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Concept and breeding strategies for waterlogging and submerged tolerance in sesame (*Sesamum indium*)

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Abstract

Submergence or waterlogging is among the most damaging abiotic stresses in low-lying areas, and agricultural damages due to waterlogging are significant. Plant breeding techniques, either traditional or genetically engineered, may be a productive and cost-effective approach of producing crops that can grow effectively in waterlogged and submerged conditions. Marker assisted selection (MAS) is a novel and much more effective method for identifying genomic areas of crops experiencing stress that could not be identified earlier. The development of complete molecular linkage maps allows us to pyramid favorable characteristics to increase submergence tolerance via MAS. Nevertheless, due to genetic and environmental combination, having too many genes encoding a characteristic, and utilizing unsuitable populations, QTL identification was impeded to maintain adequate growth and production under waterlogged circumstances. Waterlogging responses of soybean and key cereal crops such as rice, barley, maize, and sesame identification of QTL linked to waterlogging tolerance, creation of resistant varieties, and long-term prospects. In environment, such stresses play a significant role in determining the species makeup of an ecosystem. They create economic harm on agricultural land, as well as long-term societal effects. The analysis of various aspects of the stress, especially low stress, has aided knowledge of the plant's biochemical responses to these two stresses. Field crops growth and productivity have slowed due to the harsh weather conditions. Therefore, crop damage and productivity losses are considerable. The morpho-physiological responses of crops during waterlogging, such as the formation of aerenchyma, shoot elongation, adventitious roots, and radial oxygen loss barrier in roots, antioxidant defense system, Anaerobic respiration, role of ethylene, are reviewed in this study.

Keywords: Marker assisted selection, waterlogging, submergence, anoxia, ethylene, hypoxia

1. Introduction

Sesame (Sesamum indium) is an oil seed crop which is mainly grown for the edible oil purpose. It belongs to family Pedaliaceae and usually called sesamum. It is known for its good quality oil and is familiarly recognized as the "Queen of oilseeds" due to its antibacterial, antiviral properties and many health benefits for mankind. Sesame seeds contains high amount of oil 44-57% and rich source of protein 18-25%, contains carbs 13-14% (Borchani et al., 2010) [10]. The sesame seeds are also known as" the seeds of immortality" because of presence of sesamin, sesamolin antioxidants. Based on the hull color sesame is two types; White and Black (Verma1 et al., 2021)^[64]. It contains an amino acid Tyrosine which helps in preventing anxiety and depression. To obtain the maximum yield the sesame required 25°C-37°C for its entire growing season (Terefe et al., 2012)^[60]. Northeastern India climate is well suited for the production of the sesame crop. According to Directorate of oil seed Development data West Bengal is leading in production and productivity with 2 Lakh MT and 951 kg/ha followed by Madhya Pradesh and Rajasthan (http://oilseeds.dac.gov.in). In the world Sesame seed production is high in Sudan with 981K MT. The top producers of sesame in world trend follows Sudan, Myanmar, India, Nigeria, and Tanzania. Major producers of sesame from 1991-2018 are India, Myanmar, and China. Over recent years the African countries becoming more conspicuous in sesame production because of different government initiatives (TREDGE, 2020)^[62]. We are in the world where the food demand had been growing day by day and the production or farmland is going on shrinking. So, the researchers are trying new methods and technologies to increase the food production for the coming future generations. Due to ongoing COVID-19 pandemic situation, it made the consumers to reconsider the consumption habits for the healthy lifestyle which have led to the increase in demand for the nutrient rich ingredients. The global sesame seed market is expected grow at

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compound annual growth rate (CAGR) of 2.2% around the period of 2021-2026(Mordor Intelligence)Sesame flourishes well in tough environmental circumstances and requires less amount of water, fertilizers and does not require any pesticides and fungicides because of its elevated tolerance to Pests and Diseases (Myint *et al.*, 2020) ^[45]. It is greatly tolerant to drought and deficient soil conditions, even though it is readily affected by waterlogging and other stress that leads to the reduced yield and quality of the seeds (Kole, 2019) ^[33].

Waterlogging is the common problem that occurs in the areas where the annual rainfall is high. Waterlogging depending upon the level of moisture content present in the Field soil, itis also familiar with various designations like Submergence, Soil Humidity, Floods, Hypoxia and Anoxia. Sudan the leading producer of sesame in the world, The losses caused due to the floods in Sudan in 2020 is estimated at 1,00,44,942 tonnes in which sorghum accounts for 50% and sesame accounts for 25% (FAO & GoS, 2020)^[22].



Fig 1: Production tendency of major sesame seed producing countries from 1991-2018 (Source: FAOSTAT Jul 18, 2021) [58]

2. What is waterlogging

Waterlogging is the condition that arises due to the stagnation of water in the field. This condition creates diminutionof oxygen present in the rhizosphere and reduce the availability of oxygen to the roots of plants. Because, in waterlogged or submerged soils the rate of diffusion of gases is almost 100 times lower in the flooded soil which leads to reduced gaseous exchanges between the roottissue and the atmosphere (Kennedy et al., 1992)^[32]. Due to decrease in the oxygen supply the root, shoot growth and the nutrent uptake is reduced (Meyer et al., 1985)^[40]. Waterlogging-induced yield losses are aided by a variety of reasons, including changes in soil chemistry and the elements profile, which quickly reduces. The redox potential of the soil. In wet soil, denitrification of both inorganic and organic N occurs, severely impeding plant growth and development (Muirhead, 1991)^[44]. Hypoxia stress caused by waterlogging encourages soil microorganisms to produce more N2O. In respiration, these bacteria utilise nitrate as an alternate electron acceptor. The next electron acceptors are manganese oxides, followed by iron and sulphate. This raises the concentration of soluble Fe2+ and Mn2+ in the wet soil, which frequently exceeds the hazardous limit (Marschner, 1991)^[38].

2.1 Hypoxia and Anoxia

Mesophytes normally cannot tolerate the excess soil moisture for the longer period of time only few mesophytes have the ability to do metabolic function normally under the waterlogged condition. Hypoxia, the most prevalent form of stress triggered owing to decline of oxygen beneath the optimal concentration in partial submergence for short-term. Anoxia, similar form of stress triggered owing to the complete lack of oxygen in accordance with complete submergence for longer period of time. Prolonged exposure of the plant to hypoxia condition causes wilting and death of the plant (Fukao *et al.*, 2019) ^[23]. Thus, it is important for the crop to maintain its performance when roots of the crop are exposed to waterlogging and function normally after the recovery from the hypoxia stress period in the waterlogged soil prone regions. It is familiar for waterlogging to have a long-term influence on root development, even after the stress has been removed. (Dickin & Wright, 2008) ^[17].

3. Mechanisms of waterlogging tolerance

3.1 Morphological and anatomical alterations: These are the structural adaptations that are made by the plant during waterlogging condition. Morphological adaptations are helpful only when the plant is in the partial submerged condition.

3.1.1 Rapid shoot elongation

Plants belong to some plant species showed a mechanism called low oxygen escape syndrome (LOES) and enables the very survival of the submerged tissues of the plant. Most of the plant species that are grown in waterlogged prone areas have the ability to stimulate elongation of stem or leaves. The

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stimulation of fast elongation can help the plant to reach in contact with atmosphere in the partial submerged condition, Due to fast elongation the plant may end up by dying if the energy already store in the plant got depleted before the plant emergence. In complete submergence condition the plant shows Low oxygen quiescence syndrome (LOQS) it uses the carbohydrates to generate energy in the plant for its expenses without shoot elongation. The plant starts growing only after the de-submergence. (Bailey-Serres & Voesenek, 2008) ^[8].

The submergence tolerant genotype of rice FR13 contain submerged tolerance gene SUB 1Adoes not elongate the stem in submerged condition, but it starts growing after the desubmergence. Some varieties of indica and japonica showed the elongation of stem under submerged condition to escape the submergence stress (Xu *et al.*, 2006) ^[70]. Resistance in *Rumexpalustris*to submergence is due to swift stem elongation supported by ethylene (Herzog & Pedersen, 2014) ^[28]



Source: (Striker, 2012) [59]

Fig 2: Shallow submergence plant with low oxygen escape syndrome (LOES) and Deep submergence plant with low oxygen quiescence syndrome (LOQS).

3.1.2 Adventitious root growth

Adventitous roots are araised from the stimulus of outgrowth of primordia that are pre existed in the base of the stem (Jackson *et al.*, 1981)^[30]. Wei *et al.*, (2013)^[68] done experiment in sesame genotypes Ezhi-2 and ZZM2541, In

Ezhi-2 the older leaves became pale and wilted with in 4 days and the at 15 days the Ezhi-2 endured to 100% death rate but ZZM2541 leaves were normal until 8 days & by 15 days it developed dynamic AR from the submerged shoot.



Fig 3: Morphological responses of both tolerant and intolerant genotypes in Sesame ZZM2541 (Z) and Ezhi-2 (E). where Z0, Z4, Z8, Z15 & E0, E4, E8, E15 are the day of waterlogging 0, 4, 8, 15. The black arrow in Z15 is indicating the adventitious that are formed by 15 days in ZZM2541.

3.1.3 Aerenchyma formation

Aerenchyma is a specialized tissue which is formed in many plants in the waterlogged condition it contains constant gas filled channels or spaces. The transfer of O2 from the shoots to the roots is facilitated by the aerenchyma, which provides a low-resistance internal channel (Drew *et al.*, 1985)^[20]. These formed aerenchyma allows the plants survive aerobically to maintain the growth and development of the plant under the hypoxia condition (partially availability of oxygen). However,

some amount of oxygen that is delivered to roots through the aerenchyma gets defused into the rhizosphere that provides oxygen rich environment in the rhizosphere for the growth of microorganisms which in accordance with the conditions prevent the formations of toxic productsN₂O, Fe²⁺ and Mn²⁺ (Colmer, 2003)^[12]. According to M. B. Jackson & Armstrong, (1999)^[29], there are two forms of aerenchyma in plants on basis of procedure of development: Schizogenous and Lysigenous. Schizogenous aerenchyma develops species-

The Pharma Innovation Journal

specific cell arrangements and occurs regularly in the roots of wetland species without cell demise, while the lysigenous aerenchyma have developed from programmed cell demise and cellwall autolysis to the abiotic stress response. (Evans, 2004)^[21]. Aerenchyma is normally formed withiin 5 to 7 days of waterlogging or hypoxia (Thomson et al., 1990)^[61]. In the study conducted by Wei et al., (2013) [68] ZZM2541 (waterlogging tolerant genotype of sesame) under waterlogging situation roots synthesisedthe vast lysigenous aerenchyma. Further, they discovered that presence of aerenchymatous cells in the leaf vein epidermis in the ZZM2541 that are stressed. But, they have witnessed the formed disorganized aerenchyma by the collaps of parenchymatous cells in Ezhi-2 (suseptable genotype of sesame to waterlogging).



Fig 4: Transverse section of sesame plant stem showing formation of aerenchyma. Yellow arrow indicating aerenchyma. In the experiment conducted by (ANEE, 2016)^[4] A thin transverse section of sesame stem is made at the waterlogging level and observed under digital microscope had seen the formation of different aerenchyma due to waterlogging.

3.1.4 ROL (Radial Oxygen Loss) barrier

ROL is the flux of oxygen from the roots to rhizosphere. In

partial submergence condition some portion of the leaves and shoot are in contact with the atmosphere which makes it easier for the uptake of oxygen. The Oxygen that is absorbed is transported to the roots in waterlogged or hypoxia condition to avoid root anoxia. It is vital for the transport of oxygen to root apex to continue its normal function under submerged condition (Armstrong, 1980)^[6]. The O₂ that is transported through the aerenchymas roots to the root tip may be used for metabolic purpose or lost into the rhizosphere is approximately 30-40% through the process of radial diffusion from roots (Yamauchi et al., 2018) [71]. ROL leads to the decrease in the supply of oxygen to the plant root apex and reduce the root growth in the hypoxia or partial submerged condition, But it oxygenate the soil surrounding the roots in the waterlogged condition and helps in the growth of beneficial microorganisms (M. B. Jackson, 1984). Some plants are able to reduce the loss of oxygen to rhizosphere by the formation barrier to ROL (Pedersen et al., 2021) [46]. Colmer, (2003)^[12] conducted study on spatial motif of ROL through roots uncovered the barrier is located at the basal region of roots, but no barrier at the root apex. So, even then many wetland plants have strong barrier to ROL, some amount of O_2 is released through the root apex. Release of oxygen into the rhizosphere creates O₂ rich surroundings for roots and it reduces the formation of toxic ions Fe²⁺ and Mn²⁺andsulphides (Armstrong & Armstrong, 2005)^[5]. Suberin is the main contender functioning as barrier to O₂outflow (Shiono et al., 2011; Ranatunga et al., 2011)^[57, 48]. Shiono et al., (2011)^[57] Based on the histochemical work done by him, suberin deposition is considered more important than the lignin because suberin increased before the changes in lignin. Suberin deposition on the cell wall of outer cortex in submerged condition showed the importance in ROL reduction.



Source: (Striker, 2012)^[59].

Fig 5: Showing different models of ROL (Radial oxygen loss) from the roots. (a) These are the roots without barrier to ROL in outer cortex. This, results in the loss of oxygen from all positions of the roots caused poor apex O2, and short roots under waterlogging condition. (b) These are the roots of species with strong barrier to ROL. Which results in the supply of oxygen to the root apex efficiently and oxygenates the Rhizosphere. Physical barrier to Radial loss of oxygen is due to presence of suberin deposition in the cell wall of exodermis. Suberin is indicate by red line in the (Figure 5) thickness showing the amount of it present and thickness of grey arrows showing the quantity of O2 available.

Abiko & Miyasaka, (2020)^[1] had strained adventitious roots of *Colocasia esculenta* with methylene blue they observed that there is no formation of blue coloured area in the middle of roots and blue colour is found in the root tips only. This indicate that there is leakage of oxygen in the root tips and there is no leakage in the other portion of the roots.

3.1.5 Metabolic Adaptations

The first metabolic adaptation of the plant to injury and anaerobic conditions is improved by (Crawford, 1978). Plant tissues suffer from the lack of energy due to decrease in the respiration under the hypoxia or anoxia condition in waterlogging intolerant and waterlogging tolerant genotypes (Gibbs and Greenway, 2003). The tolerant plant genotypes can overcome the energy crunch by different metabolic adaptations such as anaerobic respiration, preventing cytoplasmic acidification, Continuous energy metabolism and sugar supply, Development of antioxidants for the survival under anaerobic conditions (A Setter *et al.*, 1997)^[54].

3.1.6 Anaerobic respiration

In the presence of oxygen, plant cells produce energy by aerobic respiration, which comprises glycolysis, the TCA or Krebs cycle, and oxidative phosphorylation. In the absence of oxygen (anoxia), the Krebs cycle and oxidative phosphorylation are inhibited, and cells must resort to anaerobic respiration to meet their energy needs (Davis, 1980) ^[15]. Glycolysis and fermentation are types of anaerobic respiration. Glycolysis is the main source of energy generation under anaerobic conditions. The regeneration of NAD+, a cofactor derived from NADH, is required for the glycolytic process to continue to function (Drew, 1997)^[19]. To recycle NADH to NAD+, large amounts of pyruvate produced as a by-product of glycolysis must be transformed to alternate products. The most significant mechanism for

recycling NADH to NAD+ under oxygen deficiency is ethanol fermentation or lactate fermentation (Kennedy et al., 1992; Ricard et al., 1994) [32, 49]. Pyruvate is the substrate of pyruvate decarboxylase (PDC), which produces CO2 and acetaldehyde, which is reduced to ethanol by alcohol dehydrogenase oxidising NADH to NAD+. In lactic fermentation, pyruvate is the substrate of lactate dehydrogenase (LDH), which converts NADH to NAD+ to produce lactate. The efficiency of glycolysis and fermentation in producing energy is substantially lower than that of aerobic respiration. Furthermore, the cell is exposed to the endproducts of the glycolytic and fermentative pathways, such as ethanol, lactic acid, and CO₂. The persistence of active glycolysis and the development of fermentative metabolism have been well documented as adaptive processes for plant tolerance to anoxia (Kennedy *et al.*, 1992; Sairam *et al.*, 2008) ^[32, 51]. Anoxia is always preceded by hypoxia in a wet environment (Setter and Waters, 2003), and hypoxia is considered hypoxic pre-treatment prior to exposing the plants to anoxia (Waters et al., 1991). Hypoxia speeds up the induction of glycolytic and fermentative enzymes such aldolase and enolase, as well as ADH and PDC (Albrecht et al., 2004). This induction can help anoxic plants increase their tolerance to anoxia by improving or at least maintaining their glycolytic rate. On the set of anoxia, anoxic cells may perform lactic fermentation rather than ethanolic fermentation, but ethanol is the less degrading product of fermentation (Davies, 1980) [15]. Menegus et al., (1991) [39] The increased lactate transport out of the roots and into the surrounding medium, on the other hand, may help to prevent cytoplasmic acidification (Xia and Saglio 1992)^[69]. Furthermore, decreased cytoplasmic pH causes PDC activation and LDH inhibition (Davis, 1980)^[15], resulting in a shift from lactate to ethanolic fermentation.



Fig 6: Flow chart of aerobic and anaerobic respiration

3.2 Oxidative stress & Antioxidant defence system

Plants are subjected to oxidative stress when they are exposed to most unfavourable situations, such as hypoxia or anoxia, which results in the creation of reactive oxygen species (ROS) such as superoxide radicals, hydroxyl radicals, and hydrogen peroxide, which inhibit plant growth (Mittler et al., 2004)^[43]. High concentration of ROS can cause leaf membrane to lipid peroxidation and delipidating, damage to DNA, proteins, which leads to damage of cell membranes and cell organelles (Baxter et al., 2014). Exposure of the plant to normal O2 condition after a period of O2 stress can cause serious injury by ROS (Crawford, 1982)^[13]. The inability of the scavenging system to metabolise harmful active oxygen due to increased ROS production or decreased scavenging enzyme activity is the most common cause of oxidative stress (Yordanova et al., 2004)^[72]. Under waterlogged condition plants had developed certain endogenic antioxidant systems. They are enzymatic and non-enzymatic antioxidants components. Enzymatic components are catalase (CAT), Superoxide dismutase (SOD), Monodehydroascorbate reductase (MDHAR), Peroxidases (POX), Glutathione reductase (GR), Glutathione peroxidase (GPX), Dehydroasorbate reductase (DHAR), Glutathione s-transferase (GST). Non-Enzymatic are Glutathione (GSH), Ascorbate (AsA), Tocopherols, Carotenoids & Pro (Hasanuzzaman et al., 2012) [27]. Cajanuscajanwhen exposed to waterlogging for 6 days showed increases in SOD, GR, APX, CAT activity (Sairam et al., 2009) [53]. Oryzasativa exposed to waterlogging for 12 days they observed increase in LDH, ADH, PDC, APX, SOD, CAT & Ethylene (Damanik et al., 2010) [14]. Zea mays waterlogged for 10 days showed increase in SOD, POD, APX, CAT, GR activity (Bin et al., 2010) [10]. Vignaradiataexposed to waterlogging for 8 days showed an increase in SOD, GR, APX activity (Sairam et al., 2011)^[52]. During waterlogging experiments on Brassica juncea (L.) seedlings, Lee et al. (2014) [35] discovered that a CATencoding gene was downregulated, while SOD and POD genes were upregulated. By converting H2O2 to O2, CAT may play a role in regulating H2O2 levels. Down-regulation of this gene would result in an increase in H2O2 levels in the leaves of rape seedlings, causing photosynthetic organ damage and premature ageing. Wei et al. (2013)^[68] conducted studies on Sesamum indicum waterlogged sesame crop for 8 days and observed an increase activity of ADH, LDH, PDC, APX, SOD, MDA up to 6 days and then decreased. The information given by different researchers showed that ROS scavenging capacity of different plants can be augmented by increase in antioxidant chemicals, Oxidative damage caused due to waterlogging in the resistance genotypes can be resisted by greater antioxidant activity.

3.2.1 Enhanced accessibility of solvable carbohydrates

The amount of solvable carbohydrates presents in the roots of the plants and the enzymes that can hydrolyse carbohydrates also determines the waterlogging tolerance of a crop (Sairam *et al.*, 2009)^[53]. During the waterlogged condition the change of energy use to anaerobic from aerobic under hypoxia or anoxia condition the amount of energy required for the plant tissue is drastically reduced to very little number of ATPs produced from one molecule of glucose. It is consequently critical to maintain a high level of anaerobic metabolic rate in hypoxic or anoxic roots to provide the energy charge required to sustain metabolism in roots for plant survival (Jackson and Drew, 1984). Zeng *et al.* (1999)^[73] observed the two enzymes responsible for the sucrose hydrolysis, the enzyme activity of sucrose invertase (SI) is downregulated and the sucrose synthase is upregulated under hypoxia in maize seedlings. The roots of tolerant varieties showed higher amount of solvable carbohydrates content as compared to susceptible genotypes in pigeon pea. Further, in waterlogged tolerant genotypes it showed an increased activity of sucrose synthase by increase in the expression of mRNA for sucrose synthase, but susceptible varieties showed very low expression under hypoxia (Sairam *et al.*, 2009)^[53].

3.2.2 Role of ethylene production under waterlogged condition

Rapid build-up of ethylene in the roots is the most important adaptation under waterlogged condition shown by the tolerant plants. Ethylene is the gaseous hormone and the rate of diffusion of ET under waterlogging is very slow (Hartman *et al.*, 2019)^[26].

ACC (1-amino cyclopropane 1-carboxylic acid) is the precursor of the ethylene which increases the production of ethylene in the roots of plants under waterlogging (Bradford K. J. N. D and Yang S. F, 1980)^[31]. ACC formation can occur under anaerobic condition, but the formation of ethylene is not possible under anaerobic condition.so, it requires oxygen in the roots for the ethylene production. In the absence of oxygen, the accumulation of ACC increases to the shoot (Alamgir. H et al., 2011)^[24]. Ethylene production and the perception are essential for the formation of Adventitious roots. Vidoz et al. (2010)^[65] conducted an experiment on 4 weeks old tomato seedlings by treating with the waterlogging and above-ground portions were sprayed daily with 500 M aminoethoxy vinyl glycine (AVG), an inhibitor of ET production. As soon as plants waterlogged, plants that were not treated with AVG were submerged for 72 hours, Adventitious root primordia appeared at the base of the stem. These primordia lengthened and produced a high number of ARs within 7 days. Significantly fewer ARs were detected in tomato plants treated with AVG compared to untreated plants. Formation of aerenchyma is normally initiated by the ethylene production (M. B. Jackson & Armstrong, 1999)^[29].

4. Breeding for water logging tolerance

Breeding methods rely heavily on the presence of wild relatives, elite cultivars, and landraces to allow for the selection of superior lines for improvement (Akbar *et al.*, 2011)^[2]. Due to lack of oxygen during and after waterlogging the plants may got affected with root rot and there is decrease in growth and yield. Waterlogging or submerged tolerance is controlled by one or few genes with little effect (Mohanty H. K & Khush G. S, 1985)^[25]. Waterlogging tolerant cultivar like Zhongzhi No. 13 are crossed with the distinct genotype for the product of superior varieties with the desired traits (Wang *et al.*, 2016)^[66].

4.1 Selection of parents for breeding for water logging tolerance

Sesame genotypes that are more resistant to waterlogging during the vegetative stage were selected by an experiment in pot culture, which examined physiological responses as well as antioxidative enzyme activities. This study compared flooded (during the vegetative stage) and control (no waterlogged) conditions for four sesame genotypes: BD-6980, BD6985, BD-6992, and BD-70112.Plant height, root volume, root dry, root length weight, and leaf area per plant reduced substantially in all four sesame genotypes under waterlogged conditions as compared to the control condition during vegetative stage It was shown that waterlogged plants had a higher SPAD (Soil and Plant Analyzer Development) score as well as a higher specific leaf mass compared to controls during the waterlogging phase. All the genotypes exhibited improved root, stem, leaf, and petiole performance when it came to waterlogging tolerance. For all components, BD 6980 demonstrated greater resistance to waterlogging than any other genotype. However, most antioxidant enzyme activities such as Peroxidase (POD), Catalase (CAT), Glutathione peroxidase (GPX), Ascorbate peroxidase (APX) and Superoxide dismutase (SOD) exhibited an increasing tendency in waterlogged plants than that of control plants in all genotypes. It is believed that sesame genotype BD 6980 is extremely resistant to waterlogging because to its low MDA concentration and strong antioxidant activity, whereas the other three genotypes are somewhat tolerant (Saha et al., 2017)^[50].

Sesame genotypes for waterlogging tolerance were evaluated by Athul et al., (2017) in Kerala, India. At the seedling stage (20 days after planting), thirty genotypes were screened for waterlogging tolerance by flooding them for 24 hours, 48 hours, and 72 hours. All genotypes survived 24 and 48 hours of waterlogging, however only 17 genotypes survived 72 hours. Observations of genotypes that survived 72 hours of flooding were recorded, and the findings revealed that the genotypes differed considerably for the characteristics under investigation. The ten genotypes with the best survival percentages were chosen for the field experiment. Ayali, Sesamummalabaricum, SC 207, Thilarani, Thilak, GT 10, SV 2, TKG 308, TKG 22 and Rama. Flooding was forced in the field experiment for 72 hours, and biometrical characteristics were collected and statistically analysed. The genotypes indicated substantial differences in all the characteristics. Ayali, a native variety, had the largest yield per plant (7.46g) while Sesamummalabaricum had the lowest (2.92g). Thilak (48.6 percent) had the greatest oil content, while Sesamummalabaricum, a wild species, had the lowest (32.5 percent).

4.2 MAS (marker assisted selection) breeding for waterlogging tolerance

Since the mid-1990s, key genes important for waterlogging tolerance have been identified, making it easier for researchers to focus on modification or use. Use of such genes to create a new waterlogged-tolerant crop Rice, maize, wheat, barley, soybeans and other grains are examples. In the instance of rice, the Sub1 gene was introgressed to a specific genotype, markers aided backcrossing (MAB) types for various Land kinds, farmer preferences, and the addition of new genotypes it became feasible to create new kinds through genetic engineering.

For genetic diversity research, molecular marker methods such as random amplified polymorphic DNA (RAPD), simple sequence repeats (SSR), amplified fragment length polymorphism (AFLP), and inter simple sequence repeats (ISSR) are often utilised (Laurentin & Karlovsky, 2006)^[34]. These are the QTL for waterlogging that are identified in the mid-1990s. In Rice (*Oryzasativa* L.) theSub1 in chromosome number (Ch. 9) is identified by using the SSR marker by

marker assisted selection method (Xu et al., 2006) [70]. In Barley (Hordeumvulgare L.) tfy2.1-1, tfy1.1-2, tfy1.2-1 are identified by using RFLP marker by MAS (H. Li et al., 2008). In Maize (L.) the gene for waterlogging is identified on Ch. 4, 9 by using SSR marker by Composite interval mapping(CIM) method (Qiu et al., 2007)^[47]. Sesame is quite sensitive to waterlogging stress. After 2-3 days of waterlogging, the crop's development and yield are reduced, which is common when they are cultivated on poorly drained soils (Ucan et al., 2007) [63]. Wang et al., (2012) [67] discovered 13,307 DEGs (differentially expressed genes) for sesame during waterlogging stress. A larger investigation discovered a total of 1,379 genes as the main genes that acts in relation to waterlogging. They found 66 genes that might be candidates for increasing sesame resistance to waterlogging (Wang et al., 2016) ^[66]. Simultaneously, six OTLs (qEZ09ZCL13, qEZ10ZCL07, qWH09CHL15, qEZ10CHL07, and qWH10CHL09, qWH10ZCL09) which were related to waterlogging characteristics, and an SSR marker (ZM428) strongly linked to qWH10CHL09 was revealed as an efficacious marker for marker-assisted selection (MAS) against waterlogging tolerance (Zhang et al., 2014)^[75].

4.3 Waterlogging tolerance through genetic engineering

Manipulation of a specific gene in plant for increasing the production or tolerance to a particular stress is becoming necessary day by day (Lemay & Moineau, 2020)^[36]. The production of agronomical and horticulture crops against the climatic stress is becoming difficult, genome editing can help decreasing the environmental effect in in the production(Lemay & Moineau, 2020)^[36]. Through genetic engineering we can increase or decrease the expression of endogenous genes. The development of editing technology has ushered in a new age of discoveries in a variety of biotechnology sectors, including agricultural investigation (Doudna and Charpentier, 2014)^[18]. Nevertheless, there is one exception. There has been one documented case of gene manipulation in Stress caused by submergence/waterlogging. Yamauchi et al. (2017) modified truncated rice respiratory burst oxidase homolog (RBOHH) genes to highlight the critical function that peroxide plays This enzyme's output influences waterlogging signalling. and the development of aerenchyma. Unfortunately, homozygous plants found to be infertile, preventing further phenotyping. A new study presents an intriguing paradigm for genome editing for plant biotechnology applications. Miao et al. (2018)^[41] used Cas9 to generate mutants for all Pyrabactin resistance 1 (PYL) ABA receptors in rice and tested all combos for Among biotechnologically interesting genotypes. all conceivable combinations, pyl1/4/6 boosted growth and productivity by being free of ABA-related actual growth limitations while retaining ABA-controlled positive traits such as undesired seed sprouting, which are found in several other mutant combos. They believe that the gathered understanding of submergence/flooding stress is advanced enough to apply these types of strong gene and genome editing methods with many of its regulating branches, particularly the complicated network of TF groups. These potential innovation methods can generate variants ranging from single base editingto gene fusions and replacements and maybe even transgene-free genomes (Miki et al., 2018; Chen et al., 2018; Zhang Y. et al., 2016) [42, 11, 74]. Great number of studies have shown that WRKY gene families are expressed sturdily with the abiotic stresses, drought, salt stress and waterlogging (Diao et al., 2016) [16]. To discover sesame WRKY proteins, all Arabidopsis WRKY candidate genes were utilised as query in the Basic Local Alignment Search Tool (BLAST). There were 61 putative WRKY genes discovered in all, and anticipated protein sequences lacking a domain were excluded. Twelve differential WRKY expression SiWRKY genes were chosen, and their expression levels measured by qRT-PCR at different intervals following the beginning of each abiotic stress to validate the identification of some of the genes crucial for waterlogging and drought resistance. For both the waterlogging-tolerant and -sensitive cultivars, six SiWRKY genes were transcribed at various periods after the commencement of the waterlogging treatment (P < 0.05). During the waterlogging treatment, the expression levels of SiWRKY13, SiWRKY35, and SiWRKY43 rose, albeit every gene's expression spiked at a different period. SiWRKY35 reached its maximal expression before SiWRKY13 and SiWRKY43. Waterlogging, on the other hand, reduced the expression of SiWRKY17, SiWRKY59, and SiWRKY63. In the study conducted by them the variable expression patterns of SiWRKY genes in various cultivar tissues revealed that these genes play distinct functions in sesame growth and many display tissue-specific transcriptional pattern. Furthermore, SiWRKY gene expression studies indicated that some were significantly elevated or negatively regulated in relation to waterlogging and drought stress. These findings will aid future research into the roles of WRKY genes involved in abiotic stress responses, as well as the creation of molecular breeding strategies to improve abiotic stress tolerance in sesame (D. Li et al. 2017) [37]

5. Conclusion

In this review we had understood completely about the waterlogging and how it is affecting the crop production especially in the sesame. By this we can conclude that the waterlogging is the major problem that occurring in the sesame crop. Waterlogging tolerance is every important for the sustainability of the crop in the frequently waterlogged areas. Phenotypic based Plant breeding techniques is time consuming, and it have lot of other problems as we seen, and it is not enough for developing a plant that are tolerant to waterlogging in a short period of time. Mapping of QTLs for waterlogging tolerance is very much necessary for the identification of small effect contributed by many genes and should use techniques like MAS which increases the precision for the selection for the screening of plants in a population which is simple and precise as compared to the phenotypic selection.

6. References

- 1. Abiko T, Miyasaka SC. Aerenchyma and barrier to radial oxygen loss are formed in roots of Taro (*Colocasia esculenta*) propagules under flooded conditions. Journal of Plant Research. 2020;133(1):49-56. https://doi.org/10.1007/s10265-019-01150-6
- 2. Akbar F, Ashiq Rabbani M, Shinwari ZK, Khan SJ. Genetic divergence in sesame (*Sesamum indicum*) landraces based on qualitative and quantitative traits. Pakistan Journal of Botany. 2011;43(6):2737-2744.
- 3. Albrecht G, Kammerer S, Praanik W, Wiedenroth EM. Fructan content of wheat seedling (*Triticum aestivum L.*)

under hypoxia and following re-aeration. New Phytol. 1993;123:471-476

- 4. Anee TI. Morpho-Physiological, Yield and Oxidative Stress Responses of Sesame Under Waterlogging Stress Taufika Islam Anee Department of Agronomy Sher-E-Bangla Agricultural University June, 2016 Stress Responses of Sesame Under Waterlogging Stress. 2016.
- 5. Armstrong J, Armstrong W. Rice: sulphide–induced barriers to root radial oxygen loss, Fe2+ and water uptake, and lateral root emergence. Annals of Botany. 2005;96:625-638.
- 6. Armstrong W. Aeration in Higher Plants. Advances in Botanical Research. 1980;7(C):225-332. https://doi.org/10.1016/S0065-2296(08)60089-0
- Athul V. Evaluation of sesame genotypes for tolerance to waterlogging. M. Sc. (Ag.) Thesis, Kerala Agricultural University, Thrissur. 2016, 50-75.
- Bailey-Serres J, Voesenek LACJ. Flooding stress: Acclimations and genetic diversity. Annual Review of Plant Biology, 2008;59:313-339. https://doi.org/10.1146/annurev.arplant.59.032607.09275 2
- Bin T, Shang-zhong XU, Zou XL, Zheng YL, Qi FZ. Changes of antioxidative enzymes and lipid peroxidation in leaves and roots of waterlogging-tolerant and waterlogging-sensitive maize genotypes at seedling stage. Agric. Sci. China. 2010;9:651-661.
- Borchani C, Besbes S, Blecker C, Attia H. Chemical Characteristics and Oxidative Stability of Sesame Seed, Sesame Paste, and Olive Oils. J Agr. Sci. Tech. 2010;12:585-596.
- Chen L, Li W, Katin-Grazzini L, Ding J, Gu X, Li Y, et al. A method for the production and expedient screening of CRISPR/Cas9-mediated non-transgenic mutant plants. Hortic. Res. 2018;5:13. DOI: 10.1038/s41438-018- 0023-4
- Colmer TD. Long-distance transport of gases in plants: A perspective on internal aeration and radial oxygen loss from roots. Plant, Cell and Environment. 2003;26(1):17-36. https://doi.org/10.1046/j.1365-3040.2003.00846.x
- Crawford RMM. Physiological responses to flooding. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology, new series, vol. 12B, Physiological plant ecology II. Springer, Berlin, Germany. 1982, 453-477
- Damanik RI, Maziah M, Ismail MR, Ahmad S, Zain AM. Responses of the antioxidative enzymes in Malaysian rice (*Oryza sativa* L.) cultivars under submergence condition. Acta Physiol. Plant. 2010;32:739-747.
- 15. Davies DD. Anaerobic metabolism and the production of organic acids. In: Davies DD (ed) The biochemistry of plants. Academic Press, NY, USA. 1980;2:581-611.
- 16. Diao WP, Snyder JC, Wang S, Bin Liu JB, Pan BG, Guo GJ, *et al.* Genome-wide identification and expression analysis of WRKY gene family in *capsicum annuum* L. Frontiers in Plant Science. 2016;7(FEB2016):1-15. https://doi.org/10.3389/fpls.2016.00211
- Dickin E, Wright D. The effects of winter waterlogging and summer drought on the growth and yield of winter wheat (*Triticum aestivum* L.). European Journal of Agronomy. 2008;28(3):234-244. https://doi.org/10.1016/j.eja.2007.07.010
- 18. Doudna JA, Charpentier E. The new frontier of genome

engineering with CRISPR-Cas9. Science. 2014;346:1258096. DOI: 10.1126/science.1258096

- 19. Drew MC. Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. Annu Rev Plant Physiol Plant Mol Bio. 1997;48:223-250.
- Drew MC, Saglio PH, Pradet A. Larger adenylate energy charge and ATP/ADP ratios in aerenchymatous roots of *Zea mays* in anaerobic media as a consequence of improved internal oxygen transport. Planta. 1985;165(1):51-58. https://doi.org/10.1007/BF00392211
- 21. Evans DE. Aerenchyma formation. New Phytologist. 2004;161(1):35-49. https://doi.org/10.1046/j.1469-8137.2003.00907.x
- FAO, GoS. The Sudan 2020 Flood impact rapid assessment. 2020 Sept. http://www.fao.org/3/cb1463en/cb1463en.pdf

http://www.fao.org/3/cb1463en/cb1463en.pdf 23. Fukao T, Barrera-Figueroa BE, Juntawong P, Peña-

- 23. Fukao 1, Barrera-Figueroa BE, Juntawong P, Pena-Castro JM. Submergence and waterlogging stress in plants: A review highlighting research opportunities and understudied aspects. Frontiers in Plant Science. 2019;10(3):1-24. https://doi.org/10.3389/fpls.2019.00340
- 24. Alamgir H, Uddin SN. Mechanisms of waterlogging tolerance in wheat: morphological and metabolic adaptations under hypoxia or anoxia, Australian Journal of Crop Science. 2011;5(9):1094-1110.
- 25. Mohanty HK, Khush GS. Diallel analysis of submergence tolerance in rice, *Oryza sativa* L, eoretical and Applied Genetics. 1985;70(5):467-473.
- 26. Hartman S, Liu Z, Van Veen H, Vicente J, Reinen E, Martopawiro S, *et al.* Ethylene-mediated nitric oxide depletion pre-adapts plants to hypoxia stress. Nat. Commun. 2019;10:1-9.
- 27. Hasanuzzaman M, Hossain MA, da Silva JAT, Fujita M. Plant responses and tolerance to abiotic oxidative stress: antioxidant defense is a key factor. In: Bandi, V., Shanker, A. K., Shanker, C. and Mandapaka, M. (eds) 91 Crop stress and its management: perspectives and strategies. Springer, Berlin. 2012a, 261-316.
- Herzog M, Pedersen O. Partial versus complete submergence: Snorkelling aids root aeration in Rumex palustris but not in R.acetosa. Plant, Cell and Environment. 2014;37(10):2381-2390. https://doi.org/10.1111/pce.12284
- Jackson MB, Armstrong W. Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. Plant Biology. 19991(3):274-287. https://doi.org/10.1111/j.1438-8677.1999.tb00253.x
- 30. Jackson Michael B, Drew MC, Giffard SC. Effects of applying etnylene to the root system of Zea mays on growth and nutrient concentration in relation to flooding tolerance. Physiologia Plantarum. 1981;52(1):23-28. https://doi.org/10.1111/j.1399-3054.1981.tb06028.x
- 31. Bradford KJND, Yang SF. Xylem transport of 1aminocyclopropane-1-carboxylic acid, an ethylene precursor, in waterlogged tomato plants, Plant Physiology. 1980;65:322-326.
- Kennedy RA, Rumpho ME, Fox TC. Anaerobic metabolism in plants. Plant Physiology. 1992;100(1):1-6. https://doi.org/10.1104/pp.100.1.1
- Kole C. Genomic designing of climate-smart oilseed crops. In Genomic Designing of Climate-Smart Oilseed Crops. 2019, (100). Springer International Publishing. https://doi.org/10.1007/978-3-319-93536-2

- Laurentin HE, Karlovsky P. Genetic relationship and diversity in a sesame (*Sesamum indicum*) germplasm collection using amplified fragment length polymorphism (AFLP). BMC Genetics. 2006;7:1-10. https://doi.org/10.1186/1471-2156-7-10
- 35. Lee Y-H, Kim K-S, Jang Y-S, Hwang J-H, Lee D-H, Choi I-H. Global gene expression responses to waterlogging in leaves of rape seedlings. Plant Cell Rep. 2014;33:289-299. DOI: 10.1007/s00299-013-1529-8
- 36. Lemay ML, Moineau S. How are genes modified? Crossbreeding, mutagenesis, and CRISPR-Cas9. In Genetically Modified and Irradiated Food: Controversial Issues: Facts versus Perceptions. Elsevier Inc. 2020. https://doi.org/10.1016/B978-0-12-817240-7.00003-6
- 37. Li D, Liu P, Yu J, Wang L, Dossa K, Zhang Y, *et al.* Genome-wide analysis of WRKY gene family in the sesame genome and identification of the WRKY genes involved in responses to abiotic stresses. BMC Plant Biology. 2017;17(1):1-19.

https://doi.org/10.1186/s12870-017-1099-y

- Marschner H. Mechanisms of adaptation of plants to acid soils. Plant and Soil. 1991;134(1):1-20. https://doi.org/10.1007/BF00010712
- 39. Menegus F, Cattaruzza L, Mattana M, Beffagna N, Ragg E. Response to anoxia in rice and wheat seedlings. Changes in the pH of intracellular compartments, glucose-6-phosphate level, and metabolic rate. Plant Physiol. 1991;95:760-767.
- 40. Meyer WS, Barrs HD, Smith RCG, White NS, Heritage AD, Short DL. Effect of irrigation on soil oxygen status and root and shoot growth of wheat in a clay soil. Australian Journal of Agricultural Research. 1985;36(2):171-185. https://doi.org/10.1071/AR9850171
- Miao C, Xiao L, Hua K, Zou C, Zhao Y, Bressan RA, *et al.* Mutations in a subfamily of abscisic acid recepto genes promote rice growth and productivity. Proc. Natl. Acad. Sci. U.S.A. 2018;115:6058-6063. DOI: 10.1073/pnas.1804774115
- 42. Miki D, Zhang W, Zeng W, Feng Z, Zhu J-K. CRISPR/Cas9- mediated gene targeting in Arabidopsis using sequential transformation. Nat. Commun. 2018;9:1967. DOI: 10.1038/s41467-018-04416-0
- 43. Mittler R, Vanderauwera S, Gollery M, Breusegem FV. Reactive oxygen gene network of plants. Trends Plant Sci. 2004;9:490-498.
- 44. Muirhead WA. Flood Irrigation of Wheat on a Transitional Red-brown Earth. 1988, 1991.
- 45. Myint D, Gilani SA, Kawase M, Watanabe KN. Sustainable sesame (*Sesamum indicum*) production through improved technology: An overview of production, challenges, and opportunities in Myanmar. Sustainability (Switzerland). 2020;12(9):1-21. https://doi.org/10.3390/SU12093515
- 46. Pedersen O, Sauter M, Colmer TD, Nakazono, M. Regulation of root adaptive anatomical and morphological traits during low soil oxygen. New Phytologist. 2021;229(1):42-49. https://doi.org/10.1111/nph.16375
- 47. Qiu F, Zheng Y, Zhang Z, Xu S. Mapping of QTL associated with waterlogging tolerance during the seedling stage in maize. Annals of Botany. 2007;99(6):1067-1081. https://doi.org/10.1093/aob/mcm055

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- 48. Ranathunge K, Lin J, Steudle E, Schreiber L. Stagnant deoxygenated growth enhances root suberization and lignification's, but differentially affects water and NaClpermeabilities in rice (*Oryzasativa* L.) roots. Plant, Cell & Environment. 2011;34:1223-1240.
- 49. Ricard B, Couee I, Raymond P, Saglio PH, Saint-Ges V, Pradet A. Plant metabolism under hypoxia and anoxia. Plant Physiol Biochem. 1994;32:1-10.
- 50. Saha R, Ahmed F, Mokarroma N, Rohman M, Golder P. Physiological and biochemical changes in waterlog tolerant sesame genotypes. SAARC Journal of Agriculture. 2017;14(2):31-45. https://doi.org/10.3329/sja.v14i2.31243
- 51. Sairam RK, Kumutha D, Ezhilmathi K, Deshmukh PS, Srivastava GC. Physiology and biochemistry of waterlogging tolerance in plants. Biol Plant. 2008;52:401-412.
- 52. Sairam RK, Dharmar K, Lekshmy S, Chinnusam V. Expression of antioxidant defense genes in mung bean (*Vigna radiata* L.) roots under waterlogging is associated with hypoxia tolerance. Acta Physiol. Plant. 2011;33:735-744.
- 53. Sairam RK, Kumutha D, Ezhilmathi K, Chinnusamy V, Meena RC. Water-logging induced oxidative stress and antioxidant enzymes activity in pigeon pea. Biol. Plant. 2009;53:493-504.
- 54. Setter TL, Ellis M, Laureles EV, Ella ES, Senadhira D, Mishra SB, *et al.* Physiology and genetics of submergence tolerance in rice. Ann Bot. 1997;79(A):67-77.
- 55. Settler TL, Waters I. Reviews of prospects for germplasm improvement for waterlogging tolerance in wheat, barley and oats. Plant Soil. 2003;253:1-34.
- 56. Sharma P Jha AB, Dubey RS, Pessarakli M. Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Bot. 2012, 217037.
- Shiono K, Ogawa S, Yamazaki S, Isoda H, Fujimura T, Nakazono M, *et al.* Contrasting dynamics of radial O2– loss barrier induction and aerenchyma formation in rice roots of two lengths. Annals of Botany. 2011;107:89-99.
- 58. Source: FAOSTAT (Jul 18, 2021). (n.d.). 2021. http://www.fao.org/faostat/en/#compare
- 59. Striker GG. Flooding Stress on Plants: Anatomical, Morphological and Physiological Responses. Botany, March. 2012, 3-28.
- 60. Terefe *et al.* Sesame Production Manual. 2012 March. https://www.researchgate.net/publication/301771324_Ses ame_production_manual
- 61. Thomson CJ, Armstrong W, Waters I, Greenway H. Aerenchyma formation and associated oxygen movement in seminal and nodal roots of wheat. Plant, Cell & Environment. 1990;13(4):395-403. https://doi.org/10.1111/j.1365-3040.1990.tb02144.x
- 62. Tredge MI. 2020 Industry Report : Sesame Seed Sesame Seed Market : The Queen of. November. 2020.
- 63. Uçan K, Killi F, Gençoğlan C, Merdun H. Effect of irrigation frequency and amount on water use efficiency and yield of sesame (*Sesamum indicum*) under field conditions. Field Crops Research. 2007;101(3):249-258. https://doi.org/10.1016/j.fcr.2006.11.011
- 64. Vermal H, Sakuonuo Theunuol AK, Baishyal LK, MK, Rajkhowal DJ. Prospects of Sesame Cultivation in

NorthEastern India. Bioticainternational. 2021;3(5):330-331.

- Vidoz ML, Loreti E, Mensuali A, Alpi A, Perata P. Hormonal interplay during adventitious root formation in flooded tomato plants. Plant J. 2010;63:551-562. DOI: 10.1111/j.1365-313x.2010.04262.x
- 66. Wang L, Li D, Zhang Y, Gao Y, Yu J, Wei X, *et al.* Tolerant and susceptible sesame genotypes reveal waterlogging stress response patterns. PLoS ONE. 2016;11(3):1-18.

https://doi.org/10.1371/journal.pone.0149912

- Wang L, Zhang Y, Qi X, Li D, Wei W, Zhang X. Global gene expression responses to waterlogging in roots of sesame (*Sesamum indicum*). Acta Physiologiae Plantarum. 2012;34(6):2241-2249. https://doi.org/10.1007/s11738-012-1024-9
- Wei W, Li D, Wang L, Ding X, Zhang Y, Gao Y, Zhang X. Morpho-anatomical and physiological responses to waterlogging of sesame (*Sesamum indicum*). Plant Science. 2013, 2018 Nov;208:102-111. https://doi.org/10.1016/j.plantsci.2013.03.014
- 69. Xia JH, Saglio PH. Lactic acid efflux as a mechanism of hypoxic acclimation of maize root tips to anoxia. Plant Physiol. 1992;100:40-46
- 70. Xu K, Xu X, Fukao T, Canlas P, Maghirang-Rodriguez R, Heuer S, *et al.* Sub1A is an ethylene-response-factorlike gene that confers submergence tolerance to rice. Nature. 2006;442(7103):705-708. https://doi.org/10.1038/nature04920
- 71. Yamauchi T, Colmer TD, Pedersen O, Nakazono M. Regulation of root traits for internal aeration and tolerance to soil waterlogging-flooding stress. Plant Physiology. 2018;176(2):1118-1130. https://doi.org/10.1104/pp.17.01157
- 72. Yordanova RY, Christov KN, Popova LP. Antioxidative enzymes in barley plants subjected to soil flooding. Environ. Exp. Bot. 2004;51:93-101.
- 73. Zeng Y, Avigne WT, Koch KE. Rapid repression of maize invertase by low oxygen: Invertase/sucrose synthase balance, sugar signaling potential and seedling survival. Plant Physiol. 1999;121:599-608.
- 74. Zhang Y, Liang Z, Zong Y, Wang Y, Liu J, Chen K, *et al.* Efficient and transgene-free genome editing in wheat through transient expression of CRISPR/Cas9 DNA or RNA. Nat. Commun. 2016;7:12617. DOI: 10. 1038/ncomms12617
- 75. Zhang Y, Wang L, Li D, Gao Y, Lu H, Zhang X. Mapping of sesame waterlogging tolerance QTL and identification of excellent waterlogging tolerant germplasm. Sci. Agric. Sin. 2014;47:422-430.