

Oryza glaberrima: A source for the improvement of *Oryza sativa*

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African rice *Oryza glaberrima* ($2n = 24$, AA) has many unique traits such as weed competitiveness, drought tolerance and the ability to grow under low input conditions. These traits have been recently combined with high yield of *Oryza sativa* to develop NERICA (NEW RICE for AfriCA). The new rice varieties are high-yielding, drought- and pest-resistant and are uniquely adapted to the growing conditions of West Africa. The major problems in combining useful traits of both cultivated *Oryza* species are sexual incompatibility and hybrid sterility. Reproductive barriers between the two species have been studied and genetic models based on sporogametophytic interactions proposed. The availability of a molecular linkage map of *O. glaberrima* and molecular markers linked to sterility loci would aid in the introgression of desirable traits and elimination of sterility loci quickly. The use of *O. glaberrima* in rice breeding is challenging, but promising. The genetic base of Asian rice *O. sativa* can be widened for obtaining higher yields under adverse conditions and using non-transgenic approaches.

Keywords: Hybrid sterility, NERICA, *Oryza glaberrima*, *Oryza sativa*, weed suppression.

RICE is cultivated in India in about 45 million hectares under irrigated (46%), rainfed lowland (28%), rainfed upland (12%) and flood-prone (14%) ecosystems. Since the major portion of area under rice is rainfed, production is strongly linked to the distribution of rainfall. Drought and flood often in the same year limit productivity in some areas. Soil acidity is a problem in parts of southern and eastern India and soil salinity and alkalinity in parts of northern India. In addition to diseases, insect pests and abiotic stresses, weeds are becoming major factors constraining productivity and profitability in rainfed areas. Most farmers in such areas cannot afford necessary inputs for full exploitation of the yield potential of modern rice varieties. Also, herbicides are often not affordable and hazardous. *Oryza glaberrima* Steud (African rice) has many useful traits such as weed competitiveness, drought tolerance and low input responsive nature that are unique to rice species. If these traits are introgressed into *Oryza sativa* cultivars, yield in rainfed areas may be considerably improved. The sexual barriers between *O. sativa* and *O. glaberrima* and sterility of the hybrids

between them thwarted earlier attempts to combine the high yield potential of *O. sativa* and the adaptability of *O. glaberrima* (www.scienceinAfrica.co.za/nerica.htm).

In the history of rice breeding, high-yielding rice varieties have been obtained for the first time from crosses between African rice (*O. glaberrima*) and Asian rice (*O. sativa*). The dramatic development of new varieties called NERICA (NEW RICE for AfriCA) at WARDA, Ivory Coast has led to yield increase by 50% in upland rice ecology of Africa. These replaced the low-yielding, lodging and shattering-prone *O. glaberrima*. About 3000 lines were developed in the 1990s and many varieties have been released and are being grown by farmers in West African countries. NERICAs are projected to cover two lakh hectares by 2007. The high-yielding new rice varieties are drought- and pest-resistant. Their unique adaptation to the growing conditions in West Africa has helped increase yield and has potential to benefit 20 million farmers there. The World Food Prize for 2004 was shared by (Monty Jones) for the development of NERICAs (www.warda.org/warda1/main/Achievements/nerica.htm; www.worldfoodprize.org/) and Yuan Long Ping for development of hybrid rice.

In this review we provide an update on the characteristics of *O. glaberrima* and focus on the problems and prospects of its hybridization with *O. sativa* to obtain high-yielding derivatives rapidly.

Origin, evolution and distribution of *O. glaberrima*

O. glaberrima (genome AA, $2n = 24$) is a cultivated rice species endemic to Africa. Two major ecotypes are recognized in this species – floating photosensitive ecotype grown in deep water, including coastal mangrove areas, and an early erect ecotype grown in upland or moderately inundated lowlands¹. The Asian rice species *O. sativa* (genome AA, $2n = 24$) is spread in large parts of the world and is more diverse than *O. glaberrima*. *O. sativa* is broadly divided into *indica* and *japonica* subspecies. The genus *Oryza* is believed to have originated in Gondwanaland², the ancient land mass from which India, Africa, South America and Australia drifted apart. The two cultivated species, namely *O. sativa* and *O. glaberrima* are considered to have evolved later by independent and parallel evolutionary processes in Asian and African continents. *O. glaberrima* originated around 1500 BC in swampy basins of the upper river delta of Niger

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in West Africa, which is the primary centre of origin of this species. Two secondary centres appeared in Guinea coast^{2,3} around 1000 BC. The hypothesis of parallel lines of evolution of the two cultivated species has been confirmed by cytological studies^{4,5}. Major portions of chromosomes of *O. glaberrima* could not be distinguished from those of *O. sativa*. Position and organization of two ribosomal RNA gene clusters (45s rDNA and 5s rDNA) were also found similar in the chromosomes of the two species⁵. The two cultivated species have been classified within the group of A-genome species but formed separate clusters within it, as shown by results from isozymes⁶ and molecular marker⁷⁻⁹ studies. Similarities were observed using miniature inverted transposable element amplified fragment length polymorphism (MITE-AFLP), and greater variation was detected in ancestral wild species than in cultivated species¹⁰. It is believed that both the cultivated species might have evolved from an unknown common ancestor following a sequence from wild perennial to wild annual to cultivated annual ancestors (Figure 1). Both *O. glaberrima* and *O. barthii* are restricted to West Africa, but *O. longistaminata* is widely distributed in most parts of Africa, except the north. It is well established that *O. barthii* is the progenitor of *O. glaberrima*, while *O. rufipogon* and *O. nivara* gave rise to *O. sativa*^{3,11-14}. Recently, *O. glaberrima* genome has been used as a reference to unravel the sequence of evolution in *O. sativa* subspecies¹⁵. *O. glaberrima* differs from *O. sativa* in many qualitative and quantitative traits. The two species can be distinguished in the field by differences in ligule shape and panicle branching (Table 1).

Useful traits of *O. glaberrima*

O. glaberrima has many important traits such as weed competitiveness, drought tolerance and ability to respond to low input conditions, traits that are unique to this rice species. It is resistant to pests and diseases, and is a good source of variation for important abiotic stresses also (Table 2). It has the ability to grow in a wide range of difficult ecosystems such as rainfed hilly areas, deep-water floating conditions and in coastal mangrove areas.

The weed competitive ability of *O. glaberrima* is due to the early vigour, low extinction coefficient, high light use efficiency, and high specific leaf area leading to high canopy growth for given amount of assimilates. It has droopy leaves which prevent sunshine from reaching the soil surface. Further, its high root biomass accumulation and thin roots with better soil penetration ability help compete effectively with weeds for nutrients. *O. glaberrima* has the ability to produce extra tillers (up to 8 tillers/hill) between 40 and 80 days after germination, and thus can compensate for any early loss in tillering suffered due to weeds¹⁶. The short basic vegetative phase and the ability to produce more biomass within a short time allow *O. glaberrima* to successfully compete with the weeds. An *O. glaberrima* accession CG14 developed strikingly more leaf area (two times at zero N and 3.5 times under 80 kg nitrogen treatment), than *O. sativa* accession WAB 56-104¹⁶. Such phenomenal capacity for leaf area growth helps in competing with weeds. This assumes greater importance in upland conditions of Asian and African countries, where poor farmers are unable

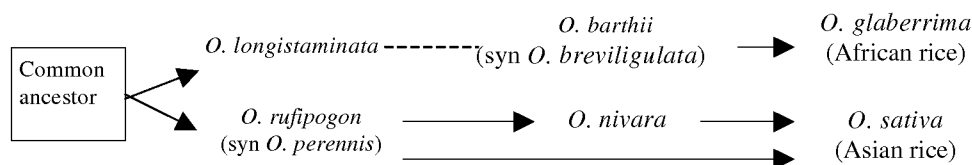


Figure 1. Proposed evolutionary pathway from perennial wild to annual wild to cultivated rice species. Broken line indicates that molecular evidence for the link is missing. All are A genome species and diploid, $2n = 24$ (adapted from Chang² and Khush¹⁴).

Table 1. Distinguishing characters between *Oryza glaberrima* and *Oryza sativa*

| Character | <i>Oryza sativa</i> | <i>Oryza glaberrima</i> |
|----------------------|---------------------------------|-----------------------------|
| Distribution | Cosmopolitan | Endemic to West Africa |
| Habit | Essentially perennial | Annual |
| Varietal differences | High variation | Limited variation |
| Lodging | Rare | Frequent |
| Drought resistance | Poor | High |
| Ligules | Long 40–45 mm, pointed, thin | Short 6 mm, oblong, thick |
| Panicle branching | Many | None or few |
| Grain number | High (up to 250 grains/panicle) | Low (75–100 grains/panicle) |
| Grain | Easy to mill | Difficult to mill |
| Seed dormancy | Low | High |
| Seed shattering | Low | High |
| Protein | Low | High |

Table 2. Resistance or tolerance of *O. glaberrima* to abiotic and biotic stresses

| Abiotic stress | Reference |
|---------------------------------|-----------------------------|
| Weed competition | 16, 17, 65, 66 |
| Drought tolerance | 16, 22, 67–69 |
| Submergence tolerance | 70 |
| Acidity | 69 |
| Salt tolerance | 61, 71 |
| Iron toxicity | 23, 69, 72 |
| Aluminium toxicity | 73 |
| Biotic stress | |
| <i>Rice yellow mottle virus</i> | 50, 74–76 |
| Blast | 65, 77, 78 |
| Sheath blight | 48 |
| Nematode | 79, 80 |
| Stem borer and hispa | 81 |
| Stalked eye fly | 82, 83 |
| Bacterial leaf blight | Kuldeep Singh, pers commun. |
| African gall midge | 84, 85 |

to take up timely and complete weeding because of less resources and poor labour availability. Several accessions such as IB19, CG14, IG10, CG20 and Biyagero of *O. glaberrima* were identified as weed-competitive¹⁶. In the presence of weed competition, IG10 produced higher yields than *O. sativa* cultivars Moroberekan and IDSA6, but without competition from weeds, grain yields did not differ between the cultivars^{16,17}. Although *O. glaberrima* has been used as a source of resistance to many pests and diseases found in West Africa, tests are needed to estimate the durability of its resistance or tolerance in Asia. *O. glaberrima* accessions resistant to many pathotypes of bacterial leaf blight have been identified at Punjab Agricultural University and the resistance in these accessions is recessive (Kuldeep Singh, pers. commun.).

Among abiotic stresses, drought is the major stress that affects rice yields. *O. glaberrima* has several drought-escaping mechanisms. The ability to mature early and synchronized maturity towards the end of the wet season are unique features. In addition to its ability to withstand drought, it has the capability to recover fast on receipt of moisture with the help of its thin leaves and roots. The thin leaves roll quickly to retain water and thin roots penetrate effectively, coming in close contact with the soil particles to effectively mine water and nutrients¹⁸. These traits are useful in breeding for drought tolerance in rice^{19–22}. Among the *O. glaberrima* accessions evaluated for drought tolerance, 32 were highly resistant and 217 were moderately resistant¹⁶. *O. glaberrima* is a source of resistance to other abiotic stresses as well. Its ability to tolerate acidic conditions has helped utilize rock phosphate. It also tolerates iron and aluminium toxicity. An accession CG14 of *O. glaberrima* showed remarkable tolerance at an iron-toxic site at Ivory Coast²³.

The survival capacity under low input conditions, high nitrogen use efficiency, high photosynthetic efficiency per unit of Rubisco²⁴, high specific leaf area, rapid canopy establishment, droopy leaves^{16,25,26} and high root biomass¹⁹ in *O. glaberrima* varieties are the other traits that could be exploited to develop new plant types for both rainfed and irrigated ecosystems. Some of the short-statured and thick-leaved accessions of *O. glaberrima* such as oldAyoma, Fufore-yola, UG75 (1), UG75 (2), NG26(3), CG66, Katasina ala and Shendam are also rated as resistant to lodging¹⁶. Some useful quality traits identified by the West African farmers in *O. glaberrima* include: faster cooking, good keeping quality of cooked rice, good taste with salt and pepper and suitable for feeding weaning babies (<http://www.Unu.edu/enu/plec>). Thus *O. glaberrima* is also a potential source of genes to enhance milling, cooking and eating qualities of Asian rice.

Interspecific hybridization

The sexual cross-compatibility varies with the combination of specific *O. glaberrima* and *O. sativa* accessions. In general, *O. sativa indica* accessions are more compatible than *japonica* accessions for interspecific hybridization with *O. glaberrima*. The *O. glaberrima* accessions used influence seed set. For example, F₁ seeds were obtained from four of its 14 *O. sativa* parents in the interspecific crosses using WO 25 as the *O. glaberrima* parent, and 12 when CG 13 was used as the *O. glaberrima* parent²⁶. Season, parental genotypes and cytoplasm are significant factors that influence the interspecific crossability between the two species²⁷. Although on an average 30–56% seed set has been reported in interspecific crosses between the two species, there is no consensus on the extent of crossability. Crosses made using *O. glaberrima* as female and *O. sativa* as male parent resulted in a range of sterility and seed set. Out of 335 spikelets, pollinated seeds were formed only in 190 spikelets²⁸. In another study involving 170 crosses, 99 crosses produced 0–21 seeds²⁶. Jones *et al.*¹⁶ made 48 interspecific crosses between *O. sativa* and *O. glaberrima* in an attempt to improve upland rice. Only in seven crosses seed set was successful (5% from 6783 spikelets pollinated)¹⁶. In interspecific crosses with *O. glaberrima*, a major problem was abscission of clipped spikelets within a day of pollination. This could not be prevented by spraying GA₃ + NAA (Kuldeep Singh, pers. commun.). In most of the cases, F₁s exhibited normal vigour and intermediate plant type and rarely transgressed the parents. But a deviation towards *O. glaberrima* was seen in several crosses, indicating the dominant effects of *O. glaberrima* genome²⁹. The intermediate ligule length observed in F₁ helps identify hybrids.

Hybrid sterility

Both *O. glaberrima* and *O. sativa* are AA genome species with minor sub-genomic differences which do not hinder

normal chromosome pairing and gamete formation in the hybrids³⁰. Yet, complete sterility is the general rule in *O. sativa* and *O. glaberrima* F₁ hybrids, irrespective of the combinations of parental varieties^{2,31}. Various causes such as meiotic irregularities^{26,32-34}, low proportion of viable pollen, low pollen germination, cytoplasm and its interaction effects from male side and early elimination of female gametes and zygotes from female side^{3,35} have been ascribed for sterility.

Pollen development in F₁ in an interspecific hybrid is arrested at the microspore stage. Three types of pollen – empty, intermediate and fully stained have been reported based on staining with iodine solution (I₂KI). Pollen studies in some hybrids showed pollen sterility to an extent of 80%, of which 7–48% pollen was of intermediate type and 51–92% was completely empty. In rice intraspecific (*indica* × *japonica*) hybrids, it has been shown that though pollen stainability with iodine was 50%, only 10% germinated *in vitro*. Thus stainability with iodine or acetocarmine may not correctly indicate pollen fertility. Whether the same is true for interspecific hybrids between *O. sativa* and *O. glaberrima* is not known. The ability of intermediate type of pollen to germinate is also not known. Studies on pollen germination and pollen tube growth in different interspecific hybrids would help devise methods to improve seed set. The exact cause for pollen sterility is not known.

Genetic models based on one locus sporo-gametophytic interactions have been proposed after extensive analyses of reproductive barriers between the two species^{36,37}. According to this model, pollen killer and gametic eliminator loci are responsible for sterility. In the pollen killer model, it is proposed that only the pollen are killed and female gametes are unaffected (if *S/Sa* is the sterility locus, only *Sa* pollen is killed, *Sa* ovule is normal). In the gametic eliminator model, both the male and female gametes are killed (both *Sa* pollen and *Sa* ovule are killed). A sterility locus *S-1* causing hybrid sterility was identified by Sano³⁸. Later, a number of sterility loci such as *S18* on chromosome 10, and *S20* and *S21* on chromosome 7 have been reported^{39,40}. The high sterility and semisterility in interspecific hybrids are governed by loci *S18* and *S1* respectively. Dayun *et al.*⁴¹ reported three nonallelic gamete eliminator loci and two pollen killer loci derived from *O. glaberrima*. The mode of action of genes underlying these sterility loci is not known.

The position of the sterility locus *S1* (= *S10*) was inferred from the marker segregation ratios in BC₁ population from the cross *O. sativa* × *O. glaberrima*⁴². Strong segregation distortion (95% plants were heterozygous for these markers compared to the expected 50%) was observed on chromosome 6, close to the microsatellite markers OSR19 and OSR 25 in the *wx* gene, indicating the presence of a sterility locus. The sporo-gametophytic sterility factor *S10* in heterozygous state leads to a total elimination of male gametes. In addition, female gametes carrying the *O. glaberrima* allele of *S10* are selected against those carrying the *O. sa-*

tiva allele. This confirms earlier studies⁴³ that hybrid sterility is correlated with a heterozygous *S1* locus linked to waxy gene on chromosome 6. It should be possible to use these markers in the seedling stage to select rare, semi-fertile BC₁ individuals that are homozygous for *O. sativa* allele of *S-10*.

Spikelet sterility in *O. sativa* × *O. glaberrima* hybrids was correlated with total spikelet number⁴⁴. Similar correlations have been reported with plant height in *O. sativa indica* × *japonica* hybrids and with spikelet number when spikelet sterility was exceptionally high due to heat. Semi-sterile plants had a high straw weight and 8% more spikelets/panicle than fertile plants. In these hybrids apparently, the translocation of metabolites from vegetative parts into grains was affected. In all probability, hybrid plants produced more spikelets/panicle to offset the effect of high frequency of abnormal female gametophyte development and thus ensured a minimal seed set. In interspecific hybrid progenies, semi-sterility was maintained until the F₄ generation. It is interesting to note⁴⁵ that the gametophyte lethal 2 locus was linked to the semidwarf gene *d60* on chromosome 7. It is not known if QTLs/genes for spikelet number are also linked to semi-sterility.

Hybrid sterility is a common phenomenon not only in interspecific crosses, but also in intraspecific crosses between subspecies of *O. sativa*⁴⁶. The *indica-japonica* sterility could be overcome by use of wide compatible varieties (WCV) having neutral sterility loci (*Sⁿ*). Individual *Sⁿ* loci are sufficient to restore fertility in intraspecific crosses between *indica* and *japonica* hybrids. But the wide compatible varieties could not restore fertility in interspecific hybrids. The sterility in interspecific hybrids is caused by genes that are apparently distinct from those causing sterility in *O. sativa indica* × *japonica* hybrids, since F₁ hybrids from the cross *O. glaberrima* × *O. sativa* (with *WC* genes) are completely sterile⁴⁴.

Methods to overcome sterility

Strategies have to be developed to overcome or circumvent the crossing barriers and F₁ hybrid sterility^{16,26,37}. Accessions of *O. glaberrima* and *O. sativa* which give fertile F₁ and BC₁F₁ need to be identified. For example, one accession of *O. glaberrima* (IRGC 101800) yielded fertile F₁ and BC₁F₁ with both Pusa 44 and PR114, whereas another accession IRGC 102356 yielded fertile F₁ and BC₁F₁ only with Pusa 44 (Kuldeep Singh, pers. commun.). Backcrossing and biotechnological tools such as embryo rescue techniques⁴⁷, anther culture¹⁶, and specially molecular markers are helpful in obtaining desirable plants rapidly (Figure 2).

Backcrossing

Repeated backcrossing can restore fertility^{11,17,48} since some embryo sacs are fertile in F₁. The extent of fertility resto-

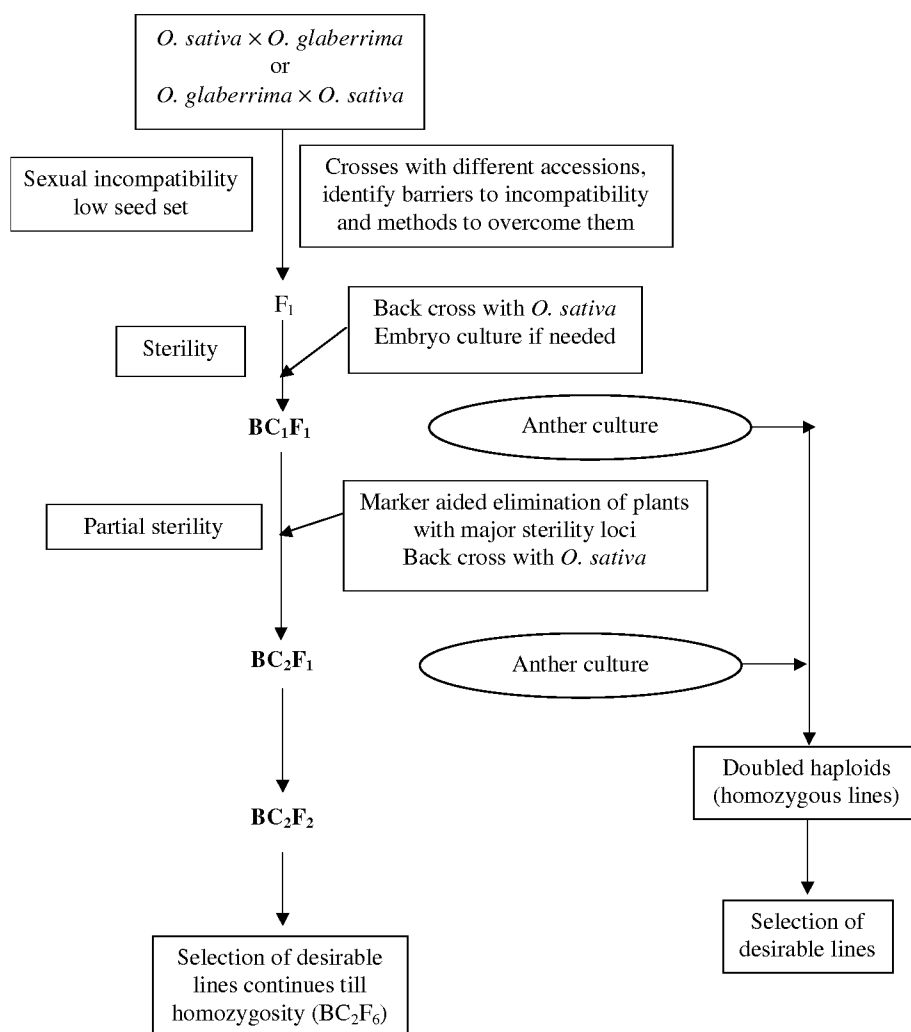


Figure 2. Proposed scheme to obtain fertile lines from interspecific crosses between *O. sativa* and *O. glaberrima*.

ration varied from 30 to 65% (ref. 16) to 90% (ref. 26) or even 98% (ref. 29), after two backcrosses. However, crossability in *O. glaberrima* is still limited to a few parental accessions and desirable traits are often lost in the fertility restoring process.

Anther culture

The rapid genetic fixation through chromosome doubling of haploids after anther culture has the advantage of retaining genes which could be lost through conventional selection. Callus induction and plant regeneration vary widely with genotypes. Callus induction ranged from 0 to 18.6% upon culture of 45,400 anthers from 75 F₁s derived from crosses between *O. sativa* and *O. glaberrima*. Anthers of only 41 F₁s showed on an average 1.35% callus induction, and plant regeneration ranged from 0 to 77%. In different F₁ hybrids, callus induction and plant regeneration varied with genotypes. The 562 doubled haploid lines showed high (56 to 100%) seed sterility⁴⁹. Anther culture in BC₁F₁ may be more useful.

Molecular markers

Contig line concept was proposed by Ghesquiere *et al.*¹ to bypass the sporogametic interaction by monitoring sterility loci using molecular markers. It was proposed that contig lines containing an alien chromosome fragment of 15–20 cM be developed. Since each contig line has only a fragment of alien chromosome, it can be effectively monitored to eliminate sterility loci, retaining the useful and recessive traits tightly linked to such sterility loci, which are otherwise not possible to transfer through conventional backcrossing. For example, efforts to transfer *Rice yellow mottle virus* (RYMV)⁵⁰ resistance from a variety of *O. glaberrima* TOG 5681 by conventional backcrossing was not successful. If such traits are linked to sterility loci such as *SI* (*S10*), they get eliminated during backcrossing.

Recently developed linkage map of *O. glaberrima* permits the identification, location and introgression of various genes of interest to new genetic backgrounds. The map was developed using 129 markers representing 112 discrete loci⁴².

O. sativa and *O. glaberrima* maps showed good collinearity with only small nonsignificant marker inversions, implying that no major rearrangement like inversions or translocations have occurred between the two species. Linkage map helps in marker-assisted elimination of sterility locus to restore fertility quickly. Markers in the region of putative sterility loci can be developed. Introgression of desirable genes is possible using tightly linked molecular markers. Favourable QTL alleles have been mapped for improved per cent rice bran, per cent milled rice, alkali spreading value, per cent protein and grain length/width ratio in derivatives from *O. sativa* × *O. glaberrima*^{51,52}.

Interspecific hybrids and their derivatives

Exploitation of heterosis is one of the major ways to boost yield in rice. But the three line system of hybrid seed production is highly dependent on WA (wild abortive) cytoplasmic male sterile lines as sterility source. Its cytoplasm is known to have undesirable effects on the hybrid seed quality. Cytoplasmic male sterile lines have been developed using *O. glaberrima* cytoplasm and are in use for commercial hybrid seed production in China⁵³.

The interspecific hybrids between *O. sativa* and *O. glaberrima* are more vigorous than the *O. sativa* intraspecific hybrids. A significant standard heterosis of *O. glaberrima* × *indica* and *O. glaberrima* × *japonica* hybrids over *indica* × *japonica* hybrids has been reported for dry weight and number of tillers per plant⁵³. The derivatives of such vigorous interspecific hybrids perform better under low input and poor management conditions. For example, a line WAB-450-24-2-3-P33-HB yielded 4.7 t/ha under poor management¹⁶. These were found suitable for unfavourable temperature, flood and shifting cultivation.

In addition, *O. glaberrima* seeds show dormancy. It can be used to develop varieties with different dormancy patterns to suit different ecologies. Varieties with high dormancy periods are suitable for lowland ecologies, while those with short dormancy are required for double-cropping. Lines with low initial germination but reaching 100% germination quickly, are suitable for rainfed uplands⁵³. Lines P31 (WAB450-11-1-p31-HB) and P38 (WAB-1-BP-38-HB) with different dormancy have been developed from interspecific progenies to suit upland and lowland ecologies⁵⁴.

NERICA

NERICA rice varieties are also called as interspecifics (though in the strict sense of the word these are not interspecific hybrids, i.e. F₁s, but lines derived from interspecific hybrids), because they bridge the genetic gap between two distinct species of rice. These were developed to combine the superior traits of *O. glaberrima* and *O. sativa*. Thus lines which resemble *O. glaberrima* during early growth stages and *O. sativa* during later stages were developed. Signifi-

cantly, the selected recombined new plants expressed the weed competitive ability of *O. glaberrima* at the vegetative stage and high-yielding capacity of *O. sativa* at the reproductive stage. The NERICAs have strong stem, produce more tillers and bear longer panicles than either parent. The strong stem can support heavy panicles, each with more than 400 grains that are held together tightly without lodging to prevent them from shattering. NERICAs have inherited the primary branching trait of *O. glaberrima* and forked branching trait of *O. sativa*, thus increasing the number of spikelets. These mature in 90–100 days. This helps to take up double cropping and crop rotation with a legume and enrich the soil with nitrogen. In addition, NERICAs escape late-season insects and diseases, thus preventing yield losses. NERICAs have raised the yield ceiling of upland rice by 50%. The new rice can produce 6 t/ha in the best condition and up to 2.3 t/ha under drought. Its thin leaves and roots help withstand drought. Tolerance to acidic soils enables the utilization of huge repositories of rock phosphate, which is soluble only in acid medium. The NERICA line WAB450-1-P181-22-1-HB has high level of resistance to African gall midge (www.fao.org/ag, www.undp.org, www.warda.org).

Perspective

Rice varieties with higher yield potential, increased tolerance to biotic and abiotic stresses and superior grain quality need to be continuously developed. The breeding and success of NERICA rice in Africa has shown the tremendous potential of favourable combinations of useful genes from both the cultivated species of rice. Although *O. glaberrima* has not been bred as intensively as *O. sativa*, it can carry numerous agronomically important alleles. Phenotypically inferior accessions can contribute trait-improving alleles, as has been shown with wild species. Even though some alleles may be inferior to *O. sativa* alleles individually, it is the transgressive segregants that are obtained in interspecific progeny that are valuable. The NERICAs are a good example of transgressive segregation for various traits. Such transgressive segregants which outperform either parents in several traits have been reported in backcross progeny of interspecific hybrids of *O. sativa* with *O. rufipogon*⁵⁵⁻⁵⁹, *O. glumaepatula*⁶⁰ and other wild species. Since *O. glaberrima* and *O. sativa* evolved from different progenitors and in different continents, the two species are likely to have different coadapted gene complexes. While the resistance of *O. glaberrima* to RYMV, African rice gall midge and drought is of particular interest to African rice systems, weed competitiveness and tolerance to various abiotic stresses would be of particular interest for improving Asian rice systems.

Rainfed upland rice occupies six million hectares in central and eastern parts of India. The productivity levels are low (0.6 to 1.5 t/ha). Drought and weeds are the major factors limiting yield. There are fewer high-yielding varieties

released for rainfed upland regions compared to irrigated regions. Traditionally, land races adapted to upland conditions have been good sources for improvement of upland rice. *O. glaberrima* can be an important source for yield improvement in upland rice. The resistance of *O. glaberrima* accessions to pests and diseases in Asia needs to be assessed. A combination of favourable genes from the two species is likely to help in breeding for better rice.

While the value of wild species for improving rice yield has been recognized, access to the gene pool of cultivated African rice has so far been limited. Hybridization between *O. sativa* and *O. glaberrima* has been attempted since the last fifty years. Questions on interspecific incompatibility still remain unanswered. The sterility of F₁ hybrids and semi-sterility in subsequent generations remain a major problem. A similar problem of sterility in *indica-japonica* hybrids of *O. sativa* was overcome by the use of *indica* or *japonica* lines having genes for wide compatibility. Such wide compatible lines were not useful in overcoming interspecific crossability with *O. glaberrima*. The identification of compatible *O. glaberrima* and *O. sativa* accessions for interspecific hybridization would facilitate broader access to the African rice gene pool. The development of large backcross population increases likelihood of obtaining fertile progenies, since recombination occurs frequently. There is no genome-wide barrier to recombination during meiosis, although segregation distortion is reported in a few regions of the genome. Thus many combinations of favourable alleles from both the species are possible. Backcrossing and selection of fertile plants in successive generations is time-consuming and labour-intensive. Anther culture has been used to speed up this process. Any improvement in the efficiency of anther culture procedures would enable quicker recovery of useful recombinants to reduce sterility. Doubled haploid lines have been used to develop NERICAs and map agronomically useful traits. In addition, chromosomal segment substitution lines are being developed in the background of IR64 (*indica*) and Caiapo (*japonica*) at Cornell University, USA and International Centre for Tropical Agriculture, Colombia. Each of these lines will have one segment of a chromosome substituted by the corresponding *O. glaberrima* segment. Thus a series of *O. sativa* lines with introgressions covering the entire *O. glaberrima* genome will be developed (Susan McCouch, pers. commun.).

The availability of molecular maps would help in tagging and mapping both useful and undesirable genes in *O. glaberrima*. Rapid loss of old varieties of *O. glaberrima* is a cause for concern. In an anthropological essay, Linares⁶¹ mentions an old *O. glaberrima* variety called 'ejonken', which is still grown in southern Senegal as it is used in some important rituals. Such varieties that grow in tidal channels may serve as good sources for salt tolerance. It is important that the remnant populations of *O. glaberrima* be conserved because of its qualities as a subsistence crop in difficult ecologies. Introgressions from *O. sativa* are reported to have influenced the genetic structure of *O. glaberrima*

populations in West Africa. About 198 accessions of *O. glaberrima* have been grouped into five sub-groups based on genome-wide linkage disequilibrium of nuclear microsatellite markers. Two subpopulations clustered with *O. sativa* indicate admixture in *O. glaberrima*. An average of 9.4 alleles per locus was detected with a range of 2–27 alleles per locus, indicating abundant variability⁶². It is also important that national and regional breeders gain quick access to increased genetic variability required for faster genetic gain^{63,64}. The success of NERICAs in West Africa can then be repeated for other poor regions of the world.

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