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Incorporating stress tolerance in rice

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Introduction

Crop genetic improvement and management intensification, as well as expansion of cropped area (especially in Africa), often referred to as the Green Revolution, have allowed food production to largely keep up with human need since the 1970s. Breeders incorporated dwarfing genes to develop short and stiff varieties that partition more biomass to developing grains than to straw production, and are photoperiod insensitive, of shorter duration and responsive to fertilisers, unlike the old and traditional varieties. The key genes responsible for these effects encode mutations that interfere with the action of the plant growth hormone gibberellin, resulting in short, stiff stems that can support a heavy grain load when fertiliser is applied (Hedden 2003). Because of their visible differences from taller traditional varieties, their dissemination was relatively easy: farmers could clearly see their advantages in simple field demonstrations and they were widely adopted (Evenson and Gollin 2003).

Yields of the major food crops (maize, rice, wheat and soybean) need to be doubled by 2050 to maintain global food security. However, the current annual rate of yield increase in these crops is far slower than the projected 2.4% needed to reach this goal (Ray *et al.* 2013). The decline of yield growth rates can be attributed to diminishing investments in agricultural research, and continued use of breeding and seed dissemination methods that were appropriate during the Green Revolution but that are ineffective in generating and delivering genetic gain for quantitative traits (Atlin *et al.* 2017). Much of the yield gain required to feed the world's population by 2050 will need to come from intensification of agriculture in sub-Saharan Africa, where fertiliser use remains much lower than the global average, and old, low-yielding varieties still predominate. Genetic improvement will also need to contribute to yield gains in regions where input use is already high and modern varieties have been widely adopted. In such relatively favourable environments, post-Green Revolution genetic gains for yield have resulted mainly from rapid-cycle breeding programs that incrementally improve the frequencies of genes controlling **quantitative traits**, or traits controlled by many genes, each with small effect. However, even in favourable locations, drought, floods and temperature stresses that may increase in frequency and severity as a result of climate change can reduce rainfed rice production. Under these conditions, recently characterised large-effect alleles for tolerance to stresses such as drought and flooding tolerance, found at very low frequency in elite germplasm, can make important

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contributions. A better understanding of the adaptive traits controlled by these alleles, often found only in landraces and wild relatives, and their physiological and molecular bases, will facilitate breeding varieties that are more resilient in particular environments.

Improved approaches for developing and delivering crop cultivars combining tolerance of abiotic stresses and with improved yield potential are critical for the ability of farming systems to adapt to climate change. Developing countries in tropical areas are likely to suffer significantly from the consequences of climate change, with more erratic and intense rains causing floods and droughts, and increasing salt intrusion especially in coastal areas caused by sea level rise, changing flow in rivers and increased incidence of storms and cyclones. Furthermore, challenges with pests and diseases, soil erosion and land degradation are expected to escalate (Rosegrant and Cline 2003). Marginal lands are becoming increasingly important as potential sources for food because of the steady loss of productive lands to urban and industrial encroachment. Maintaining food security in the face of a changing climate and intensifying cropping systems will require both investment in improved abiotic stress tolerance needed on marginal lands and steadily increasing productivity in favourable environments.

Green Revolution technology was adopted primarily in favourable areas where water resources are secured through irrigation or reliable rainfall. Several rounds of breeding and variety replacement delivered improvements in traits that were deficient in the initial GR, particularly in resistance to insects and diseases, and grain quality, leading to steady adoption, and gains in productivity (Estudillo and Otsuka 2013; Evenson and Gollin 2003; Ismail and Mackill 2014). A 'maintenance breeding' approach predominated after initial spectacular productivity gains, leading mostly to enhanced adaptation to specific environments and preventing yield reductions due to evolution of new strains of pests and diseases. The breeding methods that resulted in the Green Revolution in rice and wheat were based largely on visual selection for the semi-dwarf plant type and disease resistance under favourable conditions, with inadequate selection pressure applied for yield in multi-location replicated trials (Atlin *et al.* 2017), and inadequate attention to abiotic stress tolerance. As a result, adoption of new varieties has been limited: the average age of rice varieties in farmers' fields remains above 20 years in the wet season in India and Bangladesh (Tsusaka *et al.* 2015). Increasing the rate of genetic gain and driving increased rates of varietal replacement in these areas is challenging and will require considerable research and development through a restructuring of the breeding programs to enhance grain yield gains in farmers' fields (Atlin *et al.* 2017; van Ginkel and Ortiz 2018; see Chapter 9). Throughout the developing world, breeding programs are using obsolete strategies and approaches that limit the rate of genetic gain delivered to farmers. Typically, insufficient attention is paid to culinary quality, breeding cycles are too long, and inadequate selection pressure for yield in multi-environment trials is applied. Breeding strategies are now being optimised in public rice breeding programs in Asia to increase genetic gains by shortening breeding cycles, increasing selection differential for yield, increasing phenotyping throughput through digitisation and mechanisation, and the application of diagnostic molecular markers in forward breeding (Collard *et al.* 2013). Proper crop management strategies also need to be in place to narrow the current and future gaps between attainable yields and what the farmers are actually achieving in their fields (see Chapter 14).

The productivity gains achieved in favourable areas did not benefit most farmers in less favourable agro-ecological systems, especially areas affected by water shortage or excess, soil problems including excess salts, nutrient deficiencies or toxicities and temperature extremes. This is because the breeding programs that led to the Green Revolution focused mainly on yield enhancement (through input responsiveness) in favourable areas. In rice, there is evidence that the modern semi-dwarf varieties lost many of the adaptive traits present in local landraces and old varieties, because these traits were not selected for. This is particularly evident for rice in most rain-fed areas where several abiotic stresses are encountered. Although modern semi-dwarf varieties saw some adoption in these areas because of their early maturity, they were highly susceptible to drought, submergence and water stagnation. Increasing the contribution of these less favourable areas for food production requires new varieties that incorporate the adaptive traits and alleles required to tolerate particular weather or edaphic stresses while maintaining their high yield and market quality. This chapter will focus on rice as a model crop where progress was made in developing abiotic stress-tolerant varieties, and where opportunities exist for further improvements through mining the enormous genetic diversity available in preserved collections worldwide. It presents examples from the progress made in developing submergence-, drought- and salt-tolerant rice.

Challenges and opportunities in breeding rice varieties for less favourable areas

Rice is regarded as the most widely adapted cereal crop. It is grown from 50°N in northern China to 35°S in New South Wales, Australia and in Argentina. It is also grown across a wide range of altitudes, from below sea level in Kerala, India to higher than 3000 m in the uplands of Nepal and Bhutan (Office of the Gene Technology Regulator 2005). Rice is also adapted to variable types of soils and hydrological conditions, from fully aerated soils in uplands to flooded soils in irrigated and rain-fed lowlands, and to inundation for long durations with several metres of water for most of the season in flood-prone and deepwater areas. This considerable variation in adaptation resulted in substantial genetic diversity within the rice gene pool. The T.T. Chang Genetic Resources Center of the International Rice Research Institute (IRRI) currently holds close to 130 000 accessions of landraces and wild relatives collected worldwide. This vast plasticity in adaptation in rice provided a rich source of diversity for use in breeding resilient rice varieties that could potentially withstand current and future climate stresses (Ismail and Mackill 2014).

Despite the progress made in favourable areas with the adoption of the semi-dwarf, high-yielding varieties, yields in less favourable areas stayed low and unstable, typically at 1.0–2.0 t ha^{-1} in areas where landraces still dominate. This is attributed to the effects of several abiotic stresses including drought, floods, excess salt, and nutritional deficiencies and toxicities. In South and South-East Asia, ~23 million ha of rice production are estimated to be affected by drought, 22 million ha by submergence (complete inundation) and 16 million ha by excess salts in soil and water each year (Huke and Huke 1997). These abiotic stresses cause substantial crop losses, with social and humanitarian consequences usually overlooked in estimates of financial losses, because most of these areas support large populations of the poorest communities. These communities often have limited options for livelihood, and usually forced to take grave measures upon disastrous weather incidents, sometimes forcing them to liquidate their assets merely to survive, further limiting their future options. Frequent crop losses due to abiotic stress disincentivise farmers from investing in fertiliser inputs, further depressing yields in marginal areas (Emerick *et al.* 2016)

Improving adaptation to less favourable areas

The early domestication of the *Oryza* species, dating back to ~9000 BC in China (Molina *et al.* 2011), and the broader geographic and ecological distribution of cultivated rice, led to greater genetic diversity relative to other crops. Fortunately, this diversity is largely preserved, with over 750 000 *Oryza* species accessions globally conserved in gene banks, the largest collection of which (20%) is maintained at the International Rice Research Institute (IRRI) Genetic Resources Center (Jackson 1997; Hay *et al*. 2013). These resources are being used to improve adaptation of existing high-yielding varieties to abiotic stresses, extending their benefits to less favourable areas. About half of the genetic resources conserved in IRRI gene bank (38 000 at the time) were screened under different abiotic stresses in the 1970s and 1980s. Only a few accessions were identified as potential donors, suggesting that tolerance traits are relatively rare (Palada and Vergara 1972; Khush and Coffman 1977; Ismail and Mackill 2014). Parallel research activities were also carried out in other countries, including Thailand, India and Japan (Yamada 1959; Richharia and Misro 1960; IRRI 1975). However, abiotic stress-tolerant varieties suitable for farmers' needs were never developed because of the difficulty of retaining high yield and other desirable traits while incorporating stress tolerance using phenotypic selection alone. Linkage drag resulted in the incorporation of substantial amounts of the donor genome in addition to the target trait, often preventing full recovery of the yield potential and culinary quality of the recurrent parent. Recent advances in molecular marker technology have made it possible to localise and precisely transfer large-effect alleles for tolerance to abiotic stresses using marker-assisted backcrossing (Tanksley *et al*. 1989), facilitating the development of rice varieties for the less favourable areas. Their adoption by farmers demonstrates their potential for improving rice production in areas that missed the benefits of the Green Revolution. Using modern plant breeding technologies made it possible to locate and transfer adaptive traits and tolerance mechanisms from old landraces into modern high-yielding varieties, making them suitable for cultivation in unfavourable areas.

Progress in developing flood-tolerant varieties

Waterlogging and floods cause substantial losses in cereal crops worldwide. Most dryland cereals (maize, wheat, rye, barley) are sensitive to waterlogging, causing up to 20% yield losses in irrigated areas and more than 40% losses in rain-fed areas (Setter and Waters 2003; Herzog *et al*. 2016). In flooded or waterlogged soils, root growth and function are impaired because of oxygen shortages causing impaired root respiration and growth (Ismail 2018). Gases such as ethylene, CO_2 and H_2S, and other phytotoxins such as reduced iron and zinc and organic acids increase in the root zone, causing serious damage to roots (Drew and Lynch 1980; Colmer *et al*. 2014; Kirk *et al*. 2014). Genetic variability in waterlogging tolerance was reported in some dryland cereals, such as wheat, barley and rye, but with little to no significant progress in breeding tolerant varieties (Drew 1997; Setter and Waters 2003).

In contrast to dryland cereals, rice is peculiar in its ability to survive waterlogged and even flooded soils, due to its ability to aerate its roots and the rhizosphere through its extensive aerenchyma system, which helps overcome the stresses associated with low oxygen in roots and surrounding soil (Jackson and Ram 2003; Jackson and Ismail 2015). However, this tolerance is limited to waterlogging and shallow flooding, and is ineffective under prolonged partial (more than 25 cm to a few metres) or complete submergence that are common in rain-fed lowlands and flood-prone areas. The excessive wetness in these areas during the height of the tropical rainy season leaves the farmers no options but to grow rice: rural poverty and food insecurity are widespread in these areas. Yields in affected areas are low and unstable, and farmers rely on traditional landraces and old varieties that are better adapted to partial flooding and submergence than modern varieties. Farmers also use fewer inputs because of the risks of crop loss in flood-prone areas and the poor responsiveness of these old varieties to fertilisers. Although flood incidence and duration are expected to worsen in many flood-prone regions of the tropics due to climate change (Kemp *et al.* 2011; Coumou and Rahmstorf 2012), the diversity available among rice landraces that evolved in contrasting hydrological conditions will likely make it feasible to breed varieties suitable for current flooding conditions, and for future climates. This chapter presents examples of the progress made in developing rice varieties that tolerate complete submergence.

Considerable efforts were devoted over the last five decades to breed submergence-tolerant varieties. Several tolerant landraces were identified and used for studying the physiology and genetics of submergence tolerance and in breeding (Mackill *et al.* 2012; Ismail *et al.* 2013; Ismail and Mackill 2014). Early studies suggested that submergence tolerance is highly heritable, and semi-dwarf breeding lines with high tolerance were identified after breaking the association between poor grain quality and yield inherited from the donor landraces such as FR13A. These breeding lines were evaluated in several countries, and a few were released, but they were not widely adopted because they did not meet the quality standards of the high-yielding varieties being used by farmers, even though they are much more tolerant of submergence (Mackill *et al.* 1993).

The most significant stride in breeding submergence-tolerant rice varieties was the discovery and cloning of the *SUB1A* gene, identified from the Indian landrace FR13A, (Xu and Mackill 1996; Xu *et al.* 2006). The development of a diagnostic marker facilitated its deployment to farmers by backcrossing the gene into the background of several widely grown mega-varieties, each grown on at least 1 million ha, that were preferred by farmers for their high yield, adaptation to favourable rainfed lowlands and good grain quality. The identification of *SUB1* provided an opportunity to further improve these mega-varieties for submergence tolerance while preserving their desirable characteristics, and their popularity made it possible to use them to quickly deploy submergence tolerance in target areas (Mackill *et al.* 2010, 2012; Ismail *et al.* 2013). *SUB1* was initially transferred into eight popular varieties using marker-assisted backcrossing (MABC). These varieties included IR64, Swarna, Samba Mahsuri, Sabitri, BR11, TDK1, BSBRc18 and Ciherang, all popular in South and South-East Asia (Neeraja *et al.* 2007; Septiningsih *et al.* 2009; Iftekharuddaula *et al.* 2011). More recently, several varieties were developed via MABC by national programs in India (Singh *et al.* 2016a) and Vietnam (Cuc *et al.* 2012; Lang *et al.* 2015), and *SUB1* has been introgressed into the widely grown West African varieties WITA4 and NERICA-L-19, creating the submergence-tolerant varieties FARO 66 and FARO 67, respectively (R. Venuprasad *pers. comm.*). The new introgression lines were extensively evaluated under field conditions with farmers, and were observed to be phenologically and agronomically identical to their recurrent parents, with similar yield and grain quality under control conditions. However, when subjected to submergence, usually for 7 to 18 days in farmers' fields, these Sub1 varieties showed strong submergence tolerance, with yield advantage generally ranging from 1 to 3.5 t ha^{-1} above that of the intolerant parental varieties, depending on the submergence duration and floodwater conditions (Das *et al.* 2009). This yield advantage was attributed to higher survival and faster recovery after submergence of the Sub1 varieties (Fig. 13.1A) (Sarkar *et al.* 2009; Singh *et al.* 2009; Bailey-Serres *et al.* 2010; Mackill *et al.* 2012; Ismail *et al.* 2013). IRRI-developed Sub1 varieties have been disseminated in several countries, including India, Bangladesh, Nepal, Myanmar, Laos, Indonesia and the Philippines (Collard *et al.* 2013). Performance of these varieties was consistent across countries and continents when submergence was encountered from early seedling stage to about a week before panicle initiation.

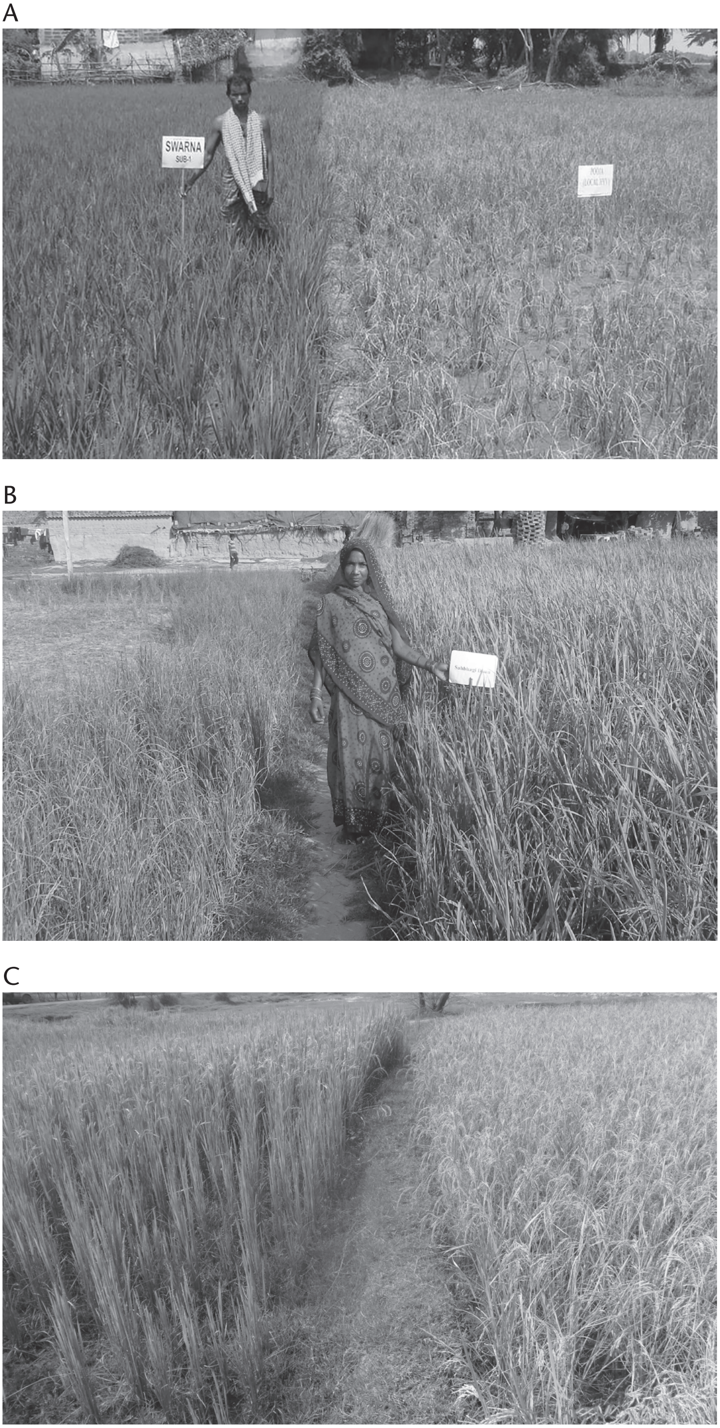

Fig. 13.1. Impact of abiotic stress tolerance in farmers' fields: **(A)** submergence-tolerant Swarna-Sub1, left, **(B)** drought-tolerant Sahbhagi dhan, right, and **(C)** salt-tolerant CSR43, right; all compared with local sensitive varieties. Source: Photos courtesy of the International Rice Research Institute.

In addition to sustaining productivity in submergence-prone areas, Sub1 varieties also carried several unforeseen benefits to resource-poor farmers in affected areas, including reducing the need for re-transplanting damaged fields that lowers productivity and grain market quality. Farmers invested more in their crops and used more inputs further improving their productivity. The potential of these varieties triggered policy changes that speeded up varietal release and improved seed systems. Private sector involvement in seed systems also accelerated dissemination in affected areas, reaching millions of farmers (Sarkar *et al.* 2006, 2009; Mackill *et al.* 2012; Ismail *et al.* 2013; Ismail and Mackill 2014; Emerick *et al.* 2016). The success of Sub1 varieties also helped generate substantial international support for their outscaling, including support from the Bill & Melinda Gates Foundation (BMGF) through STRASA (Stress-Tolerant Rice for Africa and South Asia) project, and from USAID (United States Agency for International Development) and IFAD (International Fund for Agricultural Development). Several government programs, notably India's National Food Security Mission and the 'Bringing Green Revolution to Eastern India' program also provided additional funds and logistic support to produce and distribute seeds of Sub1 varieties to farmers in flood-prone areas, as in India, Bangladesh, Indonesia and the Philippines. These varieties now rank high in total breeder seed requests in India (Table 13.1). Cultivation of these varieties is enhancing productivity, contributing to

Table 13.1. Breeder seed (BS) of some of the stress-tolerant varieties released in India: total seed indent, amount produced by government institutions and allocation to certified seed producers by the Ministry of Agriculture and Farmers Welfare (MoAFW), India, during the wet season of 2017.

Data does not include BS sold directly by the source to private companies and other seed producers. The data showed that some of the stress-tolerant varieties such as Swarna-Sub1 (I) and Sahbhagi dhan (II) already occupy the top of the list of BS demands (Source: MoAFW, India).

Variety	Stress tolerance	Year of release	Indent (tons)	Production (tons)	Allocation (tons)
Swarna-Sub1	Submergence	2009	55.3 (I)[a]	48.52	47.5 (I)
Sahbhagi dhan	Drought	2010	33.9 (III)	34.581	33.9 (II)
Samba Mahsuri-Sub1	Submergence	2012	13.4	30.0	13.4 (VI)
Bina dhan11	Submergence	2016	3.6	9.0	3.6
DRR 44	Drought	2014	4.4	6.3	4.4
DRR 42	Drought	2014	18.3	5.5	5.5
DRR 46	Drought	2016	1.9	2.4	1.9
DRR 43	Drought	2014	2.6	2.0	2.0
CR10009-Sub1	Sugmerbence	2016	4.5	2.0	1.0
CSR 36	Salinity/alkalinity	2005	0.4	1.8	0.4
CSR 43	Alkalinity	2011	0.25	1.0	0.25
DRR 39	Drought	2009	1.4	0.84	0.84
Total BS of STRVs			140.0	143.9	115.69
Proportion of total BS production			27.3%		26.7%
Total BS of all 312 varieties			511.60		432.50

[a] Data in parentheses represent ranking out of the 312 rice varieties currently in the breeder seed chain.

poverty alleviation and securing food supply for millions of impoverished farm households in Asia, and is disproportionately benefiting the poorest farming communities who are forced to live off these flood-affected lands, providing insurance against submergence and supporting their livelihood and food supply (Dar *et al.* 2013; Emerick *et al.* 2016).

Progress in developing drought-tolerant varieties

Drought is the most important abiotic stress affecting rice production in both Asia and sub-Saharan Africa. It reduces yield on over 20 million ha in Asia alone, where 90% of the world's rice is produced and consumed (Pandey *et al.* 2000). The semi-aquatic nature of rice makes it more sensitive to drought than other cereal crops. There are four major hydrological environments for rice production that can be defined in terms of toposequence position, or the relative elevation of a rice field within a watershed consisting of terraced fields that drain into each other and the resulting effects on the hydrological environment (Wade *et al.* 1999):

1. Unbunded uplands that never retain standing water
2. Bunded but drought-prone upper fields that retain standing water only briefly after a rainfall
3. Well-drained mid-toposequence fields that receive a reliable supply of water from fields higher in the watershed, but that rarely experience stagnant flooding
4. Poorly drained lower fields in which water accumulates to depths of 1 m or more during the rainy season.

Separate breeding pipelines are needed for each of these hydrological environments. Unbunded uplands and bunded upper fields are the main hydrological environments frequently affected by drought. Of these, bunded upper fields, which are managed as lowland (i.e. puddled and often transplanted) environments, are the most extensive in Asia; unbunded uplands are widespread in Africa.

As in other ecologies, traditional varieties used to dominate drought-prone areas, but were gradually replaced by the semi-dwarf, fertiliser-responsive, high-yielding varieties developed for irrigated and favourable rain-fed systems. Although initial screening of rice genetic resources reported good genetic variability within cultivated rice for drought response (Palada and Vergara 1972; Khush and Coffman 1977; Ismail and Mackill 2014), there is evidence that the development of modern varieties resulted in the loss of much of this drought tolerance due to linkage with undesirable traits such as plant height (Vikram *et al.* 2015). Modern varieties were frequently adopted in upper bunded fields because of their short growth duration (allowing them to escape terminal drought as the monsoon withdraws in Asia), but have been shown to be extremely susceptible to drought (Verulkar *et al.* 2010).

Early drought tolerance breeding and genetic analysis efforts focused on use of subsidiary traits associated with drought responses, such as shoot and root traits, canopy temperature and water potential, but with little success in translating to varietal drought tolerance (Babu *et al.* 2003; Kamoshita *et al.* 2008; Deivanai *et al.* 2010; Dixit *et al.* 2015). The focus of breeding and genetic analysis for rice drought tolerance at IRRI shifted around 2002, when it became apparent that yield under drought stress imposed by withholding irrigation and (in lowland fields) draining paddies during the wet season is usually less expensive to measure and often more heritable than physiological traits thought to be associated with drought tolerance, such as stomatal conductance, osmotic adjustment or root architecture (Atlin and Lafitte 2002).

Abiotic stress breeding and genetic analysis programs must be able to impose stress in a reliable manner that is predictive of yield under stress in the target population of environments. Managed stress screening is relatively simple in rice, a species that exhibits reduced biomass production and seedset whenever soil is less than fully saturated. Stress can usually be imposed, even in the rainy system, by withholding irrigation and draining paddies. Rice is most susceptible to drought stress during panicle exsertion and anthesis, but stress during tillering and panicle initiation can significantly reduce biomass, tiller number and spikelet number (Bernier *et al.* 2008). Because of the intermittent nature of drought stress in bunded upper fields, the most effective managed stress protocol for both breeding and genetic analysis of yield under stress is to repeatedly drain and re-irrigate paddies, beginning shortly after transplanting and continuing through flowering and grain-filling, re-irrigating when soil water potential reaches –20 to −60 Kpa at a depth of 20–30 cm, depending on the targeted stress level (Verulkar *et al.* 2010). Because of the variability of stress occurrence in farmers' fields, and because the trait being measured is yield under stress, drought tolerance screening must be conducted in multi-location, replicated trials to be reliable. Managed stress is more easily imposed in the dry season than in the wet season, but growing conditions (irradiation, temperature, vapour pressure deficit and diseases) differ substantially between the wet season, when rain-fed rice is grown, and the dry season. Line performance under dry season screening must therefore be evaluated in the wet season before it is incorporated in a breeding pipeline. Managed stress screening in the dry season at IRRI has been shown to be moderately predictive of performance under naturally occurring stress in the wet season in South Asia (Verulkar *et al.* 2010).

Because of the vast area covered by drought-prone bunded upper fields, particularly in South Asia, IRRI and Indian national partners at nine drought-prone locations in Eastern India established a breeding pipeline designed to develop drought-tolerant varieties. Because drought stress occurs unpredictably within and across years, farmers require cultivars that are tolerant to stress but responsive to favourable conditions when they occur (Bernier *et al.* 2008). The key element of any breeding program for regions affected by abiotic stresses is to systematically incorporate routine screening for yield under both stress and optimal conditions in selection decisions. Yield under stress may be positively or negatively correlated or uncorrelated with performance under non-stress conditions (Atlin and Frey 1989). The relative weights given to trials conducted under stress versus non-stress trials should be a function of the heritability of yield in the two types of trials, the genetic correlation between stress and non-stress environments, and the frequency of occurrence of the stress. A low but positive correlation between yield under favourable and drought conditions and relatively high genetic variability for grain yield under drought was consistently noted by IRRI researchers (Venuprasad *et al.* 2007, 2008; Kumar *et al.* 2008). This permits simultaneous improvement of both yield potential and yield under drought stress.

The IRRI-India drought breeding network, in operation in its current form since 2005, permits promising breeding lines from IRRI, Indian state agricultural universities and the Indian Council of Agricultural Research (ICAR) breeding centres to be evaluated in multiple locations under optimal irrigation, as well as under moderate and severe stress. Heritabilities for yield under severe drought stress typically range from 0.5 to 0.7 in multi-location trials (Venuprasad *et al.* 2007; Kumar *et al.* 2008; Verulkar *et al.* 2010). In combined analysis over locations and years, the IRRI-Indian drought-breeding network identified promising breeding lines out-yielding widely grown varieties such as Swarna by ~0.5 t ha^{-1} under moderate stress and 0.7–1.0 t ha^{-1} under severe stress (Verulkar *et al.* 2010). Several of these varieties have now been released and are being disseminated in India, Nepal and

Bangladesh. In total, ~30 drought-tolerant varieties have been developed and commercialised through this approach in South and South-East Asia and in sub-Saharan Africa since 2011 (Dixit *et al.* 2014; Kumar *et al.* 2014; Sandhu and Kumar 2017). These varieties are demonstrating significant positive impacts on rice productivity in drought-affected areas, with yield advantages of 0.5–1.8 t ha^{-1} under stress, compared with the varieties being used by farmers. A good example is the breeding line 'IR74371–70-1–1' released as Sahabhagi dhan in India, BRRI dhan 56 in Bangladesh and Sukha dhan 3 in Nepal (Anantha *et al.* 2016) being grown widely by farmers in drought-prone areas and with high demand for its seeds (Fig. 13.1B; Table 13.1). It should be noted that an increase in yield of even 0.5 t ha^{-1} for a farm family can reduce the potential ruinous impact of a drought year.

In addition to its use in breeding pipelines, managed-stress screening for yield in intermittently drained paddies and drought-stressed upland fields has been extensively used by IRRI for the genetic analysis of yield under drought stress over the last 15 years. Numerous mapping populations were developed and analysed, usually involving crosses or backcrosses between a widely grown but susceptible parent and a drought-tolerant landrace or variety. These experiments are repeated over several seasons to ensure that a high level of heritability for grain yield under stress is achieved, and they are also conducted under fully irrigated conditions to differentiate alleles affecting yield potential from those affecting yield under stress. A large-effect quantitative trait locus (QTL) explaining over 50% of the genetic variation for yield under upland drought stress in the Vandana/Way Rarem population was localised on chromosome 12 by Bernier *et al.* (2007). Since that time, a total of 12 QTL alleles affecting yield under stress have been identified by IRRI researchers in crosses between widely grown mega-varieties and drought-tolerance donors, seven of which have demonstrated positive effects on yield when introgressed into more than one susceptible background (Sandhu *et al.* 2018). Their physiological and molecular bases have also been described but are not yet well understood (Henry *et al.* 2014; Dixit *et al.* 2015; Anantha *et al.* 2016). Several of these QTL alleles have been introgressed into mega-varieties such as IR64, Swarna and Sambha Mahsuri via marker-assisted backcrossing, and new varieties carrying these QTLs were recently released in India, Nepal and Myanmar (Kumar *et al.* 2014; Sandhu and Kumar 2017). This is yet another case illustrating the enormous genetic diversity within the pool of cultivated rice ensuing from its adaptation to a wide range of geographic, thermal and hydrological conditions (Ismail and Mackill 2014).

Although QTLs with moderately large effects on yield under drought stress have been identified in rice, the genetic architecture of the trait is oligogenic or even polygenic in comparison with the submergence and anaerobic germination tolerances discussed earlier. In general, each new mapping population involving a cross between a tolerant donor and susceptible recurrent parent identifies new QTLs, although some of these appear to function in other genetic backgrounds, and no drought tolerance QTL has effect sizes and consistency across backgrounds as large as that of *SUB1*. Although the drought tolerance QTLs have been introgressed into susceptible mega-varieties and generated detectable improvements in yield under stress, MABC is unlikely to be the optimum method for exploiting QTL alleles affecting yield under stress. As is the case for submergence tolerance, the production of drought-tolerant versions of obsolete varieties is unlikely to lead to wide-spread adoption if increases in stress tolerance are not coupled with improved yield potential, quality and disease resistance. Alleles mined from drought-tolerant donors will begin to have widespread impact when they are deployed in a forward breeding strategy that allows for allele frequencies at many loci to be changed simultaneously.

Progress in breeding salt-tolerant varieties

Salinity limits rice productivity in over 16 million ha of irrigated and rainfed areas in South and South-East Asia, particularly along the tropical coasts where salinity is encroaching inland, leading to a gradual increase in the affected area. This is owing in part to climate change, causing sea level rise, decreased flow of fresh water from upper catchments of major rivers and increased incidence of coastal storms (Ismail and Tuong 2009; Smajgle *et al.* 2015). As in other unfavourable environments, rice yields in salt-affected soils are low, averaging less than 2.0 t ha^{-1}. This is attributed to the high sensitivity of rice to salt stress, with a threshold of 1.9–3.0 dS m^{-1} for impacting grain yield (Maas and Hoffman 1977; Grattan *et al.* 2002).

Despite this sensitivity, the capability of rice to survive in flooded soils, and the resulting dilution and leaching effects on salt concentration, makes it the best cereal crop choice for these salt-affected soils (Ismail and Tuong 2009). Several landraces that can tolerate high salinity were identified and subsequently used in breeding salt-tolerant varieties. These landraces also helped in ascertaining the major mechanisms involved in salt stress responses in rice, reflecting complex inheritance, with several traits associated with tolerance and several genes associated with each trait. Intriguingly, only one or a few of these traits are highly associated with tolerance of a particular landrace, making it possible to develop varieties with higher tolerance by selectively combining superior alleles associated with the tolerance traits from different landraces (Ismail *et al.* 2007; Platten *et al.* 2013; Ismail and Horie 2017).

Numerous salt-tolerant rice varieties were recently developed and commercialised in several countries in Asia, delivering substantial benefits to farmers in salt-affected areas (Fig. 13.1C). These varieties provided additional yield gains of up to 2 t ha^{-1} in saline and sodic soil, stabilising productivity in affected areas, and encouraging farmers to use more inputs and expand production in lands previously abandoned because of high salinity (Islam *et al.* 2016; Singh *et al.* 2016a). However, the conventional breeding methods used to develop these salt-tolerant varieties took 10–15 years from the time a cross is made until a variety is released, with consequent high costs. Alternative breeding approaches including use of genomic tools and modern breeding advances are now in place to speed up the development of salt-tolerant varieties combining several traits. This is aided by the methodical analyses and understanding of the bases of tolerance in several landraces and cloning of several genes controlling critical processes for salt homeostasis (Thomson *et al.* 2010a, 2012; Platten *et al.* 2013; Ismail and Horie 2017).

Large-effect QTLs associated with tolerance of salt stress were mapped using several tolerant landraces; the most important of these is *Saltol* on chromosome 1. *Saltol* was recently transferred into popular varieties and showed positive effects in saline fields. Several other QTLs with moderate to large effects at both seedling and reproductive stages are being identified from several salt-tolerant landraces and markers are being developed at IRRI for use in breeding (Thomson *et al.* 2010b, 2012; Tiwari *et al.* 2016; Bimpong *et al.* 2016). Novel alleles underpinning major traits associated with salt tolerance are being identified through diversity studies; these will be combined in high-yielding backgrounds using forward-breeding approaches. Moreover, the large number of genes involved in the control of sodium and other harmful elements needs to be evaluated for allelic variation and marker development for use in breeding (Ismail and Horie 2017). The scarcity of large-effect QTLs for salinity tolerance, their dispersal among donors, and the difficulty of screening large numbers of selection candidates in managed stress environments indicate strongly that cultivar development for saline and sodic environments should be based on multi-environment yield testing in those environments, with rapid breeding cycles facilitated by genomic selection.

Breeding for areas affected by several abiotic factors

Farmers in rain-fed lowlands and flood-prone areas are vulnerable because of the extreme variation in rainfall patterns and intensity. Multiple abiotic stresses are regularly encountered in these areas in different seasons, and sometimes at different times within the same season. The obvious examples are: drought and floods in inlands, which are intermittent and unpredictable in their occurrence and intensity, with uncertain predictability; and salinity and floods in coastal deltas, with high salinity during crop establishment at the beginning of the rainy season and floods any time later in the season (Mackill *et al*. 1996; Ismail *et al*. 2008). Effective breeding strategies are required to combine tolerances of these abiotic stresses to develop more resilient varieties as a requisite for food security in these areas, while also increasing yield potential, disease resistance and grain quality. These breeding programs also need to keep up with a changing climate and rapidly evolving commercial environment that is becoming more demanding in terms of grain quality as consumer incomes increase as a result of economic growth.

In flood-affected areas, *SUB1* can provide protection against submergence for up to 2 weeks, but additional tolerance genes are required for survival for extended periods of submergence. This can be accomplished through incorporating other shoot and root adaptive traits being discovered recently, such as lasting gas films and underwater photosynthesis and better root aeration and growth (Ismail 2018). Furthermore, *SUB1* provides protection when plants are completely inundated, but not when plants are partially flooded for longer durations as in stagnant floods (SF) and deepwater areas. Direct seeding is becoming the preferred system over transplanting in rice because of labour and water scarcity, besides other benefits (Ismail *et al.* 2012), yet its wide adoption is hindered by waterlogging or flooding if it rains early in the season, because of the high sensitivity of rice to flooding during germination. Reasonable progress has been made in identifying sources of tolerance of anaerobic conditions during germination (AG) and SF. Markers were also developed for major QTLs associated with AG tolerance and are being used for developing breeding lines capable of germinating in flooded soils (Ismail *et al.* 2009; Kretzschmar *et al.* 2015; Lal *et al.* 2018). Remarkably, tolerance of these three types of flooding – AG, SF and submergence conferred by *SUB1* – were largely independent, making it possible to combine them into new high-yielding varieties for direct seeded systems in rain-fed and flood-prone areas (Mackill *et al.* 2010; Singh *et al.* 2011; Mackill *et al.* 2012).

The success in breeding drought-tolerant varieties, together with the discovery and effective incorporation of major QTLs into new varieties, made it possible to combine drought tolerance with other adaptive traits such as submergence tolerance. Several varieties have recently been released, such as CR dhan 801 in India and Baghuguni dhan1 and 2 in Nepal, that combine both *SUB1* and drought tolerance QTL (Dixit *et al.* 2017). Moreover, varieties tolerant of submergence and salinity are being developed, by combining *SUB1* with *Saltol*, or by incorporating *SUB1* into older salt-tolerant varieties developed conventionally. A recent salt-tolerant variety carrying *SUB1* (BRRI dhan 78) was released for coastal areas in Bangladesh. Besides tolerance of major abiotic stresses, new varieties should essentially incorporate resistances to major pests and diseases, because several genes for major rice diseases such as blast and bacterial blight are now available. Incorporating these adaptive and protective traits into high-yielding short-to-medium-duration varieties with good grain quality and market value will provide farmers in less favourable areas with better options to replace their older, less productive varieties, and even to add a second crop of rice or another non-rice crop. Access to such resilient varieties provides assurance for farmers to invest in more fertilisers and other agrochemicals, and manage their crops better, securing food supply and sustaining income. However, selecting for complex haplotypes, in which desired alleles are dispersed among several parents, while simultaneously maintaining adequate selection pressure for the polygenes that are also critical to yield potential and yield under stress, is difficult. It is likely to require the redesign of breeding programs to increase population sizes and accelerate cycles using genomic prediction. Traditional pedigree breeding and marker-assisted backcrossing will not be adequate to combine favourable stress tolerance QTL rapidly with the other traits needed by farmers, millers and consumers.

Impact of developing stress-tolerant varieties

Elements of success and implications on national policies

The success of stress-tolerant varieties in stress-prone areas caught the attention of national governments in South Asia, because stress-affected areas have been long viewed as unproductive with insurmountable challenges. This is particularly important for policy makers because these parts of eastern India and south and central Bangladesh have very large and extremely poor populations. In a recent review, Yamano *et al.* (2016) showed that stress-tolerant varieties were identified as one of the most promising technologies and are being quickly disseminated among farmers in South Asia. These varieties were also reported to have disproportionately benefited the most impoverished marginal households (Dar *et al.* 2013). Moreover, these varieties are reducing weather-induced risks of crop losses, leading to increased input use, expansion of cultivated area, more modern production technologies and access to credit, all of which positively influence the economic and social behaviours of smallholder farmers living in affected areas (Emerick *et al.* 2016).

Although there has been considerable adoption of stress-tolerant varieties in areas where the occurrence of damaging stress is very frequent (or in the case of salinity, assured), there has been relatively little adoption in more favourable rain-fed areas where the occurrence of crop loss due to drought or flooding is less frequent (IRRI unpublished data). This is likely because farmers in such areas are more concerned about yield potential in favourable years than losses in unfavourable ones. The stress frequency threshold needed to drive adoption of stress-tolerant varieties is not known, but it may be that farmers who experience major crop loss due to flooding or drought in fewer than one year in five have limited incentive to adopt varieties solely on the basis of improvement in stress tolerance. These farmers will require genes for stress tolerance to be delivered in cultivars that also have improved yield potential. For this large segment of South Asian rice growers, marker-assisted introgression of QTLs such as *SUB1* into older mega-varieties is unlikely to drive adoption. Through GIS and remote sensing, areas affected by specific stresses are being more precisely mapped, and this information made available to both public and private seed producers to help match seed supply of specific varieties with the demand for seeds in specific villages where the variety is most adapted (see Chapter 19).

Several factors contributed to the success of these stress-tolerant varieties in highly stress-prone regions of South Asia:

1. The decision to use varieties that are popular among farmers is extending their benefits to less favourable areas, with assured and stable yields, considerably shortening the time for further evaluation and adoption (Ismail *et al.* 2013; Singh *et al.* 2013).
2. The strong ownership developed through partnerships with the public sector is playing a major role in increasing uptake and eventual adoption.

3. The involvement of extensive networks of partners along the value chain, including the private sector, is supporting quality seed production and helping build effective distribution systems.
4. Effective awareness and knowledge transfer programs have targeted appropriate partners, including policymakers and farmers.
5. National and regional policy changes are resulting in more favourable and enabling environments for varietal release, certification and commercialisation.
6. The additional investments made by national programs and international development organisations are accelerating production of high-quality seeds and timely delivery to farmers in affected areas.

Several models were being used to demonstrate the value of these varieties in farmers' fields, including: 'minikit' distribution of 2–5 kg of seeds once to a few progressive farmers in a village; large field demonstrations of one or two varieties in target areas; head-to-head demonstrations where new varieties are demonstrated by a few farmers side by side with existing varieties; and 'crop cafeterias' where several new varieties are planted to synchronise their flowering time, then demonstrated to seed producers and dealers, millers, policy advisors and also farmers, to participate in the selection of future varieties and to gain their support for varietal release and commercialisation. The use of head-to-head demonstrations and crop cafeterias are attracting substantial interest and are proving to be efficient in generating interest and demand for the new stress-tolerant varieties (IRRI unpublished data).

Head-to-head demonstrations are extremely useful for the initial introduction of a new stress-tolerant variety, but demonstration is only effective when there is a visually striking difference between the new variety and the variety currently grown by farmers. After the first introduction of a new plant type or large-effect stress tolerance genes, highly effective breeding programs can deliver genetic gains of only ~1.5% annually. This means that 7 years of effective breeding will generate gains of only ~10%. Farmers cannot reliably detect a 10% yield difference between cultivars in a demonstration plot. In future, a much greater investment in on-farm testing will be needed to identify and recommend new varieties that outperform the current cohort of stress-tolerant varieties. Currently, few international or national breeding programs conduct on-farm testing programs of adequate scope and quality to reliably detect a 10% yield advantage for new varieties. In most cases, the environmental and management variation within the target population of environments (TPEs) served by international breeding networks is much greater than the variability facing breeders serving cropping systems in North America or Europe, but the number of on-farm trials they conduct is usually far lower. Major US seed companies evaluate candidate soy and maize varieties on many hundreds, and even thousands, of farms annually (Gaffney *et al.* 2015). The CIMMYT maize program in Eastern and Southern Africa, which operates the largest formal on-farm trial network in the CGIAR, tests new candidate hybrids on a maximum of 70 farms per TPE, an order of magnitude (at least) lower than testing levels used by companies in the much less variable US Corn Belt. IRRI is initiating a large on-farm testing and demonstration network in India, and managed 8000 head-to-head comparison sites in 2017 (Manzoor Dar *pers. comm.*), but data are collected from relatively few of these trials. To generate enough data to predict confidently that a new variety will outperform what farmers are currently growing, breeding organisations need to link with partners such as seed companies, NGOs and farmer organisations to conduct a large number of on-farm trials. No hard and fast minimum number can be given for the size of the on-farm testing network needed, but variance components estimated from the CIMMYT Regional On-Farm Testing Network for maize in Eastern and Southern Africa indicated that at least 100 trials are needed to reduce the LSD (0.05) to 0.3 t ha^{-1}, or ~10% of the mean yield of these trials (calculated from data presented by Setimela *et al.* 2012). The ability to reliably detect a 5% yield improvement would require ~400 on-farm trials.

The demand of farmers for seeds of stress-tolerant varieties stimulated dialogues that helped in reforming national policies and guidelines to provide enabling policy environments that accelerate reaching needy communities. For example, the Indian Ministry of Agriculture decided that varieties improved for stress tolerance via marker-assisted backcrossing could be released after only one year of testing to confirm they retain the characteristics of the original varieties and are stress tolerant. Moreover, seed production of these varieties can start before release and up to 10 t of breeder seeds can be produced for distribution once a variety is notified. These policy adjustments shortened the time from the start of the final evaluation process until a variety reaches farmers by ~50%. Another step taken in India to accelerate varietal replacement was the removal of varieties that are older than 10 years from the national seed subsidy program and to halt their breeder seed production to encourage replacement of older varieties. Private sector partnerships were also strengthened to assume active roles in production and distribution of certified and truthfully labelled seeds of new varieties, by eliminating major bottlenecks, such as tackling shortage of breeder seeds through diversifying production sources. Responsibility for provision of breeder seeds is now extended beyond the institution that releases a particular variety. These reforms need to be extended to other rice-producing countries in Asia and sub-Saharan Africa.

Implications on regional policies

The rice policy reforms triggered by stress-tolerant varieties are now bridging borders within South and South-East Asia. This was made possible through a series of high-level inter-government agreements made in Bangladesh (2013), Nepal (2014) and more recently in Cambodia (2017), organised and mediated by the IRRI. These agreements provided formal means for exchange of knowledge and seed of newly released rice varieties across all participating countries. The main highlights of these seed policy agreements include:

- varieties released in any of the member countries could be immediately released for similar ecologies in other countries and after only one year of testing in different ecologies
- sharing and recognition of evaluation data among countries for release of new breeding material
- pre-release seed multiplication and promotion of breeding lines in the final stages of testing to facilitate faster outreach
- encouraging strong participation of private sector to develop an effective and sustained seed production, demonstrations and delivery networks
- harmonising the guidelines for varietal release and seed systems across countries
- member countries agreed to recognise each other's seed certification systems and to accept the seed certified by other member countries, to facilitate faster movement of seeds across borders to fill in gaps in seed supply at regional level
- encouraging germplasm and knowledge exchange as well as exchange of visits.

This regional cooperation has now been put into practice and several varieties released in India, Bangladesh and Nepal were formally commercialised in other countries without further testing. Moreover, the agreement is being extended to crops other than rice, including other cereals, pulses, oilseeds, vegetables (non-hybrid), sugarcane and fibre crops. The agreement is expected to accelerate varietal release and seed movement between countries. This is particularly important in cases of seed supply shortages that are common after natural disasters such as typhoons and floods. Several countries ratified this agreement including India, Bangladesh, Nepal and Sri Lanka in South Asia, and Cambodia and Myanmar in South-East Asia. Other countries in Asia, such as Laos, Vietnam and Bhutan are expected to join the agreement in near future. Discussions have also been initiated with several countries in sub-Saharan Africa to help introduce modern varieties developed in Asia and to facilitate strengthening of their varietal release and seed sector development and outreach. These developments are also expected to encourage Asian seed companies to engage in the rice value chain in Africa, especially seed and paddy production, post-harvest processing and marketing. Several issues still need to be worked out including: strict quarantine measures to avoid spread of diseases, insects and weeds; proper material transfer agreements; intellectual property management; and trade implications. Substantial efforts are needed to ensure application and maintenance of these agreements and to expand them across Asia and Africa.

Future prospects: accelerating adoption and change

In less favourable rain-fed ecosystems where rice-based agricultural systems predominate, poverty and food insecurity are still high, despite the potential for production of more food. Our viewpoints for exploiting these areas for rice production are now changing. The recent progress made in developing and deploying high-yielding varieties tolerant of common abiotic stresses results from the design of breeding pipelines that integrate selection both for yield potential and yield under the target stress in rigorously validated managed stress screens, as well as from the identification and deployment of QTLs with large effects on abiotic stress tolerance. IRRI's success in developing and disseminating stress-tolerant varieties with national partners indicates that there is considerable potential for transforming stress-prone areas when adapted varieties are provided to farmers in combination with access to other critical inputs and management advice. Most of the stress-tolerant varieties deployed so far are tolerant to one or two abiotic stresses, when in fact most rain-fed areas are simultaneously subject to multiple weather adversities, soil problems and biotic factors. The marker-assisted breeding approach used in developing most of these varieties is a conservative approach designed to achieve the maximum benefit of stress tolerance in as short a time as possible, by upgrading the stress tolerance of existing varieties. It therefore leaves some important issues unresolved, especially the need for varieties that are both more resilient under multiple stresses and have improved yield under optimal conditions. For most trait combinations tested so far (e.g. tolerances of submergence, drought, salinity and resistances to various diseases), there are no obvious barriers for their combinations in high-yielding backgrounds, but the integration of abiotic and biotic stress-tolerance haplotypes dispersed among several parents while simultaneously selecting for quality and yield potential is a complex task that will require breeding programs to move beyond marker-assisted backcrossing and pedigree breeding to rapid-cycle genomic selection for population improvement, using simulation and modelling tools to optimise breeding pipelines (Cameron *et al.* 2017). More effort is needed to identify and combine useful alleles for critical traits that can synergistically improve grain yield, adaptation and resilience. This is now becoming feasible through the use of modern breeding strategies and molecular tools to shorten the breeding cycles and accelerate varietal replacement. The capacity of national breeding programs needs to be strengthened to modernise their breeding strategies to fast track breeding of varieties that are more widely adapted in less favourable areas, and to replace older varieties. Confidently recommending to ministries of agriculture, farmers, extensionists and seed producers that a new stress-tolerant variety should replace what farmers currently grow will require a significant expansion of on-farm testing effort to generate reliable data on performance under the difficult conditions faced by smallholder farmers.

Reforms of agricultural policies and regulations, both at national and regional levels, are taking place and are providing enabling environments for effective knowledge and germplasm exchange. Rice seed systems are still lagging behind other crops, and most farmers still rely on their saved seeds, with considerable losses to productivity and quality. Stronger public–private sector partnerships are necessary to ensure far-reaching networks along the value chain, supported by effective awareness, communication and monitoring programs. Research leaders and policy advisors are calling for rapid access to reliable sources of information for forecasting and to inform decision-making processes, especially when dealing with issues related to national food security and responses to natural and human-made disasters. Our ultimate goal is to develop resilient rice-based production systems that produce sufficient food in the face of worsening climate and shrinking natural resources.

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