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DIFFERENT RATES OF GENOME DIVERGENCE PRESUMED BETWEEN TWO SPECIES GROUPS IN THE GENUS *ORYZA**

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Two independent species groups in the genus *Oryza* are widely distributed throughout the tropics from Southern China to Northern Australia and to Pakistan as well as in intertropical Africa and America.

One, the *O. sativa* group, comprises, as is suggested in its name, all cultivated forms and their closest wild relatives. They are all diploid and share only one genome AA as reported in the literature on the basis of chromosome pairing at meiosis in F_1 hybrids. The cultivated forms will not be considered here but it should be emphasized that many *wild* plants collected from Asia are rather weedy.

The other *O. latifolia* group includes no domesticated form but four genomes are recognized: B, C, D and E. The B, C and E genomes are known at diploid level

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Such a programme needs time not only because of the production of the hybrids and allopolyploid plants but especially because of the difficulties of the pachytene studies. But the results, which are to be expected, would certainly give more precise information on the phylogenetic status of the potato than all the findings existing so far in this field. Not only our own experiences but also the pachytene studies of Ramanna and Hermsen (1979) in tuber-bearing *Solanum* species demonstrate that the performance of this programme is in principle possible.

Summary

The question, whether the potato (*Solanum tuberosum* $2n=4x=48$) has an auto - or an allopolyploid origin, is discussed since decades. The primitive cultivated species. *S. stenotomum* and the two wild species *S. sparsipilum* and *S. vernei* are regarded to belong to the diploid ancestors of the potato.

In the present review, the meiotic behaviour of the potato is discussed with regard to the mode of its origin. In contrast to all the other cytological findings available in the literature, the pachytene was used for interpreting the evolutionary development of the species. In this early meiotic stage, the fine structure of the chromosomes as well as their pairing behaviour can be utilized giving considerably more reliable information than findings obtained in later meiotic stages.

The identification of all the pachytene chromosomes of the potato is possible; they are partially heterochromatic. The species has 4 structurally identical chromosome complements. The pairing behaviour agrees completely with that of experimentally produced autotetraploid tomatoes. Homologous bivalents are present which undergo secondary pairing; moreover, partner exchange figures are formed in which all the 4 homologous chromosomes of each type are united giving quadrivalents in metaphase I.

These results strongly support the hypothesis of an autotetraploid origin of the potato. According to pachytene studies, the diploid species *Solanum stenotomum* or a closely related form not yet known seems to be the ancestor of the autotetraploid species *Solanum tuberosum*.

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with maximum distribution in Africa, South Asia and Australia, respectively. The D genome is not known at diploid level; it was assumed to correspond to *O. officinalis* in China (5) although this remains to be proven as its cytogenetic relationship with other genomes has not been studied yet. Two allotetraploid genomes are known in nature: BBCC in Africa and Asia and CCDD mainly in America but probably in Asia.

Most of the available world collection (except from China) were studied at a few discriminant isozyme loci and a condensed collection was constituted on the basis of the taxonomical classification, the geographical and ecological origins and preliminary isozyme survey on a few polymorphic loci. The condensed assembly of strains was further studied for additional isozyme loci.

For the *O. sativa* group, 181 strains were analyzed at 24 isozyme loci. In order not to make any *a priori* classification, Nei's standard genetic distances (D) were computed strain to strain in all possible combinations and the matrix of these distances was analyzed by a Principal Coordinate Analysis computer programme.

The clusters of strains assembled on the plane defined by the two first components extracted are shown on figure 1-A. The Australian strains formed a cluster with some of New Guinean origin although morphologically they differ. They are at a maximum genetic distance from all others with a value of D up to 1·26 for some of the Australian strains. Another cluster consisted of the African perennial species *O. longistaminata* only. The third cluster was composite, comprising all Asian and American strains (*O. rufipogon*), some New Guinean strains and the annual African species *O. breviligulata*. It was a surprise that the morphologically divergent American strains could not be distinguished clearly from their Asian counterparts. *O. breviligulata* could be clearly isolated on the basis of some specific electromorphs as well as morphological characters. Also, when only Asian strains were considered, it appeared that some Chinese strains were clearly distinguished from their South Asian counterparts as shown in figure 1-B. These were strains collected in remote areas, isolated from cultivated rice fields.

In short, 4 main areas of geographic differentiation appear in the Old World: Africa, South Asia, China and Australasia. The American taxa are not clearly distinguishable from the Asian ones and only in Africa can the annual and perennial life forms be distinguished.

The largest genetic distances found between the Australian and other strains point to many millions years of divergence assuming the calibration of the molecular clock adopted in other organisms. The primitive features and wide diversity of the genus *Oryza* among grasses allow to assume its existence in the widely distributed tropical paleoenvironment of tertiary era. It is thus plausible that migration of *Oryza* to Australasia occurred at the time of its collision with South East Asia, that is around 15 million years (m.y.) ago. Rice could have remained isolated in Australia until the present Era. It is remarkable that, assuming such calibration of the isozyme clock, the genetic structure of the *O. sativa* group can be understood as resulting primarily of the isolation of four areas in the Old World through tectonic or climatic events as follows:

(*i*) Progressive appearence of inhospitable land for rice between Africa and Asia, due to the aridity and/or cooling of climate. In accordance with the observed genetic distances, it is logical that migration might have been interrupted earlier (10 m.y.) for the perennial life forms adapted to flooded areas than for the annual life forms adapted to temporary pools in arid savannahs (2 or 3 m.y.).

(*ii*) Progressive emergence of the Himalayan mountain range known to be geologically very young mountain. It seems to have stopped the migration of Hipparion fauna across it, hence of wild rice, only 2 or 3 m.y. ago.

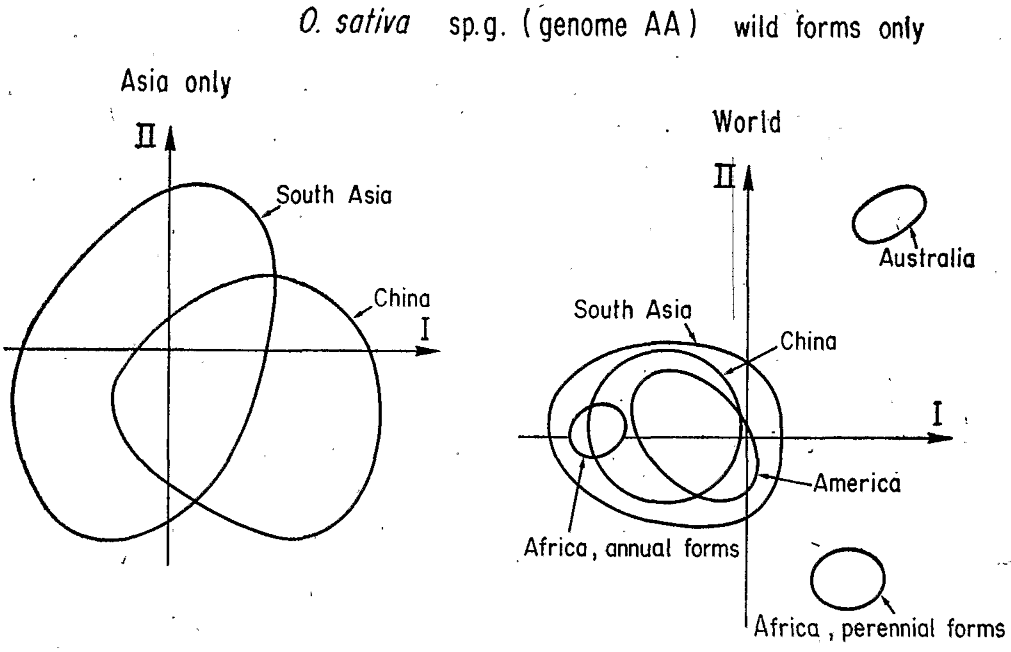

Fig. 1

(*iii*) Migration of life forms between Australia and Asia has been very limited as is attested by the so-called "Wallace line".

The picture which emerges is thus one of independent evolution in four areas for 2 to 15 million years followed by that of migration between continents in the Old World and to the New World, through the agency of Man. Interest of Man for rice started probably very early in the paleolithic for food but was extended to cultivation and to use as medicinal herbs and also as fodder for animals. Opportunities for artificial migration of seeds on one hand and opening up of new ecological niches in disturbed habitats to which genetically heterogeneous populations may be adapted, on the other hand, have dramatically increased in historical time. These factors may be undermining the original paleostructure through reciprocal introgression of genes.

One way to test this model was to look into the genetic structure of the *O. latifolia* group which is independent and is also widely distributed. Twenty-five strains were chosen among a collection of 155 observed and they were screened at 17 isozyme loci. The same multivariate analysis of the data as used in the *O. sativa* group is shown in figure 2. A putative DD diploid genome was deduced from the comparison of isozyme patterns between CCDD and CC genomes and was included in the analysis. It is evident that the diploid BB, CC, DD and EE genomes are readily distinguished at isozyme level. It is remarkable that: (*i*) the genetic distances found between them did not significantly exceed the maximum distances found within the AA genome. (*ii*) The allotetraploid genome BBCC appears to be truly intermediate between the diploid genomes BB and CC in that it shows both their isozyme patterns. This suggests their recent origin. (*iii*) The heterogeneity of the CC genomes may be the result of introgressions of genes between the old South Asian stock (CC_1 in figure 3) and the African BB genomes. This is coherent with the fact that intermediate genomes CC_2 and CC_{ei} are found in areas where the allotetraploid BBCC is also found.

In short, although more convincing evidences must await further collection, there appears to be a close parallel between the genetic structure of the two species groups: the geographical pattern may be interpreted in terms of primarily four areas of differentiation with intermediates due to recent intermixing and migration to America.

Taking into account that the *O. latifolia* group is better adapted to shade than the *O. sativa* group, its genetic structure in terms of isozymes appears to fit largely into the evolutionary model proposed above. There is however one important difference between the two groups in terms of genome divergence. If the model is correct, there would have been a more rapid differentiation of genomes in the *O. latifolia* group than in the *O. sativa* group. Also there should be an incipient genome divergence within the AA genome. That is actually what was reported in several instances. Incidentally, it should be of far reaching practical implications, in an attempt to tetraploidize cultivated rice, to take into account the genetic structure of genome AA.

Another difference between the two species groups which may be worth connecting with the genome divergence is that in the total nuclear DNA content. There are several reports in the literature which state that the chromosomes of the *O. latifolia* group are generally larger, with more heterochromatin than those of the *O. sativa* group. The 2C value of DNA content per diploid genome indicates that the former is about twice as rich in DNA as the latter (wild species only) although more data are certainly needed (1·78 to 2·02 versus 1·03 to 1·35 pg) (3).

It could be that the extra DNA in the *O. latifolia* group accounts for its greater rate of genome divergence. This would be in line with Flavell's (2) hypothesis that the genomes of organisms with large DNA content diverge more rapidly than the genomes of organisms with low DNA content.

I would like to suggest here that such an hypothesis could account for the classical observation by Avdulov in 1931 (in 6) that, particularly in the grass family, small chromosomes are observed in species of continuously warm tropical climates or arid environments while the largest chromosomes are found in species inhabiting temperate climates. For example, among cereals, rice has relatively small chromosomes while wheat, rye and barley have big ones.

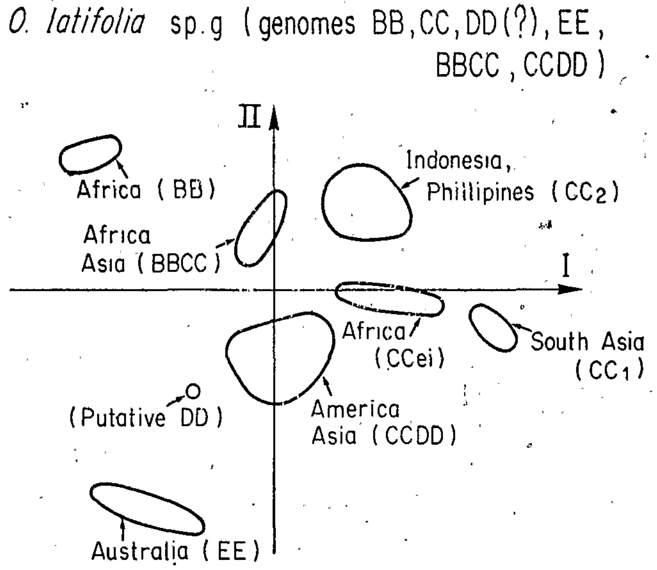

Fig. 2

If we recall that the extension of temperate and mediterranean climate areas is relatively recent while the tropical and subtropical ones have been retreating, it makes sense that species with large DNA amount were selected during this climate shift as they had the ability to speciate more rapidly. This could be an alternative hypothesis (although not exclusive) to the direct adaptative significance of DNA amount proposed by Bennett (1).

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CYTOTAXONOMY OF THE OCTOPLOID AND DECAPLOID SPECIES OF HIBISCUS SECT. FURCARIA (MALVACEAE)*

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The genus *Hibiscus* L. contains 350-400 described species of which about 50 may be assigned to sect. *Furcaria* DC. as defined by Hochreutiner (3). The name *Furcaria* derives from the forked involucral bracteoles that characterize some but not all of the species, a trait that is usually dominant or epistatic in hybrids between species with forked and unforked bracteoles. The section comprises an extended alloploid series (2x to 10x) based on x = 18 small metacentric to submetacentric chromosomes of rather uniform size.

Thirty-eight species studied in the living collection at Florida State University include 10 diploid, 15 tetraploid, eight hexaploid, four octoploid and one decaploid species. Analysis of morphology, chromosome numbers, and geographical distribution of species, chromosome pairing in about 125 different types of interspecific hybrids (4-12), pollen exine morphology (1, 2) and isozyme profiles (Hancock *et al*, unpub) led to a general understanding of relationships among the diploid, tetraploid and hexaploid species. Diploids and tetraploids occur mainly in Africa and South America, whereas the hexaploids are confined to Australia and New Guinea (see 5). Relationships among the higher polyploids, the subject of the present study, are less well studied.

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