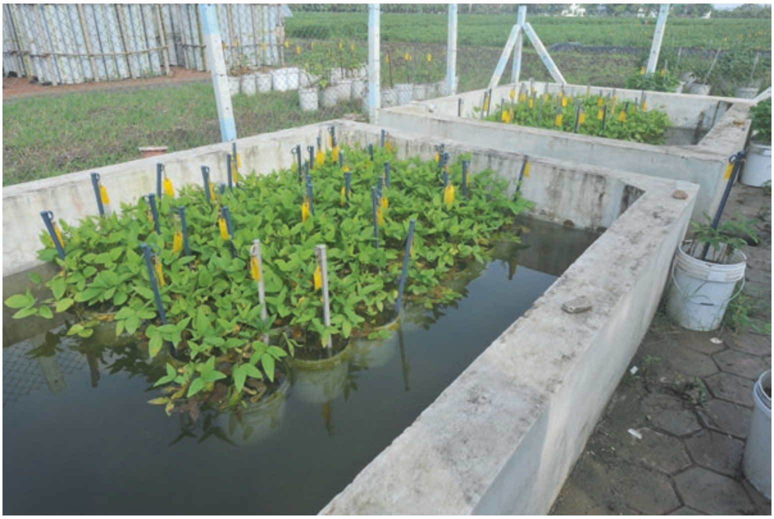

Fig. 3.2 Soybean genotypes in waterlogging structures during evaluation

stages (Sallam and Scott 1987). Reduction in canopy height was found to be greater at full flowering (R_2 stage) (Scott et al. 1989) than at the fourth trifoliate stage (V_4) (Fehr and Caviness 1977). Waterlogging stress at the flowering stage leads to severe chlorosis and stunted growth (Griffin and Saxton 1988). Waterlogging stress at the reproductive stage causes more severe yield loss as compared to stress at the vegetative stage (Linkeme et al. 1998).

The duration of stress period directly correlates with yield loss under waterlogged condition (Scott et al. 1989). Phenotyping for waterlogging tolerance at germination stage or vegetative establishing stage is done with observations of relative germination percentages, delay in coleoptile emergence, biomass/dry weight of the plant, and root architectures after waterlogging stress (Wu et al. 2017c; Rajendran et al. 2019), while at early vegetative and reproductive stage, waterlogging tolerance is being measured on the basis of plant survival rate (PSR), foliar damage score (FDS), stem elongation rate, differences in leaf chlorosis, coefficient based on yield/dry weight reduction in waterlogging stress, and other yield-related traits (Wu et al. 2017a, b; Anonymous 2018, 2019). Soil texture also plays a role in variable response to waterlogging conditions (Scott et al. 1989; Rhine et al. 2010), so type of soil environments should be similar during evaluation of genotypes.

3.4 Conventional Breeding Approaches for Improvement

Soybean is a self-pollinated crop, and conventional breeding methods, like pure line selection, pedigree method, single-seed descent method, etc., can be used for the genetic improvement of soybean crop. The main objective of any breeding program is to develop high-yielding genotypes under different environmental conditions. Waterlogging tolerance is a complex character and different characters contribute to it. Traits like root and shoot length, adventitious root formation, root surface area, and dry weight are important indicators in response to waterlogging stress. Besides the number of pods per plant, seeds per pod and 100 seed weight help in determining yield under water stress conditions (Ohashi et al. 2009). Substantial genetic variation in seed yield has been reported in soybean genotypes under waterlogged/flooded conditions. Nguyen et al. (2012) reported about loss of 40–57% in yield due to flooding stress during the reproductive stage of soybean and identified tolerant genotypes subsequently. Wu et al. (2017a) standardized the methodologies to screen soybean genotypes at R_1 and V_5 growth stages and identified the tolerant genotypes against flooding among 40 soybean genotypes studied. In a study, a total of 128 soybean genotypes were screened for pregermination anaerobic stress tolerance to waterlogging, and 10 genotypes showed germination percentage of 50–59% (Rajendran et al. 2019) identified as tolerant ones. Again, Wu et al. (2017b) evaluated 772 soybean genotypes at R_1 growth stage, and 52 genotypes were found to be tolerant for waterlogging stress. Arya et al. (2014) screened 50 genotypes at R_1 stage in small pots; during their investigation genotypes, JS 97-52, Bhatt, Cat 3299, and JS 93-05 were found relatively better based on percent increase in plant height and percent reduction in dry weight of plants. During the study of the genetics pattern of waterlogging tolerance, Anonymous (2020) reported polygenetic inheritance for foliar damage score in the F_2 population at $V_{2–3}$ stage. Shrivastava et al. (2014) evaluated 25 soybean genotypes for waterlogging tolerance and genotypes, viz., JS 95-60, JS 20-87, JS 20-69, and RVS 2007- 1, which are reported as tolerant for excessive moisture conditions. Furthermore, Shrivastava et al. (2014) also suggested the preponderance of additive gene action for seed yield plant^{-1} and yield attributes in waterlogged environment. So, there are a lot of genetic variations for traits associated with waterlogging tolerance have been recorded; some identified donors/tolerant genotypes are depicted in Table 3.1. Landraces that are highly adapted to climatic conditions are an important source of genetic materials for developing waterlogging-tolerant varieties. Wild soybean (*Glycine soja*) is also an important genetic resource for breeding varieties with improved waterlogging tolerance, and there is a possibility of increasing the genetic variability in cultivated soybean by introgression of genes from wild soybean. Hence, different germplasm should be evaluated using conventional and nonconventional methods for identifying/characterization of genes holding natural genetic variation for waterlogging tolerance so that different regulatory mechanisms can be better understood.

3.5 Molecular Breeding Approaches for Improvement

In the last some decades, accelerated progress in soybean genomics leads to several outcomes in area of molecular breeding of soybean. It resulted in recognizing of genomic regions/SNPs associated with several traits and identifying structural

Table 3.1 Potential genetic resources for waterlogging stress tolerance

Tolerant genetic resource/genotype	Source	References
Edison, GR 8836, CX 415, Archer	USA	VanToai et al. (1994, 2001)
Archer, Misuzudaiz, PI408105A, PI561271, PI567651, and PI567343	Korea	Shannon et al. (2005)
Misuzudaizu	Japan	Githiri et al. (2006)
91210-350, 91210-316	USA	Henshaw et al. (2007)
Kefeng No. 1, Peking	China	Wang et al. (2008) and Sayama et al. (2009)
Nam Vang, VND2, ATF15-1	Cambodia	VanToai et al. (2010)
AGS 313	Bangladesh	Ara et al. (2015)
JS 97-52 and JS 20-38	India	Anonymous (2015)
Iyodaizu, Kokubu 7, Maetsuezairai 90B, Yahagi	Japan	Nguyen et al. (2017) and Suematsu et al. (2017)
UA 5615C, R10-4892, R13-12552, R07-6669, Walters, R04-342, S11-25108, S12-1362, S11-25615	USA	Wu et al. (2017a)
PI 561271, PI 567651, PI 567343, PI 407184,PI 603910C, PI 567394B, PI 467162, PI 479751, PI 407229, PI 597459C, PI 424082, PI 378699A, PI 424107A, PI 366124	USA	Valliyodan (2017)

variation and copy number variations in soybean genetic resources (Kim et al. 2010; Schmutz et al. 2010). The advancement in next-generation sequencing (NGS) approaches and cheap sequencing cost has revolted soybean research in various forms of molecular tools, viz., whole-genome resequencing (WGR), de novo sequencing, genotyping by sequencing (GBS), and transcriptomic analysis. These advances have played a significant role in molecular breeding of crop through marker development such as SSRs (Hwang et al. 2009), SNPs (Kim et al. 2010; Valliyodan et al. 2017), and insertion/deletion (INDEL) markers (Song et al. 2015). Furthermore, the technical growth and availability of ample amount of SNPs have facilitated the development of high-density array-based genotyping chips such as Illumina Infinium array (SoySNP50 K iSelect Bead Chip) for _50,000 SNPs (Song et al. 2013), and Axiom Soya SNP array for approximately 180,000 SNPs (Lee et al. 2015), which are being used for the genotyping of soybean germplasm lines (Chaudhary et al. 2019). GBS is becoming one of the popular sequencing-based genotyping strategies that has significantly reduced labor and time and upgraded accuracy in identifying associated genes compared to the conventional PCR-based genotyping approach; additionally, it helps in the detection of new variants in the population of interest (Chaudhary et al. 2019).

3.5.1 QTL Mapping for Flooding Tolerance

A few studies were conducted on the genetic and molecular aspects of flooding tolerance since the last 15 years. Till now, around 30 QTLs associated with flooding/waterlogging tolerance in soybean have been documented in SoyBase (http://www.soybase.org). QTLs for waterlogging tolerance have been summarized in Table 3.2. VanToai et al. (2001) identified one QTL near to Sat_064 located on chromosome 18 which was associated with flooding tolerance, using two RIL populations. However, Reyna et al. (2003) could not find this QTL (Sat_064) associated with waterlogging tolerance in near-isogenic line (NIL) populations due to different genetic background or location/soil types of studies. Cornelious et al. (2005) had reported five QTL markers, i.e., Satt485 on chr.3, Satt599 on chr.5, and Satt160, Satt269, and Satt252 on chr. 13, associated with flooding tolerance using two RIL populations with tolerant parent Archer. Githiri et al. (2006) identified seven QTLs (ft1 to ft7) associated with yield under waterlogging stress. Three QTLs, viz., Satt531-A941V (chromosome 1), Satt648-K418_2V (chromosome 5), and Satt038--Satt275 (chromosome 18), associated with soybean flooding tolerance were identified by Wang et al. (2008). Sayama et al. (2009) identified four QTLs, viz., Sft1, Sft2, Sft3, and Sft4, using RILs derived from a cross between Peking and Tamahomare; same parents were also used by Rizal and Karki (2011) to identify genomic regions linked for flooding tolerance in terms of alcohol dehydrogenase content. Nguyen et al. (2012) identified two new QTLs associated with both flooding injury score and flooding yield index on chromosomes 11 and 13. Furthermore, Nguyen et al. (2017, 2021) fine mapped QTL for flooding tolerance using RILs (96) derived from cross Tachinagaha × Iyodaizu. Recently, Dhungana et al. (2020) identified 20 QTLs associated with flooding tolerance index based on chlorophyll content and dry weight explaining phenotypic variation ranging from 5.8% to 33.3% on nine chromosomes. However, all of these identified QTLs were discovered by the use of linkage mapping with limited recombination events (restriction resolution) in a biparental population.

3.5.2 Genome-Wide Association Mapping for Flooding Tolerance

Genome-wide association mapping strategy maps the genes or identifies the linked markers with more precision than biparental QTL mapping approach by exploiting historical and evolutionary recombination in genetically diverse mapping panel (Zhu et al. 2008). A genome-wide association studies was conducted by Yu et al. (2019) in a panel of 347 soybean germplasm to identify the quantitative trait nucleotides associated with flooding tolerance. Three seed-flooding tolerance related traits, viz., germination rate (GR), electric conductivity (EC), and normal seedling rate (NSR), using genotypic data of 60,109 SNPs. They identified three major

Table 3.2 Overview of QTLs identified for waterlogging tolerance in soybean depicting parents, mapping population, associated trait, chromosome, and markers and phenotypic variance explained

Parents involved[a]	Population/size	Traits related to drought tolerance	Linked marker(s)	Type of marker	LG/Ch No.	QTLs/genes	PVE (%)	References
Archer × Noir 1 and **Archer** × Minsoy	RILs (122), RILs (86)	Flooding tolerance in terms of yield and plant height	Sat_064	SSR	18	1 QTL	-	VanToai et al. (2001)
A5403 × **Archer** and P9641 × **Archer**	RILs (103), RILs (67)	Waterlogging injury score	Satt269, Satt385	SSR	3, 5, 13	3 QTLs	10–16	Cornelious et al. (2005)
Misuzudaizu × Moshidou Gong 503	RILs (60)	Flooding tolerance index based on seed yield	Satt100, Sat_238, A520	SSR, RFLP, AFLP	2, 6, 7, 10, 11, 14, 19	7 QTLs	6.8–49.2	Githiri et al. (2006)
Kefeng No. 1 × Nannong	RILs (184)	Flooding tolerance in terms of plant survival rate	Satt531, Satt648, Satt038	SSR	1, 5, 18	3 QTLs	4.4-7.6	Wang et al. (2008)
Peking × Tamahomare	RILs (96)	Seed flooding tolerance	Sat_175, Satt187, Satt338, Sat_279	SSR	2, 4, 8, 12	4 QTLs	-	Sayama et al. (2009)
Su88-M21 × Xinyixi-aoheidou	RILs (175)	Plant height increment and flooding injury score	Satt229-Satt527 and Satt527-Sat_286	SSR	19	2 QTLs	10.10–12.34%	Sun et al. (2010)
Peking × Tamahomare	RILs (96)	Flooding tolerance in terms of alcohol dehydrogenase content	Satt184, Sat_134, Sat_309	SSR	1, 8, 9, 13, 19	5 QTLs	14–35	Rizal and Karki (2011)

PI 408105A × S99-2281	RILs (188)	Flooding tolerance in terms of plant injury and yield index	BARC-016279-02316, BARC-024569-04982	SSR	11, 13	2 QTLs	7.7–19.7	Nguyen et al. (2012)
Tachinagaha × **Iyodaizu**	RILs (94)	Flooding tolerance in terms of root traits	Satt342, Satt469, Sat_177, Sat_342	SSR	4, 9, 11, 12, 13, 14	17 QTLs	1–23	Nguyen et al. (2017)
S99-2281 × **PI 561271**	RILs (182)	Flooding injury score	Gm03_3087237_A/G, Gm10_43840376_T/C	SNP	3, 10	2 QTLs	8.5–33.1	Ye et al. (2018)
5002T × **91210-350** and RA-452 × **Osage**	RILs (111), RILs (79)	Flooding damage score, plant survival, and chlorophyll content	Gm11_27896148_A_G, Gm13_28041039_G_A	SNP	1, 3, 6, 7, 11, 13, 14, 17, 19, 20	29 QTLs	9–29	Hummer (2018)
Linhe × **M8206** and Zhengyang × **M8206**	RILs (104), RILs (126)	Seed flooding tolerance in terms of seedling length	LDB_1_46012724, LDB_13_29032373_29059156, LDB_17_8879391_9078832	SNPLDB/SNP	1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 17, 19, 20	33 QTLs	0.5–4	Ali et al. (2020)
Paldalkong × NTS1116	RILs	Foliar damage at V_1/V_2 stage	–	SNP	10, 12, 13, and other 6 chr.	20 QTLs	5.8–33.3%	Dhungana et al. (2020)
Tachinagaha × **Iyodaizu**	NIL	Root development in seedlings	–	–	12	1 QTL	–	Hien et al. (2020)
Tachinagaha × **Iyodaizu**	RILs (94)	Seed flooding tolerance in terms of seed germination	Satt05,-Satt302	SSR	12	1 QTL	11–19%	Nguyen et al. (2021)

[a] Tolerant parent depicted in bold letters

QTNs, viz., QTN13, qNSR-10, and qEC-7-2; among the three, QTN13 was through different methods and multiple environments (Yu et al. 2019). Wu et al. (2020) conducted GWAS in a panel of 384 PIs for flooding with 42,291 SNP markers utilizing 4 different models and subsequently identified 14 SNPs associated with flooding tolerance crossways all environments and models.

3.5.3 Transcriptomic Approaches to Develop Waterlogging Tolerance

Identifying appropriate genes, transcription factor, and proteins is crucial for the development of waterlogging responsiveness. For waterlogging stress conditions, many transcriptome and proteome studies have been carried out to identify the protein involved in flood tolerance responses (Dennis et al. 2000, Ahsan et al. 2007a, b). For example, in a root proteome study on tomato seedling under flooding conditions, the change in expression of a wide range of genes has been recorded (Ahsan et al. 2007a, b). Proteomic study in germinated soybean seedlings under submergence stress also provided better understanding about molecular avenues of flooding stress in this crop (Sakata et al. 2009). Most of the protein identified in these studies is involved in adaptive responses foremost to development of aerenchyma and adventitious roots which help in overcoming deleterious side effects of flooding stress. Since transcription factors can act as repressors or inducers of gene expression in molecular pathways, waterlogging tolerance candidate genes may be either negatively or positively expressed in response to stress. Alterations in protein involved in calcium signaling and carbohydrate metabolism were observed in soybean seedling under waterlogging condition (Yin et al. 2014; Nanjo et al. 2010). Comparative proteomic analysis of differentially expressed proteins using crude proteins in soybean highlighted the importance of cell wall metabolism during flooding stress. In soybean root, ROS-scavenging and jasmonic acid biosynthesis suppresses lignification under waterlogged condition (Komatsu et al. 2010). Plasma membrane proteome analysis in soybean identified the stress signaling and antioxidant system protein which plays a crucial role in oxidative stress protection, prevention of protein degradation, and maintenance of ion homeostasis (Komatsu et al. 2009). Alam et al. (2010) investigated the proteome expression and identified the novel proteins that are differentially regulated genes (DEGs) in soybean plants at the early vegetative stage upon exposure to waterlogging stress. They identified proteins involved in carbon metabolism and other energy-related (UDP-glucose pyrophosphorylase, phosphofructokinase, cytosolic phosphoglycerate kinase, enolase, alcohol dehydrogenase, coproporphyrinogen oxidase, auxin amidohydrolase), antioxidant and nitrogen metabolism proteins, programmed cell death proteins, and some proteins of unknown function (NUDIX/mutT hydrolase family protein). Such studies on gene expression, transcriptome, and proteome provide better insight into waterlogging stress tolerance in crops. In flood-tolerant genotypes, upregulated transcript levels and enhanced protein abundance of eukaryotic aspartyl protease and glycine-rich RNA-binding protein 3 were reported as compared with wild-type soybean. This suggests that RNA metabolism plays an important role in flooding tolerance (Yin et al. 2016). Lin et al. (2019) selected Qihuang 34, a highly flooding resistance variety for better understanding of the mechanisms of submergence tolerance in soybean. In transcriptome and proteome analyses, a number of upregulated /downregulated pathways and the corresponding genes playing a role in mechanism of submergence tolerance have been identified. The metabolic pathways such as glycolysis/gluconeogenesis, fatty acid degradation, mitogen-activated protein kinase signaling, lignin biosynthesis, as well as isoflavonoid biosynthesis were upregulated. A comparative study on the expression of root-related transcription factor between contrasting cultivars was conducted in flooded soil (Valliyodan et al. 2014). Expression of gene associated with ethylene biosynthesis pathway and adventitious root formation was increased in the roots of the flooding-tolerant genotypes. They identified two MYB domain TFs, GLB1 hemoglobin and leucine zipper TF gene, during the 10-day flooding stress (Valliyodan et al. 2014). Dhungana et al. (2020) conducted RNA sequencing-based analysis of differentially expressed genes (DEGs) in the soybean leaf tissues of tolerant (“Paldalkong” and “Danbaekkong”) and susceptible (“NTS1116”) cultivars under flooding stress. Out of 22,468 genes which were differentially expressed, some genes, i.e., lipoxygenase, expansin, glutathione S-transferase, and sugar efflux transporter, were upregulated in tolerant genotypes than in the susceptible cultivar (Dhungana et al. 2020). Other than those, some abscisic acid-related TFs of basic leucine zipper domain and myeloblastosis families were also greater in the tolerant cultivars than in the susceptible genotypes (Dhungana et al. 2020). In order to adapt to waterlogging stress, plants bring adaptational changes in morphological and anatomical changes. The endogenous content of plant hormones like ethylene and gibberellic acid was reported to be high under waterlogging stress in waterlogging-tolerant lines compared to susceptible lines. On the other hand, endogenous abscisic acid content was low in tolerant cultivars as compared to susceptible cultivars (Kim et al. 2015). Under hypoxia and anoxia conditions, ethylene cross talks with other hormones such as gibberellic acid, auxin, abscisic acid, and cytokinin adapt to waterlogging stress conditions (Dat et al. 2004; Xu et al. 2006; Bailey-Serres and Voesenek 2008; Shimamura et al. 2014). The glycoside hydrolase family enzyme (xyloglucan endo-transglycosylases/hydrolases (XTH)) activity is associated with changes in abiotic stresses, and that hormones play an important role in tuning XTH activity during plant development under abiotic stress. Transgenic *Arabidopsis* overexpressing CaXTH3 showed improved tolerance to water deficit and less tolerance to high salinity than wild type (Cho et al. 2006). GmXTH genes play a significant role in regulating soybean stress responses under waterlogging conditions. Gene expression study in soybean revealed that the expression level of GmXTH genes was associated with ethylene and flooding stress. Furthermore, overexpression of the *Arabidopsis* AtXTH31 gene in soybean improved waterlogging stress tolerance in soybean (Song et al. 2018).

Plastoglobules are lipoprotein bodies in chloroplast attached to the thylakoid membrane. They store lipids and antioxidants such as carotenes, tocopherols, and plastoquinones which stabilize the photosynthetic apparatus during photo-oxidative stress under any stress (Austin et al. 2006; Vidi et al. 2006). Under drought and flood, stress-tolerant varieties contain more plastoglobin under stress than the susceptible ones (Ytterberg et al. 2006; Giacomelli et al. 2006). Plastoglobules contain ubiquitous proteins, i.e., fibrillins, which play an important role in maintaining the plastoglobule structural integrity and thus play a role in stress tolerance (Yang et al. 2006; Youssef et al. 2010). In soybean, fibrillin gene has seven isoforms. In soybean under waterlogging, stress expression level of all seven fibrillin genes was upregulated in flooding-tolerant cultivar, whereas only three fibrillin genes (FBN2, FBN7a, FBN8) were upregulated in the susceptible genotype. This suggests the possible role of fibrillin proteins by regulating the formation of plastoglobules. Proteomic analysis of soybean seedlings under flooding stress identified cytosolic ascorbate peroxidase 2 (cAPX 2) gene as an important regulator of flooding stress response. Northern hybridization results showed that the abundance of cAPX 2 transcript decreased significantly after flooding, resulting in a significant decrease in ascorbate peroxidase activity (Shi et al. 2008).

In rice, under waterlogging stress, two mechanisms of stress tolerance are involved. One escape mechanism involves gibberellic acid-mediated elongation of internodes regulated by multigenic SNORKEL1 and SNORKEL2. The second one is quiescence which involves slow growth along with the reduced activity of starch metabolism to conserve energy, mediated by SUBMERGENCE1A, SUBMERGENCE1B, and SUBMERGENCE1C (SUB1A, SUB1B, and SUB1C) (Xu et al. 2006; Hattori et al. 2009). Several rice orthologues of SNORKEL (15) and SUBMERGENCE (3) genes were reported in soybean (Syed et al. 2015). It was suggested that escape mechanism (SNORKEL1, SNORKEL2) of waterlogging tolerance is not very active in soybean. Furthermore, SUB1A gene which plays an essential role in conferring tolerance to prolonged submergence in rice (Xu et al. 2006; Bailey-Serres and Voesenek 2008; Bailey-Serres et al. 2012a, b) is absent in soybean. This indicates that in soybean, SUB1B and SUB1C genes may be more important in conferring tolerance to partial flooding conditions (Syed et al. 2015). The generation of molecular information about the differentially expressed gene transcription factor under flooded condition would be valuable to improve the flooding tolerance in soybeans.

3.6 Recent Concepts and Strategies Developed

The accessibility of genetic variations in soybean germplasm including wild relatives is critical for soybean breeding programs targeting waterlogging tolerance. But insufficient genetic diversity and limited germplasm and mutant collections restrict both basic and applied research, particularly in area of abiotic stresses. The recent availability of genome-editing tools provides ample opportunity to triumph over these limitations. These tools provide ease to use methodologies for introgression of targeted mutation/insertion/deletion and precise sequence alteration using tailored nucleases in soybean (Satpute et al. 2020). There are various genome editing tools like meganucleases, transcription activator-like effector nucleases (TALEN), zinc finger nucleases (ZFN), and clustered regularly interspaced short palindromic repeat (CRISPR)/CRISPR-associated nuclease protein (Cas) system, which have offered targeted gene modification in crop plants (Shukla et al. 2009; Li et al. 2012a, b, 2013a, b; Cermak et al. 2015). Among these, the CRISPR-Cas9 system is the easiest to use and is highly proficient. For abiotic stresses, CRISPR-Cas9 is exploited for various crop plants likewise in maize; this approach was utilized to enhance the expression level of the ARGOS8 gene (negatively regulate ethylene response) to improve moisture stress tolerance (Hirai et al. 2007). Similarly, SAPK2 and SIMAPK3 genes were targeted to improve drought tolerance in rice and tomato, respectively, using this tool (Wang et al. 2017; Lou et al. 2017). Recently, genome-editing tools were utilized in soybean for improving agronomic and seed quality traits. Haun et al. (2014) targeted fatty acid desaturase 2 gene family using TALEN for improving soybean oil quality. A new high-oleic acid (80% oleic acid) soybean cultivar has been developed utilizing TALEN tool (Calyxt Inc. 2019; Splitter 2019). For abiotic stresses, both CRISPR/Cas9 and TALEN were utilized by Curtin et al. (2018); they modified heritable changes in small RNA processing concerned to moisture stress tolerance in soybean. Similarly, desired modifications may be introgresed in potential candidate gene involved in waterlogging tolerance in soybean. This non-transgenic approach definitely would lead in development of climate-resilient soybean cultivars in future.

Recently, several advances were reported in cultural aspects to counter waterlogging stress in soybean. Nakayama et al. (2004) reported more damage of waterlogging stress during germination in soybean cultivars which have lower moisture content. Thus, sowing of seeds with optimum moisture content may be a practical strategy to manage waterlogging stress without any chemical control. Chandra et al. (2019) suggested adopting broad-bed furrow (BBF) technique for soybean sowing/cultivation in low-lying area of India which is also useful in case of drought stress. Ridging is also very efficient for avoiding waterlogging stress, especially in soil surfaces with poor drainage facilities; it improves root growth and nodulation via increased N_2 fixation in stress conditions (Takahashi et al. 2006). Yoshinaga (2012) proposed the interrow stripe tillage method, where a gap of 22 cm wide remained untilled during sowing with 45 row spacing; this strategy will improve the growth and yield of soybean in fields that had been transformed from paddies. So novel plant breeding tools (NPBT), viz., CRISPR/Cas9, TALEN, etc., along with conventional and marker-assisted breeding strategies would offer better opportunities for developing waterlogging-tolerant soybeans. Integration of genetic and novel cultural strategies to enhance the waterlogging tolerance should lead to more stable production of soybean in the world.

3.7 Conclusions and Future Perspectives

In the last two decades, extreme damage of soybean crop due to waterlogging/excessive moisture stress has been reported in different parts of the world. In the last one decade, we have witnessed a remarkable progress in soybean genomics. We have observed development of high-density genetic maps, identification of putative QTLs, EST sequencing and analysis, gene expression analysis, assembling of cDNA and oligo arrays, and sequencing and comparison of homologous segments. These resources may fasten the progress in our basic and applied research aspects in field of waterlogging tolerance in soybean. Recently, abundant progress has been made in the mapping through biparental approaches, but still there is a lot scope to identify responsible SNPs using association strategies including wild accessions. Still, a lot of phenotypic information with multiple traits needs to be generated for characterization of responsible genes of pathways/mechanisms of waterlogging tolerance. Once the fundamental gene sequence is completely distinguished, haplotype analysis of the structural variants identified in the underlying genes for waterlogging tolerance could find out novel and useful alleles. After identification of different flooding-tolerant (FT) genes, prioritization of FT genes is also important for experimental validation of each of the flooding tolerance candidate genes (Zhai et al. 2016). Recently, Lai et al. (2021) prioritized 83 flooding tolerance genes (FT genes) from 36,705 test genes collected from various genomic features linking to soybean flooding tolerance. These kinds of studies would contribute in research on variety development in soybean. Due to advances in genomics and cultural aspects, we will be able to further face the challenges of different kind of abiotic stresses in soybean cultivation.

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