International Journal of Botany

ISSN: 1811-9700

science alert

ANSInet
an open access publisher
http://ansinet.com

International Journal of Botany 4 (1): 33-40, 2008
ISSN 1811-9700

Meiotic and Population Dynamics in the Indigenous Representatives of the A-genome Complex of the Genus *Oryza* Linn.

Francisca O. Aladejana and J.O. Faluyi and Chinyere C. Nwokeocha
Department of Botany, Obafemi Awolowo University, Ile-Ife, Nigeria

Abstract: The savanna agroecology of Nigeria was surveyed for the occurrence of wild rice-three species of the A-genome complex (*O. barthii*, *O. glaberrima* and *O. longistaminata*) were found to be endemic. A total of 32 accessions of these species, including *O. sativa* were studied *in situ* and *ex situ*. Chromosome studies revealed regular pairing as 12II in the accessions *per se*. The *O. glaberrima*×*O. sativa* crosses showed a preponderance of bivalent pairing as 12II, other associations like 24I, 10II + 1IV, precocious movement at Metaphase I and occurrence of two pairs of satellited chromosomes. The crosses were infertile. The *O. glaberrima*×*O. barthii* cross was highly pollen and spikelet-fertile. A modal chromosome association of 12II was recorded. A translocation was seen at pachynema. The *O. barthii*×*O. sativa* cross was sterile with only a few shriveled seeds. The chromosomes showed many associations at diakinesis and budding of microspores was experienced during pollen mitosis. Some fertility was restored in the BC_1 generation of the *O. glaberrima*×*O. sativa* crosses; more fertility was restored in the BC_1 F_2 Fertility was not restored in the BC_1F_2 of the backcrosses involving *O. glaberrima*. Various meiotic disturbances were monitored in the backcross generations. Rice farming in the savanna agroecology of Nigeria (particularly in Jebba) is a peasant affair in small holdings circumscribed by wild rice. This creates an opportunity for natural hybridization. The population dynamics and phylogeny of the A-genome complex are enunciated based on this fact and the results of the cytogenetic studies carried out.

Key words: Savanna, A-genome complex, natural hybridization, phylogeny

INTRODUCTION

Three species of rice in the A-genome complex-*Oryza barthii* A. Chev. and Roehr., *Oryza glaberrima* Steud. and *Oryza longistaminata* A. Chev. and Roehr.-are native to West Tropical Africa. *Oryza sativa* Linn., the Asiatic rice, has become the main cultivated rice crop having displaced *O. glaberrima*, the so-called African Rice or Red Rice. The rice culture is more than 450 years old in West Africa (Grist, 1975). Prior to the introduction of *O. sativa*, *O. glaberrima* was under cultivation. There is evidence to suggest that the *glaberrima-sativa* cultures have produced genetic variability over time (Faluyi and Nwokeocha, 1993).

Genome A was assigned to *O. sativa*, *O. glaberrima* *O. barthii* and *O. longistaminata* on the basis of regular metaphase pairing in the F_1 hybrids (Morinaga and Kuriyama, 1960; Nezu *et al*., 1960). Two African species: *O. brachyantha* A. Chev. and Roehr., *O. eichingeri* Peter belong in the FF and CC genomes, respectively. These species are compatible when crossed but they are separated by many reproductive barriers; the F_1 hybrids among them are infertile (Tao *et al*., 2002a, b). Zymographic and molecular tools have also been used in phylogenetic studies in rice (Endo *et al*., 1971; Katayama and Chern, 1973; Abbasi *et al*., 1999; Sujatha *et al*., 2004).

O. glaberrima, *O. longistaminata* and *O. barthii* occur in the savanna agroecology of Nigeria where *O. sativa* is intensively cultivated on peasant holdings. As a result, regular interphases are maintained between *O. sativa* and these wild rices, particularly in one of the locations of this study Jebba, Nigeria (09°08”N; 04°50”E). This study reports the results of cytogenetic investigation carried out on these wild accessions, their hybrids and advanced generations. The population dynamics of the A-genome complex and the phylogeny of the component species studied are enunciated.

The main objective of this study is to reconstruct the reproductive and population dynamics that produced the hybrid swarms observed in the field and thereby elucidate further the phylogeny of the A-genome complex which have been worked out by various workers (Oka, 1964; Second, 1986; Doi *et al*., 1995; Abe *et al*., 1999; Sujatha *et al*., 2004).

Corresponding Author: J.O. Faluyi, Department of Botany, Obafemi Awolowo University, Ile-Ife, Nigeria

MATERIALS AND METHODS

This study was carried out in the Department of Botany, Obafemi Awolowo University in Nigeria between 1998 and 2004.

A total of 32 accessions involving *O. barthii*, *O. glaberrima*, *O. longistaminata* and *O. sativa* were collected either during surveys in the savanna agroecology of Nigeria or from the Genetic Resources Unit of the International Institute of Tropical Agriculture, Ibadan, Nigeria. Interspecific and intravarietal crosses were carried out among these accessions to investigate species relationships and the mode of inheritance of some morphological and agronomic attributes. Hybridization was carried out by physical emasculation and transfer of pollen at blooming. The markers established in the screen house studies were used to identify hybrids in the wild. Three hybrids including their advanced generations were studied cytogenetically in this study.

Detailed chromosome studies were carried out on all the accessions, their hybrids and in some cases, backcrosses involving them. Flower buds of all the accessions, the F_1 hybrids and some backcross plants were harvested and fixed in 1:3 acetic-alcohol. Slides were prepared by squash techniques and stained in FLP Orcein (2 g of Orcein in 100 cm^3 of solution containing equal parts of formic acid, lactic acid, propionic acid and distilled water; Lasebikan and Olorode, 1972). Pollen Mother Cells were examined and cells with good chromosome spreads were photographed under phase contrast on a Leitz DIALUX research microscope. Pollen stainability was determined by counting the number of well-formed and well stained pollen grains in Cotton Blue in Lactophenol. Spikelet fertility was assessed as the percentage of filled caryopses in each accession. Species relationship was monitored through meiotic behaviour and hybrid sterility indicators like pollen grain size and stainability and spikelet fertility/seed set.

RESULTS AND DISCUSSION

The general trends in the study of chromosomes of the accessions show regular pairing as 12II without any multivalents. The hybrids generated represent a broad spectrum of the cross combinations expected in the A-genome complex with the exception of *O. barthii*× *O. longistaminata* and *O. glaberrima*×*O. longistaminata*.

Table 1 shows a summary of the meiotic configurations in the hybrids obtained in this study. The general features of the *O. glaberrima*×*O. sativa* crosses are: preponderance of bivalent pairing as 12II; associations like 24I; 10II + 1IV and others; precocious movement at Metaphase I and occurrence of two pairs of satellited chromosomes (Table 1 and Fig. 1).

The *O. glaberrima*×*O. barthii* cross showed high pollen and spikelet fertility; the modal chromosome association is 12II with a few others shown in Table 1. Normal Anaphase 1 constitutes 95% of the meiotic configurations while Anaphase I with a bridge was 5%. The occurrence of a translocation, possibly a reciprocal translocation at pachynema (Fig. 2) is a significant event in the meiosis of this cross. It is also significant that the cross produced fertile seeds (70% seed set; Table 2) whose seedlings segregated for Mendelian ratios in the F_2.

The *O. barthii*×*O. sativa* cross (TOB 10835 × TOS 1585-W) segregated for all sorts of chromosome associations shown in Table 1. The chromosomes were joined by heterochromatin connections. Pollen mitosis showed some budding microspores resulting in very small infertile pollen grains; some medium-sized pollen grains were of low fertility. These probably resulted in the low pollen and spikelet fertility (Table 2).

The *O. glaberrima*×*O. sativa* crosses were all sterile but backcrosses were obtained in the screen house and the wild. The main cytological events in the backcrosses are shown in Table 1. Anaphase was 100% normal except with Plant 1 which showed abnormal cells with non-disjunction and a bridge. The meiotic events resulted in a low spikelet fertility (5.36-15.63%) of the backcrosses. This value is significant because the F_1 was completely sterile. Fertility was further restored in the BC_1 F_2 plants.

The F_1 between *O. sativa* and *O. longistaminata* was infertile but the backcrosses showed some levels of restoration of pollen fertility ranging from 16.37 to 48.85%; the plants still remained highly sterile, however. The major cytological events are precocious separation at Diakinesis and Metaphase I in (TOS × TOL) × TOL and (TOS × TOL) × TOS-3; asynchrony was observed in the meiotic stages of (TOS × TOL) × TOS-3 but the tetrad was normal and anaphase configurations were 100% normal. Nwokeocha (1998) reported some regular pairing (12II, 35%) with occasional univalents and an array of abnormal associations probably due to the multiple heterochromatin connection in her F_1 between TOB 10838 × IJ86-W, an *O. barthii*× *O. sativa* cross. She reported a low seed set. Faluyi (1985) reported a seed set of 29.92% to a pollen fertility of 51.16% in a cross between *O. barthii* and *O. sativa*.

A thorough assessment of agricultural practices in the Fadama around Jebba revealed that rice farming is

Table 1: Chromosome associations in the accessions studied and their hybrids

Accession	Modal chromosome association	Comments
TOB 8218	11 ring II + 1 rod II	
TOB 5645	10.01 ring II + 1.99 rod II	
TOB 10838	11.05 ring II + 0.95 rod II	
TOB 5660	11.25 ring II + 0.75 rod II	
TOB 7382	10.60 ring II + 1.40 rod II	Paucity of Pollen Mother Cells, high level of synchrony.
TOB 8226	10.19 ring II + 1.81 rod II	Some level of asynchrony (from pachynema to Anaphase I). Some bivalents assume figure of 8.
TOB 7307	9.72 ring II + 2.28 rod II	Big meiotic cells, clear cytoplasm, high level of synchrony, some bivalents assume figure of 8.
TOB 5646	11.10 ring II + 0.90 rod II	Some bivalents assume figure of 8
TOB 7337	11.47 ring II + 0.53 rod II	
TOB KARI 83	11.05 ring II + 0.95 rod II	
TOB 7311	10.35 ring II + 1.65 rod II	Small meiotic cells, not typical
TOG 16771	8.27 ring II + 3.73 rod II	Asynchrony
TOG 12083	10.05 ring II + 1.95 rod II	Asynchrony, small meiotic cells.
TOG 5236	11.06 ring II + 0.94 rod II	
TOG 5282	11.26 ring II + 0.73 rod II	Large bud size, large meiotic cells.
TOG 5281	10.28 ring II + 1.72 rod II	Asynchrony, large meiotic cells, delayed first cytokinesis, resolves between Met II and Ana II
TOG 5284	11.01 ring II + 0.99 rod II	
TOG 10985	10.70 ring II + 1.30 rod II	
TOG 5283	9.87 ring II + 2.13 rod II	
TOG JEBBA 1	10.00 ring II + 2.00 rod II	
TOG JEBBA 2	10.65 ring II + 1.25 rod II	
TOG GARKAWA	11.09 ring II + 0.24 rod II	Some bivalents assume figure of 8
TOL BIDA	9.52 ring II + 2.48 rod II	"
IJ86 Br	11.65 ring II + 0.35 rod II	
TOS 15223	11.01 ring II + 0.09 rod II	
TOS JEBBA 1	11.00 ring II + 1.00 rod II	
TOS JEBBA 2	10.96 ring II + 1.04 rod II	
TOG 10985 × IJ86 Br	12II = 9.25 ring II + 2.75 rod II (56.6%) 24 I (16.70%) 10 II + 1 IV (26.70%)	Precocious separation at diakinesis and metaphase I, tetrad is normal.
TOG 5236 × TOB 7382	12II = 10.18 ring II + 1.82 rod II (68.75%) 10 II + 1 IV (25%) 4 II + 16 I (6.25%)	Precious movement at metaphase I, High level of synchrony, tetrad is normal.
TOS PURPLE × TOG 16771	12II = 11.15 ring II + 0.85 rod II (95.2%) 10 II + 1 IV (4.8%)	Asynchrony. Precocious separation at Metaphase I. There is heterochromatin connection at diplonema. Normal tetrad.
TOG JEBBA × TOS JEBBA	12II = 10.52 ring II + 1.48 rod II (70.50%) 10 II + 1 IV (23.25%), 2 II + 20 I (6.25%)	Asynchrony, precocious separation at metaphase I.
TOG JEBBA × TOL JEBBA	12II = 9.1 ring II + 2.9 rod II (63.34%) 2II + 20 I (6.67%), 1 II + 3 IV + 2 V (3.33%) 4 II + 16 I (6.67%), 3 II + 3 IV + 1 VI (3.33%) 4 II + 4 IV (3.33%), 2 II + 3 IV + 1 VIII (3.33%) 8 II + 2 IV (3.33%), 24 I (6.67%)	Meiotic cells very small. Tetrad normal. Asynchrony.
TOB 10838 × TOS IJ86-W	12II (35%; 10II + 1IV (15%); 8II + 2IV (25%); 6II + 3IV (15%); 16I + 2IV (5); 24I (5)	
(TOG × TOS) × TOG-1	12II = 11.10 ring II + 0.90 rod II (52.95%) 5 II + 14 I (5.88%), 9 II + 6 I (5.88%), 1 II + 20 I (11.76%), 24 I (23.53%)	Precocious separation at Metaphase I. Synchrony.
(TOG × TOS) × TOG-2	12II = 8.75 ring II + 3.25 rod II (100%)	Meiotic cells small. Synchrony.
(TOG × TOS) × TOG-3	12II = 7.23 ring II + 4.77 rod II (83.33%) 10 II + 1 IV (16.67%)	
(TOS × TOL) × TOL	12II = 10.76 ring II +1.24 rod II (82.62%) 8 II + 2 IV (8.69%), 10 II + 4 I (8.69%)	Synchrony in meiotic cells, tetrad not synchronised. Precocious separation at metaphase I.
(TOS × TOL) × TOS -1	12II = 10.01 ring II + 1.99 rod II (90.0%) 10 II + 4 I (5.0%), 10 II + 1 IV (5.0%)	
(TOS × TOL) × TOS-3	12II = 9.52 ring II + 2.48 rod II (75.0%) 10 II + 4 I (6.25%), 11 II + 1 2 I (18.75%)	Asynchrony. Precocious separation at diakinesis tetrad normal.
(TOS × TOL) × TOS-5	12II = 10.42 ring II + 1.58 rod II (84.5%) 10 II + 1 IV (7.75%), 10 II + 4 1 (7.75%)	

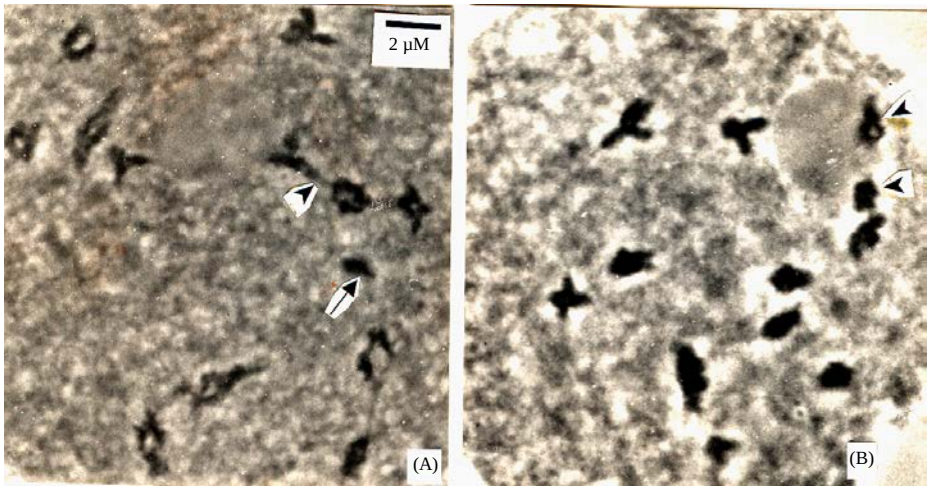

Fig. 1: Chromosome configurations in *O. glaberrima*×*O. sativa* crosses. (A) Diakinesis in TOG10985 × IJ86BR showing 10II + 1III + 1I. Arrow shows univalent; arrowhead shows trivalent and (B) Late Diakinesis shows two satellited pairs in TOS PURPLE × TOG 16771

Table 2: Pollen stainability and spikelet fertility in the hybrids and backcrosses studied

Accession	Pollen stainability (‰)	Spikelet fertility (‰)
TOG 10985 × IJ86BR	0.00	0.00
TOG 5236 × TOB 7382	95.83	70.00
TOS PURPLE × TOG 16771	0.00	0.00
TOG JEBBA × TOS JEBBA	0.00	0.00
TOB 10838 × TOS IJ86W	6.10	3.20
TOS JEBBA × TOL JEBBA-1	0.00	0.00
(TOG × TOS) × TOG-1	21.80	8.75
(TOG × TOS) × TOG-2	84.50	15.63
(TOG × TOS) × TOG-3	40.86	5.36
(TOS × TOL) × TOL	48.85	1.71
(TOS × TOL) × TOS-1	16.37	1.46

essentially a peasant affair dominated by small holdings in permissive locations around inaccessible natural bodies of water. *O. longistaminata* is the dominant component of the vegetation in the location studied. This situation leads to pockets of holdings surrounded by wild rice (*O. longistaminata*).

There are four critical aspects of this cytological study: 1. the hybrids between *O. longistaminata* and *O. sativa* were sterile in spite of a modal chromosome configuration of 12II 2. the F_1 between *O. glaberrima* and *O. barthii* was fertile with a spikelet fertility of 70%, a modal chromosome configuration of 12II (68.75%) and a translocation at pachynema 3. restoration of fertility in the BC_1F_1 of the *O. glaberrima*×*O. sativa* cross and segregation for genetic ratios in the F_2 4. progressive increase in bivalent association (12II = 78.7-83.08%) and improvement in fertility of backcrosses of hybrids involving *Oryza sativa*, *Oryza glaberrima* and *Oryza longistaminata*.

The crosses that were not obtained in this study are those involving *O. longistaminata O. barthii* and *O. glaberrima*. Dania Ogbe and Williams (1978) concluded that there may be gene flow in the direction of *O. longistaminata* to *O. glaberrima* based on biosystematic evidence. Dania Ogbe (1993) suggested that the annual *O. barthii* evolved from *O. longistaminata*. Second (1986) had demonstrated through zymographic studies that two alleles frequent in *O. sativa*, but never found in *O. barthii*, were found in weedy strains of *O. barthii* suggesting that there is gene flow between *O. sativa* and *O. barthii*. Faluyi (1985) and Nwokeocha (1998) provided direct evidence for gene flow through the generation of hybrids between these two species.

The observation of regular meiosis in the hybrid between *O. sativa* and *O. glaberrima* has been made by many workers (Oka, 1964; Sano, 1986; Sano *et al*., 1979). The occurrence of two pairs of satellited chromosomes suggests that *Oryza* is probably a secondarily diploidized polyploid and confirms a basic number of 6. Sano (1986) implicated a one locus sporophytic sterility, one locus sporogametophytic interaction and duplicate genetic lethals in the sterility of *O. sativa*×*O. glaberrima* crosses. The observation of a bridge and non-disjunction at anaphase I (Fig. 3) suggests that chromosome rearrangements, possibly an inversion, might be involved in the reproductive isolation between the two species. The genetic models proposed by Sano (1986) do not necessarily preclude gross chromosomal involvement in reproductive isolation between the two species.

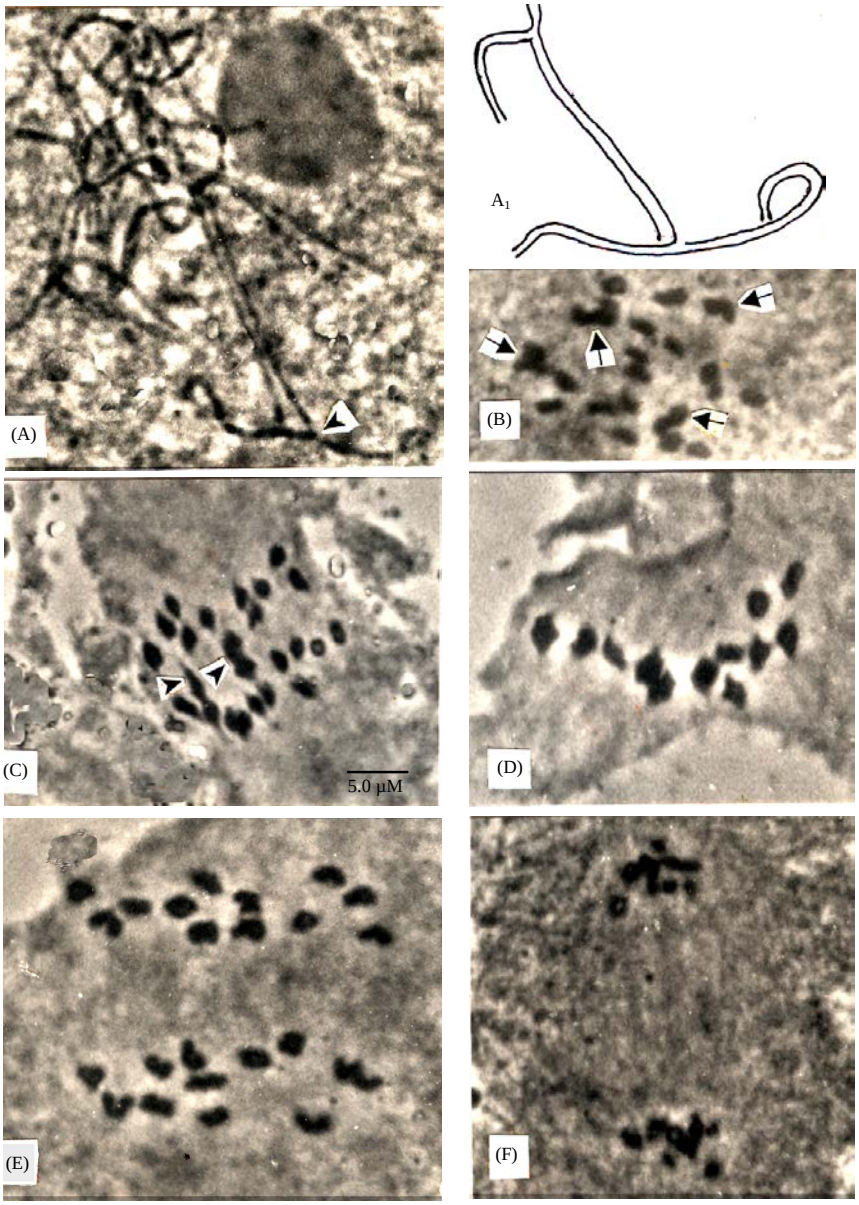

Fig. 2: Chromosome configurations in *O. glaberrima*×*O. barthii* (TOG 5326 × TOB 7382). (A) Pachynema showing a translocation. The arrowhead shows a breakpoint. A1 Interpretation of A. (B) Diakinesis showing 4II + 16I. Arrows show bivalents. (C) Non disjunction at early Anaphase I, (D) Normal Metaphase I showing 12II. (E) Anaphase I (normal) and (F) Telophase I (normal)

The cytology of the F_1 between *O. glaberrima* and *O. barthii* clearly shows that the two species are separated by at least one translocation. The non-disjunction observed is probably due to the translocation. There was a distinct segregation for levels of seed set in the F_2 similar to the situation in the BC_1F_1 of the *O. sativa*×*O. glaberrima* cross. Many of the F_2 plants died as a result of hybrid weakness. From the weight of evidence obtained in this cross, it can be concluded that chromosome rearrangement (probably a reciprocal translocation) and hybrid weakness at the level of the F_2 are the post-zygotic mechanisms involved in the reproductive isolation between *O. glaberrima* and *O. barthii*.

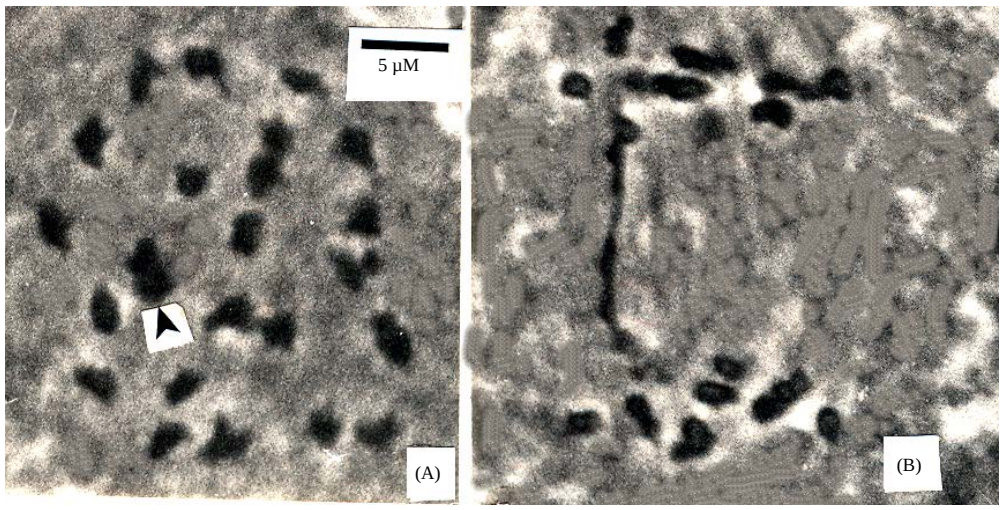

Fig. 3: Chromosome configurations in a backcross involving *O. glaberrima* and *O. sativa*, (A) Metaphase I in (TOG JEBBA × TOS JEBBA) × TOG JEBBA-1 (1II + 22I) and (B) Late Anaphase I showing a bridge in the same backcross

The results obtained for the *O. sativa*×*O. glaberrima* cross have indicated a very close relationship between the two species. Doi *et al.* (1995) grouped these two species together using nuclear DNA RFLP. The study of Abe *et al.* (1999) showed that *O. glaberrima* and *O. barthii* are very close. These results agree with earlier studies using morphology, cytology, morphometry and zymography (Katayama, 1989; Second, 1985). Kwon *et al.* (2006) used the *Rim2/Hipa* analysis to show that the African species: *O glaberrima*, *O. longistaminata*, *O barthii* clustered with the American taxon *O. glumapaetala.* The chromosome behaviour in the hybrid between *O. sativa* and *O. longistaminata* is similar to that between *O. sativa* and *O. glaberrima.* One difference is that while fertility was restored in the BC_1 in the hybrid between *O. sativa* and *O. glaberrima*, it was not in the BC_1 of *O. sativa*×*O. longistaminata.* Indeed, Khush *et al.* (1990) actually did four backcrosses to restore the fertility of his *O. sativa*×*O. longistaminata* cross in the process of transferring the gene for bacterial blight resistance to *O. sativa.* Chu and Oka (1970) proposed a complementary gene model with dosage-dependent lethal effect for the reproductive barrier between the two species.

The location of this study is in the savanna agroecology of the Middle Belt of Nigeria, specifically in Jebba and Bida. In Jebba, there is an upsurge in rice farming leading to the opening up of new pockets of land for rice cultivation. Inaccessible natural impoundments around which *O. longistaminata* and patches of *O. glaberrima* grow are a common feature. The above situation inevitably creates opportunities for the occurrence of interphases among *O. sativa*, *O. longistaminata* and *O. glaberrima.*

Figure 4 presents a model enunciating the population dynamics in the A-genome complex based essentially on the results obtained in this study. The major processes identified are hybridization and introgression leading to restoration of fertility of hybrids and segregation either as F_2 (as in the *O. barthii*×*O. glaberrima* cross) or as BC_1F_2 as in the other hybrids. The incidence of a translocation in the *O. glaberrima*×*O. barthii* cross and a bridge in the *O. glaberrima*×*O. sativa* cross provide evidence that chromosome rearrangements are involved in the process of speciation in the genes *Oryza.*

The model makes provision for the primary pool of variability which consists of the species *per se*, the active pool which consists of the hybrids which can undergo introgression to produce events like BC_nF_2, F_n, BC_nF_n, etc. thereby producing the secondary pool of variability. Experience in the wild shows that the perennial habit of *O. longistaminata* is an advantage in holding the ground and producing hybrid swarms. Ghesquire (1986) reported the occurrence of self compatible plants called Obake in his survey of 31 populations of *O. longistaminata.*

The evidence from this study suggests that *O. barthii* and *O. glaberrima* are closely related and that one, *O. glaberrima* arose from the other through chromosome rearrangement. This is consistent with the findings of Oka (1964), Second (1986), Doi *et al.* (1995), Abe *et al.* (1999), Cheng *et al.* (2002) and Kwon *et al.* (2006). *O. sativa* is closer to *O. glaberrima* than it is to

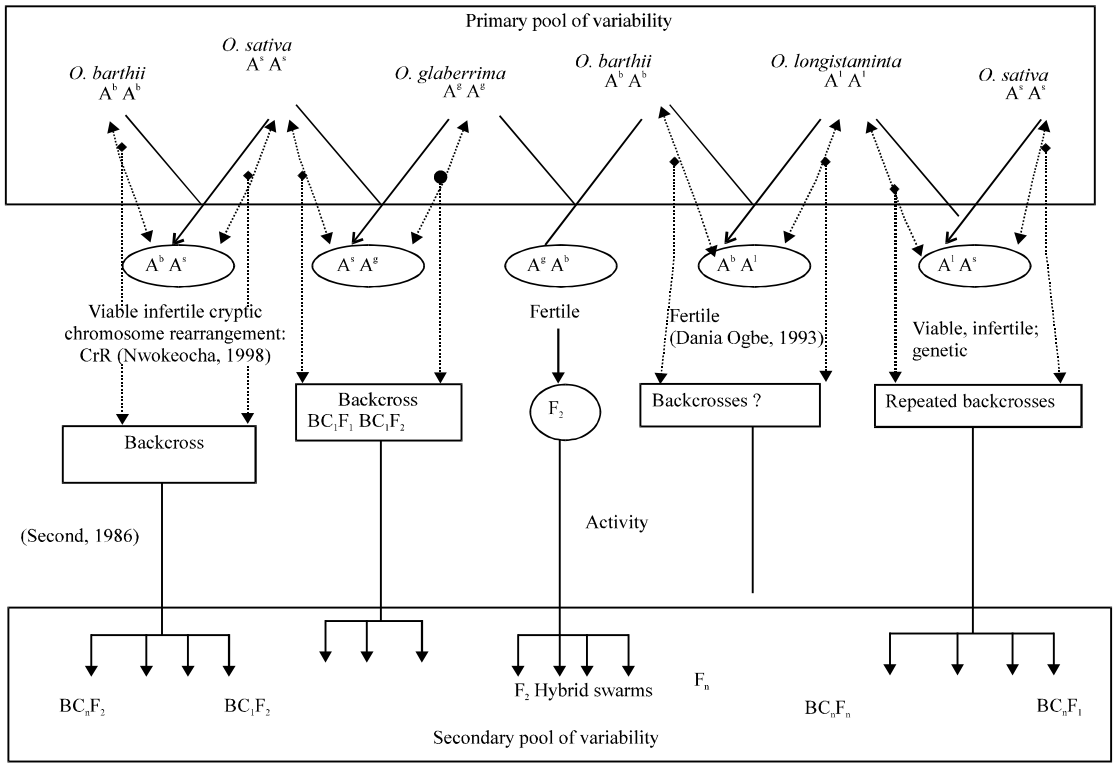

Fig. 4: Model (primary and secondary pool of variability) enunciating the population dynamic in A-genome complex

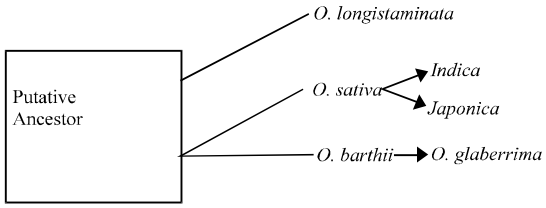

Fig. 5: Phylogenetic relationship among the species of the A-genome complex

O. longistaminata based on the relative ease with which fertility was restored in the backcross with *O. glaberrima*. The meiotic data from the *O. sativa*×*O. barthii* cross show that *O. barthii* is closer to *O. glaberrima* than it is to *O. sativa*. Ghesquire (1986) had reported lack of introgression between *O. longistaminata* and *O. barthii*.

Figure 5 shows the phylogenetic relationship in the A-genome complex based on the findings of this study. The species are supposed to have arisen from a common putative ancestor; *O. glaberrima* probably arose from *O. barthii* while *O. sativa* and *O. glaberrima* probably evolved independently from their progenitor. *O. longistaminata* probably took a different root in its evolution from the common ancestor. Evidence from this research does not support direct evolution of *O. sativa* from *O. barthii*. The occurrence of the japonica-indica differentiation in *O. sativa* suggests a more advanced evolution than in the other species.

REFERENCES

Abbasi, F.M., D.S. Brar, A.L. Carpena, K. Fukui and G.S. Khush, 1999. Detection of autosyndetic and allosyndetic pairing among A and E genomes of *Oryza* through genomic *in situ* hybridization. Rice Gene. Newslett., 16: 24-25.

Abe, T., T. Edami, E. Adachi and T. Sasahara, 1999. Phylogenetic relationships in the genus *Oryza* based on mitochondrial RFLP. Genes Genet. Syst., 74: 23-27.

Cheng, C., S. Tsuchimoto, H. Ohtsubo and E. Ohtsubo, 2002. Evolutionary relationships among rice species with AA genome based on SINE insertion analysis. Genes Genet. Syst., 77: 323-334.

Chu, Y.E. and H.I. Oka, 1970. The genetic basis of crossing barriers between *Oryza perennis* subsp. *barthii* and its related taxa. Evolution, 24: 135-144.

Dania Ogbe, F.M. and J.T. Williams, 1978. Evolution of indigenous West African rice. Econ. Bot., 32: 59-64.

Dania Ogbe, F.M., 1993. Lost Crops of Nigeria: West African Rice. In: Lost Crops of Nigeria: Implications for Food Security. Okojie, J.A. and D.U.U. Okali (Eds.), University of Abeokuta.

Doi, K.A., Y.M. Nakano and N. Iwata, 1995. Phylogenetic study of A-genome species of genus *Oryza* using nuclear RFLP. Rice Genet. Newslett., 12: 160.

Endo, T., B.B. Shasi and C. Pal, 1971. Genetic convergence of the specific acid phosphatase zymograms in *Oryza sativa*. Jap. J. Genet., 46: 147-152.

Faluyi, J.O., 1985. Cytogenetic studies in the genus *Oryza* L. I. Investigation of two interspecific hybrids and an intervarietal cross. Nig. J. Genet., 6: 1-16.

Faluyi, J.O. and C.C. Nwokeocha, 1993. Agro-botanical studies of some populations of the *Oryza sativa-Oryza glaberrima* complex of peasant agriculture. Nig. J. Bot., 6: 1-11.

Ghesquire, A., 1986. Evolution of *Oryza longistaminata*. Rice Genetics. IRRI, Manila, Philippines, pp: 15-25.

Grist, D.H., 1975. Rice. Longman Group. London, pp: 108-133.

Katayama, T. and J.L. Chern, 1973. Zymographic studies on diploid *Oryza punctata* and its related species. Jap. J. Breed., 23: 329-333.

Khush, G.S., E. Bacalango and T. Ogawa, 1990. A new gene for resistance to bacterial blight from *O. longistaminata*. Rice Genet. Neweslett., 7: 121-122.

Kwon, S., J.K. Lee, S. Hong, Y. Park, K.L. McNally and N. Kim, 2006. Genetic diversity and phylogenetic relationship in AA *Oryza* species as revealed by *Rim2/Hipa* CACTA transposon display. Genes Genet. Syst., 81: 93-101.

Lasebikan, A.B. and O. Olorode, 1972. Morphological variations and cytological aberrations in natural populations of *Zonocerus variegatus* L. (*Orthoptera: Pyrgomorphidae*). Bull. Entomol. Soc. Nig., 3: 127-133.

Morinaga, T. and H. Kuriyama, 1960. Interspecific hybrids and genomic constitution of various species in the genus *Oryza*. Agric. Hortic., 35: 935-938.

Nezu, M., T.C. Katayama and H. Kihara, 1960. Genetic study of the genus *Oryza*. I. Crossability and chromosomal affinity among 17 species. Seikenziho, 11: 1-11.

Nwokeocha, C.C., 1998. Botanical and cytogenetic studies in the genus *Oryza* Linn. Ph.D Thesis, Obafemi Awolowo University, Ile-Ife.

Oka, H.I., 1964. Pattern of interspecific relations and the evolutionary dynamics in Oryza. Rice Genet. Cytogenetics. IRRI. Elsevier, New York, pp: 70-90.

Sano, Y., Y.E. Chu and H.C. Oka, 1979. Genetic studies of speciation in cultivated rice II. Character variations in backcross derivatives between *Oryza sativa* and *O. glaberrima*: M-V linkage and key characters. Jap. J. Genet., 55: 19-39.

Sano, Y., 1986. Sterililty barriers between *Oryza sativa* and *O. glaberrima*. In: Rice Genetics IRRI, Manila, Philippines, pp: 109-118.

Second, G., 1986. Isozymes and phylogenetic relastionship in Oryza. Rice Genetics IRRI, Manila, Philippines, pp: 27-39.

Sujatha, K., R. Upadhyay, K. Kaladhar, N.S. Rani and N. Saria, 2004. Genetic relationship among aromatic short grain and Basmati rice based on ISSR and SSR markers. Rice Genet. Newslett., 21: 24-25.

Tao, D., P. Xu, J. Li, Y. Yang, F. Hu, J. Zhou, X.L. Tan and M. Jones, 2002a. Inheritance of japonica upland rice restoration lines and their restoration gene mapping. Rice Genet. Newslett., 19: 23-27.

Tao, D., F. Hu, Y. Yang, Y. Zhou and H. Chen, 2002b. Studies on crossabililty between two cultivated rice species *Oryza sativa* and *O. glaberrima*. Rice Genet. Newslett., 19: 27-29.