BIOCHEMICAL, PHYSIOLOGICAL AND MOLECULAR ASPECTS OF WATERLOGGING TOLERANCE IN ECONOMICALLY IMPORTANT OILSEED CROPS RAPESEED, SESAME AND SOYBEAN

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Climate change poses a significant threat to agricultural sustainability. As the frequency of heavy rainfall has increased globally, waterlogging has become a pressing global issue that has a significant impact on the growth and development of oilseed crops. Due to decreased aerobic respiration in the rhizosphere, various physiological processes, including metabolic reactions, hormone production, and signaling cascades, are adversely impacted by waterlogging. These physiological changes impair reproductive health, resulting in decreased oilseed crop yields. In response to waterlogging, the most common resistance mechanisms developed by crop plants are development of aerenchyma, adventitious roots, and radial oxygen loss barrier. Consequently, the identification and selection of parents with resistance mechanisms, as well as their incorporation into breeding programmes, are essential for sustaining crop production. Thus, a better understanding of the physiological and biochemical mechanisms during waterlogging followed by identification of underlying key regulatory molecules would greatly facilitate the oilseed breeding programs. This review systematically summarizes the response of crop plants to waterlogging through adaptations and the strategies for introduction of waterlogging resistance in oilseed crops.
        Keywords: adventitious roots, aerenchyma, reactive oxygen species, signalling molecules, waterlogging tolerance

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INTRODUCTION

Optimal development of plants is achieved by maintaining the balance between root water absorption and leaf transpiration. While the requirement of sufficient water is necessary for normal growth, saturation of the soil's water-holding capacity, or stagnant water in the field, can quickly lead to waterlogging stress. Reduced root respiration and build-up of toxic chemicals caused by waterlogging stress, lead to severe yield loss(es) or even harvest failure (XU *et al.* 2013; HERZOG *et al.* 2016; TIAN *et al.* 2019; DING *et al.* 2020). To ensure sustainable agriculture in light of projections of increasingly frequent heavy rainfall and flood disasters, establishment of the cause and mechanisms underlying waterlogging tolerance has become mandatory (BAILEY-SERRES *et al.* 2012; NISHIUCHI *et al.* 2012, MONDAL *et al.* 2020).

Oilseed crops, a vital part of semi-tropical and tropical farming, store energy mostly as oil. Being a source of readily available and incredibly nutrient-rich food for both humans and animals, their economic importance has increased exponentially over the years (WEISS, 2000). Sesame (*Sesamum indicum* L.), a diploid annual species (2n=2x=26), offers one of the most nutrient-dense edible oils among the significant oilseed crops that are widely farmed around the world, including rapeseed, peanut, soybean, and sunflower (PATHAK *et al.* 2017). Being rich in natural antioxidants such as sesamol, sesamin, and sesamolin, the oil that makes up between 50 to 60% of the seed has extraordinary stability (ANILAKUMAR *et al.* 2010). Sesame oil's chemical composition, marked by a low amount of saturated fatty acids (< 15%) and high concentration of antioxidants, has been linked to a variety of health benefits, including reduced incidence of cancer (HIBASAMI *et al.* 2000, MIYAHARA *et al.* 2001) and decrease in blood pressure and cholesterol levels in humans (SANKAR *et al.* 2005). Likewise, other oilseed crops, such as Rapeseed (*Brassica napus*, AACC, 2n = 38) and Soybean (*Glycine max* L. Merr., 2n=2x=40) are cultivated for bio-diesel and high protein food/feed in addition to healthy edible oils, thus playing a significant commercial role (VALLIYODAN *et al.* 2014; PULLEN and SAEED 2015).

While droughts are a significant concern globally, floods are also a prevalent natural disaster affecting various regions around the world, particularly, Bangladesh, India, Indonesia, and Vietnam, Nigeria, Egypt, Miami, Netherlands, Brazil, Peru etc. The unpredictable climatic changes pose a serious threat to sustainable agriculture. With the increasing incidences of heavy rainfall followed by flooding, waterlogging has become a global issue that substantially reduces productivity of oilseed crops (VAN NGUYEN *et al.* 2017). Flattening of land, rising water tables, and inadequate drainage (JITSUYAMA, 2017) have all contributed to an increase in waterlogging frequency by roughly 65% over the past 25 years (CONFORTI *et al.* 2018). Indian sub-continent being surrounded by three huge water bodies is particularly vulnerable to waterlogging conditions. Waterlog-prone areas account for approximately 12.5% of India's land area, with the state of Uttar Pradesh having the largest percentage, followed by other states like Bihar, Punjab, Rajasthan, Assam, and West Bengal (SHARMA *et al.* 2021). Among oilseed crops, Sesame is highly vulnerable to waterlogging stress as waterlogging stress of 2-3 days causes a decline in output of the crop (UÇAN *et al.* 2007). Similarly, waterlogging stress has been reported to cause yield losses in rapeseed upto 55.5%, 34.9% and 93.2% at seedling establishment stage, seedling stage and maturity stage, respectively (ZOU *et al.* 2014). Among abiotic conditions causing the biggest economic losses in soybean, waterlogging ranks second following drought (MITTLER 2006; VALLIYODAN *et al.* 2014). It has been demonstrated that waterlogging in clay soil during early

vegetative or reproductive growth in soybean can impair production by as much as 27% (TAMANG *et al.* 2014). Waterlogging has been documented to have a significant impact on reproductive development, altering physiological and growth processes as well as reducing yields in a variety of plant species (EZIN *et al.* 2010; PALTA *et al.* 2010; KUMAR *et al.* 2013). Under waterlogged conditions, the roots, shoots, and nutrient uptake is impaired as a result of the decreased oxygen supply (HERZOG *et al.* 2016). Numerous factors, including changes in the soil chemistry and its' elemental profile, lower the redox potential of the soil, contributing to waterlogging-induced yield losses.

IMPACT OF WATERLOGGING ON PLANT SYSTEM

Waterlogging significantly impairs the normal biochemical and physiological functioning of oilseed crops due to declined oxygen levels in the rhizosphere, ultimately decreasing the oxygen supply to plant roots and repressing root respiration. Inhibited gaseous exchange also causes a rapid breakdown of plant hormones and reduce the plant's ability to withstand waterlogging (HATTORI *et al.* 2009; KUROHA *et al.* 2018). Reduced oxygen availability also hampers ATP synthesis (BAILEY-SERRES and VOESENEK 2008; LIMAMI *et al.* 2014), leading to build up of toxic metabolites such as lactic acid, ethanol, and aldehydes as well as an increase in reactive oxygen species (ROS), particularly hydrogen peroxide, that have lethal effect on cells causing plant senescence (TAMANG *et al.* 2014). Study by CHUGH *et al.* (2024) have demonstrated higher levels of Superoxide dismutase (SOD) in flooding tolerant sesame genotypes relative to sensitive genotypes. In addition, waterlogging leads to decrease in stomatal conductance and photosynthetic activity (ZENG *et al.* 2021). Long-term waterlogging adversely affects all the growth stages in the life cycle of a plant, which eventually reduces productivity (HERZOG et al. 2016). Research on soybean, cereals, canola, and wheat (ANDRADE *et al.* 2018; WOLLMER *et al.* 2018; ZHOU *et al.* 2020) demonstrated the vegetative stage to be the most vulnerable to flooding since plant development is impeded under stressed conditions.

RESPONSE OF PLANTS TO WATERLOGGING CONDITION

The developmental stage, duration and intensity of waterlogging determine the response of plant to the flooding stress (SHAO *et al.* 2014; WU *et al.* 2018). Plant's ability to withstand waterlogging is largely a function of the stress resistance that has evolved over the time (BORELLA *et al.* 2019). Plants respond to waterlogging stress with a myriad of physiological, biochemical, and molecular changes that help them endure the situation (ARGUELLO *et al.* 2016; HERZOG *et al.* 2016; ZHANG *et al.* 2016a; JOGAWAT 2019).

Conceptually, a plant's response to waterlogging can be separated into three stages where the first stage involves the activation of a group of signal transduction components, followed by next stage of metabolic adaptation involving fermentation pathways enzymes (ethanol, lactic acid, and alanine fermentation) and the final stage of plant tolerance, involving morphological adaptations like development of aerenchyma/gas-filled air gaps and/or adventitious roots (MUI *et al.* 2021).

Signaling transduction pathways in response to waterlogging stress

The immersion of plant organs in water alters the endogenous concentration of oxygen, carbon dioxide, ethylene, and nitric oxide, the gases essential for signal transduction pathways that result in adaptive processes including physiological, biochemical, metabolic and morphological adaptations. Amongst these, ethylene is the most constant, ubiquitous, and reliable indicator of early flooding stress (ALPUERTO *et al.* 2016; HARTMAN *et al.* 2021). Waterlogging tolerant soybean genotypes produce higher levels of endogenous ethylene as compared to the susceptible genotypes.

A group of APETALA2/ERF (AP2/ERF) TFs known as group VII ethylene response factors (ERFVIIs) play a crucial role in mediating wide range of genes involved in adaptive response to oxygen deprivation and flooding. ERFVIIs function as transcriptional activators for the genes that code for regulatory proteins and other fermentative enzymes. The loss of oxidation of the N-terminus proteins associated with ERFVIIs signals low oxygen levels. Under waterlogging, ERFVIIs mediate metabolic adaptation and developmental reprograming. Additionally, increased internode elongation is induced by ERFVIIs during waterlogging, enabling plants to grow above the water level. NO, a key signaling molecule with a functional role in response to abiotic stress, is involved in cellular processes such as PCD, ROS homeostasis, and aerenchyma production in plant organs. During hypoxia, nitrite is converted more frequently by the enzyme nitrate reductase or by the mitochondrial electron transport chain to NO, which raises NO levels. The genes encoding ACC synthase and ACC oxidase are upregulated as a result of hypoxically induced NO. Together with ERF1, NO also promotes the formation of aerenchyma. The respiratory burst oxidative homolog/NADPH oxidase (RBOH/NOX) gene, which is crucial for aerenchyma production, is induced by NO. Similar to ethylene, NO may also accumulate to larger concentrations in flooded tissues as a result of constrained gas diffusion. DOSSA *et al.* 2019 discovered the core abiotic stress-responsive genes in sesame to comprise of many TFs, with ethylene response factor (ERF), myeloblastosis viral oncogene homolog (MYB), basic helix loop helix (bHLH), and WRKY being the more predominant families. Numerous studies have highlighted the significance of ERF genes in reposnse to abiotic stimuli mediated by ethylene (ZHANG *et al.* 2004; KLAY *et al.* 2018). MMADI *et al.* (2017) identified 287 SIMYB genes expressing SIMYBs, key transcription factors involved in regulating the drought and waterlogging stress. The WRKY genes work mostly through ABA-mediated pathways and are among the top four TF families highly active in transcriptional reprogramming during stress (CHEN *et al.* 2014; PHUKAN *et al.* 2016). In a thorough investigation of the WRKY gene family in sesame, Li et al. 2017 discovered 71 SiWRKYs., of which 65 of the genes were assigned to 15 linkage groups in the sesame genome. According to an analysis of the SiWRKY gene expression patterns, 33 and 26 SiWRKYs, respectively, respond substantially to waterlogging and drought conditions. Yin et al. 2014 suggested protein phosphorylation in soybean root tips to be one way that ethylene signaling pathways contribute to plant tolerance mechanisms in the early phases of waterlogging stress.

Biochemical and Metabolic adaptation

Waterlogging-induced damage to roots causes some biochemical changes, such as decreased activity of glycolate oxidase, phosphoglycolate, and ribulose bisphosphate carboxylase (RuBPC), as well as the destruction of chloroplast membranes, which reduces the efficiency of photosynthetic electron transport and photosystem II(ASHRAF,2012). Because of this impairment

in photosynthesis, plants under waterlogging stress produce more reactive oxygen species (ROS), including superoxide (O2•), singlet oxygen ($_1O^2$), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH•) which are damaging to plants (ASHRAF, 2012) . Numerous cellular organelles, including mitochondria, chloroplasts, peroxisomes, etc., have been identified as the sources of ROS (SAIRAM and SRIVASTAVA 2002). Under waterlogging stress, insufficient O_2 causes a rise in intracellular ROS(BAILEY-SERRES and CHANG 2005; PUCCIARIELLO *et al.* 2012) that leads to lipid peroxidation, protein degradation, and enzyme inactivation. Thus, excess ROS functions as a signalling molecule in stressed plant cells. Plant NADPH oxidase is a crucial enzyme in the synthesis of ROS and is essential for the signal transduction mediated by ROS. A well-balanced antioxidant defence system, which includes enzymatic components like catalase (CAT), glutathione peroxidase (GPX), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR), as well as non-enzymatic components such as ascorbate (AsA); glutathione (GSH); tocopherols; and carotenoids helps scavenge the harmful ROS(APEL and HIRT 2004; HASANUZZAMAN *et al.* 2012). The duration of the stress and the plant genotype have a significant impact on the activity of the components in this system (HASANUZZAMAN *et al.* 2017). Another hazardous substance generated spontaneously in the glycolysis pathway under stress conditions is methylglyoxal (MG) which is detoxified by glyoxalase system, constituted by two enzymes, glyoxalase I (GlyI), which transforms MG into S-D-lactoylglutathione using GSH (SLG) and glyoxalase II (GlyII), restores GSH while converting SLG into D-lactic acid (HASANUZZAMAN *et al.* 2017). Plants are able to survive under stress conditions owing to the coordinated action of the antioxidant defence and glyoxalase systems (HASANUZZAMAN *et al.* 2012). Glutathione S-transferase DHAR2 and GSH activity have been reported to be upregulated in ethephon-treated soybean plants under waterlogging conditions, thus improving ROS scavenging (KIM *et al*. 2018). Different enzymatic activities of the youngest fully developed green leaves of sesame genotypes under control and waterlogged plants in both the waterlogging period and the recovery period showed the levels of malondialdehyde (MDA), a marker of ROS injury to biological lipids, to be higher in waterlogged plants than in control plants. Compared to the sensitive sesame genotypes, the tolerant genotypes showed enhanced SOD, POD, CAT, and proline content activities with lower MDA content (SAHA *et al.* 2017; HABIBULLA *et al.* 2021). In winter rape, uniconazole, a powerful and active member of the triazole family, enhances root development and the activities of antioxidant enzymes and chlorophyll content under waterlogged condition (LEUL and ZHOU, 1999).

In waterlogged conditions, dissolved oxygen levels are approximately 4 times lower relative to stress-free situations. Hypoxia leads to energy insufficiency and consequent suppression of root respiration, which are some of the most severe issues in plants experiencing waterlogging (LORETI *et al.* 2016). Reduced oxygen availability disturbs the electron transport chain and thus prevents the synthesis of adenosine triphosphate (ATP), which disrupts the mitochondrial respiration (BAILEY-SERRES and VOESENEK 2008; LIMAMI *et al.* 2014). Glycolysis and ethanol fermentation are the alternate pathways with which plants fulfill their energy requirement to alleviate the energy deficit resulting from waterlogging stress (BAXTER-BURRELL *et al.* 2002*)*. Alcohol dehydrogenase (ADH) and pyruvate decarboxylase (PDC) are essential components of the ethanol fermentation pathway, since the activities of these enzymes are key indicators of the level of waterlogging tolerance in a plant. By regulating the expression of genes encoding ADH,

PDC, and other related enzymes, waterlogging-tolerant plants increase the rate of fermentation to temporarily supply the requisite energy for plant development (ZHANG *et al.* 2016b). This is evident from plants including soybean and cotton, wherein up-regulation of genes involved in anaerobic metabolism, such as those encoding PDC and ADH indicates fermentation to be an essential step in the energy metabolism during waterlogging (KOMATSU *et al.* 2011; XU *et al.* 2013; ZHANG *et al.* 2015).Expression of GmADH2 gene has been reported to be increased during glycolysis and ethanol fermentation (KOMATSU *et al.* 2011).Tougou et al. 2012demonstrated the ability of GmADH2-transgenic soybeans to have better germination rate during waterlogging. The energy produced by glycolysis and fermentation can transiently overcome the energy deficiency created by the respiratory suppression in roots; however, the buildup of toxic anaerobic metabolites, such as lactic acid, alcohols, and aldehydes, ultimately proves to be detrimental over prolonged waterlogging conditions (TAMANG *et al.* 2014).
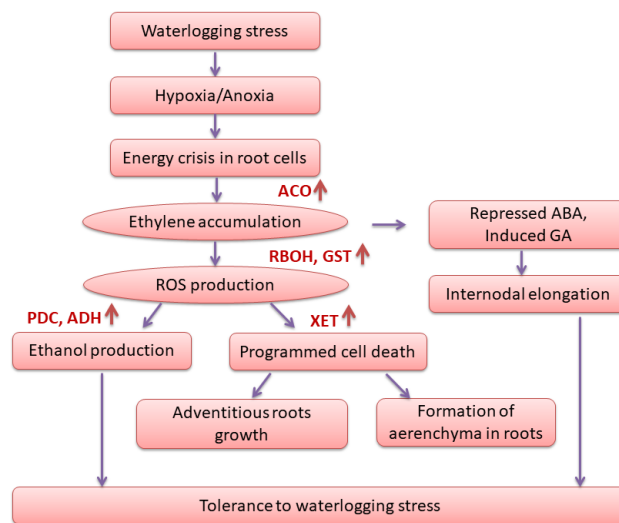

Figure 1. Schematic representation of the primary metabolic adaptations that plants use to cope with waterlogging stress. ACO: 1-amino-cyclopropane-1-carboxylic acid oxidase, RBOH: respiratory burst oxidase homolog, GST: glutathione S transferase, PDC: Pyruvate decarboxylase, ADH: Alcohol dehydrogenase, XET: xyloglucan endo-transglycosylase

Morphological and Anatomical adaptation

Several crops, including oilseed crops, exhibit distinct morphological modifications that help alleviate root respiratory depression and harm brought on by disturbed energy metabolism during waterlogging. But morphological modifications are useful only in the case of partial submersion. The classic adaptive morphological modification is the formation of adventitious roots (ARs) in the base of stem of flooding tolerant soybean genotypes as documented by SATHI

et al. 2022. ARs promote gaseous exchange in addition to water and nutrient absorption. By partially replacing the primary roots that perish under hypoxic stress, AR development has been reported to preserve metabolic cycles and promote healthy growth and development (XU *et al.* 2016; EYSHOLDT-DERZSÓ and SAUTER 2019; LIN and SAUTER 2019). Study by Wei *et al.* 2013demonstrated the resistant sesame genotype ZZM2541 to develop AR from the submerged shoots compared to susceptible genotype, Ezhi-2, which wilted and died in a fortnight under waterlogging conditions.

Another specialized tissue with continuous gas filled channels/gaps known as Aerenchyma develops in response to waterlogging conditions, facilitating the passage of oxygen from the shoots to the roots (KADEMPIR *et al.* 2013). Generally, aerenchyma formation occurs after 5 to 7 days of waterlogging in majority of oilseed crops like soybean (GARCIA *et al.* 2020, SHIMAMURA *et al.* 2010) with a few exceptions as observed in case of oilseed rape (*Brassica napus* L.), making the latter highly prone to flooding stress. Formation of extensive lysigenous aerenchyma by the roots and presence of aerenchymatous cells in the epidermis of the stressed ZZM25 sesame genotype conferred waterlogging stress tolerance in contrast to the disordered aerenchyma following collapse of parenchymatous cells in the susceptible genotype, Ezhi-2(WEI *et al.* 2013). Kim et al. 2018 demonstrated exogenous applications of ethephon, a synthetic plant growth regulator that breaks down to produce ET, to greatly enhance the occurrence of ARs on soybean plants as well as the root surface area.

Exogenous application of ethephon (ETP; donor source of ethylene) greatly raised the photosynthetic pigments and concentrations of Gibberellic acid (GA)and amino acids, promoted adventitious root initiation, increased root surface area, and dramatically increased the expression of glutathione transferases and relative glutathione activity compared to those of non-ETP-treated soybean plants (KIM *et al.* 2018).

The study of anatomical characteristics of the root and stem in sesame, soybean and rapeseed land races during waterlogging have demonstrated damage to the epidermis, hypodermis, and vascular bundle, leading to noticeable hollow stem. Thus, the tolerant genotypes are less sensitive to hypoxia than the susceptible genotypes due to the former's greater ability to grow aerenchyma in root, stem and additional adventitious roots, as well as by decreased demand for fermentative respiration and more efficient antioxidant enzyme system (SOD, APX, and CAT), capable of better coping up with ROS generated by episodes of waterlogging (WEI *et al.* 2013; JITSUYAMA 2015; SUEMATSU*et al.* 2017; NABLOUSSI *et al.* 2019; ISLAM and KHATOON 2020; LINH *et al.* 2021).

STRATEGIES FOR WATERLOGGING TOLERANCE

Hormonal induced resistance

The regulation of life cycle of a plant is strongly influenced by endogenous plant hormones, and a healthy balance among these hormones is essential for adequate metabolism, growth, and development (BARTOLI *et al.* 2013; MIRANSARI and SMITH 2014).Plants manage the balance between the synthesis and transport of plant hormones, thus controlling the response to waterlogging through complex signaling. According to several studies (BENSCHOP *et al.* 2006; YAMAUCHI *et al.* 2017; WU *et al.* 2018), plant hormones are crucial endogenous signals for the waterlogging tolerance mechanism. As an early response to waterlogging, ET production

stimulates auxin transport to waterlogged areas of the plant, and auxin build up leads to induction of aerenchyma. External application of auxin transport inhibitor 1-naphthylphthalamic acid (NPA) to tobacco, cucumber, and tomato (MCDONALD and VISSER 2003, VIDOZ *et al.* 2010, QI *et al.* 2019) led to inhibition of AR growth. The auxin polar transport carrier protein PIN (PIN-FORMED) mediates the dynamic transport of auxin in plants. DAWOOD *et al.* 2016 demonstrated suppression of the development of ARs was in PIN expression-deficient mutants of *Solanum dulcamara*, providing evidence that auxin transport was necessary for AR creation. On the contrary, soybean plants exposed to waterlogging led to decrease in the amount of IAA (SHIMAMURA *et al.* 2016). Despite physiological testing showing no appreciable difference in endogenous IAA concentration in the hypocotyl between the waterlogged and control groups after 72 hours, the hypocotyl produced ARs and aerenchyma after waterlogging period, demonstrating IAA buildup to be irrelevant for the generation of secondary aerenchyma in soybean hypocotyls. subjected to waterlogging.

Gibberellic acids (GA) primarily function by regulating cell size and quantity to govern a variety of processes involved in plant growth and development (NELISSEN *et al.* 2012). Studies on several genotypes of soybean varying in their response to waterlogging stress revealed GA content to be significantly greater in the waterlogging-tolerant lines as compared to the sensitive lines (KIM *et al.* 2015). Salicylic acid (SA) induced increased expression of stress-related genes, improves the coping ability of plants to unfavorable situations by regulating the cellular antioxidant mechanism. (ZHOU *et al.* 2009; HAYAT *et al.* 2010; ARIF *et al.* 2020). SA promotes flooding tolerance by facilitating two distinct physiological reactions (KIM *et al.* 2015). First, a rise in intracellular SA initiates programmed cell death, increasing lipid peroxidation in the root cellular walls, promoting the growth of aerenchyma cells inside the root. Second, SA buildup also promotes the development of AR primordia, thus improving waterlogging tolerance. (KIM *et al.* 2015) quantified the SA content in soybeans after 5 and 10 days of waterlogging and discovered the waterlogging-tolerant soybean genotype PI408105A to have significantly higher SA content than the control, while the waterlogging-sensitive soybean S99-2281 had no significant difference in SA content relative to the control. Thus, increased SA amount escalates gaseous exchange besides promoting AR formation, leading to waterlogging tolerance.

Jasmonic acid (JA), a fundamental plant growth hormonewell-known for abiotic stress induced defense response. However, limited studies have demonstrated a connection between JA and waterlogging tolerance (PER *et al.* 2018; FARHANGI-ABRIZ and GHASSEMI-GOLEZANI 2019; WANG *et al*. 2020a; RAZA *et al*. 2021). In waterlogged soybeans treated with JA compared to the control, 649 distinct proteins were discovered, largely connected to the stress response metabolite pathway, glycolysis, ethanol fermentation, and cell wall and cell tissue metabolism. By altering the proteome profile, JA treatment greatly decreased waterlogging-related injury to soybean plants and increased plant development (KAMAL and KOMATSU, 2016).

Abcissic acid (ABA), a key hormone for regulating water potential in plant cells, is responsible for altering the size of stomatal guard cells and is regarded as a crucial hormone in response to water stress (ZHU 2016). Waterlogging for 5-10 days has been reported to decrease the concentration of ABA in soybean hypocotyls as compared to the control group (KIM *et al.* 2015), indicating a negative connection of ABA with the ability to withstand waterlogging. However, in cotton (ZHANG *et al.* 2016b) and wheat (NAN *et al.* 2002) waterlogging significantly

increased the level of ABA. By promoting stomatal closure and accumulating more H_2O_2, ABA improved plants' tolerance to waterlogging and other harsh environmental conditions while also reducing water loss from transpiration (LIU *et al.* 2012).

Planting techniques and parental selection

One of the most crucial components of modern production technology are planting methods, which guarantees improved crop establishment besides efficient irrigation water use, particularly when the crops are sown on ridges or beds. Various studies have demonstrated the advantage of furrow and bed planting over flat planting in terms of better water use efficiency (AGGARWAL and GOSWAMI 2003). Bed planting ensures adequate spacing for light penetration, thus, sowing sesame on beds and ridges led to larger number of capsules per plant and more seed weight (ASLAM *et al.* 2015).Thus, planting sesame on beds or ridges effectively prevent water logging stress in the root zone.

As a secondary selection criterion for waterlogging tolerance, it is important to consider the value of morpho-physiological characteristics. Several characteristics are associated with waterlogging resistance during germination. (SAYAMA *et al*. 2009) reported smaller soybean seeds to exhibit a higher germination rate than larger seeds. Numerous investigations determining the role of testa in preventing cellular damage during imbibition revealed that seeds with cracked testa and seeds without testa had quicker imbibition and more solute leakage relative to seeds with intact testa and no cracks in crops like soybean, navy bean (*Phaseolus vulgaris* L.). Additionally, a brief period of seed submergence (i.e., 24 h) resulted in rapid imbibition that caused solute leakage and was linked to low seedling vigor in soybean (YAKLICH *et al.* 1979) and faba bean (KANTAR *et al.* 1996). The ability to tolerate waterlogging at germination appears to be strongly influenced by testa integrity. Similarly (HOU and THSENG 1991; UENO and TAKAHASHI 1997) established a correlation between color of the testa (seed coat) and waterlogging tolerance where dark (red/black/brown) testa genotypes in rapeseed, wheat and soybean are more resistant to waterlogging than light (white/yellow) testa genotypes (HOU and THSENG 1991; UENO and TAKAHASHI 1997). ZHANG *et al* 2008 determined dark testa genotypes in rapeseed to have higher quantities of phenolic compounds relative to sensitive light testa genotypes. The higher concentration of phenolic or tannin compounds in the testa pose barrier to imbibition (DEBEAUJON *et al.* 2000; ZAMAN *et al.* 2019), thus enhancing flooding tolerance. Thus, testa pigmentation acts as a safeguard against imbibition damage caused by waterlogging stress.

QTL mapping

Precise screening of diverse genotypes for waterlogging tolerance under controlled conditions is a pre-requisite for conducting research (SINGH *et al.* 2021; KUMAR *et al.* 2022). Accurate genotyping coupled with precise phenotyping can help dissect genomic regions underlying complex traits (MALIK *et al.* 2022). Under waterlogging stress in sesame, WANG *et al.*(2012) discovered 13,307 differentially expressed genes associated with various pathways such as glycolysis, nitrogen metabolism, starch and sucrose metabolism, and plant hormone signal transduction, suggesting the activation of pathways like glycolysis/glycogenesis. Significant alterations in the gene expression for pathways such as flavone and flavanol biosynthesis, steroid biosynthesis, photosynthesis, cysteine and methionine metabolism, glutathione metabolism, as

well as phenylpropanoid biosynthesis, spliceosome, and circadian rhythm were also discovered. Furthermore, in-depth analysis revealed a set of 1,379 genes to respond to waterlogging, of which 66 candidate genes enhancing resistance to waterlogging have been postulated (WANG *et al.* 2016). Meanwhile, six QTLs (*qWH09CHL15*, *qEZ10ZCL07*, *qWH10ZCL09*, *qEZ10CHL07*, and *qWH10CHL09*) associated with waterlogging traits were discovered (ZHANG *et al* 2014). ZHANG *et al.* 2014 reported an efficient SSR marker (ZM428) strongly associated with qWH10CHL09 for marker-assisted selection (MAS) toward waterlogging tolerance in sesame. Similarly (VALLIYODAN *et al.* 2016) identified a few cultivated germplasm lines of soybean native to USA, Archer, Misuzudaiz, PI 408105A, PI 561271, PI 567651, and PI 567343 to be prospective donors for breeding for waterlogging tolerance. (GITHIRI *et al.* 2006) used donor alleles from Misuzudaizu to map seven quantitative trait loci (QTLs) for yield under flooding stress. Using a recombinant inbred line (RIL) population and a high-density SNP map, (WANG *et al.* 2020b) discovered seventeen consensus QTLs for waterlogging tolerance using seedling death rate (SDR) as the index following total plant submersion in *Brassica napus*. Of which, three QTLs, *cqSDR.C3-2*, *cqSDR.C8-1*, and *cqSDR.C8-2*, were stably expressed in two studies, and *cqSDR.C3-2*, the largest QTL, explained between 10.30 and 23.32 percent of the phenotypic variance. Using a set of reciprocal introgression lines (ILs) produced from the cross GH01 x ZS9, (DING *et al.* 2020) discovered QTLs associated with three waterlogging tolerance-related characteristics, including relative root length (RRL), relative hypocotyl length (RHL), and relative fresh weight (RFW). At the seedling establishment stage, 66 unique QTLs were found for waterlogging tolerance, including 31 for RRL, 17 for RHL, and 18 for RFW. Twenty QTLs present in both genetic backgrounds were combined into six clusters that can be targeted in rapeseed breeding to increase waterlogging tolerance by marker-assisted selection (MAS). The summary of QTLs linked to waterlogging tolerance are listed in Table 1.

Table 1. Summary of major QTLs associated with waterlogging tolerance in rapeseed, soybean and sesame

Species	Chr	QTL	Trait	Position (Mb)	LOD	PVE	Population	Population type	Population size	Reference
Brassica napus L.	A3	*qRRL.A3b*	Relative root length	9.32	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	A3	*qRFW.A3b*	Relative fresh weight	9.32	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	A6	*qRRL.A6-2a*	Relative root length	6.96	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	A6	*qRHL.A6a*	Relative hypocotyl length	6.96	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	A6	*qRFW.A6-1a*	Relative fresh weight	6.96	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	A7	*qRRL.A7-2a*	Relative root length	10.49	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	A7	*qRFW.A7a*	Relative fresh weight	20.93	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	A7	*qRHL.A7b*	Relative hypocotyl length	22.23	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	A7	*qRFW.A7b*	Relative fresh weight	22.23	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C1	*qRFW.C1b*	Relative fresh weight	3.14	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C1	*qRHL.C1b*	Relative hypocotyl length	3.36	-	-	GH01×ZS9	IL	108	Ding et al. 2020

Brassica napus L.	C1	*qRRL.C1-1b*	Relative root length	3.84	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C1	*qRRL.C1a*	Relative root length	5.98	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C1	*qRFW.C1a*	Relative fresh weight	5.98	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C1	*qRRL.C1-2b*	Relative root length	6.45	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C3	*qRFW.C3b*	Relative fresh weight	47.57	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C3	*qRRL.C3b*	Relative root length	47.82	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C6	*qRRL.C6b*	Relative root length	34.39	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C6	*qRHL.C6b*	Relative hypocotyl length	34.34			GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C6	*qRHL.C6-2a*	Relative hypocotyl length	34.34			GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRRL.C7-1b*	Relative root length	34.86	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRHL.C7-1b*	Relative hypocotyl length	35.64	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRFW.C7-1b*	Relative fresh weight	35.64	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRRL.C7-2a*	Relative root length	36.07	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRHL.C7a*	Relative hypocotyl length	40.10	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRRL.C7-2b*	Relative root length	40.77	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRHL.C7-2b*	Relative hypocotyl length	40.77	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRFW.C7-2b*	Relative fresh weight	40.77	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRRL.C7-3b*	Relative root length	43.61	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRHL.C7-3b*	Relative hypocotyl length	43.61	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	C7	*qRFW.C7-3b*	Relative fresh weight	43.61	-	-	GH01×ZS9	IL	108	Ding et al. 2020
Brassica napus L.	A2	*qSDR.A2*	Seedling death rate	36.61	3.06	6.09	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	A5	*qSDR.A5-1*	Seedling death rate	39.61	2.61	5.31	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	A5	*qSDR.A5-2*	Seedling death rate	42.61	2.68	5.14	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	A5	*qSDR.A5-3*	Seedling death rate	51.81	5.42	11.31	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	A5	*qSDR.A5-4*	Seedling death rate	70.21	3.85	7.55	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	A5	*qSDR.A5-5*	Seedling death rate	81.81	4.45	9.23	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	A10	*qSDR.A10-1*	Seedling death rate	1.01	3.96	7.4	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	A10	*qSDR.A10-2*	Seedling death rate	16.01	2.91	5.85	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	C3	*qSDR.C3-1*	Seedling death rate	0.21	3.22	6.55	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	C3	*qSDR.C3-2*	Seedling death rate	15.31	4.47	10.3	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	C3	*qSDR.C3-3*	Seedling death rate	76.51	2.65	9.17	APL01× Holly	RIL	189	Wang et al. 2020
Brassica napus L.	C7	*qSDR.C7*	Seedling death rate	81.81	2.55	4.91	APL01× Holly	RIL	189	Wang et al. 2020

Brassica napus L.	C8	*qSDR.C8-1*	Seedling death rate	14.92	4.18	8.14	APL01×Holly	RIL	189	Wang et al. 2020
Brassica napus L.	C8	*qSDR.C8-2*	Seedling death rate	20.80	2.93	6.89	APL01×Holly	RIL	189	Wang et al. 2020
Brassica napus L.	C8	*qSDR.C8-3*	Seedling death rate	27.21	4.55	15.92	APL01×Holly	RIL	189	Wang et al. 2020
Brassica napus L.	C8	*qSDR.C8-4*	Seedling death rate	89.61	2.51	4.62	APL01×Holly	RIL	189	Wang et al. 2020
Brassica napus L.	C9	*qSDR.C9*	Seedling death rate	96.11	2.77	5.46	APL01×Holly	RIL	189	Wang et al. 2020
Glycine max L. Merr.	3	*qSFT_3-38*	Flooding tolerance	36.8-40.9 cM	5.14	11.8	Danbaekkong×NTS1116	RIL	152	Dhungana et al. 2021
Glycine max L. Merr.	3	*qSFT_3-64*	Flooding tolerance	62.8-71.3 cM	3.39	8.3	Danbaekkong×NTS1116	RIL	152	Dhungana et al. 2021
Glycine max L. Merr.	4	*qSFT_4-17*	Flooding tolerance	267.5-290.6 cM	3.51	8.2	Danbaekkong×NTS1116	RIL	152	Dhungana et al. 2021
Glycine max L. Merr.	6	*qSFT_6-86*	Flooding tolerance	200.5-215.2 cM	4.55	10.4	Danbaekkong×NTS1116	RIL	152	Dhungana et al. 2021
Glycine max L. Merr.	7	*qSFT_7-3*	Flooding tolerance	77.9-115.2 cM	3.98	30.7	Danbaekkong×NTS1116	RIL	152	Dhungana et al. 2021
Glycine max L. Merr.	7	*qSFT_7-14*	Flooding tolerance	116.3-134.5 cM	4.22	12.8	Danbaekkong×NTS1116	RIL	152	Dhungana et al. 2021
Glycine max L. Merr.	13	*qSFT_13-53*	Flooding tolerance	66.1-72.6 cM	3.64	8.1	Danbaekkong×NTS1116	RIL	152	Dhungana et al. 2021
Glycine max L. Merr.	15	*qSFT_15-67*	Flooding tolerance	125.3-140.9 cM	4.7	10.6	Danbaekkong×NTS1116	RIL	152	Dhungana et al. 2021
Glycine max L. Merr.	16	*qSFT_16-40*	Flooding tolerance	43.8-76.3 cM	3.85	9.7	Danbaekkong×NTS1116	RIL	152	Dhungana et al. 2021
Glycine max L. Merr.	16	*qSFT_16-62*	Flooding tolerance	83.7-87.2 cM	3.78	8.9	Danbaekkong×NTS1116	RIL	152	Dhungana et al. 2021
Glycine max L. Merr.	5	*Gm05*	Flooding injury	-	-	0.1	A5403×Archer	F6:11 RIL	103	Cornelious et al. 2005
Glycine max L. Merr.	13	*Gm13*	Flooding injury	-	-	0.16	A5403×Archer	F6:11 RIL	103	Cornelious et al. 2005
Glycine max L. Merr.	18	*Gm18*	Flooding injury	-		-	Archer×Minsoy	RIL	208	VanToai et al. 2001
Glycine max L. Merr.	11	*FTS-11*	Flooding injury	87 cM	8.97	19.7	PI408105A×S99-2281	F7 RIL	188	Nguyen et al. 2012
Glycine max L. Merr.	13	*FTS-13*	Flooding injury	26 cM	7.75	18.3	PI408105A×S99-2281	F7 RIL	188	Nguyen et al. 2012
Glycine max L. Merr.	3	*FTS-03*	Flooding injury	-	-	0.17–0.30	PI408105A×S99-2281	F7 RIL	188	Nguyen et al. 2012
Glycine max L. Merr.	10	*FTS-10*	Flooding injury	-	-	0.12–0.16	PI408105A×S99-2281	F7 RIL	188	Nguyen et al. 2012
Glycine max L. Merr.	3	*qWT_Gm03*	Flooding injury	-	-	18.1	S99-2281×PI 561271	F7 RIL	182	Ye et al. 2018
Glycine max L. Merr.	10	*qWT_Gm10*	Flooding injury	-	-	15.4	S99-2281×PI 561271	F7 RIL	182	Ye et al. 2018
Sesamum indicum L.	13	*qEZ09ZCL13*	Waterlogging tolerance	0 Mb	-	10.2	Zhongzhi No.13×Yiyangbai	RIL	-	Zhang et al. 2014
Sesamum indicum L.	15	*qWH09CHL15*	Waterlogging tolerance	8 Mb	-	7.55	Zhongzhi No.13×Yiyangbai	RIL	-	Zhang et al. 2014

Sesamum indicum L.	7	*qEZ10ZCL07*	Waterlogging tolerance	4.5 Mb	-		8.14	Zhongzhi No.13×Yiyangbai	RIL	-	Zhang et al. 2014
Sesamum indicum L.	9	*qWH10ZCL09*	Waterlogging tolerance	7 Mb	-		5.67	Zhongzhi No.13×Yiyangbai	RIL	-	Zhang et al. 2014
Sesamum indicum L.	7	*qEZ10CHL07*	Waterlogging tolerance	4.5 Mb	-		6.69	Zhongzhi No.13×Yiyangbai	RIL	-	Zhang et al. 2014
Sesamum indicum L.	9	*qWH10CHL09*	Waterlogging tolerance	7 Mb	-		17.19	Zhongzhi No.13×Yiyangbai	RIL	-	Zhang et al. 2014

MAS breeding

Since the mid-1990s, key genes for waterlogging tolerance have been discovered, including *Sub1* in rice(XU *et al.* 2006), *Qwt4-1*, *tfy2.1-1*, *tfy1.1-2*, *tfy1.2-1*, *tfy1.1-3*, *tfsur-2*, *tfsur-1*, *tfy1.1-1*, *tfmas*, *tfy2.1-2* in barley (LI*ET al.* 2008), and *Rps* in soybean(CORNELIOUS *et al.* 2005).Combining the tolerance features from the promising donor lines and their introgression into current cultivars can enhance flooding tolerance. QTL mapping by (VANTOAI *et al.* 2001) in two soybean recombinant inbred (RI) populations, "Archer" x "Minsoy" and "Archer" x "Noir I," comprising of two hundred eight lines identified a single QTL associated to marker sat_064 linked with waterlogging tolerance. Improvements in plant growth and grain yields of 11–18% and 47–180%, respectively, under waterlogging environments were attributed to the parent Archer. Another experiment by CORNELIOUS *et al.*(2005) employed two populations of 103 and 67 $F_{6:11}$ RI lines, respectively, to map QTLs linked with waterlogging tolerance using SMA (single marker analysis) and CIM (composite interval mapping) techniques and identified 17 and 15 SSR markers in population 1 and 2 respectively related to waterlogging tolerance. Most of the markers shared a close relationship with the *Rps* gene or QTL that confers resistance to Phytophthora (*Phytophthora sojae*). In both groups, five markers Satt59, Satt160, Satt269, Satt252, and Satt485 were linked to waterlogging tolerance (CORNELIOUS *et al.* 2005). Three waterlogging-tolerant soybean germplasm lines (S12-1362, S13-15764, and S13-15999) have been established by the University of Missouri breeding programme through MAS. The yield potential of these lines is 90 percent that of commercial checks under non-stress conditions, and they outperform commercial checks by 0.7 to 1.0 tonnes/hectare under extreme flooding conditions (VALLIYODAN *et al.* 2016). Similarly, MAS has been utilized to incorporate Sub1A allele in high-yielding rice varieties to make them submergence tolerant (SARKAR and PANDA, 2009).

CONCLUSION

The ability of oilseed crops to withstand waterlogging is largely a function of the stress resistance that has evolved over the time. The alteration of various physiological properties, such as photosynthesis, stomatal conductance, gas exchange, etc., as well as biochemical adaptations, including increased glycolysis supply, increased fermentative enzyme content, and energy depletion are defining characteristics of tolerance under waterlogging. Oilseed crops respond to waterlogging stress with a myriad of physiological, biochemical, and molecular changes that help them endure the situation. Thus, identification of the role of various endogenous phytohormones and signalling molecules need to be thoroughly investigated. Plants manage the balance between

the synthesis and transport of plant hormones, thus controlling the response to waterlogging through complex signalling. A thorough understanding of the role of transcription factors, DNA methylation patterns would greatly facilitate deciphering the molecular aspects of waterlogging. The best way to increase plant tolerance to waterlogging will be better cultivation management to lessen the direct harm that waterlogging causes to crops, and the use of cutting-edge molecular biology advanced technologies like genome editing, genetic engineering to identify the key genes regulating waterlogging tolerance and validate their functions. Thus, identification of QTLs/genomic regions associated with waterlogging tolerance followed by their introgression via MAS breeding holds potential in accelerating the breeding programs aimed at incorporating waterlogging tolerance in oilseed crops.

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BIOHEMIJSKI, FIZIOLOŠKI I MOLEKULARNI ASPEKTI TOLERANCIJE NA NAVODNJAVANJE U EKONOMSKI VAŽNIM ULJANIM USEVIMA REPE, SUSAMA I SOJE

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Izvod

Klimatske promene predstavljaju značajnu pretnju održivosti poljoprivrede. Kako se učestalost obilnih padavina povećala na globalnom nivou, preplavljivanje je postalo hitno globalno pitanje koje ima značajan uticaj na rast i razvoj uljarica. Zbog smanjenog aerobnog disanja u rizosferi, na različite fiziološke procese, uključujući metaboličke reakcije, proizvodnju hormona i signalne kaskade, negativno utiče preplavljivanje. Ove fiziološke promene narušavaju reproduktivno zdravlje, što dovodi do smanjenja prinosa uljarica. Kao odgovor na preplavljivanje, najčešći mehanizmi otpornosti koje razvijaju usevi su razvoj aerenhima, adventivnih korena i radijalne barijere za gubitak kiseonika. Shodno tome, identifikacija i odabir roditelja sa mehanizmima otpornosti, kao i njihovo uključivanje u programe oplemenjivanja, su od suštinskog značaja za održavanje biljne proizvodnje. Stoga bi bolje razumevanje fizioloških i biohemijskih mehanizama tokom preplavljivanja, praćeno identifikacijom ključnih regulatornih molekula u osnovi, u velikoj meri olakšalo programe oplemenjivanja uljarica. Ovaj pregled sistematski rezimira odgovor biljnih useva na preplavljivanje kroz adaptacije i strategije za uvođenje otpornosti na zalijevanje uljarica.