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.scienceafrica.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 WARDIA, 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.wardia.org/warda/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 lowlands\(^1\). 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 Gondwanaland\(^2\), 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 around 1000 bc. The hypothesis of parallel lines of evolution of the two cultivated species has been confirmed by cytological studies. 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 species. 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 isozymes and molecular marker 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 species. 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*. *O. glaberrima* genome has been used as a reference to unravel the sequence of evolution in *O. sativa* subspecies. *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 weeds. 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 56-104. 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 to manage competition of weeds.
Table 2. Resistance or tolerance of *O. glaberrima* to abiotic and biotic stresses

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

The survival capacity under low input conditions, high nitrogen use efficiency, high photosynthetic efficiency per unit of Rubisco, high specific leaf area, rapid canopy establishment, droopy leaves, and high root biomass 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 old Ayoma, Fufere-yola, UG75 (1), UG75 (2), NG26(3), CG66, Katasina ala and Shendam are also rated as resistant to lodging. 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* parent. Season, parental genotypes and cytoplasm are significant factors that influence the interspecific crossability between the two species. 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 spikelets. In another study involving 170 crosses, 99 crosses produced 0–21 seeds. Jones et al. 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). 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, *F₁* 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* genome. 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 hybrids. Yet, complete sterility is the general rule in O. sativa and O. glaberrima F1 hybrids, irrespective of the combinations of parental varieties. Various causes such as meiotic irregularities, low proportion of viable pollen, pollen germination, cytoplasm and its interaction effects from male side and early elimination of female gametes and zygotes from female side have been ascribed for sterility.

Pollon 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 pollen stainability with iodine was 50%, only 10% germinated in vitro. Thus stainability with iodine or aceto-carmine 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 sporophyto-gametophytic interactions have been proposed after extensive analyses of reproductive barriers between the two species. According to this model, pollen killer and gametic eliminator loci are responsible for sterility. In the pollen killer model, it is supposed 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). The gametic eliminator model, both the male and female gametes are killed (both Sa pollen and Sa ovule are killed). A sterility locus S-I causing hybrid sterility was identified by Sano. Later, a number of sterility loci such as S18 on chromosome 10, and S20 and S21 on chromosome 7 have been reported. The high sterility and semisterility in interspecific hybrids are governed by loci S18 and S1 respectively. Dayun et al. 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. 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 of the wx gene, indicating the presence of a sterility locus. The sporophyto-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. sativa allele. This confirms earlier studies that hybrid sterility is correlated with a heterozygous Si locus linked to waxy gene on chromosome 6. It should be possible to use these markers in the seedling stage to select rare, semi-sterile 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 number. 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 ensures a minimal seed set. In interspecific hybrid progenies, semisterility was maintained until the F2 generation. It is interesting to note that the gametophyte lethal 2 locus was linked to the semi-dwarf gene d60 on chromosome 7. It is not known if QTLs genes for spikelet number are also linked to semisterility.

Hybrid sterility is a common phenomenon not only in interspecific crosses, but also in intraspecific crosses between subspecies of O. sativa. The indica-japonica sterility could be overcome by use of wide compatible varieties (WCV) having neutral sterility loci (S0). Individual S0 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 sterile.

Methods to overcome sterility

Strategies have to be developed to overcome or circumvent the crossing barriers and F1 hybrid sterility. 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 techniques, amther culture and specially molecular markers are helpful in obtaining desirable plants rapidly (Figure 2).

Backcrossing

Repeated backcrossing can restore fertility 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*.

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

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Molecular markers

Contig line concept was proposed by Ghesquiere *et al.* to bypass the sporogamic 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) 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 *S1* (*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 loci.
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, alkalai spreading value, per cent protein and grain length/width ratio in derivatives from O. sativa × O. glaberrima.

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 China.

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 plant. 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 management. 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 rained uplands. 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 ecologies.

NERICA

NERICA rice varieties are also called as interspecifics (though in the strict sense of the word these are not interspecific hybrids, i.e., F1's, 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. Significantly, 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, O. glumaepatula 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 NERICA cultivars and map agronomically useful traits. In addition, chromosomal segment substitution lines are being developed in the background of IR64 (indica) and Calapo (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, Linares 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 variability. It is also important that national and regional breeders gain quick access to increased genetic variability required for faster genetic gain. The success of NERICA cultivars in West Africa can then be repeated for other poor regions of the world.

REVIEW ARTICLES


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