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Nitrogen Use Efficiency in Rice under Abiotic Stress: Plant Breeding Approach

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Abstract

Nitrogenous fertilizer has remarkably improved rice (*Oryza sativa* L.) yield across the world since its discovery by Haber-Bosch process. Due to climate change, future rice production will likely experience a wide range of environmental plasticity. Nitrogen use efficiency (NUE) is an important trait to confer adaptability across various abiotic stresses such as flooding, drought and salinity. The problem with the increased N application often leads to a reduction in NUE. New solutions are needed to simultaneously increase yield and maximize the NUE of rice. Despite the differences among flooding, salinity and drought, these three abiotic stresses lead to similar responses in rice plants. To develop abiotic stress tolerant rice varieties, speed breeding seems a plausible novel approach. Approximately 22 single quantitative trait loci (QTLs) and 58 pairs of epistatic QTLs are known to be closely associated with NUE in rice. The QTLs/genes for submergence (*SUB1A*) tolerance, anaerobic germination (*AG*, *TPP7*) potential and deepwater flooding tolerance (*SK1*, *SK2*) are identified. Furthermore, phytochrome-interacting factor-like14 (*OsPIL14*), or loss of function of the slender rice1 (*SLR1*) genes enhance salinity tolerance in rice seedlings. This review updates our understanding of the molecular mechanisms of abiotic stress tolerance and discusses possible approaches for developing N-efficient rice variety.

Keywords: abiotic stress, crop establishment, climate change, QTLs, food security

1. Introduction

Nitrogen is the most abundant (78%) of the atmosphere in gaseous form as an N_2 molecule. But it is not directly available to the plants for their growth and development [1]. It is the foremost important major essential nutrient element involved in the physiological processes in plants. Globally, nitrogen deficiency is a crucial growth-limiting factor for plants, especially under abiotic stresses. The nitrogen use efficiency (NUE) is defined as the output of any crop plant per unit of nitrogen applied under a specific set of soil and climatic conditions [2]. Agronomist usually considers the amount of rough rice produced per unit of nitrogen applied as the

efficiency of nitrogen, but physiologist defined it as the amount of rough rice produced per unit of nitrogen absorbed [3, 4]. The latter is also termed as N utilization efficiency. Apparent N recovery is based on N uptake measurement in the above-ground plant parts and assumes that fertilized and control crops absorb the same amount of soil N. On the other hand, physiological and agronomic efficiencies are based on grain yield rather than total dry matter production. However, the enhancement of NUE under an abiotic stressful environment has paramount importance to the future rice breeder.

Rice (*Oryza sativa* L.) is grown in a wide range of ecosystems from the tropic to the temperate regions, but productivity is severely tormented by various abiotic stresses [5, 6]. Farmers may encounter flooding or waterlogging if heavy rain occurs immediately after seeding before or after transplanting. The flooding can cause complete crop failure because of the high sensitivity of rice to anaerobic conditions caused by flooding during germination [7, 8]. There are various forms of flooding caused by directly from heavy rains and/or flooding from adjacent rivers, leading to drastic reductions in rice yield, ranging from 0.5 to 2.0 t ha⁻¹ [9]. Flash floods are relatively short durations, prevailing some days to a couple of weeks. Apart from this, stagnant flooding (30–50 cm water depth) may occur at any time of the monsoon. Sometimes, the stagnant flooding may have coincidence with the flash flood resulting in severe impacts on rice production. In deepwater areas, stagnant water present from 0.5 m to a few meters in the field, usually for 4–6 months. The depth of water in some of these deepwater areas can exceed 4 m as in floating-rice areas. Rice breeders have been trying to develop a unique rice variety having specific adaptive traits to tackle these types of floods [10–12]. Recently, the Bangladesh Rice Research Institute has developed a deepwater rice variety, BRRI dhan91, for the deepwater ecosystem. However, the application of nitrogenous fertilizer is very challenging to the deepwater rice field and the NUE of this ecosystem is not yet been well investigated.

Another one among the most important abiotic stresses is drought. Despite the importance of drought as a major factor in yield reduction in rainfed ecosystems, few efforts have been made to develop high-yielding drought-tolerant rice variety. Impending rice production will experience a range of drought stress. The root architectural plasticity is taken into accounts as a very important characteristic to confer tolerance to drought stress [13]. Deciphering the genetic and molecular mechanisms controlling root phenotypic plasticity is important for effective screening, selection and rice breeding efforts. Despite the likely genetic complexity behind the regulation of trait expression in line with environmental conditions, phenotypic plasticity is heritable and selectable. The QTLs have been identified incur for plasticity in aerenchyma development and lateral root growth in response to drought stress in rice [14]. These QTLs can be used in advanced breeding for the development of a drought-tolerant rice variety. Due to global climate change, rice crops will face diverse stresses, including prolonged drought stress, poor soil fertility, and unpredictable rainfall. Rice establishment, either by transplanting or direct seeding, depends upon the rainfall pattern. Therefore, the identification of root phenotypic plasticity traits suitable for adaptation to the particular range of conditions faced by rice crops, as well as the genetic regions responsible for those plasticity traits, may facilitate selection for wide adaptation of rice genotypes to variable conditions to confer sustainable yield. Quantification of root architectural plasticity possesses significant value to detect which root traits may play the pivotal roles in rice adaptability to drought. It is reported that the most plastic genotypes in root traits may show the most yield stability under various dynamics of drought stress [11]. In this regard, many drought-tolerant cultivars, like N22 and Moroberekan, have been selected from rainfed ecosystems through traditional processes. These cultivars

harbor genes for tolerance to abiotic stresses, including a wide range of drought [15]. But due to their low yield potential and poor grain quality, farmers and consumers are reluctant to prefer these cultivars. This provides a unique opportunity for rice breeders to develop high-yielding drought-tolerant varieties.

Salinity is another major abiotic stress that is globally distributed in both irrigated and non-irrigated areas [16, 17]. On a global basis, salinity stress ranked second after the drought [18]. Salt stress affects many aspects of rice growth and development, especially during seed germination and seedling growth [19]. It is one of the most prevalent environmental threats to global agricultural productivity, especially in arid and semi-arid climates, where population growth, water shortage and land degradation are major concerns [1, 20]. Salt-affected soils are identified by high electrical conductivity (EC), sodium adsorption ratio (SAR) and pH, calcareousness, poor organic matter, less biological activity and imbalance in physical soil conditions. Salinity causes toxicities of ions like Na^+ and Cl^- , osmotic stress and ionic imbalance to the root zone or in the soil body, including soil impermeability [21], resulting in nutrient uptake problems in rice plant. Salt stress is the osmotic stress expressed on seedling to the reproductive stage when they are growing under high saline conditions. The N is the essential element for the synthesis of chlorophyll, amino acids, nucleic acids, and proteins. Reduction in plant dry matter is sometimes observed under severe NaCl salt stress and N deficiency. This phenomenon possibly happens because of the decrease in sugar or starch accumulation [1, 22]. The NUE of nitrogenous fertilizers in saline soil depends upon its mineralization pattern, soil salinity levels, soil texture, temperature, freshwater irrigation and soil pH [23]. As NUE for rice plants under salt-affected soils is relatively lower than those on normal soils, the judicious use of nitrogenous fertilizer application in saline soil is needed. Breeders involved in salinity tolerant rice, it is groundbreaking news that the over-expression of PHYTOCHROME-INTERACTING FACTOR-LIKE14 (*OsPIL14*), or loss of function of the DELLA protein SLENDER RICE1 (*SLR1*), accelerate mesocotyl and root growth under salt stress and minimize the sensitivity to NaCl-induced hindrance of seedling growth in rice [17].

2. Crop establishment methods under abiotic stress

Crop establishment under abiotic stress is crucial for farmers, even though farmers are coping with this stress condition. There are many more abiotic stresses; out of those, we will discuss only flooding, drought and salinity stress.

2.1 Crop establishment under flooding stress

Proper rice establishment is significantly important in flood-prone areas because of its sensitivity to flooding during germination (**Figure 1**) and early seedling stage relative to other growth stages [24, 25]. In most areas of Asia, irrigated rice is established by transplanting of seedlings into puddle soil [26, 27], after which the fields are flooded for a prolonged time and recession of water is done before harvesting. Puddling gives some advantages such as it reduces water loss by percolation, assists weed control through destroying weeds, burying weed seeds and maintaining anaerobic conditions that impede weed germination, and makes the soil soft for transplanting [28, 29]. In many rainfed areas of Bangladesh and the eastern part of India, water deposits in the field to around 30 cm or more within a few days after the onset of the rainy season, making the farmers to transplant taller and older seedlings being their only viable option in their hand [30]. Many variations in direct-seeding are being practiced depending on water availability

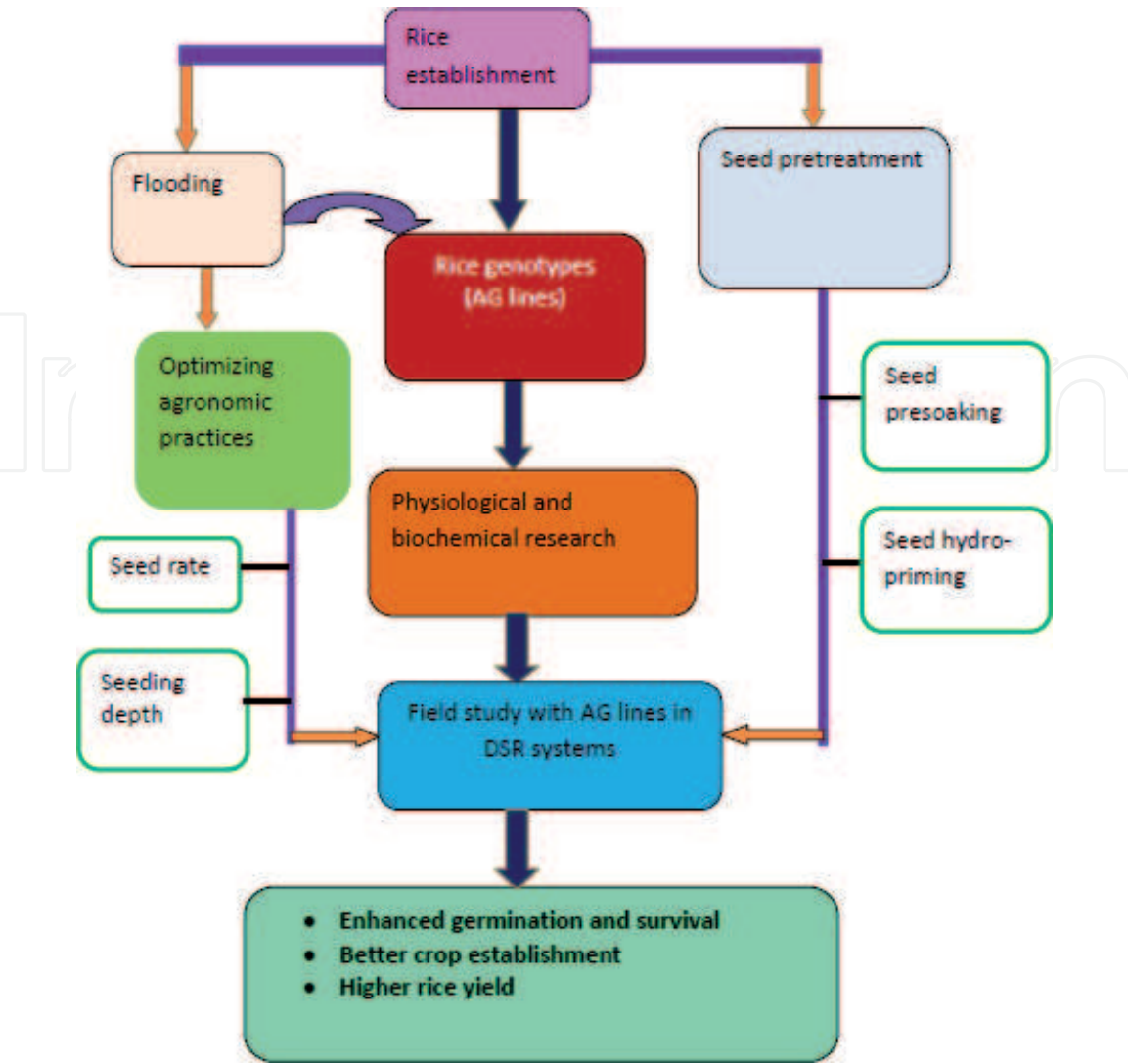


Figure 1. Crop establishment methods and seed management options under early flooding stress using anaerobic germination (AG) potential rice genotypes in direct-seeded rice (DSR) system under field condition.

and field conditions [29]. Due to increasing labor scarcity and cost, however, the need to shift a more suitable establishment method with much lower labor requirement than manual transplanting is conducted. This can be achieved by changing to mechanical transplanting or direct-seeding, which also enable timelier planting/seeding and improved crop stand [31]. Researchers in China [32], South Asia [33], and Australia [34] reported that rice could be successfully grown using dry-seeding. Dry-seeding rice has been developed as an alternative establishment method of rice that alters labor requirements and other inputs while increasing or maintaining economic productivity and alleviating soil degradation problems in cropping systems [35, 36].

The three basic methods of direct seeding are water seeding (broadcasting seed into standing water), dry-seeding and wet-seeding [31]. In wet seeded rice (WSR), the pre-germinated seeds are broadcasted or sown in rows on the saturated soil surface, typically after puddling. Dry-seeding involves broadcasting or preferably drilling the seed into non-puddled soil, usually after dry tillage [31]. Water seeding involves pre-germinated rice seeds broadcast in standing water and is practiced in some cooler areas like in California, Central Asia and Australia [30]. The main advantage of this method is that the standing water suppresses the majority of weed species. This is common in temperate irrigated areas, but could potentially be adapted in flood-prone rainfed lowlands in the tropical area where farmers can

practice early sowing without waiting for a complete recession of floodwater, to minimize the risk of delayed maturity and late-season drought [26]. Once the rice crop has been established in direct-seeded systems and based on water availability, the field is flooded to suppress weed growth and water depth is then maintained at 5–10 cm through most of the season, later water is gradually drained prior to harvest [30]. The type and degree of adoption of alternative rice crop establishment methods to puddling and manual transplanting vary across Asia. In some parts of South East Asia (Philippines, Malaysia, and Vietnam) and Sri Lanka, transplanting has been replaced in large areas by wet-seeding on puddled soil [2, 26]. In the more developed East Asian countries, like Japan and South Korea, transplanting in puddled soil using specialized machinery has been a common practice for many years, and there is now emerging interest in mechanical transplanting into either puddle or non-puddle/dry tilled soil in parts of India. In parts of South Asia, especially in the rice-wheat systems of north-west India, dry-seeding of rice is at the early stages of adoption. The same seed drill can also be used for sowing other crops; thus, dry-seeding may be more conducive to the mechanization of rice establishment than the use of a single purpose mechanical transplanters in regions where farmers also grow non-rice crops [37].

The establishment methods involving puddling have several disadvantages, including higher tillage costs, adverse effects on soil structure for upland crops grown in rotation with rice, and high water requirement for crop establishment. Irrigation cost for crop establishment can be reduced by avoiding puddling, with or without a change in the crop establishment method. For example, both mechanical transplanting and wet-seeding can be done in non-puddled soil after saturating the soil (after dry tillage or no-tillage) [38]. Dry-seeding into dry or moist soil, can further reduce the water requirement for crop establishment, with or without prior dry tillage as for transplanted and wet seeded rice. Nevertheless, direct-seeded rice in the field for 2–3 weeks is longer than transplanted rice, increasing the length of the irrigation season. It has been observed that the extraction of water is more uniform across depths with direct-seeded rice because of better root growth than with transplanted rice [39]. At the early stage of crop growth, up to 60 days after sowing (DAS) growth rate is relatively higher in DSR and WSR than transplanted rice, having more plant density per unit area compared to transplanting [40].

2.2 Crop establishment under drought stress

Drought is an environmental occurrence imposed by the synergistic effect of hydrological, climatic, and natural forces that result in insouciant precipitation for agricultural production over a long period [41]. Globally drought severity is one of the serious concerns because of its immense impacts [42]. The frequency and severity of global drought remain omnipresent and the incidence or extremity of drought has been increasing globally, such as in the Mediterranean region [43], Central China [44], and Africa [45]. Drought is a major constraint to rice production worldwide, as it can occur for varying lengths of time and intensity at any stage of rice growth and development. With the increasing human population and depleting water resources, the development of drought-tolerant rice is of supreme importance to minimizing rice yield losses from drought stress [46]. The major obstacle of rain-fed rice production is drought [47]. Irrigated conditions induce shallow root systems to uptake the resources from the top layer of the soil, whereas rain-fed conditions favor a deep and robust root system, needed to extract the water and nutrients from a wider volume of soil [48]. Three common types of drought can be found for rice production: early water scarcity that causes a delay in seedling

establishment through transplanting, mild sporadic stress having cumulative effects, and late stress affecting long duration varieties [49].

Drought stress induces different physiological and biochemical changes in rice at various developmental stages [50]. It is reported that the plant acclimatized to drought stress through modification of its roots into thicker and longer to uptake nutrient and water from a relatively higher depth of soil and it is found that assimilates are translocated to roots instead of shoots in response to drought stress [51]. In contrast, some researchers opined that root growth in rice decreases under drought stress [52]. These findings show that the response of roots to water stress is highly dependent on the rice genotype, period and intensity of stress [53]. The impact of drought stress on rice yield also depends on the growth stages, with the seedling, tillering, flowering, but if rice plant faces severe drought at the panicle initiation stage might be the most sensitive stage resulting huge loss in yield [54].

2.2.1 Role of root to uptake water under drought

As roots uptake water and nutrients from the soil; hence, the morphological and physiological characteristics of roots play a vital role in determining shoot growth, successive development and ultimate crop production [55]. The access of water to a plant is measured by its root system, root properties, root structure, and distribution of root and rootlets, so improving root traits to expedite the uptake of soil moisture and uphold the productivity under drought stress is of paramount interest [56, 57]. Herbaceous plants like rice have a root system comprised of coarse roots, which include the primary roots that originate from the taproot system and the nodal/seminal roots of fibrous root systems, easily distinguishable from the finer lateral roots [58]. Moisture deficiency can be recovered through modification of the root-shoot ratio and maintain leaf gourd cell-mediated process under drought stress [59]. The optimal dry matter partitioning theory proposes that a plant distributes the assimilates among its different parts for optimum growth and development [60]. It further suggests that the shoot ratio and some other signaling processes may change the ratio to balance the assimilates that alter plant growth even the plants produce certain root for adaptation [61]. Roots having a small diameter and a high specific root length expedite the surface area of roots in contact with soil water and also increase the influx of the xylem through the apoplastic pathway [62, 63]. Moreover, the decrease in root diameter also assists in enhancing water access and upraises the productivity of plants under drought stress [64].

Agronomic adjustments to root plasticity may occur when plant combat with multiple resources limitation [65]. Root architecture varying with rice seedling establishment methods; dry direct seeding prone to more edaphic stresses than irrigated transplanted methods [31]. Moreover, the adjustments in high yield potential among genotypes showing the highest degree of root plasticity may be due to genetic potentiality rather than functional adjustments. Undesirable traits to drought stress such as tall plant height and very early flowering have been reported previously, later in high-yielding, medium-duration drought-tolerant rice varieties developed [66, 67]. So the exact identification and fine-mapping of the QTLs governing the root plasticity traits identified [68]. The positive plasticity values noticed in response to stress indicate that the growth of that particular root trait was increased due to stress application. This response is distinct from an allometric response, in which larger root biomass is related to larger shoot size, because though root growth increased under drought stress but shoot growth down-regulated under stress [68]. The genotypes showing most root-plasticity have positive correlations for root architectural traits between and drought suggest that the most root-plastic genotypes would consistently show a plastic response in different drought environments

either in transplanting or direct seeding or in other soil types [68]. The genotypes having the most root-plasticity under drought also would show a relatively greater degree of plasticity under low phosphorus content soil, depending on the soil depth [68]. Combinations of multiple root plasticity traits in response to drought and/or low-phosphorus have been related to genotypic variation for adaptation to various environments [69]. It is reported that no single functional parameter was strongly incurred to trends in root plasticity or yield [68]. In line with root architectural plasticity, traits such as root anatomy, water use efficiency, and phenology has been reported to be related to more stable plant establishment across versatile environments in various species [70, 71]. In the case of rice, phenological plasticity in response to drought may be difficult to assess because rice exhibited delayed flowering under drought, and this delay can be reduced by plasticity in root architectural traits, which improve moisture uptake. A set of QTLs has been identified related to root architectural plasticity traits and phenotypic plasticity traits in rice, resulting in getting a better understanding of rice establishment under drought stress [68].

2.3 Crop establishment under salinity stress

Generally, rice plants are very sensitive to salinity stress during the early stages of seedling establishment, post-germination and reproductive stage and relatively less sensitive during tillering and grain filling stages [72, 73]. Under salinity altering in the shoot to root ratio as a consequence of root length reduction was supposed to be the avoidance mechanism of the seedlings from salt stress. Salinity accumulates the toxic ion in plants, causing a mineral imbalance. The essential ions are reduced and do not meet the demand resulting in hindrance in normal physiological activities of rice plants. High salt stress impedes the seed germination process, while low salt stress induces seed dormancy [74]. To cope with such stress conditions, seeds develop a mechanism of maintaining low water potential, other specific avoidance, escaping, or tolerance mechanisms to protect the damage by salt stress [75]. Salinity limits germination in a number of ways. From reducing the osmotic potential of soil, which makes a decline in water imbibitions by seed [74] to the creation of ionic toxicity, which alters enzymatic action involved in nucleic acid metabolism. Other effects of salt stress on seed germination include changes in the metabolic process of protein [76]. Seeds are usually more sensitive to salt stress due to close association to the surface of the soil. Accumulation of NaCl to a toxic level in soil, ionic stress decreases the rate of germination [77]. Seed could not absorb water properly because of lower water potential induced by salt stress resulting in toxic effects to the developing embryo and delay in the germination process [78]. The average time of seed germination depends on salinity severity and genotype's inherent quality. There is a strong negative co-relationship between the strength of salinity stress and the rate of germination [79]. Salinity exhibits an immense effect on the germination index and seed size [80]. Small-sized seeds show a relatively higher germination index than large size seeds under salinity stress. Salinity has a negative effect on germination percentage, rate of germination and germination speed [81]. After germination, in successive growth of the seedling, salinity reduces shoot and root dry matter production in rice genotypes [82], and the magnitude of reduction increased with increasing salinity level (**Table 1**).

2.3.1 Plant physiology under salinity

Higher amounts of salt in the soil cause a serious threat to various metabolic processes of plants, which results in a reduction of crop yield. Soil salinity limits the uptake of essential ions into the plants resulting in metabolic disorder leading to

Genotype	Salinity level (dS m ⁻¹)							
	0	5	10	15	0	5	10	15
	Shoot dry weight (g/10 plants)				Root dry weight (g/10 plants)			
IR20	0.060	0.05 (17)	0.028 (53)	0.016 (73)	0.068	0.048 (29)	0.036 (47)	0.016 (76)
POKKALI	0.134	0.116 (13)	0.064 (52)	0.044 (67)	0.152	0.076 (50)	0.026 (83)	0.018 (88)
IR29	0.140	0.07 (50)	0.036 (74)	0.014 (90)	0.06	0.048 (20)	0.022 (63)	0.012 (80)
NERICA 1	0.084	0.064 (24)	0.024 (71)	0.008 (90)	0.054	0.038 (30)	0.018 (67)	0.01 (82)
NERICA 5	0.076	0.054 (29)	0.032 (58)	0.02 (74)	0.13	0.056 (57)	0.016 (88)	0.004 (97)
NERICA 12	0.092	0.068 (26)	0.046 (50)	0.028 (70)	0.062	0.04 (35)	0.024 (61)	0.01 (84)
NERICA 19	0.054	0.038 (30)	0.014 (74)	0.004 (93)	0.036	0.028 (22)	0.002 (94)	0.0 (100)
IWAI	0.090	0.068 (24)	0.032 (64)	0.02 (78)	0.068	0.046 (32)	0.028 (59)	0.016 (76)
Values in parenthesis indicate percent reduction to respective controls.								

Table 1.
Effect of salinity on shoot and root dry weight (g/10 plants) of different rice varieties [82].

downstream in plant growth rate [83]. Excess salt concentration in the root zone of plants causes a change in plant water potential. Salinity causes a reduction in turgor pressure in plant cells due to less water uptake by the plants. Insufficient water limit cell division and regulation of stomatal aperture, which lead to low photosynthesis rate and in severe case causes plant tissues death [84]. Aside from this, reduction in turgor pressure causes stomatal closure, resulting reduction in gaseous exchange of transpiration [20]. Salinity causes other physiological disorders, like changes in membrane permeability, leading to misfolding of membrane proteins [85] and suppression of the photosynthesis [86]. Reduction in enzymatic activities and photopigments causes a lowering of photosynthesis rate [87]. Many plant physiological and biochemical processes, photosynthesis [88], water conductance through stomata [75, 89] are affected by salinity, resulting in an adverse effect on biological processes and crop yield reduction.

2.3.2 Plant anatomical change under salinity stress

Rice adopts various strategies in response to salinity through their anatomical modification, which allows them to cope with the stress. Plants with growth in high salt concentration have more thickness of leaves [90], epidermis, cell walls and cuticles. The higher the salt concentrations, the higher the mesophyll cell layers and cell size up to some extent [91], due to more elasticity in the cell wall at high turgor pressure [92]. Salinity expedites the density of stomata at the lower side of leaves [93] with increased palisade tissues [94]; however, salinity downregulates the number of cells per leaf. Salinity reduces the number of stomata on the surface of the epidermis [95], vessels number [94]. However, salinity accelerates suberinization inside the roots resulting in hindrance in nutrient uptake from soil [96]. In rice, it is reported that stem diameter was reduced [97], while trichome and stomata density increased. Salt stress reduced cell size, the epidermal thickness of leaves, apical meristem, diameter of the cortex and central cylinder [98]. Salinity induced thickening of exodermis and endodermis [99] and assist in developing sclerenchymatous tissues [98]. Once the seed has germinated, the next goal for the plant is an establishment. Salinity causes a reduction in crop establishment by reducing shoot growth, sealing leaf development and expansion, reducing the growth of internodes and inducing abscission of leaf [91, 100]. Salinity causes some complexity to plants, like osmotic stress, ion toxicity and nutrient imbalance, which are detected as the most prominent reasons for a reduction in crop growth, resulting in crop failure in severe cases. Nonetheless, different developmental stages like germination, vegetative growth, flowering, spikelet's setting and grain filling of rice behave differently with salinity. It is reported that salinity decreased biomass and leaf area in rice [101].

3. QTLs and genes of nitrogen use efficiency

In soil, inorganic nitrogen is available for plants as nitrate (NO_3^-) in aerobic upland condition and ammonium (NH_4^+) in flooded wetland or acidic soils. Nitrogen use efficiency (NUE) is a complex trait that is controlled by multiple genes. Many genes and/QTLs associated with NUE have been identified in rice. Studying and understanding the mechanisms of N utilization at a molecular level may help to improve rice varieties for N deficiency tolerance under different abiotic stresses. Researchers [102] identified 14 putative QTLs for NUE components and 63 QTLs for 12 physiological and agronomic characteristics with six hotspot regions using 174 recombinant inbred lines derived from the IR64/Azucena cross at the

vegetative phase in the hydroponic Yoshida solution with three different N concentrations: 1X (standard), 1/4X and 1/8X. In line with this, it is reported that eight QTLs for plant height in hydroponics with two N supply levels in the Yoshida culture solution and 13 QTLs for plant height in a soil mediated experiment with two N supply treatments [103]. Twelve QTLs were detected for root weight, 14 for shoot weight and 12 for biomass from 239 rice recombinant inbred lines (RILs) derived from a cross between two *indica* parents (Zhenshan97/Minghui63) under hydroponics medium using two N treatments [104]. In another pot experiment, seven QTLs were identified associated with nitrogen use and the yield on chromosome 3 [105]. Three candidate genes *Os05g0208000*, *Os07g0617800* and *Os10g0189600* were identified through fine-mapping of four QTLs located on chromosomes 5, 7 and 10 accelerated yield performance under low N level [106].

Five QTLs were identified on chromosomes 1, 2, 7 and 11 for grain yield (GY) using 127 RILs derived from the cross Zhanshan 97/Minghui 63 [107]. The phenotypic and genetic associations between grain NUE and GY are positive and highly significant; thus, QTLs for both NUE and GY could be used to trigger NUE and GY in a breeding program [108]. Seven QTLs for the glutamine synthetase (GS1) protein content and six QTLs for the NADH-GOGAT protein content were detected using backcross inbred lines between Nipponbare and Kasalath. Some of these QTLs were finely mapped to get a structural gene for GS1 from chromosome 2 and chromosome 1 [109]. A QTL on chromosome 2 activates cytosolic GS1 for protein synthesis in older leaves, resulting in more active tillers during the vegetative stage and a more panicle number and total panicle weight [110]. Using 166 RIL populations, 22 single QTLs and 58 pairs of epistatic QTLs associated with physiological NUE in rice have been identified [111]. With the same mapping population, 28 main effect QTLs and 23 pairs of epistatic QTLs were detected [112]. It is reported that [113], using 38 chromosome segment substitution lines derived from a cross between “Koshihikari,” a *japonica* variety, and “Kasalath,” an *indica* variety, identified a major QTL *qRL6.1* on the long arm of chromosome 6 associated with root elongation under deficient and sufficient NH_4^+ condition. The “Kasalath” allele at this QTL region promoted significant root elongation. The marker interval was C11635–P3A2 and phenotypic variance explained by this QTL was 76.4%.

A set of RILs grown in four different seasons in two locations with three nitrogen fertilization treatments was analyzed for QTL for grain yield components and two main effect QTLs were detected viz., grain yield per panicle on chromosome 4 and grain number per panicle on chromosome 12 under N zero level [114]. Four QTLs for trait differences of plant height and heading date between two N levels have been mapped on chromosomes 2 and 8 co-locating with reported QTLs for NUE [111]. In response to low nitrogen application for two years, 33 QTL have been identified in RIL population, out of which only ten QTLs were consistent under low N [115]. QTL mapping for NUE and nitrogen deficiency tolerance traits in RIL population for two years resulted in four common QTL on chromosomes 1, 3, 4 and 7 [116].

From a recombinant inbred population, 20 single QTLs (S-QTLs) and 58 pairs of epistatic loci (E-QTLs) were detected for the nitrogen concentration of grain, nitrogen concentration of straw, the nitrogen content of shoot, harvest index, grain yield, straw yield and physiological nitrogen use efficiency (PNUE) [117]. Researchers [118] identified seven chromosomal regions using 40 introgression lines (ILs) derived from a cross between “Ilpumbyeo,” a temperate *japonica* variety, and “Moroberekan,” a tropical *japonica* accession from seedlings grown in 0, 250 and 500 μM NH_4^+ . Among them, the *qRW6* QTL was detected on the long arm of chromosome 6 associated with root weight in temperate *japonica*.

Recently, a group of scientists reported [119] about a main effect QTL *qRD-WN6XB* (Table 2) on the long arm of chromosome 6, which positively confers

tolerance to N deficiency in the *Indica* rice variety XieqingzaoB, was identified using a chromosomal segment substitution line population using Zhonghui9308 and XieqingzaoB. Nine candidate genes were found in this region through fine mapping. Out of these genes, *Os06g15910* was seemed to be a strong candidate gene associated with root system improvement under low N status. However, putative

QTLs/genes	Special traits	Chr. No	Reference
<i>ARE1</i>	High-yield under N limiting condition	8	[108]
<i>qRL6.1</i>	Root elongation under deficient and sufficient NH ₄ ⁺ condition	6	[113]
<i>qRW6</i>	Enhance root traits and yield potential	6	[118]
<i>qRDWN6XB</i>	Confers tolerance to N deficiency	6	[119]
<i>qGYLN7</i>	Increases grain yield under low N	7	[106]
<i>qGYPP-4b</i>	Increases grain yield per plant under low N	4	[114]
<i>qGNPP-12</i>	Increases grain number per panicle under low N	12	[114]

Table 2.
Major QTLs/genes associated with nitrogen use efficiency under abiotic stresses.

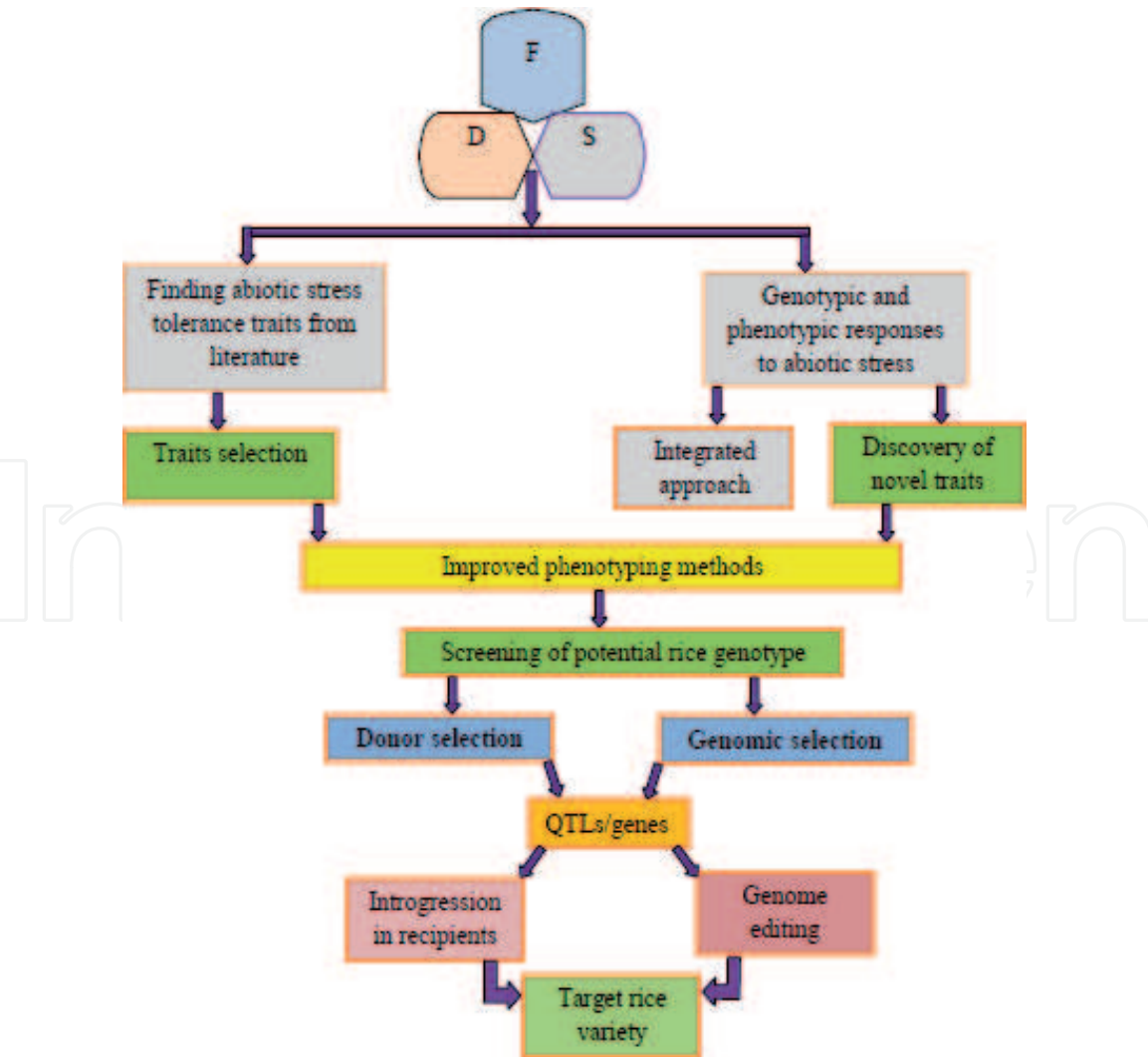


Figure 2.
Holistic breeding approach for multiple abiotic stress tolerance in rice. F = flooding, D = drought, S = salinity, QTLs = quantitative trait loci.

QTLs/genes needed for multiple abiotic stress tolerance, NUE and associated novel traits in rice could be discovered through a holistic breeding approach (**Figure 2**).

4. Hybrid rice production under abiotic stress

Adverse environmental conditions like abiotic factors, triggering abiotic stresses, run a key role in determining the productivity of rice yields. Biologically, abiotic stress is considered as a substantial deviation from the model environments in which plants are grown, inhibiting them from expressing their complete genetic potential regarding growth, development and reproduction [120]. Agriculture production in Bangladesh is dwindled mainly due to biotic and abiotic stresses. Abiotic stress ubiquitously affects the crop growth and development process worldwide. Hence, these are one of major areas of concern to fulfill the required food demand [121, 122]. The major abiotic stresses, drought, flooding, salinity are making the risks to food and nutritional security from tropics to temperate regions worldwide. Drought affects plants in numerous ways like it affects plant growth, yield, membrane integrity, pigment content, osmotic adjustments, water relations and photosynthetic activity [123]. Over the last three decades, the temperature of the country has increased significantly. It is estimated that by 2030, 2050 and 2100, the temperature may increase around 1, 1.4 and 2.4°C, respectively [124]. This is significant as an increased temperature reduces the yield of rice. Therefore, the country is in a risky situation in meeting future challenges concerning food security.

Bangladesh is facing salinity intrusion into the arable agricultural lands. The decline in rice yield under judiciously salt-affected soils is anticipated to be 68 percent [126]. Due to global warming, the rise in sea levels, surplus irrigation without appropriate drainage in the inland area under salt stress is growing. Flash flood and cold injury also cause rice production loss almost every year in Bangladesh. Rainfed conditions in Bangladesh are quite complex, where multiple stresses frequently prevail and even follow in quick succession within a single cropping season. Two or more abiotic stresses often coexist in many rainfed lowland and saline areas of Bangladesh. Most of the rainfed areas in Bangladesh are often occurred by multiple abiotic stresses such as flooding, drought and salinity even within the same cropping season near the coastal areas. Therefore, we need to breed new hybrid rice varieties that could tolerate more than one abiotic stress and yield high under normal favorable rainfed conditions as well.

Northern districts of Bangladesh are cold prone areas of the country. Usually, Boro (winter) rice is seriously affected by cold during the seedling and flowering stage. Seedling mortality sometimes goes up to 90%, especially in the northern part of the country. In recent years, more than 2.0 million hectares of rice crops in the cold prone area of Bangladesh have been seriously affected by extreme cold stress,

Years	Salinity class and salt affected area (000'ha)				Total (000'ha)
	S1 (2.0–4.0 dS/m)	S2 (4.1.0–8.0 dS/m)	S3 + S4 (8.1–16.0 dS/m)	S5 (>16.0 dS/m)	
1973	287.37	426.43	79.75	39.9	833.45
2000	289.76	307.20	336.58	87.14	1020.75
2009	328.43	274.22	351.69	101.92	1056.26

Source: Soil Resources Development Institute (2010).

Table 3.
Extent of soil salinity during the last four decades (1973–2009) in coastal areas of Bangladesh.

causing partial to total yield loss, especially in the northern part of the country. In the haor areas of Bangladesh, early planted Boro rice has to face cold stress at the reproductive stages (Panicle initiation to flowering). If the mean temperature goes down below 20°C for more than 5-6 days during the reproductive stage of the hybrid rice plant associated with spikelet sterility, cause serious yield damage.

In particular, abiotic stresses significantly constrain rice production in Bangladesh and the frequency of these stresses is, unfortunately, likely to increase with climate change. Hybrid rice breeding programs around the world have pre-emptively responded by breeding stress-tolerant rice varieties. By manipulating the heritable variation present in the germplasm, we can develop abiotic stress-tolerant cultivars through breeding techniques, but it is a cumbersome and time-consuming process. The slow progress is due to the complexity of the problem involving environmental conditions and the genetic system. The development of stress-tolerant hybrid rice varieties has gained momentum among the breeders in the recent past. The development of hybrid rice with inbuilt stress tolerance is most desirable to increase the production capacity of rice under saline conditions.

Climate change has affected Bangladeshi agriculture a lot. The most pronounced effects of climate change are the heat stress, periodic drought conditions, and salinity intrusion in coastal belts due to sudden flood and flash flood in major rice-growing areas of Bangladesh. In the last couple of decades, the salinity affected area increased drastically in Bangladesh (**Table 3**). Due to periodic drought and saline water intrusion in the coastal belt, the already existing problem of high amounts of salts in the upper surface soil has intensified. In the future, efforts should be directed to develop climate-smart hybrid rice, which can perform stably under diverse environmental conditions. Nonetheless, China is now feeding 20 percent of the world's population from only 10 percent of the world's arable land where hybrid rice covers around 57 percent of the total cultivated rice area [125]. They have achieved this success by adopting research on region-based and stress-tolerant hybrid rice development. Their way of success was not so smooth, but eventually, they overcome all the obstacles. On the other hand, rice is called "the life of the people of Bangladesh." No obvious alternative crop can replace rice presently. Initially, after the introduction of hybrid rice in Bangladesh in 1998, the area under hybrid rice cultivation significantly increased, but not up to the mark. Currently, only 7.48 percent of the total rice area is under hybrid rice cultivation in Bangladesh [126]. We have released hybrid rice for a favorable environment. It is now world-wide accepted that hybrid rice can give 15-20% more yield compared to inbred high yielding rice cultivars. Therefore, the development of abiotic stress tolerant hybrid rice is the demand of the time to sustain food security.

5. Future outlook and conclusions

Among the essential nutrient elements, nitrogen has a paramount importance for rice growth and development in natural ecosystems. To promote optimum N nutrition for the higher rice yield, it is important to explore the possible variability in NUE in rice genotypes. Understanding the molecular mechanisms of variable NUE in rice genotypes would help to develop NUE in the elite rice variety under abiotic stressful conditions using traditional and molecular plant breeding methods, including genome editing. Global climate change plunges world rice production toward various abiotic stress. Flooding, drought and salinity are correlated to cause problems in rice production. If rice seedlings experience flooding during the vegetative stage, they may suffer from terminal drought during the reproductive stage, depending on the ecosystems. Likewise, periodic drought conditions may upregulate

the existing salinity stress through intensification of a high amount of salt layer on the upper surface soil. Therefore, there is a dire need to adopt a holistic approach to address the problems of abiotic stresses for future rice breeding. Genomics and post-genomics approaches have high potentials for dissecting underlying molecular mechanisms in differential NUE in rice genotypes. With the help of molecular mapping, fine-tuning of target QTLs, genome editing of a number of major and minor QTLs associated with abiotic stress tolerance in rice have been detected in recent years. Further enhanced research endeavors are now underway toward the development of more tolerant rice varieties to abiotic stresses. The identified QTLs are valuable resources for marker-assisted selection (MAS) to develop elite rice genotypes tolerant to flood, drought and salinity. Novel approaches are needed to apply for accelerating the mitigation of the problems of abiotic stresses in rice such as marker-assisted breeding (MAB), rapid generation advance (RGA), gene editing and transgenic technology. Attempts should be taken to develop abiotic stress-tolerant rice varieties, which can perform in a sustainable manner in a wide range of environmental conditions. Identified QTLs and rice germplasms tolerant to abiotic stresses could be explored to understand the molecular genetics of flooding, drought and salt tolerance in rice. New genes involved in abiotic stress tolerance are needed to be identified. There is a need for strategic research on molecular breeding and agronomic aspects to enhance the resilience of global rice production. To achieve these goals, capacity building of rice scientists, farmers and other stakeholders involved in developing abiotic stress-tolerant rice variety might help to increase the desired NUE in rice.

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