Chapter 15
Genetics and Breeding of Flooding Tolerance in Rice

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Abstract Flooding is a frequent natural calamity, affecting global food supply and financial security. The intensity of rainfall events is expected to increase under future climate change scenarios, which will greatly impact rice production. Different flooding patterns can cause damage or complete yield loss in rice plants at different stages of growth. This includes (a) complete submergence due to flash flood at vegetative or pre-flowering stages, (b) stagnant flooding of medium-deep water and deepwater or floating rice, and (c) submergence at germination or anaerobic germination. Different molecular and physiological mechanisms underly tolerance to each type of flooding. Several major QTLs have been mapped and several key genes underlying the QTLs have been cloned. Remarkable progress has been achieved through conventional and molecular breeding strategies in developing tolerant varieties to mitigate the impact of different flood events. This effort will be continued in the future by incorporating new QTLs/genes and tolerance to other abiotic and biotic stresses according to the needs of the target regions. Genetics, genomics, and other modern technologies will also be continuously explored to further our understanding of how rice plants cope with different types of flooding stress.

Keywords Flooding tolerance · Sub1 varieties · Stagnant flooding · Deepwater rice · Anaerobic germination · QTLs · Genes · Molecular breeding

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15.1 Introduction

Rice cultivation and flooding are considered synonymous. The ancestors of modern rice cultivars were aquatic species and provided a suitable basis for development of agriculture in swampy monsoonal environments. The floods bring water and nutrients to the rice plants, but can also kill the plants if too deep or prolonged.

Flooding is the most destructive natural calamity. For example, in the first half of 2013, it was estimated that floods were responsible for 47% of the damage from all natural disasters (Wake 2013). The specter of climate change, with images of violent storms, has increased concern over damage caused by flooding. An escalation in "record-breaking" rainfall events in recent decades has been recorded (Lehmann et al. 2015). While the frequency of tropical cyclones has declined, their intensity has increased (Auffhammer et al. 2012; Kang and Elsner 2015). There is evidence that rice-growing areas will be especially impacted by high rainfall storms in the future (Cai et al. 2014; Hirabayashi et al. 2013; Singh et al. 2014). However, rice farmers have been concerned about survival of their crop under flooding long before the modern worries of climate change. Likewise, rice scientists have been studying how rice plants can cope with excess flooding over many decades.

The different flooding patterns affecting rice plants discussed in this review article are shown in Fig. 15.1. Three major types of flooding require different coping mechanisms in rice plants: (1) short-duration flooding of less than 3 weeks, referred to as submergence; (2) long-duration flooding, sometimes referred to as stagnant flooding; and (3) flooding during germination, referred to as anaerobic germination.

With shorter-term flooding, the plants are submerged for up to a few weeks (Fig. 15.1d). Perhaps the first mention of submergence tolerance in the scientific era is by Graham (1913), who classified Indian flood-tolerant varieties as those that could survive up to 15 days under water. Scientists in India knew of these varieties and selected two famous pure-line selections FR13A and FR43B from the farmers' traditional landraces *Dhalputtia* and *Bhetnasia*, respectively (Richharia and Govindaswami 1966). We do not have the exact year of their selection, but these probably were isolated at the Cuttack station, Odisha, before this was turned over to the Central Government in 1946. The Indian flood-tolerant varieties such as FR13A and FR43B are botanically *aus* varieties, although they differ from typical *aus* varieties in being photoperiod sensitive.

With stagnant flooding (Fig. 15.1b, c, e), the water depth can vary greatly. Deepwater rice (flooding deeper than 50 cm for at least 1 month in the season) is an ancient type of rice culture that originated in both Asia, from the *Oryza sativa* species, and Africa, from the *O. glaberrima* species (Catling 1992). The rice varieties grown in these areas need to elongate rapidly during the onset of the floods to keep part of the plant above the water level. Large areas of rice production are subject to medium-deep (Fig. 15.1b, e), stagnant flooded conditions, where water depths of 25–50 cm have adverse effects on rice yields (Singh et al. 2011).

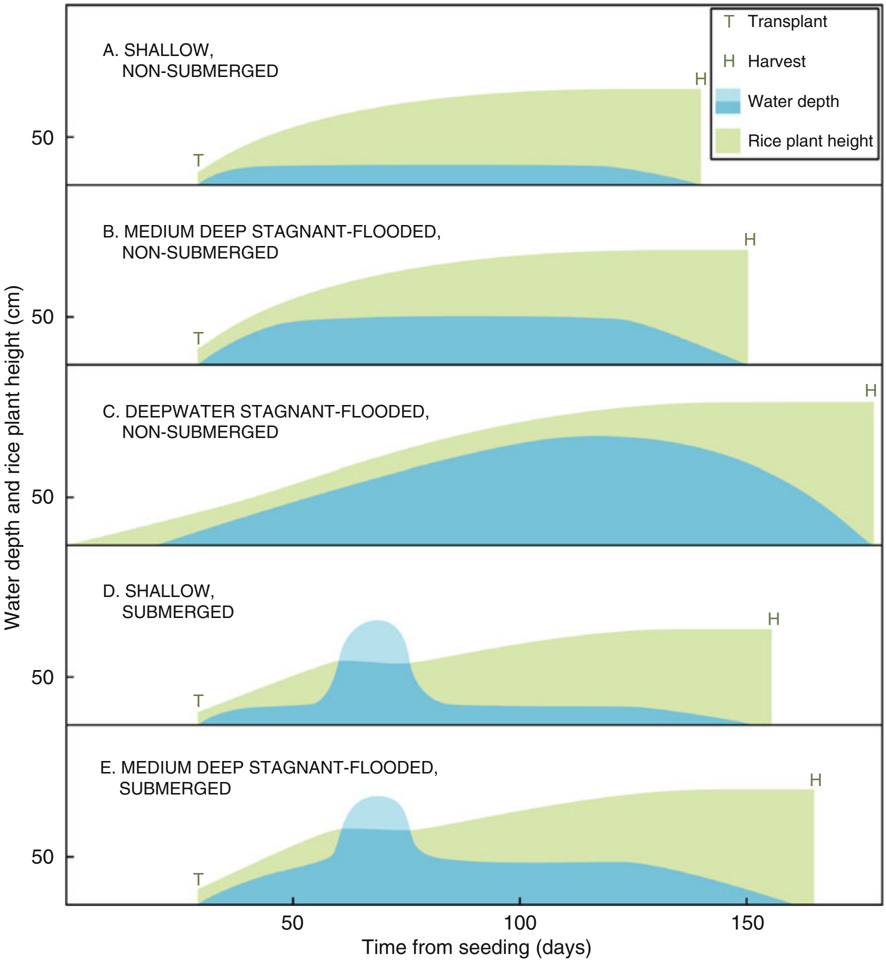

Fig. 15.1 Flooding patterns in rice. In shallow, irrigated rice (**a**), water depth usually remains well below 25 cm for the crop duration. In medium-deep conditions (**b**), water depths can remain between 25 and 50 cm for prolonged periods, and in deepwater and floating rice (**c**), water depths can go to 1 m or more for an appreciable period of the season and the rice is direct-seeded in the field. Submergence is a short-term stress of 2–3 weeks and can occur in shallow flooded (**d**) or stagnant flooded (**e**) conditions

For the third type of flooding, in areas where rice is seeded directly into the field, submergence can occur during the germination stage (Ismail et al. 2009; Yamauchi et al. 1994). This is becoming increasingly relevant as more rice-producing areas shift to direct-seeded systems.

After the formation of the International Rice Research Institute (IRRI) in the Philippines in 1960, scientists began organizing meetings to focus research on flooding stresses. International deepwater rice symposia were held in 1974

(Dhaka), 1976 (Bangkok), 1981 (Bang Khen), and 1987 (Bangkok), and their proceedings are available at https://books.google.com/. It was also recognized that flash flood causing submergence stress was a major problem in some irrigated and rainfed lowland areas, and this was also addressed in an international meeting held at Bhubaneswar, India, in 1985 (IRRI 1986). The International Rice Testing Program (later renamed the International Network for Genetic Enhancement of Rice or INGER) created nurseries addressing submergence-prone and deepwater rice, and international collaboration in breeding increased, resulting in the development of many new varieties (Mackill et al. 2013).

15.2 Genetic Networks Controlling Tolerance to Flooding Stresses

To consider the genetics and breeding of tolerance to flooding, it is critical to recognize how rice plants can survive and produce optimum yields under the different types of flooding stresses:

- Submergence at vegetative or pre-flowering stage (submergence)
- Stagnant flooding of medium-deep (25–50 cm), deepwater (50–100 cm), or floating rice (>100 cm)
- Submergence at germination (anaerobic germination, AG)

Submergence is mainly a problem in shallow to medium-deep lowland rice, but it can also occur in deepwater areas. Likewise, stagnant flooding often occurs in areas of medium-deep and deepwater systems, where poor drainage in the fields combined with high rainfall prevents the water levels from receding for weeks, or even months, at a time. Anaerobic germination is mainly required where rice is seeded directly into fields, although for transplanted rice submergence at germination can occur also in the seedbeds. Very few rice varieties can germinate when fields are flooded after seeding. There has also been interest in developing this trait for intentionally flooding fields after sowing as a means of weed control (Williams et al. 1990).

Each of these stresses can be addressed independently, and the genes conferring tolerance can be combined to confer multiple tolerances. Adaptation to stagnant flooding is not as well understood. However, for areas with deeper flood levels, rapid internode elongation is necessary, and this trait is not compatible with submergence tolerance.

15.2.1 Submergence Tolerance at the Vegetative and Early Reproductive Stage: SUB1 *and Other Genes*

Submergence tolerance in the highly tolerant FR13A (and its progeny) was found to be controlled by the *SUB1* QTL on chromosome 9 (Xu and Mackill 1996). The locus contains three ethylene responsive factors (ERFs), *SUB1A*, *SUB1B*, and *SUB1C* (Xu et al. 2006). All rice varieties studied have the *SUB1B* and *SUB1C* genes, while *SUB1A* is present in a subset of *indica* or *aus* rice varieties (Xu et al. 2006). Subsequently, it has been confirmed that within the *SUB1* gene cluster, *SUB1A* was the key determinant for complete submergence tolerance (Septiningsih et al. 2009; Xu et al. 2006). Submergence injury at the vegetative stage is increased by rapid growth, which depletes carbohydrate reserves. *SUB1A* uses a "quiescence" strategy that restrains elongation and conserves carbohydrate reserves (Fig. 15.2) (Fukao et al. 2006). The plant is consequently able to rapidly recover and regrow new tillers when the water recedes.

The frequency of the tolerant allele of *SUB1A* in rice germplasm is surprisingly low, considering the low number of submergence donors identified from numerous germplasm screenings performed at IRRI—probably less than 1%. However, based on our findings so far, this allele does not have any yield penalty or other negative effects on other important agronomic traits, and it is hypothesized that this locus was not selected against by farmers. Two common sources of tolerant *SUB1A* genes are the *aus* rices from Odisha, including FR13A and FR43B, and submergence-tolerant indica rices from Sri Lanka, including Kurkaruppan, Goda Heenati, and Thavalu (Vergara and Mazaredo 1975), and at least some of these seem to share the common tolerant haplotype for the *SUB1* locus (Singh et al. 2010). Most likely the tolerance gene originated in the *aus* rice of Odisha and was brought to Sri Lanka through migration, ultimately ending up in the *indica* landraces. Odisha has been mentioned as a possible origin for the Sinhalese people of Sri Lanka in the fifth century BC (Roychowdhury 2016; Senaveratna 1997). The *SUB1A* gene has been found in wild rice progenitor *Oryza rufipogon* (Li et al. 2011). More recently, dos Santos et al. (2017) reported that the *SUB1* locus is present in most *Oryza* species and that the *SUB1A* gene of *O. nivara* is on chromosome 1.

Varieties with and without the *SUB1A* tolerance gene generally show contrasting levels of tolerance (see Fig. 15.4), but there are differences in the degree of submergence tolerance in varieties with the *SUB1* gene that are under the control of other genes. A few smaller QTLs for submergence tolerance during vegetative stage have been identified (Gonzaga et al. 2016, 2017; Nandi et al. 1997; Septiningsih et al. 2012; Toojinda et al. 2003). It is possible that the tolerance mechanisms underlying some of these QTLs are different from *SUB1;* further investigation is needed to prove this hypothesis.

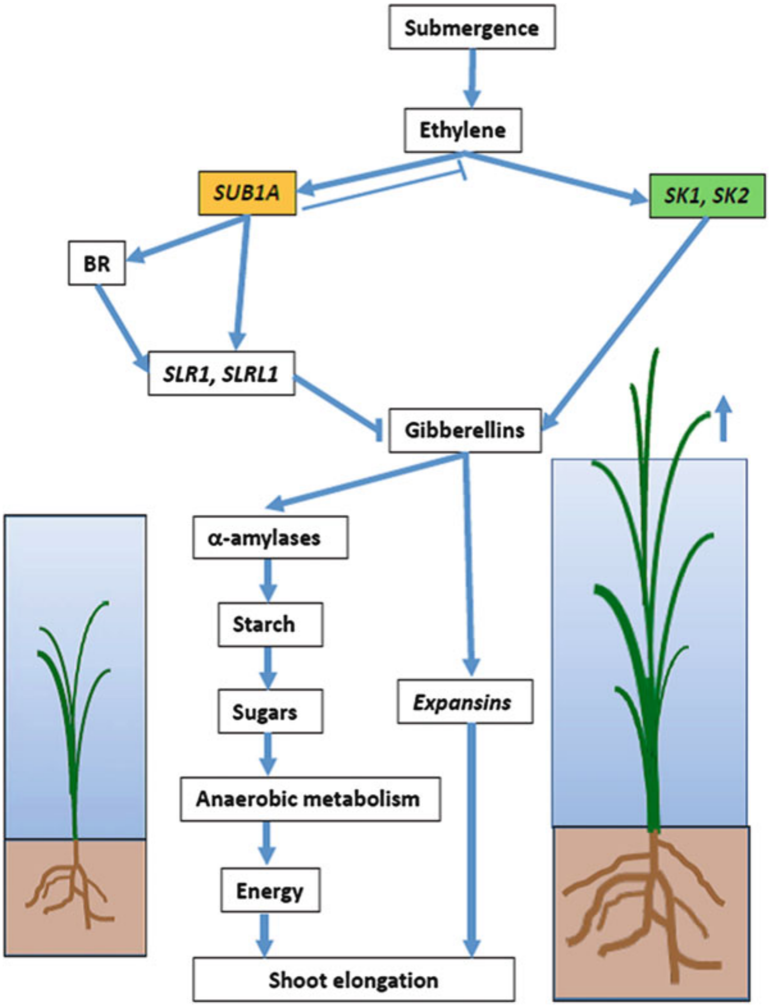

Fig. 15.2 The molecular basis of submergence tolerance during vegetative stage and deepwater rice. Under flash flooding stress (left), ethylene accumulation and perception was triggered by *SUB1A*. On the other hand, there is a feedback loop where accumulation of SUB1A transcripts will suppress the production of ethylene (Fukao et al. 2006). SUB1A maintains inhibition of GA-mediated growth responses directly through two GA-signaling repressor proteins, Slender Rice-1 (SLR1) and SLR Like-1 (SLRL1), or indirectly through the brassinosteroid (BR) pathway (Fukao and Bailey-Serres 2008; Schmitz et al. 2013). On the other hand, in deepwater rice (right), ethylene induces the transcription factors SNORKEL1 (SK1) and SNORKEL2 (SK2) that enhance GA-mediated internode elongation, keeping the rice plant's canopy above the water surface—an "escape" strategy (Hattori et al. 2009). This situation allows oxygen to be transported through aerenchyma to the submerged part of the plant

15.2.2 Adaptation to Stagnant Flooding and Rapid Elongation Ability

Even though breeding for stagnant flooding (SF) tolerance has long been one of the IRRI mainstream breeding programs for rainfed environments, thus far, there have been limited studies on this trait. Vergara et al. (2014) found wide variation in adaptation to SF among 626 rice accessions studied. Moderate elongation rate of 1.3–2.3 cm day^{-1}, as well as ability to produce more tillers, was optimum for adaptation to SF. Genetic studies have only recently been initiated (Singh et al. 2017). A recombinant inbred line population was derived from a cross of an improved high-yielding Indonesian variety, Ciherang-Sub1 (Septiningsih et al. 2015), and an IRRI elite breeding line, IR10F365, which is tolerant to both stagnant flooding and submergence during vegetative stage (Collard et al. 2013b). It was previously reported that the first generation of Sub1 varieties were susceptible to stagnant flooding (Vergara et al. 2014). The shorter the plant height of the Sub1 variety, the more susceptible it is to stagnant flooding. As an example, Swarna-Sub1, a short-stature variety, is very susceptible to stagnant flooding and is being used as a susceptible check for screening under stagnant flooding. A stagnant flooding-tolerant variety can be inherently tall or can be semidwarf but it elongates moderately with rising water to maintain its canopy above the water surface (Kato et al. 2014). Our results showed that Ciherang-sub1 was more tolerant to stagnant flooding stress compared to the first-generation Sub1 varieties. This tolerance was most likely due to its slightly tall stature; therefore even though its shoot elongation ratio and biomass are lower compared to the tolerant check, IRRI154 (NSIC Rc222), this variety still performed well under stagnant flooding. In general, grain yield was reduced by 50% due to stagnant flooding stress. Three yield QTLs and several QTL clusters for various traits that indirectly increase yield under stagnant flooding conditions were identified. The beneficial alleles of these QTLs were derived from both IR10F365 and Ciherang-Sub1 (Singh et al. 2017). Potential genes underlying these key QTLs can be further investigated to unravel the molecular mechanism underlying stagnant flooding tolerance. Furthermore, more QTLs can be mapped using new mapping populations derived from different donors—adding more targets for further physiological and molecular studies.

Deepwater and floating rice can be considered as special cases of stagnant flooding, where water depths remain above 50 cm for an appreciable part of the season. The main characteristic that distinguishes deepwater or floating rice varieties is the ability of the internodes (and shoots) to rapidly elongate when submerged. A number of QTLs for elongation ability have been identified (Hattori et al. 2007; Kawano et al. 2008; Nagai et al. 2012, 2014; Nemoto et al. 2004). Three QTLs identified by Hattori et al. (2007) were mapped on chromosomes 1, 3, and 12; the increased elongation alleles for all of them are derived from the deepwater rice variety C9285 (*Oryza sativa* ssp. *indica*). Based on comparative study of the location of the QTLs, the group also showed that the QTL on chromosome 12 is the major one for deepwater varieties (Hattori et al. 2008).

Through positional cloning, the chromosome 12 locus was found to consist of two ethylene responsive factor genes, *SNORKEL1 (SK1)* and *SNORKEL2 (SK2)*. These genes promote GA-mediated internode elongation—helping the rice plant to cope with stress by maintaining its canopy above the water surface to obtain oxygen and sunlight (Hattori et al. 2009). It was also observed that internode elongation was initiated at the sixth-leaf stage and that GA biosynthesis and signal transduction are essential for internode elongation in deepwater rice (Ayano et al. 2014). It is interesting to note that *SK1*, *SK2*, and *SUB1* are all ethylene-responsive transcription factors. As in the case of the non-SUB1 QTLs, there is also a probability that a few of the other elongation-ability QTLs could be involved in mechanisms that are completely different from *SK1* and *SK2*—this needs further study. A recent report demonstrated the role of *AtERF11* in promoting internode elongation through the ethylene biosynthesis inhibition and GA biosynthesis and signaling pathway activation. This gene is a member of the ERF subfamily VIII-B-1a of ERF/AP2 transcription factors in *Arabidobsis* (*Arabidopsis thaliana*) (Zhou et al. 2016). An ortholog of *AtERF11* that holds similar function may exist in rice. This needs further investigation. On a related issue, another recent report claimed that a novel rice protein family of OsHIGDs (hypoxia-induced gene domain), which are components of ethylene-independent hypoxia signaling, might be involved in early signaling of hypoxia-promoted stem growth in deepwater rice (Hwang and Choi 2016).

15.2.3 Submergence Tolerance at the Germination Stage: Anaerobic Germination

Tolerance of flooding during seed germination and very early seedling growth, referred to as anaerobic germination, is one of the most important traits necessary to ensure good seedling establishment in direct seeded rice (DSR) in both rainfed and irrigated ecosystems (Ismail et al. 2009). One of the most spectacular adaptive growth features of germinating rice seeds to tolerate oxygen deficiency in flooded soils is the accelerated growth of the coleoptile. Fast coleoptile elongation facilitates contact with air in waterlogged or flooded soils to maintain adequate aeration of the growing embryo. This accelerated elongation is independent of ethylene synthesis (Pearce et al. 1992), but is dependent on the extent of alcoholic fermentation and ethanol synthesis (Setter et al. 1994), which emphasizes the importance of anaerobic metabolism during germination and early seedling growth (Fig. 15.3). Several landraces with anaerobic germination (AG) tolerance have been identified (Angaji et al. 2010). Analysis of mapping populations derived from these tolerant genotypes has led to the identification of promising QTLs for molecular genetic studies and for use in breeding (Angaji et al. 2010; Baltazar et al. 2014; Septiningsih et al. 2013a, b). Additional AG QTLs have been identified from a biparental mapping population and genome-wide association studies (Hsu and Tung 2015;

Jiang et al. 2006; Zhang et al. 2017). Nonetheless, only one QTL, *qAG9-2* or *AG1*, has been fine-mapped thus far; the gene underlying the QTL, *OsTPP7*, was identified and functionally characterized. *OsTPP7* plays a role in increasing sink strength by partially alleviating feedback inhibition mediated by trehalose-6-phosphate (T6P) through increased T6P turnover. This leads to enhanced starch mobilization that generates more energy for accelerated coleoptile elongation to escape from anaerobic conditions (Fig. 15.3) (Angaji et al. 2010; Kretzschmar et al. 2015). Through over expression studies, Guo et al. (2016) demonstrated that the microRNA miR393a regulates coleoptile elongation and stomatal development

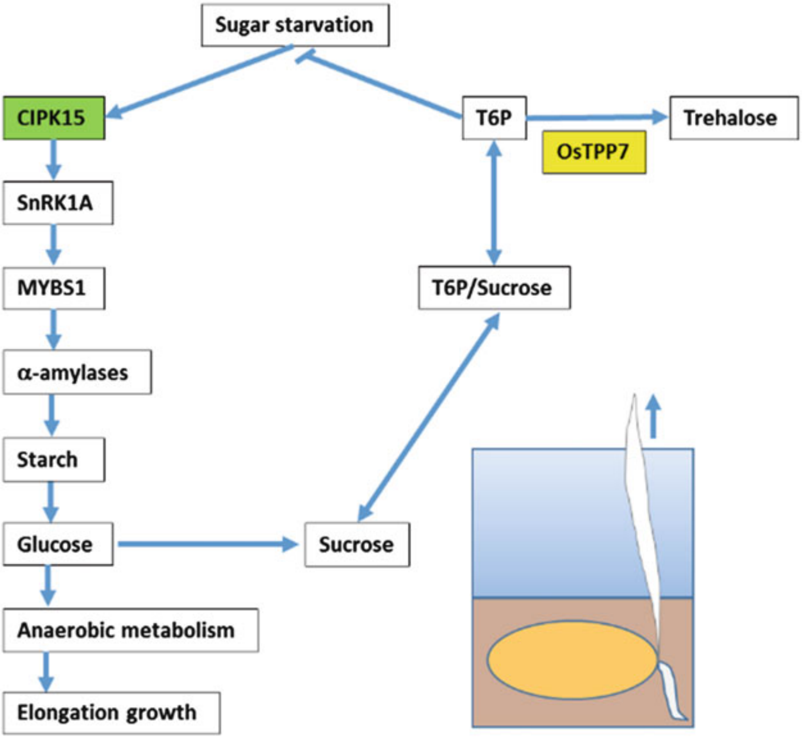

Fig. 15.3 The molecular basis of submergence tolerance during germination. Under hypoxia or anoxia, sugar starvation of an imbibed seed leads to a signaling cascade that eventually activates α-amylases through the involvement of a calcineurin B-like (CBL) protein, which targets the CBL interacting protein kinase 15 (CIPK15), which in turn triggers the SNF1-related protein kinase-1A (SnRK1A)-dependent sugar starvation-sensing cascade that induces MYBS1 transcription factor, a protein that directly binds to the promoter region of α-amylase genes (Lee et al. 2009). Only a small amount of energy is produced through glycolysis and alcoholic fermentation. Rice genotypes having functional OsTPP7 can enhance tolerance to anaerobic germination by partially alleviating feedback inhibition mediated by T6P level (Zhang et al. 2009) by indicating low sugar availability through increased T6P turnover. This leads to enhanced starch mobilization and subsequently enhanced growth of the germinating embryo and elongation of the coleoptile to facilitate timely escape from flooding (Kretzschmar et al. 2015)

via modulation of auxin signaling during seed germination and seedling establishment under anaerobic conditions. In another study, a candidate gene on chromosome 6, a DUF domain-containing protein (LOC_0s06g03520), which was highly induced by anaerobic germination, was recently claimed to be strongly associated with the trait (Zhang et al. 2017). However, further investigation is needed to better understand how these various mechanisms contribute to AG tolerance.

Unlike the *SUB1* gene that has a large phenotypic effect, major QTLs for anaerobic germination that have been identified so far have more moderate effects. However, it is assumed that different mechanisms of tolerance which are complementary can be combined to provide higher tolerance, in addition to the mechanism controlled by *OsTPP7*.

15.3 Breeding for Flood-Prone Environments

15.3.1 Flash Flood Environments

Breeding for submergence tolerance at IRRI started in the 1970s with large-scale screening of the international gene bank and identification of tolerant varieties (Vergara and Mazaredo 1975). Several of these varieties were used widely in crosses to transfer the trait into higher-yielding varieties (HilleRisLambers and Vergara 1982). The initially developed breeding lines had lower grain yields, but over several cycles of crossing and selection, some high-yielding lines were developed with strong submergence tolerance (Mackill et al. 1993). Several of them have been released in a few Asian countries. However, these were not widely adopted due to some undesirable traits, including poor grain quality and poor agronomic attributes. This problem arose due to linkage of submergence tolerance with the undesirable traits of the donor FR13A, despite its excellent tolerance to submergence.

The discovery and fine-mapping of the *SUB1* QTL, which largely contributes to submergence tolerance of FR13A (Xu and Mackill 1996; Xu et al. 2000, 2006), provided an opportunity for an accelerated and more precise breeding for submergence-tolerant rice. Closely linked and gene-based markers were developed to perform marker-assisted backcrossing (MABC) to convert susceptible mega varieties into tolerant lines without significantly altering beneficial traits of those superior varieties (Septiningsih et al. 2013a). In the beginning, IRRI successfully converted six mega varieties using two improved lines derived from FR13A, IR40931 and IR49830, as donors for submergence tolerance using the following mega varieties as recurrent parents: IR64 (Philippines); Swarna, Samba Mahsuri, and CR1009 or Savitri (India); BR11 (Bangladesh); and Tadokham 1 (TDK1; Laos) (Iftekharuddaula et al. 2011; Neeraja et al. 2007; Septiningsih et al. 2009). All six of these improved lines have been formally released in various Asian countries.

Later on, two "second-generation" Sub1 lines were developed at IRRI using IR64-Sub1 as the submergence-tolerant donor and Ciherang (Indonesia) and PSB

Fig. 15.4 Sub1 lines were grown under 25 days of complete submergence at the IRRI demonstration plot in 2014 dry season. The longer submergence duration was required because of lower than average temperature. Six pairs of the original and upgraded lines (IR64-Sub1, BR11-Sub1, PSB Rc18-Sub1, Swarna-Sub1, Ciherang-Sub1, and Samba Mahsuri-Sub1) were planted along with the susceptible check IR42. Varieties without Sub1 had high mortality

Rc18 (Philippines) as recurrent parents (Septiningsih et al. 2015). The last two improved lines were developed in a shorter time span than the former six Sub1 lines due to the use of a better donor, which was an elite variety and relatively higher genetic background similarity between donor and recipient varieties. The Sub1 lines showed a yield advantage of 2–3.5 t ha^{-1} under stress conditions compared to the intolerant parents (Singh et al. 2009) (Fig. 15.4). Most of the Sub1 lines developed through MABC in IRRI have been released in some countries in Southeast Asia and South Asia (Ismail et al. 2013; Mackill et al. 2012; Septiningsih et al. 2013a). Additionally, there have been several high-yielding lines that were conventionally bred with *SUB1* as well. The breeding line IR10F365 was developed for stagnant flooded environments (Collard et al. 2013b), but this line has also performed well in an irrigated trial in the Philippines (Gonzaga et al. 2017). Likewise, INPARA 3, which was selected and released by the Indonesian Center for Rice Research (ICRR), in Sukamandi, Indonesia, was developed for swampy areas; however, it was also found suitable for irrigated environments, especially the flood-prone regions.

The successful development of Sub1 varieties, especially Ciherang-Sub1, which was identified after only one generation of backcrossing and one generation of selfing (BC1F2), has been followed by the development of many other new submergence-tolerant lines using the elite Sub1 varieties, such as Swarna-Sub1 and BR11-Sub1, as donors of *SUB1* (Ahmed et al. 2016; Iftekharuddaula et al. 2016; Jena et al. 2015; Rao et al. 2016; Singh et al. 2016). With the discovery of additional QTLs complementary to *SUB1* (Gonzaga et al. 2016, 2017; Nandi et al. 1997; Septiningsih et al. 2012; Toojinda et al. 2003) and some new potential submergence-tolerant donors (Iftekharuddaula et al. 2015), it is expected that more robust-tolerant varieties can be bred to face the escalation of repeated and prolonged flash floods.

The released Sub1 varieties have been promoted to farmers in submergence-prone areas of South and Southeast Asia (Mackill et al. 2012). An estimated five million farmers have already adopted these varieties in South Asia (U. S. Singh, personal communication). The varieties have been evaluated in fields that are naturally submergence-prone in paired tests. For both Swarna-Sub1 and Samba Mahsuri-Sub1, average yield advantage was 1–1.5 t/ha in submergence-prone sites over their non-Sub1 parents in locations affected by submergence (Ismail et al. 2013).

15.3.2 Stagnant Flooded Environments

Breeding for stagnant flooding tolerance has been an important objective at IRRI and elsewhere for decades (Khush 1984; Mackill et al. 1996). Some criteria used to screen for tolerant genotypes have been yield, plant height, number of tillers, number of panicles, and tolerance to lodging under stagnant flooding. Among other traits, stagnant flooding tolerance is also routinely combined with *SUB1* to give additional protection in the event the plants are completely submerged, especially for rainfed lowland areas where flash floods often follow stagnant flooding events. In general, Sub1 varieties that are not too short to keep up with the raising water can survive well in this situation. A combination of bulk and pedigree breeding was used as the main method to develop new breeding lines (Fig. 15.5). Submergence screening is conducted in the F_2 and F_3 stages and again at a later stage (F_5/F_6) to make sure that there are no escapes.

Some elite breeding lines have been identified (Collard et al. 2013b; Mackill et al. 2010), and additional ones are in advanced testing. These lines have been sent to the IRRI partners, especially in South and Southeast Asia, to be tested in their affected areas. In India, for example, IRRI breeding lines together with breeding lines from the rice research centers in East India were used for selection activities among rice breeders in this region (Collard et al. 2013a). Similar activities have also been carried out in Bangladesh, Nepal, and some other countries in Southeast Asia.

Some of those advanced breeding lines are also being tested in swampy areas, such as in South Sumatra and South Kalimantan, Indonesia. In the swampy regions, however, varieties need to be also tolerant to other abiotic stresses, such as iron toxicity, aluminum toxicity, or salinity. Recently, collaboration between Indonesian and IRRI scientists identified several elite breeding lines that perform well in the swampy areas (Rumanti et al. 2016).

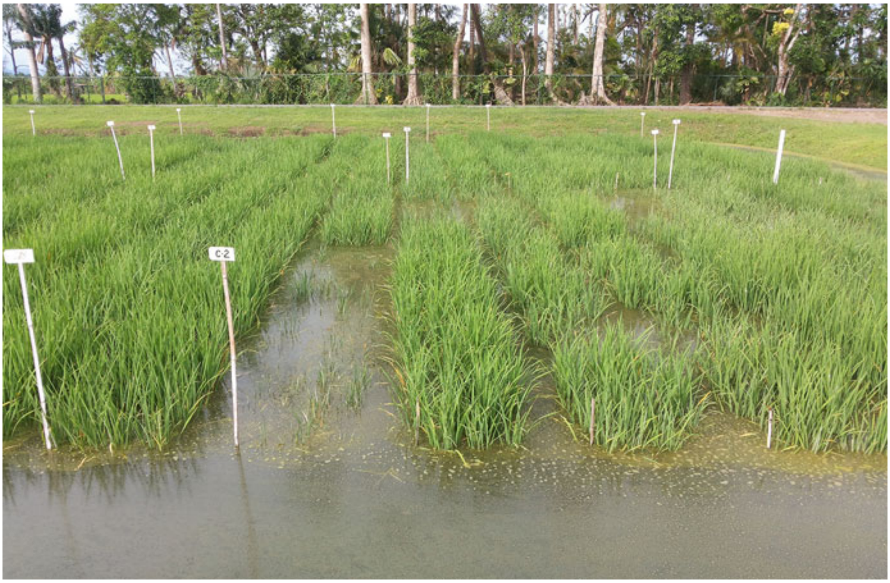

Fig. 15.5 Breeding line evaluation under stagnant flooding at the IRRI submergence field in 2014 wet season. Water was raised slowly every week starting 2 weeks after transplanting until water depth finally reached 50 cm during maximum tillering. This water depth was maintained until maturity. The plot that appears empty was Swarna-Sub1, the susceptible check. This variety almost completely died since it was too short to overcome the raising water

Nearly all deepwater and floating rice varieties are traditional landrace or pureline selections from them. There has been virtually little or no impact of modern breeding for these areas despite the advances in genetic analysis cited above. This is not due to lack of effort. Rice breeders have been working on developing improved varieties for several decades (see Catling (1992) for a history of research on deepwater rice). Early work at IRRI focused on developing improved lines combining a high-yielding plant type of semidwarf or intermediate stature with strong elongation ability (Jackson et al. 1982). These lines often performed well in areas where flooding depths were not too extreme. A few improved, high-yielding elongating rice varieties were released, such as RD19 in Thailand (Prechachat et al. 1982).

Fewer plant breeders are now working on deepwater rice because of the decline of deepwater rice production in many countries. The main cause of this decline is the widespread introduction of tube-well irrigation for dry-season rice cultivation in low-lying areas. The farmers thus replace the lower-yielding deepwater crop with a very high-yielding dry season rice crop and leave the land fallow during the rainy season. However, the discovery of the SNORKEL genes *SK1* and *SK2* for rapid elongation has created new interest in developing varieties that can cope with deepwater flood levels (Hattori et al. 2009).

15.3.3 Direct Seeded Rice (DSR) and AG

Direct seeded rice (DSR) is increasingly popular in Asia mainly due to labor shortage (Kumar and Ladha 2011) and has long been the major crop establishment method in the Americas and Europe. AG tolerance is a useful trait where flooding can kill plants at the germination stage. In the IRRI breeding program, field screening for AG tolerance is conducted in F_2 stage under 5–7 cm water right after sowing. F_3 seeds harvested from surviving F_2 plants are subjected to the same screening, and seeds are harvested from selected F_3 survivors for further selection for other traits. A small number of $F_{5:6}$ seeds will be screened in concrete benches, and the tolerant lines will be further tested under AG field screening for confirmation (Fig. 15.6). High yield is one of the most important traits required for any DSR bred with AG tolerance. Therefore, in the past few years, the selected AG tolerance breeding lines are also entered in preliminary yield trials (PYT) under both irrigated and rainfed conditions. The selected lines from either or both environments then enter multilocation yield trials (MYT).

Some AG-tolerant lines with high grain yields and other beneficial traits, such as tolerance to submergence, have been selected. Although no yield penalty of this trait has been noted, this needs to be further tested under more conditions, including evaluation under more severe or prolonged flooding stress. Several of the AG-tolerant lines have other beneficial traits such as tolerance to Zn-deficient soil. Some of the advanced breeding lines have been sent to the IRRI partners in South and Southeast Asia and to several of the IRRI research hubs in India and Africa. Yield tests for all the tolerant lines are now underway to establish them as favorable varieties.

Marker-assisted breeding has been used to develop AG-tolerant lines by transferring major QTLs to some elite genetic backgrounds. *qAG-9-2*, a major QTL derived from Khao Hlan On (Angaji et al. 2010), referred to as *AG1*, was introgressed into several genetic backgrounds such as Ciherang-Sub1, IR64, IR64-Sub1, and IR64-Sub1+Saltol (Toledo et al. 2015). A preliminary yield trial showed no yield penalty or other negative traits due to the introgression *of AG1* (Toledo et al. 2015). Another QTL derived from Ma-Zhan Red, *qAG7.1*, referred as *AG2* (Septiningsih et al. 2013b), has been pyramided with *AG1* in some varieties, such as IR64-Sub1, Ciherang-Sub1, and PSB Rc82. Preliminary data from the IRRI experiment field station of those pyramided AG lines when combined with *SUB1* demonstrated that these improved lines showed high tolerance to AG and submergence during vegetative stage. The preliminary data from the IRRI field also showed that some of the best lines have significantly higher yield compared to the local checks (S. Dixit, personal communication). Both *AG1* and *AG2* have also been introgressed into popular varieties from the Philippines and Sri Lanka by partnering with PhilRice in the Philippines and the Rice Research and Development Institute (RRDI), Sri Lanka. With the discovery of more AG QTLs, it is expected that more AG-tolerant lines carrying combinations of several QTLs will be developed through marker-assisted breeding.

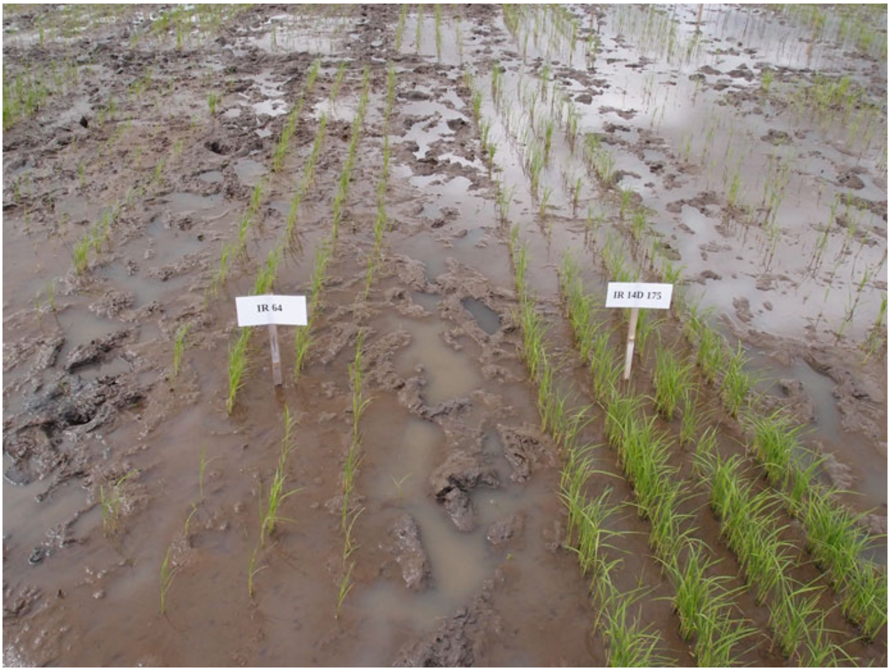

Fig. 15.6 Breeding line evaluation under anaerobic germination at the IRRI field in 2015 dry season. The field was flooded right after sowing at about 5 cm and was maintained for about 21 days to perform scoring. FR13A and IRRI154 can be used as susceptible checks; while some landraces, such as Khao Hlan On and Ma-Zhan Red, can be used as tolerant checks. Plot on the right having more survivors was IR14D175, one of the tolerant breeding lines; while plot on the left having fewer survivors was IR64, a popular high-yielding variety

15.4 Future Prospects for Flood-Tolerant Rice

There has been remarkable progress in developing breeding lines and varieties that combine tolerance to the different flooding stresses and other agronomic and grain quality traits. At this time, we can mainly document impact in flash flood environments due to the availability of Sub1 lines. Because of the MABC approach to rapidly transfer the *SUB1* gene into established varieties, the Sub1 lines have been quickly moved into production in flood-prone areas (Ismail et al. 2013; Mackill et al. 2012) and are providing benefits to rice farmers (Dar et al. 2013). Development of varieties suitable for medium-deep stagnant flooded areas has resulted in some success as well (Mackill et al. 1996; Reddy et al. 2013), and many new breeding lines developed for these conditions are under evaluation. The new breeding lines with the AG trait need further evaluation. It is not yet clear how the SNORKEL genes for rapid elongation will be utilized to develop varieties suitable for deeper flooded conditions. Determining how these genes perform in different genetic backgrounds will be important to decide which conditions they will be appropriate in. The most promising situations will be where water depths are not too extreme and higher yields can be attained. In these areas, moderate elongation may be more desirable to avoid extensive lodging after floods recede.

Many of the tolerant lines developed through both conventional and molecular breeding strategies have been used by rice breeders at IRRI and national partner institutes as parents to further develop higher-yielding varieties that are tolerant to different flooding scenarios and that could adapt well to the local environments. One example of major efforts in molecular breeding to incorporate different QTLs for submergence, drought, and salinity tolerance traits was demonstrated by Singh et al. (2016).

There are also some major molecular breeding efforts at IRRI to develop high-yielding resilient improved lines by combining several key traits, including tolerance to submergence and drought, submergence and salinity, and submergence and resistance to several diseases. These improved lines have been tested in several target regions. In the future, with the identification of more major QTLs for different flooding traits as well as other relevant traits, improved lines can be developed using some of those QTL targets to further improve the existing elite lines to develop resilient rice varieties under different stress scenarios. These novel major QTLs also open new doors to further investigate molecular mechanisms underlying these flooding tolerance traits, including tolerance to stagnant flooding—a trait that is still poorly understood.

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