Lowland ecosystems

Germplasm development for drought-prone environments: progress and implications for crop and natural resource management

A. Kumar and G.N. Atlin

Drought is the most severe constraint to rainfed rice production. Drought effects are most severe in unbunded upland fields and upper-toposequence bunded fields that do not accumulate standing water. Drought reduces productivity, both through direct effects on biomass production and grain set and through disruption of crop management operations, including transplanting, fertilizer application, and weed management. The most important of these crop management disruptions, induced by water shortage at critical times, is delayed transplanting. Drought risk is a major cause of low input use by farmers, constraining productivity, even in favorable years. There is great genetic variation in tolerance for drought stress, direct seeding in dry soil, and delayed transplanting. In areas where transplanting is likely to remain the major establishment system, varieties with tolerance for both drought and delayed transplanting are needed to reduce risk and to increase productivity. In light-textured soils, direct seeding of drought-tolerant varieties in dry soil in unpuddled fields has the potential to eliminate the risk of transplanting failure and to advance maturity sufficiently to permit the production of a post-rice crop. However, varieties for use in this establishment system must be highly weed-competitive and have a high degree of tolerance for drought at the reproductive stage. The IRRI breeding program now routinely screens lines targeted at dry direct seeding systems for rapid early biomass accumulation, a trait that has been shown to be closely associated with weed competitiveness. Lines targeted for transplanted systems are screened for yield under transplanting as 60-d-old seedlings. For both systems, advanced breeding lines are screened both for yield potential and for yield under continuous recurring stress after maximum tillering. This research has shown that yield under drought stress has a moderate positive correlation with yield potential, permitting the development of varieties with high yield potential combined with stress tolerance. It has also been shown that hybrids are higher yielding than purelines, on average, under both moderate lowland stress and delayed transplanting. Lines and hybrids combining high yield potential with yields of more than 2 t ha^{-1} under severe lowland stress and more than 1.5 t ha^{-1} under severe upland stress have been identified. Such varieties have the potential to reduce risk and increase overall productivity in drought-prone environments.

Keywords: breeding, direct seeding, drought, hybrids, rainfed rice

Drought occurs frequently in the upland and lowland rainfed rice ecosystems of South and Southeast Asia, causing severe yield loss. Worldwide, approximately 20–25 million ha of rainfed rice are frequently affected by water stress. Eastern India, with more than 12 million ha of rainfed rice area, is the worst affected (Huke and Huke 1997). In this region, drought losses are most severe in the rice bowl states of Chhattisgarh, Madhya Pradesh, Bihar, Jharkhand, Orissa, and Uttar Pradesh. Northeastern Thailand and Laos, with more than 5 million ha of drought-prone rainfed rice area, are the other severely drought-affected areas in Asia. Drought risk also reduces productivity, even in favorable years, because farmers avoid investing in inputs when they fear crop loss (Pandey et al 2005). In addition to rainfed areas, drought also affects production on millions of hectares of dry irrigated areas that depend on surface irrigation; in drought years, river flows and water impounded in ponds, tanks, and reservoirs may be insufficient to irrigate this crop (Maclean et al 2002).

There is substantial genetic variability in the rice germplasm that can be used to develop more productive varieties for water-short environments. The objectives of this paper are to identify breeding objectives for particular drought-prone target environments, assess progress in the development of more drought-tolerant cultivars for these environments, and highlight their potential contribution to productivity enhancement and risk reduction when combined with appropriate crop management systems.

Target environments for drought germplasm improvement

A local watershed in which rainfed rice is grown can often be characterized as a *toposequence*, a series of terraced fields that drain into each other. Within distances of several hundred meters, the toposequence may include unbunded uplands and bunded but drought-prone upper fields that do not retain standing water, well-drained mid-toposequence fields, and poorly drained lower fields in which water accumulates to depths of 1 m or more during the rainy season. Water-related stresses are variable across years in drought-prone upper fields because of variability in the amount and distribution of rainfall, but they occur with reasonably predictable frequency in a given field based on toposequence position and soil texture. Yield variability due to water availability can be great even within single fields due to soil texture variability and uneven soil level. This micro-scale variability results in very large estimates of genotype × location × year interaction and residual errors in the analysis of rainfed rice trials, complicating selection (Cooper et al 1999).

Farmers are experts at categorizing fields according to toposequence-driven differences in hydrology, targeting varieties with appropriate duration and plant type to specific environments. On 4–5 million ha in the eastern Indian plateau, in unbunded fields at the top of the toposequence, farmers grow extremely short-duration, drought-tolerant upland rice varieties. In upper bunded fields, farmers tend to grow short-duration, photoperiod-insensitive varieties that flower before the withdrawal of the monsoon, escaping late-season drought stress. In these fields, farmers establish rice crops either by transplanting or direct seeding, but transplanting has become widespread since the adoption of high-yielding semidwarf varieties in the 1970s. In well-drained mid-toposequence fields, farmers grow the same high-yield-potential varieties grown by farmers with irrigation and usually establish their crops via transplanting. In the lower flood-prone fields, farmers usually direct-sow photoperiod-sensitive varieties that flower as the rains cease and stagnant water levels begin to decrease (Mackill et al 1996). Individual farmers often have fields at several toposequence levels and thus often grow several varieties, each adapted to a particular hydrological environment.

The principal target environments requiring germplasm with improved drought tolerance are unbunded uplands and bunded upper fields at the top of the toposequence; drought occasionally occurs in the lower fields but is relatively rare because these fields benefit from runoff and seepage from the upper fields and usually remain saturated long after the upper fields are dry. Bunded upper fields are the largest and most important target environment for drought tolerance breeding, both because of their extent and because of their potential for improved productivity. Rainfed rice breeding programs need to develop varieties with the duration, plant type, and stress tolerance required for this environment, which recurs across millions of hectares in most rice-growing areas. But farmers rarely adopt varieties that are poor in cooking or eating quality, even if stress tolerance were improved. Rainfed farmers are also interested in varieties that combine a degree of stress tolerance with the ability to produce high yields in favorable years or in parts of the field (i.e., the lowest corner of a drought-prone field) that are more productive. Thus, quality and yield potential are also key breeding targets for drought-prone environenments. Unwillingness to compromise on quality and yield potential, particularly on bunded lands, has meant that adoption of new varieties has been infrequent in rainfed systems. A relatively few improved varieties, including Swarna, Sambha Mahsuri, IR36, IR64, BR11, and MTU 1010 (sometimes referred to as "megavarieties"), together now account for much of South Asian rainfed rice production. Most of these varieties are valued for their quality, marketability, and yield potential under favorable conditions and have proven very difficult to replace. However, they were selected under favorable irrigated conditions and are not tolerant of the major abiotic stresses of rainfed environments, including drought. They are suitable mainly for favorable, mid-toposequence fields, but their high yield potential and desirable grain quality push farmers to adopt them in fields above their optimum level of adaptation. Farmers with drought-prone fields are thus in urgent need of options, but adoption of varieties with improved stress tolerance is only likely if they retain the quality and agronomic features of current megavarieties. The key task for rice breeding programs focusing on improvement of abiotic stress tolerance is therefore the development of varieties that combine improved stress tolerance with preferred quality and high yield potential under favorable conditions.

Physiological and agronomic effects of drought and implications for germplasm improvement

Direct effects of water shortage on growth and yield

The direct effects of water shortage on growth and yield can be acute, at critical crop stages, or they may be growth-limiting effects of continually recurring nonsaturated conditions. Much more attention has been paid to the former than to the latter, but it is likely that growth reduction due to intermittent soil drying throughout the season in upper fields causes greater overall losses. Rice yield is linearly related to the number of days in the growing season in which soil is saturated (Boling et al 2004, Haefele et al, this vol). The ability to maintain biomass accumulation in relatively dry soils is therefore a key feature required in drought-tolerant varieties. Intermittent soil drying substantially reduces biomass production and, therefore, total yield potential. IRRI research has shown substantial genetic variation in the ability of upland or lowland rice cultivars to maintain biomass accumulation in dry soils. For example, in a set of lowland cultivars evaluated at IRRI under intermittently drained conditions in the wet season of 2005, yields averaged 1.6 t ha^{-1}, a reduction of more than 50% relative to the fully irrigated control. In this trial, there was a range in total biomass production among cultivars of 4.1 to 7.4 t ha^{-1}. Variation in total biomass production was more closely related to final grain yield than was harvest index (HI) in this trial (Table 1).

Table 1. Cultivar differences in yield, harvest index, and biomass production in an intermittently dried lowland field, IRRI, 2005 wet season.

Designation	Harvest index	Grain yield (t ha^{-1})	Biomass (t ha^{-1})
IR70213-10-CPA 4-2-2-2	0.28	2.1	7.6
IR79670-125-1-1-3	0.26	1.9	7.3
PSBRc 80	0.30	1.6	5.2
PSBRc 14	0.34	1.7	4.9
IR36	0.31	1.3	4.2
PSBRc 82	0.40	1.6	4.1
Mean	0.32	1.6	5.5

However, drought is especially damaging immediately before and during flowering (Atlin et al 2006, Ekanayake et al 1990, Garrity and O'Toole 1994), so tolerance at this stage is particularly critical. This is especially true in upland rice, where brief periods of drought around flowering can result in near-complete spikelet sterility. For this reason, much research on drought tolerance has focused on tolerance for stress at flowering stage. Genetic variation exists within *Oryza sativa* for the trait (Atlin et al 2006). Some varieties have a high degree of tolerance for short periods of stress around flowering, whereas others experience markedly reduced seed set and harvest index. A set of varieties was evaluated at IRRI under rainfed upland conditions in the wet seasons of 2004 and 2005. In both seasons, drought at flowering resulted in severe stress between panicle initiation and anthesis. For a subset of lines with similar days to flowering under nonstress conditions, mean yield and harvest index are presented in Table 2. In this set, yields ranged from 0.7 to 2.3 t ha^{-1}. Nearly all of the variation in yield was explained by the variation in harvest index; lines that are high-yielding under stress, such as IR71525-19-1-1 and CT6510-24-1-2, were able to maintain a high level of seed set under stress at flowering. The physiological basis for this differential tolerance is unknown.

Table 2. Mean yield and harvest index of rice cultivars exposed to severe reproductive-stage stress under upland conditions at IRRI, 2004 wet season.

Designation	Days to flowering	Yield (t ha^{-1})	Harvest index
	Non-stress	Stress	
IR71525-19-1-1	86	2.3	0.22
PSBRc 82	87	0.7	0.11
IR71700-247-1-1-2	88	1.1	0.16
IR77298-12-7	89	1.2	0.17
IR77298-14-1-2	89	0.9	0.12
PR26406-4-B-B-2	89	0.8	0.09
CT6510-24-1-2	90	2.0	0.19
IR72875-94-3-3-2	90	0.7	0.11
UPL RI 7	90	1.9	0.16
APO	91	1.7	0.18
LSD$_{0.05}$		0.7	0.06

Because crop phenological stages differ in their sensitivity to drought, researchers have devoted considerable effort to the development of screening techniques that permit genotypes of different growth durations to be evaluated in common experiments at equivalent levels of stress at key stages such as flowering. These include techniques such as line-source irrigation (Lanceras et al 2004), which subjects cultivars to a constant stress gradient throughout the season, or field designs that permit each genotype to be irrigated independently (Lafitte and Courtois 2002), allowing stress to be imposed or removed at the same stage of development for each cultivar in the trial. However, these methods are not practical in a breeding program that must screen hundreds of lines. The IRRI breeding program screens for drought tolerance using protocols (described below) where stress is repeatedly imposed on a large nursery or trial on a uniform date, starting before the first genotypes in the trial flower, with cycles of stress and re-irrigation repeated until harvest. Variety means in screens of this type are highly correlated with means from trials in which stress is precisely applied at the sensitive flowering stage (IRRI, unpubl. data).

Effects of drought on crop management and agronomic practices

Transplanting delay. To a rice farmer, the word "drought" means not only physical water shortage that affects plant growth and development but also a lack of sufficient water to support land preparation, transplanting, fertilizer application, and weed control operations. All of these operations are dependent on the presence of a standing water layer in the paddy. If they are delayed or omitted, large yield losses often ensue, even though plants have not suffered physiological water stress. Losses from these management disruptions may be as great as those from direct drought damage. Cultivars differ in their sensitivity to these management disruptions and these differences can be exploited in the development of more resilient varieties for drought-prone environments.

Transplanting is the management step that is most vulnerable to water shortage. The optimum age of seedlings at transplanting is 2–4 wk old, but rainfed farmers must often plant seedlings that are much older due to water shortage. Farmers cannot transplant until sufficient water accumulates in fields to permit puddling (usually 400–500 mm of rainfall); often, this may not occur until seedlings are 60–80 d old. Such delays result in large yield losses because of reductions in both panicle number and weight. In experiments conducted at IRRI in 2005, transplanting 65-d-old as opposed to 22-d-old seedlings resulted in a yield reduction of more than 50%, averaged across 125 cultivars. Yield reductions due to delayed transplanting were experienced on this scale in large areas of eastern India in 2004, and in the Nepali *terai* and adjoining regions of Uttar Pradesh in 2006. Even high-rainfall regions that are not considered drought-prone, such as southern Cambodia, may experience severe losses due to delayed transplanting resulting from an early-season pause in the monsoon.

Weed management. Water shortage also affects weed management. Standing water in lowland fields after sowing or transplanting suppresses the germination of weed seedlings. Under the nonflooded, aerobic conditions characteristic of upland or drought-affected lowland fields, weed seedlings germinate freely. Most upland weed species grow more quickly than rice in nonsaturated soils, resulting in greater competition from weeds under drought conditions. The widespread indigenous eastern Indian rainfed lowland establishment and weed-management practice of *beushening* (also known as *beusani* or *biasi*, among other variants), which consists of dry direct sowing, followed by uprooting the standing crop about 1 mo after broadcast seeding by plowing, followed by planking and replanting of uprooted seedlings (Singh et al 1994), is also highly sensitive to water shortage; the uprooting and replanting process is dependent on the presence of standing water in the field and cannot be conducted when early drought occurs, resulting in a failure of weed control. Extensive genetic variation among rice cultivars with respect to weed competitiveness has been documented both for upland (Zhao et al 2006a) and lowland (Haefele et al 2004) systems, but little effort has been made to exploit this variation in the development of cultivars for water-short environments. Recently, however, Zhao et al (2006b) showed that weed-suppressive ability and weed competitiveness under upland conditions are strongly associated with rapid seedling growth in the first 4 wk after sowing, a trait for which substantial variability exists within and among the major rice germplasm groups (Zhao et al 2006c).

Germplasm development for drought-prone environments

The development of cultivars adapted to drought-prone environments or to production systems that need less water requires that both high yield potential and a suite of adaptations to environment-specific types of water shortage be "packaged" in a single cultivar. Breeding methods used and progress achieved in the development of drought-tolerant, water-efficient cultivars will be considered for two specific production environments: drought-prone unbunded uplands and bunded upper terraces. These are distinctly different target environments, requiring different traits to optimize cultivar performance. As noted above, these traits include not only improved drought tolerance *per se* at the vegetative and reproductive stages but improved weed competitiveness and, in the case of transplanted crops, tolerance for delayed transplanting.

It should be noted that farmers do not usually want cultivars that are drought-tolerant but low in yield potential in favorable years. They want cultivars that not only respond to favorable conditions but that also "protect" an economically useful yield under drought conditions. Therefore, breeding lines should be screened under both stress and nonstress conditions. Most studies in which large populations of unselected lines have been screened under stress and nonstress conditions show that there is a low but positive correlation between yield under stress and yield potential (Atlin et al 2004). It is therefore possible to identify varieties with both high yield potential and relatively high yield under stress.

Developing cultivars with improved drought tolerance for bunded upper terraces

The most drought-affected lowland fields are upper-toposequence bunded fields that are established by transplanting or traditional broadcasting methods. Critical traits for these fields include the ability to maintain biomass accumulation in intermittently dry fields, tolerance for severe stress at flowering, tolerance for delayed transplanting, and responsiveness to favorable conditions when they occur.

Screening for drought tolerance. Bunded (lowland) fields regularly affected by drought are usually upper-toposequence fields with light to medium soil texture. These fields are without standing water for much of the growing season and may dry out repeatedly. Screening of cultivars targeted at this environment should mimic these intermittently dry conditions. Effective screening for lowland drought tolerance can be done even in the wet season in trials situated in upper, light-textured fields that can be easily drained. Care should be taken to ensure that the field used is at the top of the toposequence, and that there is no higher field from which water will flow into the drought screening site. Because the objective of screening is to identify cultivars with improved yield under stress, screening is conducted in replicated trials consisting of two-row plots to achieve adequate precision. Seedlings are transplanted into puddled soil in such fields, and then the trial is drained 7 d after transplanting. The field should be allowed to dry until the soil cracks and/or the surface is completely dry. The field should not be irrigated again until the local check variety is wilting, and the water table is at least 1 m below the surface. If tensiometers are installed, the field should be irrigated when soil water tension equals –40 kPa at a depth of 20 cm. When these conditions are achieved (the time needed for this to occur will vary with soil texture and rainfall), the field is then re-irrigated. One day after re-irrigation, the field is drained again. The cycle of stress followed by re-irrigation and drainage is repeated until the field is finally drained for harvest. Drought tolerance is expressed simply as the yield produced by a cultivar under stress.

Screening under this type of managed stress has identified large differences among lowland breeding lines and mega-varieties in yield under stress at IRRI (Table 3). Several lines (e.g., the pureline IR77298-14-1-2 and the hybrid IR80228H) have been identified that are comparable in yield potential to current elite irrigated varieties under nonstress conditions but that outyield them substantially under stress. Screening for grain yield under drought stress has now been incorporated as a routine cultivar evaluation step by IRRI and by several Indian breeding programs in collaboration with the IRRI-India Drought Breeding Network, a collaborative network serving drought-prone rainfed environments. This network tested a number of breeding lines developed at IRRI as well as at different national research institutes in India for their performance under drought. These lines were screened in alpha lattice design with three replications under fully irrigated conditions and two levels of stress. In one stress level, fields were drained out just after transplanting, water from rains was never allowed to stand, and the trial was never irrigated. These experiments generally had experienced more severe stress, resulting in at least 70% reduction in mean yield as compared with control mean yield. In the second stress level, fields were drained out after 35–40 d of sowing with the aim of screening the lines for reproductive stress.

The mean yield reduction in these experiments ranged between 30 and 60% and these experiments were classified as "moderate stress." Screening under severe drought, moderate drought, and irrigated control at Raipur identified breeding lines of 100–120 d duration that had yield potential between 4.0 and 5.2 t ha^{-1} and that produced a grain yield of 1.7–2.1 t ha^{-1} under severe drought stress (Table 4). These lines exhibited a combination of the drought tolerance of donors and the yield potential of high-yielding, drought-susceptible cultivars. Among the 120–140-d duration group, breeding lines with yield potential of 6.3 t ha^{-1} and yield of up 1.9 t ha^{-1} under severe drought stress (Table 5) were identified. The screening also showed that the widely grown rainfed variety Swarna is mildly tolerant, whereas the related variety Sambha Mahsuri was shown to be extremely susceptible to drought stress.

Screening for tolerance for delayed transplanting. Delayed transplanting is probably the main cause of yield loss due to drought in rainfed lowand systems, but tolerance has rarely been systematically evaluated or incorporated as a rice breeding objective. Variability in tolerance for delayed transplanting appears to be large, even in photoperiod-insensitive germplasm. In the 2005 wet-season evaluation of 125 medium-duration, photoperiod-insensitive varieties transplanted as 65-d-old seedlings, cultivar mean yields ranged from 0.3 to 3.3 t ha^{-1}. Some elite breeding lines and cultivars produced high yields when transplanted as 25-d-old seedlings but performed very poorly under delayed transplanting. A notable example is the tungro-resistant IR64 derivative IR77298-14-1-2, which yielded 4.0 t ha^{-1} under normal management, but only 1.8 t ha^{-1} under delayed transplanting. Other entries produced relatively high yields under both conditions; for example, the hybrid IR80642H yielded 4.4 t ha^{-1} when transplanted as 25-d-old seedlings, with a reduction to only 3.3 t ha^{-1} as 65-d-old seedlings. In general, hybrids were more tolerant than purelines (Table 6).

Developing cultivars with improved drought tolerance for unbunded uplands

Upland rice is grown as a subsistence crop in unbunded upper fields by some of the poorest farmers in Asia. Upland rice growers use few improved varieties and, because of risk of crop loss due to drought or weed pressure, apply only small amounts of fertilizer to their fields. Recently, studies in traditional upland

Table 3. Yield, days to flowering, and harvest index of medium-duration varieties and breeding lines under severe intermittent lowland drought stress and full irrigation, IRRI, 2006 dry season.

Line	Days to flowering		Harvest index		Yield (kg ha^{-1})	
	Stress	Non-stress	Stress	Non-stress	Stress	Non-stress
IR77298-14-1-2	94	85	0.21	0.40	1241	3278
IR80461-B-7-1	95	84	0.22	0.37	1076	3675
IR80228 H	101	85	0.27	0.46	920	5782
PSBRc 82	104	91	0.10	0.36	256	2647
Trial mean	100	88	0.10	0.34	447	2233
$LSD_{.05}$	8	2	0.10	0.16	355	944

Table 4. Yield, days to flowering, and harvest index of medium-duration varieties and breeding lines under three levels of water stress, IRRI-India Drought Breeding Network, 2005 wet season.

Line	Grain yield (kg ha^{-1})			Days to flowering			Harvest index		
	Stress level			Stress level			Stress level		
	None[a]	Moderate	Severe	None	Moderate	Severe	None	Moderate	Severe
				Tolerant lines and cultivars					
Baranideep	5523	3926	1415	82	87	87	0.42	0.40	0.38
CB00-15-24	4972	3106	1383	81	83	82	0.40	0.40	0.36
IR74371-3-1-1	4971	3872	1229	83	83	88	0.41	0.42	0.34
				Widely grown varieties					
MTU1010	2915	1922	635	86	92	91	0.28	0.21	0.13
IR64	5231	2905	516	87	90	90	0.41	0.35	0.17
IR36	4192	1993	116	85	97	94	0.41	0.27	0.04
Trial mean	4589	2763	767	84	89	91	0.38	0.32	0.22
$LSD_{.05}$	781	934	358	4	5	3	0.05	0.08	0.11

[a] Mean of 7, 3, and 1 trial for non-stressed, moderately stressed, and severely stressed trials, respectively, in southern and eastern India.

Table 5. Yield, harvest index, and days to flowering of 120–140-d duration entries from the IRRI-India Drought Breeding Network at Raipur, 2005 wet season.

Designation	Grain yield (t ha^{-1})			Harvest index			Days to flowering		
	Control	Moderate stress	Severe stress	Control	Moderate stress	Severe stress	Control	Moderate stress	Severe stress
ARB6	6.7	4.3	1.9	0.37	0.43	0.40	79	78	81
IRMBP-2	6.1	3.2	1.3	0.38	0.32	0.35	82	84	85
Mahamaya	6.5	1.9	0.6	0.34	0.19	0.14	92	93	96
PSBRc 9	5.8	4.3	1.6	0.42	0.42	0.37	90	89	91
Sambha Mahsuri	6.7	0.8	0.0	0.41	0.09	0.0	103	111	[a]
Swarna	6.0	2.1	1.3	0.38	0.25	0.34	103	110	126
(Swarna/ IR42253)-54	6.4	2.8	1.7	0.42	0.33	0.38	83	85	80
$LSD_{0.05}$	0.7	0.6	0.4	0.04	0.06	0.07	1	1	5

[a] Failed, did not flower.

Table 6. Agronomic performance of 10 hybrids versus 115 inbred purelines when transplanted at 22 or 65 d after sowing, IRRI, 2005 wet season.

Cultivar type	Days to flowering		Height (cm)		Harvest index		Yield (kg ha^{-1})	
	Seedling age at transplanting							
	22	65	22	65	22	65	22	65
Hybrid	85.0	113.5	114.7	89.8	0.41	0.38	4976	2674
Inbred	81.5	112.9	118.9	91.6	0.37	0.28	3377	1484
Pr > F	ns	ns	ns	ns	0.0012	<0.0001	<0.0001	<0.0001

rice-growing areas of Yunnan (Atlin et al 2006) and Laos (Saito et al 2006) have demonstrated that improved upland rice varieties have at least 50% higher yield potential than traditional cultivars and can serve as the basis for more productive and sustainable upland rice-based cropping systems. However, since upland systems are almost exclusively rainfed, adoption of such systems will depend on the development of varieties that combine high yield potential with high levels of drought tolerance and weed competitiveness.

Screening for tolerance for upland stress. Strategies for drought-tolerance screening under upland conditions are similar to those described above for lowland management. Most upland varieties are photoperiod-insensitive, so if temperatures permit, dry-season screening is the preferred option for reliably imposing stress. Many upland varieties have a moderate degree of vegetative drought tolerance but are often highly susceptible to stress around flowering. For this reason, screening protocols should emphasize tolerance for stress at flowering. At IRRI, drought screening is conducted in replicated yield trials of fixed lines that have been previously selected for yield potential and disease resistance. Screening trials are conducted in an unbunded, well-drained field at the top of the toposequence. There should be no irrigated or flooded trial planted above the drought screening site. Lines should be screened in trials with at least two replicates. Plots should be at least two rows. Trials are direct-sown into dry soil. The field should be irrigated to maintain soil water potential near field capacity until canopy closure, or for about 30 d after sowing, at which time the frequency of irrigation is reduced. Irrigation is withheld until the soil surface is completely dry, susceptible check varieties are severely wilted, and the water table is at least 1 m below the surface. If tensiometers are installed, the field should be irrigated when soil water tension reaches –50 kPa at a depth of 30 cm. When the target levels of soil dryness and plant stress are reached, the field should be liberally irrigated. Enough water should be applied to saturate the root zone. This is likely to require 60–80 mm of water. The stress cycle is then repeated until harvest. Yield and harvest index should be determined.

There is evidence that differences in drought tolerance measured in this screen are predictive of differences observed under natural stress in the target population of environments. For example, at IRRI, 30 varieties were screened under severe upland stress artificially imposed in the 2005 dry season. The same varieties were screened under rainfed upland conditions at IRRI in the 2004 wet season and 2005 wet season. In both of these years, severe drought stress occurred at flowering. The correlation between variety means for grain yield in the dry-season stress screen and under natural stress in the wet season was 0.87, indicating that the ability of the artificial drought screen to predict performance under natural stress was high (IRRI, unpubl. data).

Selection of random breeding lines under artificial stress has been shown to result in gains under natural stress in the wet season. Venuprasad et al (2007) screened several hundred lines from the crosses Apo/IR64 and Vandana/IR64 in the dry season of 2003. The lines were evaluated for grain yield under both severe upland stress and irrigated control conditions. Selected lines from both the stress and the irrigated control screens were then evaluated under natural stress at IRRI in the wet seasons of 2004 and 2005. Yield gains under natural stress were greater in the subset of lines selected under artificial stress than under fully irrigated conditions. Selection under stress gave no gains under nonstress conditions.

Screening for weed competitiveness. Upland rice cultivars that compete well against weeds are often thought to be tall, rapid in early growth, and have droopy leaves and high specific leaf area. These traits have been linked to low yield potential in some studies (Jennings and Aquino 1968, Kawano et al 1974) but not in others (Garrity et al 1992, Ni et al 2000, Fischer et al 2001). More recently, Zhao et al (2006b) have shown that differences in cultivar weed competitiveness in direct-sown rice are largely determined by differences in the rate of seedling biomass accumulation in the first 4 wk after sowing. They observed that, averaged over 3 yr, there was a twofold difference between the most and least competitive cultivars in weed biomass at 9 wk in plots that were hand-weeded once 3 wk after sowing, and that there was no tradeoff between yield potential and weed competitiveness. Improved weed competitiveness can be selected for in replicated trials by visually rating advanced breeding lines for total biomass 4 wk after sowing (Zhao et al 2006b). Screening for seedling biomass accumulation has been incorporated as a routine screening step in the IRRI rainfed and aerobic rice breeding programs. Cultivars with high seedling biomass accumulation tend to be erect, moderately drought-tolerant, and derived from the *indica* and *aus* germplasm groups.

Direct seeding to reduce drought risk in drought-prone upper fields

As noted above, rice establishment either by transplanting or through the traditional beushening/biasi practice in bunded upper fields frequently leads to heavy crop yield loss because of delayed transplanting, exposure of the transplanted seedlings to early drought, or failure of weed control. In crops where establishment has been delayed due to lack of standing water in fields, the risk of drought occurring during the reproductive stage or grain filling is also increased. Direct seeding in dry soil, with herbicide-based weed control, may be a useful alternative to transplanting or beushening in areas where early-season drought is frequent. Direct seeding can be undertaken in dry or moist soil starting with the earliest rains, and it therefore allows establishment to take place 4–6 wk earlier than is possible in puddled, transplanted systems. Early establishment reduces drought risk during flowering and grain filling associated with early withdrawal of the monsoon and, because direct-sown crops mature approximately 10–14 d earlier than transplanted crops seeded on the same date, increases the probability of successfully establishing a post-rice rainfed crop. Direct-seeded establishment also eliminates the risk associated with delayed transplanting, which occurs when rainfall is insufficient for main-field puddling by the time seedlings are ready to be removed from the nursery bed; planting over-aged seedlings due to early-season drought is a major cause of yield reduction in light soils and upper rainfed terraces.

Cultivars differ substantially in their adaptation to dry direct-seeded establishment. Component traits include weed competitiveness, seedling vigor, ability to maintain biomass development in intermittently dry fields, and tolerance for late-season drought. The development of adapted cultivars with these traits is therefore an important element in the design of successful direct-seeding establishment systems in rainfed upland and shallow lowland systems. Drought-tolerant upland varieties for direct seeding with a yield potential of 4-5 t ha^{-1} that produce yields of more than 1 t ha^{-1} under severe drought stress have been identified. The yield potential of these materials is not greater than that of current elite aerobic adapted varieties Apo and PSBRc 80, but yields under moderate drought stress are three- to fourfold higher (Table 7).

Hybrid rice: a technology for water-stressed environments

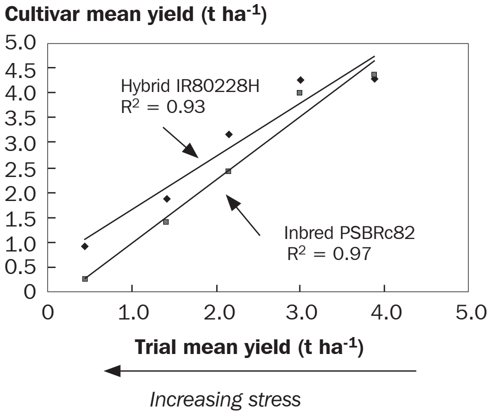
Hybrid varieties appear to offer a route to combining improved tolerance for drought stress with high yield potential, particularly in drought-prone lowland fields. In field experiments conducted at IRRI during the dry seasons of 2004 through 2006, hybrids previously not selected for drought tolerance have been compared with elite purelines from the IRRI irrigated and rainfed lowland breeding programs under the moderate intermittent drought stress protocol described above, which reduces trial mean yield from approximately 4–5 to 1.5–2.0 t ha^{-1}. Hybrids have consistently outyielded purelines under this level of stress by an average of about 1 t ha^{-1}, about 60% (IRRI, unpubl. data).

Table 7. Yield of drought-tolerant upland breeding lines under nonstress and severe intermittent upland drought stress applied following maximum tillering, IRRI, 2005 dry season.

Line	Nonstress yield (t ha^{-1})	Stress yield (t ha^{-1})	Days to flowering (nonstress)
IR78875-190-B-1-3	4.6	0.8	81
IR71525-19-1-1	4.2	1.4	85
IR78875-131-B-1-3	4.1	1.0	85
IR78875-131-B-1-2	4.0	1.0	79
IR74371-54-1-1	4.0	1.1	75
Apo	3.4	0.2	80
LSD $_{0.05}$	1.1	0.3	

The advantage of hybrids is both proportionately and absolutely greater under moderate stress than under fully irrigated conditions. This is illustrated by the comparison of yields of the elite pureline variety PSBRc 82 and the hybrid IR80228H, evaluated in five trials at IRRI under a range of hydrological conditions (see figure). The two varieties did not differ in yield under nonstress conditions, but in trials with a mean yield level of 2 t ha^{-1} or less as a result of water stress, the hybrid had a significant advantage.

The tolerance of hybrids for moderate water stress and, as noted earlier, for delayed planting, combined with their high yield potential in favorable environments, has led to their rapid adoption in eastern India, where they have been introduced by the commercial seed sector over the last 5 yr. Particularly in the drought-prone shallow lowland areas of the poorest states in the region, including Jharkhand, Bihar, Uttar Pradesh, and Chhattisgarh, smallholders have been eager to replace short-duration but drought-susceptible varieties such as IR64 and IR36 with hybrids.



Yield of an elite inbred and a hybrid compared under a range of water stress levels in five trials conducted at IRRI in the wet and dry seasons of 2005 and 2006.

Generating impact: participatory varietal selection in the target environment

To increase the probability of uptake of improved varieties, it is important to determine that their performance is maintained under the variable conditions faced by farmers, which may not be predicted by on-station performance (Atlin et al 2001), and that they have end-use and quality characteristics preferred by farmers. Experience has shown that cooking quality and performance under farmer management are the primary drivers of the adoption and spread of rainfed rice varieties (Mackill et al 1996). Low-cost and effective participatory varietal selection methods have been adapted for determining farmer preferences and assessing the performance of rainfed rice varieties under farmer management (Atlin et al 2002).

Most rainfed rice varieties with high impact in South Asia have been disseminated primarily via farmer-to-farmer spread. Measures can be taken to increase the rate of adoption of promising released varieties. Links among breeding programs, seed production programs, and agricultural development and extension organizations operating at the community level can be developed to target varieties where they are needed and to identify key farmers who will be instrumental in disseminating varieties within the community, once they are convinced of their value (Subedi et al 2001). One example of such an approach is a project to disseminate varieties with improved tolerance for submergence in low-lying areas of West Bengal (S.K. Mallik, pers. commun.). In this program, breeders collaborate with extension workers to identify communities frequently experiencing severe crop loss because of flooding and where farmers are strongly interested in obtaining tolerant varieties. Meetings are organized in the targeted communities to identify farmers with a strong interest in evaluating new varieties. These farmers serve as the conduit for improved germplasm into the community, ensuring that it is evaluated on appropriate land types. Such targeted approaches can reduce the need for expensive, large-scale seed production programs, make use of existing social arrangements for the dissemination of new varieties, and have the potential to foster the rapid spread of truly superior varieties.

Conclusions

Drought is a severe and an ongoing risk for rice producers who farm upper terraces with light soils, under both upland and lowland management. Several adaptations are required to increase productivity and reduce risk of crop loss due to drought on these lands, including increased ability to maintain vegetative biomass growth in intermittently dry soils, increase weed competitiveness, and increase tolerance in delayed transplanting and tolerance for severe drought stress at flowering. There is substantial genetic variation in all these traits. High-yielding cultivars tolerant of lowland drought stress and delayed transplanting have been developed. Hybrid varieties are particularly promising for drought-prone lowland fields due to their tolerance for moderate drying during vegetative growth and for delayed transplanting.

Direct-seeded systems offer considerable promise for drought-prone lowland fields, allowing farmers to establish their crops earlier, reducing the risk of drought during the critical flowering and grain-filling periods. Direct seeding also eliminates the risk of yield loss due to transplanting delay. Cultivars with improved yield under stress and improved adaptation to direct-seeded establishment in nonsaturated soils are best developed through direct selection for rapid early growth in dry soils, and for yield under stress imposed repeatedly after maximum tillering. This type of screening can be conducted in the dry season, or in upper, light-textured fields that can be easily drained in the wet season. This has been adopted as the principal screening method for drought tolerance by the IRRI rainfed and aerobic rice breeding programs. Drought-tolerant cultivars adapted to direct seeding, otherwise known as aerobic rice cultivars, which combine yield potential of more than 5.0 t ha^{-1}, yields of at least 1.5 t ha^{-1} under severe stress levels that reduce yield to zero in most improved lowland rice varieties, and a high level of weed competitiveness, have been developed by IRRI and collaborators. These cultivars are ready for evaluation as the basis for intensified management systems for drought-prone rainfed lowland rice environments.

References

Atlin GN, Cooper M, Bjornstad A. 2001. A comparison of formal and participatory breeding approaches using selection theory. Euphytica 122: 463-475.

Atlin GN, Paris T, Linquist B, Phengchang S, Chongyikangutor K, Singh A, Singh VN, Dwivedi JL, Pandey S, Cenas P, Laza M, Sinha PK, Mandal NP, Suwarno. 2002. Integrating conventional and participatory crop improvement in rainfed rice. In: Witcombe J, Parr LB, Atlin GN (eds.). Breeding rainfed rice for drought-prone environments: integrating conventional and participatory plant breeding for South and Southeast Asia. Proceedings of a DFID Plant Sciences Research Programme/IRRI Conference, 11-15 March 2002, IRRI, Los Baños, Laguna, Philippines. Bangor and Manila: Department for International Development (DfID) Plant Sciences Research Programme, Centre for Arid Zone Studies, and International Rice Research Institute. p 36-39.

Atlin GN, Lafitte HR, Tao D, Laza M, Amante M, Courtois B. 2006. Developing rice cultivars for high-fertility upland systems in the Asian tropics. Field Crops Res. 97: 43-52.

Atlin GN, Lafitte HR, Venuprasad R, Kumar R. 2004. Heritability of rice yield under reproductive-stage drought stress, correlations across stress levels, and effects of selection: implications for drought tolerance breeding. In: Resilient crops for water-limited environments. Proceedings of an international workshop, 24-28 May 2004, Cuernavaca, Mexico. (abstr.)

Boling A, Tuong TP, Jatmiko SY, Burac MA. 2004. Yield constraints of rainfed lowland rice in Central Java, Indonesia. Field Crops Res. 90: 351-360.

Cooper M, Rajatasereekul S, Immark S, Fukai S, Basnayake J. 1999. Rainfed lowland rice breeding strategies for northeast Thailand. I. Genotypic variation and genotype × environment interactions for grain yield. Field Crops Res. 64: 131-151.

Ekanayake IJ, Steponkus PL, De Datta SK. 1990. Sensitivity of pollination to water deficits at anthesis in upland rice. Crop Sci. 30: 310-315.

Fischer AJ, Ramirez HV, Gibson KD, Pinheiro BDS. 2001. Competitiveness of semidwarf upland rice cultivars against palisade grass (*Brachiaria brizantha*) and signalgrass (*B. decumbens*). Agron. J. 93: 967-973.

Garrity DP, Movillon M, Moody K. 1992. Different weed suppression ability in upland rice cultivars. Agron. J. 84: 586-591.

Garrity DP, O'Toole JC. 1994. Screening for drought resistance at the reproductive phase. Field Crops Res. 39: 99-110.

Haefele SM, Johnson DM, Bodj DM, Wopereis MCS, Miezan KM. 2004. Field screening of diverse rice genotypes for weed competitiveness in irrigated lowland ecosystems. Field Crops Res. 88: 39-56.

Huke RE, Huke EH. 1997. Rice area by type of culture: South, Southeast, and East Asia. Los Baños (Philippines): International Rice Research Institute.

Jennings PR, Aguino RC. 1968. Studies on competition in rice. III. The mechanism of competition among phenotypes. Evolution 22: 529-542.

Kawano K, Gonzalez H, Lucena M. 1974. Intraspecific competition with weeds, and spacing response in rice. Crop Sci. 14: 841-845.

Lanceras JC, Pantuwan GP, Jongdee B, Toojinda T. 2004. Quantitative trait loci associated with drought tolerance at reproductive stage in rice. Plant Physiol. 135: 384-399.

Lafitte HR, Courtois B. 2002. Interpreting cultivar × environment interactions for yield in upland rice: assigning value to drought-adaptive traits. Crop Sci. 42: 1409-1420.

Mackill DJ, Coffman WR, Garrity DP. 1996. Rainfed lowland rice improvement. Manila (Philippines): International Rice Research Institute. p 45-46.

Maclean JL, Dawe DC, Hardy B, Hettel GP (eds.). 2002. Rice almanac. Los Baňos (Philippines): International Rice Research Institute. 253 p.

Ni H, Moody K, Robles RP, Paller EC, Lales JS. 2000. *Oryza sativa* plant traits conferring competitive ability against weeds. Weed Sci. 48: 200-204.

Pandey S, Bhandari H, Sharan R, Naik D, Taunk SK, Sastri ASRAS. 2005. Economic costs of drought and rainfed rice farmers' coping mechanisms in eastern India. Final project report. Los Baños (Philippines): International Rice Research Institute.

Saito K, Linquist B, Atlin GN, Phanthaboon K, Shiraiwa T, Horie T. 2006. Response of traditional and improved upland rice cultivars to N and P fertilizer in northern Laos. Field Crops Res. 96: 216-223.

Singh RK, Singh VP, Singh CV. 1994. Agronomic assessment of beushening in rainfed lowland rice cultivation in Bihar, India. Agric. Ecosyst. Environ. 51: 271-280.

Subedi A, Chaudhary P, Baniya BK, Rana RB, Rijal DK, Tiwari RK, Sthapit BR. 2001. Who maintains crop genetic diversity and how? Implications for on-farm conservation and participatory plant breeding. Paper presented at the National Workshop on In Situ Crop Conservation, 24-26 April 2001, Lumle, Nepal.

Venusprasad R, Lafitte HR, Atlin GN. 2007. Response to direct selection for grain yield under drought stress in rice. Crop Sci. 47: 285-293.

Zhao DL, Atlin GN, Bastiaans L, Spiertz, HJ. 2006a. Cultivar weed-competitiveness in aerobic rice: heritability, correlated traits, and the potential for indirect selection in weed-free environments. Crop Sci. 46(1): 372-380.

Zhao DL, Atlin GN, Bastiaans L, Spiertz JHJ. 2006b. Developing selection protocols for weed competitiveness in aerobic rice. Field Crop Res. 97: 272-285.

Zhao DL, Atlin GN, Bastiaans L, Spiertz JHJ. 2006c. Comparing rice germplasm groups for growth, grain yield and weed-suppressive ability under aerobic soil conditions. Weed Res. 46: 372-380.

Notes

Authors' addresses: A. Kumar, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines; G.N. Atlin, International Maize and Wheat Improvement Center, CIMMYT, Apdo. Postal 6-641, 06600 Mexico, D.F., Mexico.