Stress Tolerant Rice Varieties for Adaptation to a Changing Climate

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ABSTRACT

Rising temperatures due to accumulation of greenhouse gasses are expected to result in declining rice yields in the tropics. In addition to the direct effect of high temperature in reducing yields, a rise in sea level coupled with more erratic and extreme weather events will result in reduced yields and increase the risks of rice farming. The abiotic stresses that are anticipated to worsen as the consequences of climate change include high temperature, drought, flooding and salinity stresses. While high temperature is not currently a major problem, the other stresses are already widespread yield limiting factors in the unfavorable environments of tropical Asia. Incorporating stress tolerance into high-yielding varieties has proven to be a very effective approach to developing varieties that can cope with these situations. These successes provide optimism that the problem of climate change can be addressed partially through development and dissemination of adapted germplasm.

Key words: Abiotic stress, Climate change, Oryza sativa, Rice.

INTRODUCTION

The prospect of global warming resulting from accumulation of greenhouse gasses is causing major concern, especially in connection with its potential effect on rice production (Wassmann et al. 2009b). While the rise in CO₂ concentration would be expected to have a beneficial effect, the overall results will be negative in the tropics, where most of the world’s poor live. Rising sea level will reclaim some of the rice lands in the coastal regions, increase salinity intrusion, and impede drainage leading to more flooding problems in low-lying areas. Increasing
frequencies of both drought and floods will result from more erratic rainfall and extreme weather events. Higher temperatures will also have a negative effect on rice production. High temperature can affect rice growth and development at all stages, and particularly if it occurs during pollination.

These damaging effects can be effectively addressed through plant breeding. Rice breeding has been a very successful activity in the past few decades, particularly in favorable areas. During the 1970s, modern, high-yielding varieties (HYVs) were rapidly adopted in irrigated and favorable rainfed lowland areas. However, these varieties were not ideal for the more unfavorable areas, where poor water control and adverse soil conditions limited yields, and most farmers in these areas continued to grow low-yielding varieties. Breeding for tolerance to abiotic stresses was rapidly expanded during this time.

The HYVs have continued to spread throughout both irrigated and rainfed areas, and now cover the majority of the production areas in tropical Asia. However, these varieties are invariably intolerant to the current major abiotic stresses that are likely to be further aggravated by climate change, such as drought, submergence, and salinity. These stresses reduce yields in millions of hectares in rice production areas; and modern HYVs have had limited impact in these areas.

The scenario of climate change is leading to a convergence of technology developed for unfavorable rainfed environments with the need for future adaptation of rice varieties to the changing climate. Rice varieties tolerant to the major abiotic stresses (drought, flooding, salinity and high temperature) will provide some protection against the adverse effects of climate change. Rapid progress has been made in developing stress tolerant varieties, and they are being rapidly disseminated to farmers in unfavorable growing environments. The present article reviews some of the advances made in genetics and breeding for stress tolerance in rice, and describes the progress made in the development of varieties for coastal areas where flooding and salinity are problems, and where rising sea-level will constrain future rice production.

**STRESS TOLERANCE: SOURCES AND GENETICS**

Drought is the most serious constraint to rice production in unfavorable rice growing areas, and most of the popular farmers’ varieties are susceptible (Serraj et al. 2009). Genetic studies on component traits have been carried out but these studies have generally not identified any QTLs that could be considered as promising targets in rice breeding programs. However, the use of direct measurement of yield under drought stress has shown more promising results. Bernier et al. (2007) detected a QTL on chromosome 12 in a large population from the cross of Vandana/Way Rarem that accounted for about 50% of the genetic variance, and was expressed consistently over 2 years. This QTL seems to be related to increased water uptake of plants under stress (Bernier et al. 2009). A chromosome 3 QTL had a large effect on drought tolerance in the cross between the tolerant variety Apo and the widely grown susceptible variety Swarna (Venuprasad et al. 2009). This is a very promising QTL for use in marker-assisted selection, because the variety Swarna is widely grown in drought-prone environments due to its high yield and other desirable traits.

Promising varieties with drought tolerance like Sahbhagi Dhan (IR74371-70-1-1) have been developed through conventional breeding and are being disseminated to farmers in drought-prone areas. These varieties perform well even during favorable years, and they provide about 1 t/ha yield advantage under severe drought stress (Verulkar et al. 2010). Most of the popular varieties grown by the farmers fail under these conditions.

Over 20 million ha in rainfed lowland areas are adversely affected by floods each year. Rice in these areas is the major crop providing food for millions of subsistence farming families. These areas are subject to either frequent flash floods or submergence; longer-term flooding of 20-50 cm (partial/stagnant, semi-deep), deep water of > 100 cm (deepwater rice), or very deep water of up to 3 or 4 meters, as in floating rice areas. Rice productivity in these ecosystems is rather low, averaging about 1.5 Mg ha⁻¹ because of the lack of high-yielding varieties tolerant of these stresses.
Enormous potential for more food production exists in these areas because of the predominance of good soils and freshwater resources. However, the challenges facing rice production in these areas are becoming ever more intricate with the enduring adverse climate changes, and the ensuing increase in storms and sea level rise in coastal areas, where rice-based systems predominate.

Submergence tolerance is an important trait where short term “flash” flooding damages rice crops. Highly tolerant varieties such as FR13A from Orissa, India, have been used in breeding programs (Vergara and Mazaredo 1975, HilleRisLambers and Vergara 1982, Mackill et al. 1993). Tolerance in these varieties is controlled by the SUB1 locus on chromosome 9 (Xu and Mackill 1996), which includes three ethylene response factor (ERF)-like genes (SUB1A, SUB1B, SUB1C) (Xu and Mackill 1996, Xu et al. 2006). The major determinant of submergence tolerance is the SUB1A gene (hereafter referred to as SUB1) (Xu et al. 2006, Septiningsih et al. 2009). The tolerance conferred by this gene is related to the suppression of elongation, which enhances survival by reducing carbohydrate consumption, thus allowing the plants to recover upon de-submergence (Fukao and Bailey-Serres 2008a). Fortunately, this gene works well in any genetic background (Septiningsih et al. 2009), and does not affect yield potential. Success in using the SUB1 gene for varietal improvement is described below.

Direct seeding is being practiced in most deepwater areas, and recently it has gained momentum in flash-flood and other rainfed areas because of its lower cost and operational simplicity. However, the uncertainties of rainfall and possibilities of flooding after seeding hinder its large-scale adoption because of the high sensitivity of germinating rice seeds to flooding and the likely failure of crop establishment. Varietal differences for submergence tolerance during germination (anaerobic germination; AG) have also been observed (Ismail et al. 2009). Submergence tolerant varieties with the SUB1 gene do not usually possess the AG trait, indicating that these two traits are independent. Some major QTLs have been identified (Angaji et al. 2010), and improved breeding lines have been developed.

In deepwater areas, the water depth increases gradually throughout the year and can remain above 50 cm for long periods. In these situations, rapid elongation ability is necessary to allow the plants to keep up with rising floodwater. Deepwater or “floating” rice varieties initiate internode elongation early in their growth period and their internodes undergo rapid elongation. The early initiation of elongation is controlled by QTLs on chromosomes 3 and 12 (Nemoto et al. 2004, Hattori et al. 2007, Kawano et al. 2008), and the rate of internode elongation is controlled by QTLs on chromosomes 1 and 12 (Hattori et al. 2007, Hattori et al. 2008, Kawano et al. 2008). The chromosome 12 QTL is the major determinant of the rapid elongation response of deepwater varieties. It has been shown to consist of two ERF genes, named SNORKEL1 and SNORKEL2, that are very similar in sequence to the SUB1 genes (Hattori et al. 2009). However, SUB1 has the opposite effect of the SNORKEL genes and inhibits elongation of leaves and internodes when induced during submergence.

Salinity and other associated soil problems are major constraints for rice production in most humid and sub-humid coastal and inland climates of Asia (Ismail et al. 2007, Ismail and Tuong 2009). The majority of these areas are not currently in use for agriculture despite being potentially suited for rice. Salinity in these areas varies with the season, being high in the dry season with the peak before the onset of rains. Salinity level in soil and water then decreases progressively during the monsoon season and reaches the ground level during June to September (Ismail and Tuong 2009). An anticipated effect of global warming is an increase in area affected and severity of salt stress, both in coastal and inland ecosystems. In coastal areas, an increase in salt intrusion has already been observed in some of the low-lying deltas such as in South Bangladesh, Vietnam and Myanmar (Wassmann et al. 2004). In inland areas, salt deposition is expected to increase as a consequence of increased evapotranspiration and water shortage with rising temperatures. Rice is suitable for reclaiming these soils because it thrives well under flooding, and with high potential for genetic manipulation.

Excellent sources for salt tolerance have been identified (Akbar and Yabuno 1977). A major QTL
was identified conferring salt tolerance on chromosome 1 and designated Saltol (Bonilla et al. 2002). This QTL has been the target of marker assisted selection (Thomson et al. 2010). A chromosome 1 QTL SKC1 that appears to be a part of this locus was isolated by positional cloning and determined to be a protein that functions as a Na⁺-selected transporter (Ren et al. 2005).

Many salt tolerant varieties have been developed and have also been adopted, especially in the inland saline/sodic areas (Singh and Mishra 2006, Rao et al. 2008). Major sources of salt tolerance of these varieties include the landrace cultivars Pokkali and Nona Bokra. For coastal areas in the wet season, both salinity and submergence are problems. Fortunately, both SUB1 and Saltol can be combined in the same variety, and these lines combine tolerance to both stresses (R. K. Singh, personal communication).

Most rice varieties are very sensitive to high temperatures. However, high temperature stress is currently not an important limitation for rice production except in a few areas where rice is grown in hot dry environments. Temperatures above 35 C can cause sterility if they occur during anthesis. This generally occurs before 1100 h in most tropical or warmer environments, so daily maximum temperatures need to be above 40 C before appreciable effects could be seen on sterility (Yoshida et al. 1981). However, higher night temperatures in tropical regions decrease rice yields appreciably (Peng et al. 2004) and reduce grain quality (Counce et al. 2005, Zhong et al. 2005, Tanaka et al. 2009). Donors for high temperature tolerance during anthesis have been identified (Satake and Yoshida 1978, Mackill et al. 1982) and QTL mapping is underway.

From the above studies it is clear that tolerance to the major abiotic stresses that will further be exacerbated as a result of climate change, can be addressed through breeding, and that these are frequently under the control of QTLs of large effect. This provides a good opportunity for applying marker assisted selection, and in particular marker assisted backcrossing (MABC) to develop cultivars with improved stress tolerance. The following section describes some of the success achieved in developing varieties for the flood prone areas, including the coastal floodplains and deltas that will be heavily impacted by future climate change.

**DEVELOPING IMPROVED VARIETIES FOR FLOOD-PRONE CONDITIONS**

1. Different types of flooding stress

Flooding is a major stress constraint to rice production, especially in rainfed lowland areas of the tropics. The flooding of the major river basins and deltas of Asia has provided the sustenance for the rice production that has been a prominent feature of the region for millennia. However, this flooding is also a cause of yield fluctuations because of erratic rainfall patterns and poor drainage of many rice fields. This results in excess water in these fields for varying depths and durations (Ismail et al. 2010). For convenience, this flooding can be classified into four types depending on the plant traits and varietal types that are adapted to the conditions:

a) **Flooding during germination** (anaerobic germination; AG): a problem when direct seeding is practiced and heavy rains result in submergence before germination.

b) **Flash flood** (submergence): plants are completely submerged for up to 2 weeks. Submergence tolerance is required for this condition.

c) **Stagnant flooding** (medium deep or semi-deep): flooding occurs for a longer duration, more than 2 weeks and often several months, at depths up to 50 cm. Varieties tolerant of stagnant flooding conditions are required.

d) **Deeper stagnant flooding** (deepwater or floating rice): water depth increases throughout the season to depths above 50 cm and often a meter or more. Varieties with tall plant height or rapid internode elongation are required.

In any particular field, more than one of these situations can occur in the same season or in different seasons. Therefore, it is preferable that varieties developed for flood-prone areas have a combination of tolerance traits when possible. This is feasible with the exception that varieties developed for deepwater areas usually need to have rapid elongation ability, and this trait is probably incompatible with submergence.
tolerance conferred by the SUB1 gene. The remaining discussion focuses on developing varieties tolerant to the first three flooding situations described above.

2. Combining tolerance to submergence and stagnant flooding

The most prominent example of breeding for flooding tolerance has been the development of submergence tolerant varieties through the use of the SUB1 gene. Sub1 versions of popular rice varieties were developed through the MABC approach (Neeraja et al. 2007, Septiningsih et al. 2009), and these varieties displayed a high level of submergence tolerance compared to their parents (Fig. 1). Because these varieties retained the desirable features of the original popular varieties, they have been accepted enthusiastically by the farmers in submergence-prone areas (for more information, see http://www.irri.org/flood-proof-rice/). These varieties typically give a 1-2 Mg ha⁻¹ yield advantage over the susceptible varieties, but can give much higher advantages under more severe submergence stress (Sarkar et al. 2009, Singh et al. 2009).

Currently, at least nine popular varieties have been converted to Sub1 type using this MABC approach, and other Sub1 varieties have been developed through the normal breeding procedures. These varieties show excellent tolerance to submergence throughout vegetative growth, and even with late floods at the panicle initiation stage (Our unpublished data). However, most of them are sensitive to stagnant flooding because of their short stature. A good example is the variety Swarna-Sub1, which has been the most popular Sub1 variety to date. This variety is being disseminated widely in eastern India, Bangladesh, and Nepal, and has been well accepted by the farmers. Researchers have observed these varieties typically give a 1-2 Mg ha⁻¹ yield advantage over the susceptible varieties, but can give much higher advantages under more severe submergence stress. (Sarkar et al. 2009, Singh et al. 2009).

Fig. 1. Widely grown rice varieties that were enhanced through introduction of the SUB1 submergence tolerance gene through MABC. The tolerant versions were planted adjacent to their susceptible parents. Plants were submerged for 14 days and fields were drained to allow the surviving plants to recover.
farmers (Reddy et al. 2010). It has shown excellent survival under natural submergence in farmers’ fields. However, it is not tolerant of stagnant flooding conditions. When the water depth increases too fast and does not recede within 2-3 weeks, the growth of Swarna-Sub1 is greatly inhibited. Rice breeders have successfully developed cultivars that have tolerance to stagnant flooding, and these cultivars are adapted to areas where water depths remain high throughout the season (Reddy et al. 2010). However, they do not possess the SUB1 gene, and they remain sensitive to short-term submergence stress.

Tolerance to submergence through SUB1 and tolerance to stagnant flooding are not incompatible traits. In a short statured cultivar such as Swarna-Sub1, the plants are sensitive to stagnant flooding if the water levels rise too rapidly because most of the canopy is under water, and the plants cannot easily elongate out of the water due to the elongation-suppressive effect of SUB1 (Fukao et al. 2006, Xu et al. 2006, Fukao and Bailey-Serres 2008b). However, in cultivars that are taller (> 100 cm) a sufficient part of the canopy remains above the water level to allow the plants to grow well. One variety developed previously at IRRI, IRRI 119 (released in the Philippines as PSB Rc68), has the SUB1 gene and is relatively tolerant to both stresses (our unpublished data). At IRRI we have been screening new breeding lines for tolerance to both water stagnation and submergence tolerance. In initial screening under relatively severe stress, breeding lines were identified that were more tolerant to stagnant flooding than the check tolerant cultivar Swarna-Sub1 (Table 1). These lines also had relatively good survival when they

Table 1. Promising breeding lines identified through screening under stagnant flooding (50 cm) in 2009 and 2010 at the IRRI farm, Los Baños, Philippines. In 2009, tolerance to submergence was assessed by measuring survival after submergence of 14 days followed by stagnant flooding of 20 cm. In the test, the check variety without SUB1, IR42, had a survival of 0 %. In 2010, yield was measured by yield test with 3 replications under shallow (10-20 cm) and stagnant flooding (50 cm). Days to flowering and plant height are from the shallow fields.

<table>
<thead>
<tr>
<th>Designation</th>
<th>2009 screening</th>
<th>2010 screening</th>
<th>Submergence + stagnant survival (%)</th>
<th>Yield (50 cm) (kg ha⁻¹)</th>
<th>Yield (shallow) flowering (d)</th>
<th>Plant height (cm)</th>
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<tr>
<td></td>
<td>Survival (%)</td>
<td>Phenotype score</td>
<td>Survival (%)</td>
<td>Phenotype score</td>
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</table>

1 Phenotype was rated visually on a score of 1 (best performance) to 9 (worst performance) before harvest.
were submerged for 14 days followed immediately by prolonged flooding of 20 cm (Table 1). Under these conditions, Swarna-Sub1 only had a survival percentage of 20%. When tested in larger plots in a replicated yield trial, these lines also performed well under both shallow and 50-cm stagnant flooding (Fig. 2, Table 1 – last four columns). It should be pointed out that some of the MABC-derived lines have moderate tolerance to stagnant flooding, and the highly sensitive variety Swarna-Sub1 can tolerate stagnant flooding that occurs gradually or develops later in the season.

3. Combining tolerance to submergence and anaerobic germination

As mentioned above, tolerance to submergence during germination is a different trait from tolerance to submergence during the vegetative stage, and \( SUB1 \) has no beneficial effect during germination. Donors for tolerance to submergence during germination were identified by screening over 8000 accessions from the IRRI rice genebank (Angaji et al. 2010). A few highly tolerant varieties were identified, among which Khaiyan (Bangladesh), Khao Hlan On (Myanmar), and Ma-Zhan (red) were found to be very promising. Crosses were made between these varieties and improved breeding lines at IRRI. From these lines, promising selections were identified that have improved plant type and yield, as well as high AG. In addition, crosses were made with submergence tolerant lines possessing the \( SUB1 \) gene for tolerance. From these crosses, advanced breeding lines were identified that have both high AG as well as \( SUB1 \)-mediated submergence tolerance. Most of these lines derived from one cross combination (IR83770 = Khaiyan/Mahsuri/IR 05F101), with Khaiyan being the source of the AG trait and IR 05F101 (Swarna-Sub1) the source of the \( SUB1 \) gene. These results show that these two traits are compatible. The increasing use of direct seeding will demand new types of varieties that can tolerate submergence both during germination and later vegetative growth stages. The results described here show that it is possible to develop rice varieties with tolerance to submergence from germination up to the early reproductive stage.

![Fig. 2. An example of a rice breeding line (IR 09F185) showing tolerance to stagnant flooding of 40 cm and that also possesses the \( SUB1 \) gene for submergence tolerance.](image)
Ideally, rice varieties with tolerance during the entire life cycle should be developed, because flooding can cause damage at all growth stages. However, there are no known varieties with tolerance to submergence at flowering or later. Otherwise, there is no apparent obstacle to combining the three traits (AG, submergence tolerance, stagnant flooding tolerance) together in a single variety. These types of varieties will be suitable to submergence-prone areas and will become more useful in the future as flooding stress intensifies.

**FUTURE PROSPECTS**

Climate change is likely to have an adverse impact on rice production in tropical Asia. This is not only due to the direct effect of higher temperatures, but to problems associated with extreme weather events and sea-level rise such as drought, submergence and salinity (Wassmann et al. 2009a). These problems will be especially acute in the coastal and delta regions, where flooding and salinity are likely to increase (Ismail et al. 2010). However, these exact conditions have existed for centuries in the coastal regions of Asia, where rice production provides the main livelihood and nourishment of the populations.

Rice is the ideal crop for these low-lying and poorly drained regions. Both short term submergence and longer-term stagnant flooding are common in these areas, and local varieties have been identified and selected by farmers that are adapted to these conditions (Mackill et al. 1996). These varieties are usually tall and low yielding, but they have provided a stable source of food in areas subjected to variable climatic conditions. Unfortunately, they cannot meet the needs of the present and future populations, who need highly productive cultivars that have the grain quality demanded by the market. Many modern rice farmers have shifted to high yielding cultivars, with devastating consequences during times of flooding. Others have abandoned rice farming, or continue to make a precarious living relying on the local varieties.

Progress on developing rice varieties for the unfavorable areas has shown that modern breeding tools can address many of the problems of farmers in these areas. Furthermore, with improved crop and soil management practices, these farmers can more than double their yields under highly stressed conditions. Achieving impacts in these areas will require continued investment in crop improvement research as well as improvements in delivery of improved seeds to the farmers. This provides some optimism that the adverse effects of climate change in rice-growing areas can be partially compensated for, through rice improvement, while certainly not removing the urgent need for mitigation initiatives.

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