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ORIGIN OF ASIAN CULTIVATED RICE AND ITS ECOTYPIC DIFFERENTIATION

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ABSTRACT

Oryza nivara **is an annual wild species that grows in small seasonal pools mainly in the plateau regions of south and southeast Asia. *O. rufipogon* Griff. is a perennial wild species adapted to swamps and margins of tanks in the coastal belts and in the lower valleys of rivers of south and southeast Asia. The cultivated rice, *O. sativa* L., which shares the same ploidy level (2n = 24) and the genome (AA) with these two wild species, has originated mainly from *O. nivara* in the same part of the world. *O. Sativa* has differentiated into ecospecies (*aus, aman, japonica* and *javanica*) and, within the ecospecies, into ecotypes. When cultivars of different ecotypes are crossed, the hybrids often express various degrees of sterility. The authors recognise the hill rices of southeast India (that includes the Jeypore tract of Orissa), the *japonica*-like cultivars of the hilly areas of southwest China (extending westward upto Nepal) and the hill rices of mainland southeast Asia as the three basic stocks that have evolved directly from *O. nivara* in their respective regions. The Proto-Australoid people who spoke Austric languages were responsible for the origin of this crop as well as for its initial spread all over south and southeast Asia before the advent of Indian and Chinese civilizations into this region. The *aus* ecotype was developed directly from the southeast Indian hill rices and the *japonica* ecotype of northern China from *japonica*-like types of southwest China. The spread of cultivation of *aus* types to the lower Gangetic valley and that of *japonica*- like types to the Brahmaputra valley resulted in the introgression of *rufipogon* genes into these types and led to evolution of *aman* and *shali* ecotypes respectively. The *aman* ecotype was successful only after iron was introduced for plough and oxen as draught animals in the lower Gangetic valley presumably by the Aryans in the second millenium B.C. Subsequently, the *aman* types were carried by Indian colonisers to Indochina and Indonesia during the ninth century A.D. The *tjereh* ecotype was developed from the aman ecotype in Indonesia. Similarly, migration of hill rices of mainland southeast Asia to Indonesia with introgression of genes of *O. rufipogon* into them has resulted in the origin of *javanica* ecotype.**

Key words: *Oryza sativa, Oryza nivara, Oryza rufipogon,* Origin of cultivated rice, ecotypic differentiation

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The origin of the Asian cultivated rice (*Oryza sativa* L.) has been a subject of debates ever since De Candolle [1] opened this topic for scientific discussion. However, as more and more data and evidences since have accumulated, our understanding of the subject has become more clear. The salient contributions in this field from Watt [2], Roschevicz [3], Ramiah and Ghose [4], Sampath and Rao [5], Richharia [6], Sampath [7], Sharma [8], Oka [9-11], Shastry and Sharma [12], Chang [13] and Morishima [14] and findings in the last decade by the authors. In this paper, the authors have tried to present a new as well as comprehensive hypothesis about the origin of Asian cultivated rice (*Oryza sativa*) and its ecotypes mainly based on their own findings and of others in the support. (Appendix I).

There are two cultivated species of rice, namely, *O. sativa* which was domesticated in south and southeast Asia and is now widely cultivated all over the rice growing areas of the world and *O. glaberrima* which was domesticated in tropical west Africa and has remained only confined to that part of the world. In fact, the Asian cultivated rice (*O. sativa*) is now so widely cultivated in the homeland of O. glaberrima that the former may edge out the latter sooner or later. Morphologically, *O. glaberrima* looks very similar to *O. sativa* but the two show parallel variation. Cytogenetically, both species have diploid chromosome number 2n = 24 and the genomic constitution, AA although the two differ at sub-genomic level [15-17]. The F1 hybrid between the two species is highly sterile. The situation in the two cultivated species is vicarious as each of the two species have a closely related annual wild and also a perennial wild species. Besides, each of the two cultivated species hybridises in nature with their annual wild relatives forming partially fertile hybrids. The situation is, however, different with regard to the relation of the cultivated species with their perennial wild species. In Asia, the cultivated species (*O. sativa*) hybridises in nature and forms partially fertile hybrids with its perennial wild relative (*O. rufipogon*) whereas Africa cultivated species (*O. glaberrima*) rarely hybridises in nature with its perennial wild relative (*O. longistaminata*) and the hybrids made artificially are highly sterile.

A perennial wild species allied to *O. rufipogon* of Asia is widely distributed in tropical America. This has been classified as a distinct and different species (*O. glumaepetula*) by Sharma [8, 18] and Chang [17] but has been considered to be a mere variant of the Asian perennial species (*O. rufipogon*) by Tateoka [19] and Vaughan [20]. Both these taxa have the same chromosomes number (2n=24) and the genome (AA) differ subgenomically [16]. However, it may be mentioned that many of the rice biosystematists classified the perennial entity of Asia (*O. rufipogon*), Africa (*O. longistaminata*) and America (*O. glumaepetula*) as a single entity and identified it as *O. perennis* Moench following Chevalier [21] and Chatterjee [22] during 1950s and

1960s. According to this view, the perennial elements of the three continents are treated as three subspecies of a single species *O. perennis* [23]. In this paper, these three elements are treated as three distinct species and the binomial *O. perennis* is discarded as suggested by Tateoka [19]. The inter-relationships of these species, their genomic constitution and habit have been indicated in Table 1 and Fig. 1.

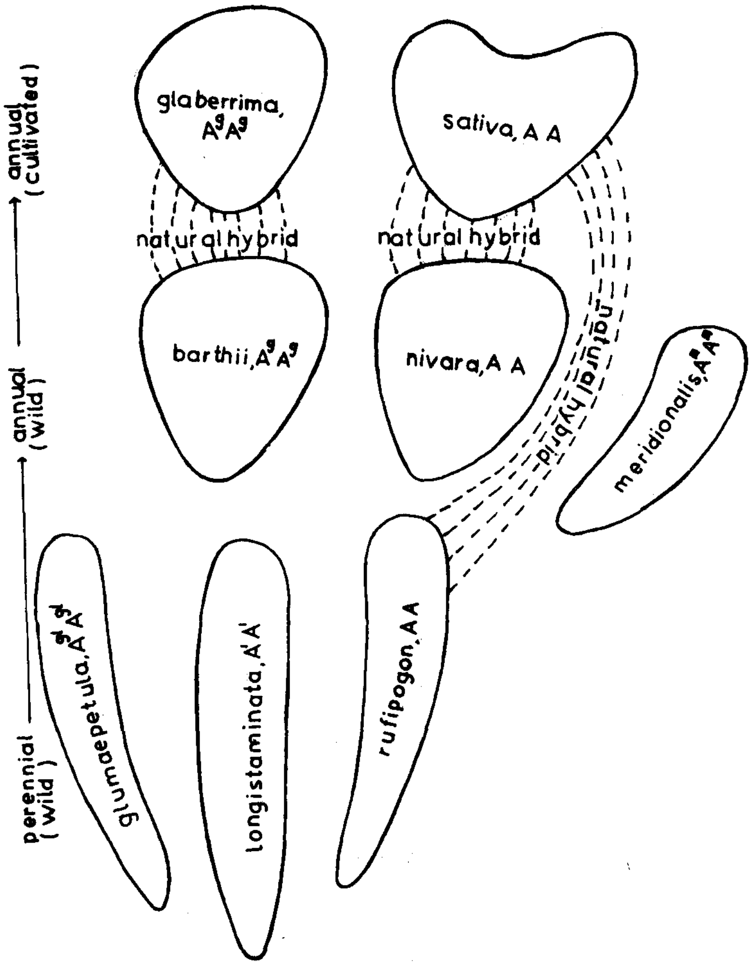

Fig. 1. Inter-relationship of Oryza spp. having genomic constitution AA

Table 1. The chromosome number, genome, habit and distribution of some *Oryza* spp.

Sl No.	Species	Chromosome No.	Genome	Habit	Distribution
01.	*O. Sativa*	2n = 24	AA	Annual, Cultivated	South & southeast Asia
02.	*O. nivara*	2n = 24	AA	Annual, Wild	South & southeast Asia
03.	*O. nivara*	2n = 24	AA	Perennial, Wild	South & southeast Asia
04.	*O. glaberrima*	2n = 24	AgAg	Annual, Cultivated	Tropical west Africa
05.	*O. barthii*	2n = 24	AgAg	Annual, Wild	Sub-Saharan Africa
06.	*O. longistaminata*	2n = 24	AlAl	Perenial, Wild	Tropical Africa
07.	*O. glumaepetula*	2n = 24	AglAgl	Perenial, Wild	Tropical America
08.	*O. officinalis*	2n = 24	CC	Perenial, Wild	South & southeast Asia
09.	*O. minuta*	2n = 48	BBCC	Perenial, Wild	The Philippines
10.	*P. coarctata**	2n = 48	????	Perenial, Wild	South Asia

* *Porteresia coarctata*. Formerly known as *O. coarctata*. Source : Chang [17].

TAXONOMIC DELIMITATION AND NOMENCLATURE

The first comprehensive monograph on genus Oryza was published in 1931 by Roschevicz [3] and was followed by another one by Chevalier [21]. Since then, many taxonomists have proposed many changes in nomenclature of *Oryza sp.* and differ with regard to delimitation of species which affects the nomenclature of species. Appendix-1 provides the nomenclature as adopted by various rice workers. The Asian cultivated rice (*O. sativa*) and its allied taxa in Asia, present a continuous array of morphological features so much so, that this whole group has been termed as *O. sativa* complex by Tateoka [19]. The first taxon of this group recognised as a species was the Asian cultivated rice *O. sativa*. The early taxonomists and flora writers [24-25] considered the wild relatives as mere variants of *O. sativa*. Subsequently, the wild relatives were assigned intraspecific ranks within *O. sativa*. e.g. Prain [26] *O. sativa* var *fatua* and Roschevicz [3] *O. sativa f. spontanea*.

Chatterjee [22] recognised three species - a perennial wild, an annual wild and the annual cultivated (*O. sativa*) - for this complex in Asia. He identified the perennial wild species as *O. perennis* Moench and called the annual wild species provisionally as *O. sativa* L. var. *fatua* Prain, pending its correct identification. Ramiah and Ghose [4] followed Chatterjee [22] and recognised the complex namely a perennial wild, an annual wild and the annual cultivated species. They referred to above three species respectively as *O. perennis*, *O. fatua* and *O. sativa*. Sampath and Rao [5], however, held the view that the Asian elements of *O. sativa* complex consist of a perennial wild species (their *O. perennis*) and the annual cultivated species (*O. sativa*) only. According to them, the annual wild types of this complex are natural hybrids between the perennial wild species (their *O. perennis*) and the annual cultivated rice (*O. sativa*). They referred to these natural hybrids as *O. sativa* var. *spontanea*. Their view was, however, based on their observation of the taxa in coastal Orissa only.

Sharma and Shastry [27, 28] extensively collected various forms of these wild rices from a wide region of India, studied their morphology, ecology, proximity to the cultivated rice fields and geographical distribution. They also studied single plant progenies of these wild rices and concluded that the *O. sativa* complex of India comprises of four distinct elements: (a) a perennial wild species identified as *O. rufipogon* following Bor [29] and Tateoka [19], (b) an annual wild species named as *O. nivara* as it lacked a valid name [28, 30], (c) the annual cultivated species *O. sativa* and (d) products of natural hybridisation between the wild and the cultivated species, and were further divided into two sub-groups : hybrids between (i) *O. rufipogon* and *O. sativa* and (ii) *O. nivara* and *O. sativa*. The said classification of *O. sativa* complex of south and southeast Asia necessitates re-examination of morphological variability within each of these species.

O. RUFIPOGON .

O. rufipogon is a perennial growing in swamps (stable habitat). It survives the drier seasons as clumps due to presence of sufficient moisture in the soil and regenerates itself during the monsoon when the water level starts rising. The culms branch out at nodes piercing through the leaf sheath (*extravaginal branching*). When the water is shallow (<15 cm.), the culm behaves like a runner, rooting at nodes and spreading horizontally. In deeper water, the branches and sub-branches remain floating in the water. The leaves are generally at right angle to the culm. The panicle is well exserted and erect, emerging from water surface. The panicle branches are open, lax and slightly drooping. The spikelets are slender, anthers are long filling the spikelet completely and stigma protrudes favouring cross pollination. The leaf sheath, apiculus, awn and stigma are pigmented, Sharma and Shastry [28].

O. rufipogon is photoperiod sensitive, flowers during November-December. It grows along the margins of ponds and lakes and by the swampy sides of roads and railway tracks. It is distributed in the coastal plains of India and also found in the lower basins of the Ganga, the Brahmaputra, their tributaries and distributaries. Outside India, it is reported in the lower valleys of rivers in south China, southeast Asia, Indonesia and New Guinea. Forms similar to *O. rufipogon* but having larger leaves, greater ramification of panicles, more number of spikelets per panicle and somewhat larger spikelets are also available in nature due to introgression of characters from *O. sativa* into *O. rufipogon*.

O. NIVARA

Compared to *O. rufipogon,* O. *nivara* is dwarf in height and semi-spreading during vegetative stage but semi-erect at maturity. It grows in shallow ditches that dry up in summer. The plants are annual and germinate from self-dispersed seeds during the rainy season. The new branches originate from the lower nodes only and grow parallel to and under the leaf sheath and come out at the point of collar (intravaginal branching). The leaves are semi-open and not so drooping as in *O. rufipogon*. The panicle is poorly exserted or even partly inserted. The number of primary and secondary branches per panicle is less as compared to *O. rufipogon*. The rachis and the branches of panicle are stiffer. The spikelets are shorter but bolder. The awns are longer and more robust. The pigmentation in plant parts shows much variation. The leaf sheath, apiculus, stigma and awn may or may not be pigmented. (Sharma and Shastry [28]).

O. nivara is photoperiod-insensitive and flowers during September- October. It occurs in small populations in seasonal ditches in north India as well as in Deccan plateau. It is distributed in the plateaus of Myanmar, Thailand, Combodia and Laos and south and southwest China [17] especially in Guangxi province and its adjoining areas [31].

O. SATIVA

The specific features of *O. sativa* are that it has differentiated into several ecogenetic groups and subgroups which Morinaga [32] recognised as ecospecies and ecotypes respectively. Summarising the earlier works as well as his own studies, he recognised four ecospecies namely, *japonica, javanica, aus* and *aman* (*indica*) within this species. When cultivars of two different ecotypes are crossed, their F1 hybrids express various degrees of pollen and spikelet sterility. The other ecogenetic groups that are of interest and have been discussed in this paper are (a) the primitive landraces of Jeypore tract of Orissa, (Sampath and Govindaswami [33] and Oka and Chang [34]) and will be referred to as southeast Indian hill rices (or by acronym "seihr"), for reasons discussed later in this paper,. (b) the *japonica* -like forms that occur in the sub-Himalayan region of Nepal, Sikkim, Bhutan, Arunachal Pradesh and southwest provinces of mainland China, (c) the hill rices of mainland southeast Asia that are closely related to javanica types (Chang et al. [17, 35] and Glaszmann and Arraudeau [36]) and referred in this paper by acronym "hrmsea", (e) the *shali* types of the Brahmaputra valley that agronomically corresponds with the aman types of Bengal and (e) the tjereh types of Indonesia that resemble aman types of India.

It is also remarkable that some of the ecotypes of O. *Sativa* are photoperiod-insensitive, while the others are photoperiod-sensitive. Besides, Asian cultivated rice is not an annual species in strict sense, as many of its cultivars have the capability to ratoon or regenerate and are partially perennial.

NATURAL HYBRIDS

The genetic barrier between the two wild species (*O. rufipogon* and *O. nivara*) and the cultivated species (*O. sativa*) is incomplete. This has led to introgressive hybridisation in either direction and occurrence of all forms of intergrades in nature. Consequently, the taxonomic distinctness of these three species in nature is blurred and the whole group appears as a species complex which has been appropriately named as *O. Sativa* complex [19].

In coastal plains and in the lower valleys of the Ganga and the Brahmaputra, *O. Sativa* × *O. rufipogon* and in Deccan plateau, *O. Sativa* × *O. nivara* form natural hybrids. These natural hybrids have been referred to as *spontanea* rices in rice literature. The *spontanea* rices which invade the rice fields are products of natural hybridisation between *O. Sativa* and *O. nivara* (in plateau regions) or between *O. sativa* and *O. nivara* (in coastal regions) followed by repeated backcrosses with *O. sativa.* As a result, the *spontanea* rices which grow along the cultivated fields closely resemble cultivated rice except for shattering spikelets at maturity (few other wild characters such as black husk, red kernel, presence of awn, etc. Farmers efforts to identify them at the vegetative stage and weed them out from the cultivated fields have acted as a selection pressure for their closer resemblance with the cultivated rice [37].

ORIGIN OF CULTIVATED RICE

Earlier Views

Earlier workers held the view that *O. sativa* has mainly originated from the wild species of *O. sativa* complex. However, as taxonomic delimitation and nomenclature of the elements of this complex were not clear earlier, different binomials have been adopted by different authors [2, 3, 21]. They held the view that, besides the species of *O. Sativa* complex, some other wild species might also have played their role in the origin of some of the cultivars of *O. sativa.* In other words, they assumed that the Asian cultivated rice had a polyphyletic origin. Among the other putative progenitors, *O. officinalis* has received the most serious consideration as this species has small sized grains, well ramified panicles and high number of spikelets per panicle — characters not identicle with either in *O. nivara* or in *O. rufipogon* but present in *O. sativa.* Besides, the distribution of *O. officinalis* is sympatric with that of *O. sativa.* However, the two species are ecologically isolated and do not hybridise in nature. Moreover, the synthesised F1's are highly sterile. Although both the species are diploid (2n = 24), their chromosomes either do not pair during meiosis [38] or pair but separate out before metaphase-I without forming chiasmata [39]. The genomic constitutions of the two species are different Table 1. Any role of *O. officinalis* in the origin of *O. sativa*, therefore, seems improbable.

Because of morphological similarities between *O. officinalis* (2n = 24, CC) and *O. minuta* (2n = 48, BBCC), the latter also assumed to have played its role in the origin of *O. sativa*. However, *O. minuta* being a tetraploid species occurring only in the Philippines, it could not play any role in the origin of *O. sativa*. *Porteresia coarctata* grows in the tidal swamps near sea coasts of south Asia. Until 1965, it was considered in genus Oryza only and was named *Oryza coarctata*. It was assumed it played a role in the origin of salinity tolerance cultivars of *O. Sativa* but it was ruled out when it was known to be a tetraploid.

During a symposium on "Origin and distribution of cultivated plants in south Asia" at New Delhi in 1951, three papers on the origin of cultivated rices were presented. Chatterjee [40] a taxonomist who had earlier worked at Kew and had published paper on enumeration of the species of genus Oryza [22] presented a classical view on the origin of cultivated rice. According to him, the annual wild species (our *O. nivara*) has played a major role in the origin of cultivated rice though he did not rule out the role of *O. officinalis*. Ramiah and Ghose [4] identified three species in the *O. Sativa* complex of Asia, i.e., a perennial wild (their *O. perennis* Moench), an annual wild (their *O. fatua* Koenig) and the cultivated rice (*O. sativa*). According to them, the annual wild species is the progenitor of cultivated species. They were the first rice scientists to attract the attention of other rice researchers towards the Jeypore tract of Orissa as "this area might form another independent centre of origin" [41]. Sampath and Rao [5] treated the perennial wild species of Asia (*rufipogon*), Africa (*longistaminata*) and America (*glumaepetula*) as single species and called it *O. perennis* Moench as suggested by Chevalier [21] and Chatterjee [22]. They proposed that the perennial form of Africa (our *longistaminata*) has given rise to *O. glaberrima* in tropical west Africa and that of Asia (our *rufipogon*) has given rise to *O. Sativa* in south and southeast Asia. Hence, Sampath and Rao proposed a monophyletic origin for cultivated rices of Africa as well as Asia. Their view was further elaborated by Richharia [6] and Sampath [7] and hypothesis popularly known as perennis hypothesis among rice researchers, supported by Oka [9-11]. He put further evidences in support of natural hybridisation between *O. nivara* (their *O. perennis*) and the cultivated rice (*O. sativa*) in Asia, but he did not support Sampath's view that perennial form of Africa (*longistaminata*) has given rise to O. glaberrima in Africa or these two species frequently hybridise in nature to produce hybrid populations. Sampath [7] himself recognised the Asian (*rufipogon*) and African (*longistaminata*) perennial elements to be two distinctly different species and demolished his own hypothesis of monophyletic origin of cultivated rices. Later on, Morishima [14] modified the perennis hypothesis to suggest that forms intermediate between the perennial and the annual types of wild rices might have given rise to the Asian cultivated rice (*O. sativa*).

THE *NIVARA* HYPOTHESIS

Sampath's [7] proposition that the perennial species (our *O. rufipogon*) is the progenitor of the culltivated species (*O. sativa*) was based mainly on field observations in coastal Orissa where the annual species (*nivara*) does not occur and all annual wilds of *O. Sativa* complex in the area are product of natural hybridisation between *O. nivara* and *O. sativa*. However, the recognition of a distinctly different annual species well distributed over the vast plateau regions of south and southeast Asia led Sharma [8] and Shastry and Sharma [12] to propose that the cultivated rice (*O. sativa*) of Asia has originated from the annual wild species (*O. nivara*). According to them, perennial wild to annual wild and annual wild to annual cultivated must have been the natural and logical sequences of evolution. Therefore, the annual (not perennial) wild species must have been the progenitor of cultivated species. In other words, the views of Ramiah and Ghose [4] were resurrected by Sharma [8] and Shastry and Sharma [12] with additional evidences, precise taxonomic delimitations and valid nomenclature [27, 28, 30].

O. nivara is an annual species which grows in shallow seasonal ditches. It is more gregarious and frugiferous than *O. rufipogon*; flowers quite synchronously with bolder spikelets and kernels. Early civilisations developed agriculture in drier regions (not in swamps). Hence it is, highly probable that early man banked upon *O. nivara* (not on *O. rufipogon*) for developing grain crop. Natural grown *O. nivara* is still harvested by tribals and economically backward people in central India for self consumption as well as for marketing at a premium for religious purpose (*deobhat*) on days of fasting.

The *nivara* hypothesis proposed by Sharma [8] and Shastry and Sharma [12] and elaborated by Chang [13] was, however, too simple to account for morphological, ecological and physiological variations available in *O. sativa*. The origin of *O. Sativa* must also account for its ecogenetic differentiation and inter-ecotypic sterility. This has led the authors to investigate genetic differentiation, if any, within *O. nivara* and its relationship with different ecotypes of *O. sativa*.

RECENT STUDIES

Biswal [42] crossed Indian collections of *O. nivara* among themselves and observed increasing F1 pollen sterility with the increase in spatial separation of *nivara* populations. She, therefore, concluded that the pollen sterility observed in the hybrids between *japonica* and *indica* was present already in the progenitor species (O. *nivara*) and has been inherited by the progeny species (O. sativa). When collections of *O. nivara* were crossed with that of *O. rufipogon*, the F1s were more fertile than many of *nivara* x *nivara* hybrids. When *O. nivara* was crossed with different ecotypes of O. sativa, pollen fertility in *aus* x *nivara* and in *japonica* x *nivara* hybrids behaved more or less like *nivara* x *nivara* hybrids while aman x *nivara* and *javanica* x *nivara* hybrids behaved like *rufipogon* x *nivara* hybrids. [42] This led Biswal to conclude (a) *aus* and *japonica* ecotypes have originated directly from two different populations of O. *nivara*, (b) introgression of *rufipogon* characters into *aus* might have given rise to aman ecotype and (c) based on the views of Chang [17] and Glaszmann and Arraudeau [36] and her own observations cited above, she proposed that migration of hill rices of mainland southeast Asia ("hrmsea") to Indonesia with introgression of *rufipogon* genes into it, could have given rise to *javanica* types.

Biswal [42] assumed that early civilization domesticated different populations of *O. nivara* at different sites in southeast India, southwest China and southeast Asia. In other words, plural sites of domestication from different *O. nivara* populations is more probable hypothesis of diffused origin of agriculture [43].

Second [44] analysed 40 isoenzyme loci in 468 *O. Sativa* collections obtained from many different countries. On the basis of their F_1 pollen sterility, he could distinguish two groups of varieties *i.e.* "ancestral" *japonica* and "ancestral" *indica.* Assuming electromorphs of these two "ancestral" groups to be "parental", he presumed that the electromorphs of other varieties could be hybrid polymorphs. Since the electromorphic diversity of wild rices is much higher than that of cultivated rice [45- 48], he concluded that "among the various phylogenetic relationships between rice varieties put forward in the literature, only the hypothesis of the independent domestication of *indica* and *japonica* types proposed by Chou [49] fits the observed pattern of isozyme variation". He, therefore, concluded; "the F_1 pollen sterility between the *indica* and *japonica* sub-species could have existed before domestication".

Tripathy [50] made many "seihr" x "seihr" crosses and observed that *F1s* show a wide range of pollen sterility as observed in *nivara* x *nivara* hybrids [42]. The various inter ecotypic combinations of "seihr" x *japonica* F1s showed high pollen sterility and in this sense behaved similar to *nivara* x *japonica* hybrids of Biswal [42]. It was, therefore, evident that the southeast Indian hill rices ("seihr") behaved like *O. nivara* in their inter-ecotypic hybrids. She, therefore, concluded that these southeast Indian hill rices of Jeypore tract and its adjacent areas might have directly originated from O. *nivara.* Tripathy [50] also crossed "seihr", *japonica, aman, shali* and *tjereh* cultivars in all inter-ecotypic combinations and based on the morphology and pollen sterility of their F_1s concluded that (a) the characters of "seihr" showed dominance over those of other ecotypes in all inter-ecotypic combinations (except "seihr" x *japonica*) not only for majority of characters but also in most of the hybrids, and (b) the characters of *japonica* showed dominance in all inter-ecotypic hybrid combinations not only for majority of characters but also in most of their F_1. She, therefore, concluded that the "seihr" types have retained more numbers of dominant genes than others and may represent a basic ecotype from which others have evolved. As *japonica* characters also showed dominance over than that of "seihr", she concluded that the former have retained more primitive characters than the latter.

The *shali* ecotype of the Brahmaputra valley is similar to the *aman* of Bengal in its ecological preferences and photosensitivity. The *shali* types are similar to *japonica* with regard to size and shape of spikelets, spikelets arrangement on primary branches and tolerance to cold, etc. Whereas in *japonica* × *shali* hybrids, the *japonica* characters were predominant; in *aman* × *shali* hybrids, the characters of *shali* showed dominance over that of aman. The inter-ecotypic *shali* hybrids, showed medium fertility with *japonica* and low fertility with *aman* types. The low fertility in *aman* × *shali* hybrids vis-a-vis medium fertility in *japonica* x *shali* hybrids indicates that the *japonica* -like forms, available in the sub-Himalayan belt of the Brahmaputra might have played a role in the origin of *shali* ecotype. The pollen fertility of *aman* x *tjereh* hybrids was highest among all inter-ecotypes of *tjereh* indicating common origin of both these ecotypes [50].

PROPOSED HYPOTHESIS

ORIGIN OF *O. SATIVA*

O. nivara frequently grows in abundance in the northeastern part of Deccan peninsula (including the Jeypore tract of Orissa) and in Central Gangetic plains. Distribution of *O. nivara* in western India is neither so frequent nor so abundant. Its occurrence is rare in south India, and is conspicuously absent in the Gangetic Bengal and whole of northeastern India. *O. nivara* is also found in the plateau regions of Myanmar, Thailand, Laos, Combodia and in southwestern China. Thus, its geographical distribution is disjunct; one found in India and the other in Indochina and China.

The small ditches and seasonal pools in plateau regions of south, southeast Asia and southwestern China provide ideal habitat for *O. nivara*. Its distribution in these regions must have been more frequent when human population was very much limited. The hilly tracts were the ideal areas for habitation by neolithic hunt-gathering man who domesticated many plants including rice. Morishima [14] rightly points out that "the deltas of big rivers were not accessible for early people. Apparently, the hilly area seems to have played an important role in making contact with rice". Therefore, it is, highly probable that the people of northeastern Deccan plateau developed the "seihr" types and the people of southwestern China developed the *japonica* types from populations *O. nivara* of their respective regions.

The Jeypore tract of Orissa comprising of hills, valleys, forests and rivulets is inhabited by many tribes who belong to Proto-Australoid ethnic stock. These people have been "harvesting" *O. nivara* which occurs naturally and frequently in seasonal ditches. These tribals have also been practising shifting cultivation by growing primitive cultivars of rice. With the increase in population and dwindling forest coverage, they have given up shifting cultivation and are adopting upland rice cultivation but still continue to patronise age-old rice cultivars. Ramiah [41] was impressed with the varietal diversity of this area, and proposed that this area probably represents another independent centre of origin of cultivated rice . During 1955-60, the Central Rice Research Institute, Cuttack collected more than 1700 traditional cultivars of rice from this area. Oka and Chang [34], studied these cultivars, and regarded them as intermediate forms between cultivated and wild types "still staying in the midst of differentiation".

The primitive upland rice cultivars of Jeypore tract have many special features *viz.* short height, thin culm, few tillers, small panicles and often (not always) black husk, red kernel and awn. They are short-duration, photoperiod -insensitive cultivars. In fact, similar types of rice cultivars are often cultivated as a rainfed upland crop especially in unbunded fields in the whole of eastern Madhya Pradesh (Chhattisgarh region), western Orissa and southern Bihar (Jharkhand region) by resource-poor farmers. These landraces (*tikradhan* in eastern Madhya Pradesh, *bhathadhan* in western Orissa and *garodhan* in southern Bihar) have been collectively referred to as "southeast Indian hill rices" (or acronym "seihr") in this paper. As discussed already, these "seihr" types have retained many primitive features, express dominance for many of their charactrs in their F1 hybrids with other ecotypes and, with regard to sterility of their hybrids, behave like *O. nivara.* The "seihr" types are, therefore, assumed to have directly originated from *O. nivara* of southeast India.

According to Sharma *et al.* [51], Hakim and Sharma [52], Asthana and Majumdar [53] and Sharma [54] there are gradations in *japonica*-like cultivars that are cultivated by tribals of Arunachal Pradesh in northeast India. The higher in altitude one moves up in the Himalayas, the greater one finds the expression of *japonica* traits in rice cultivars. The landraces in Tawang district of Arunachal Pradesh probably set a unique example of *japonica*-like rice cultivars which occurs at lower latitude (27°N) but in higher altitude (1800 m.). The situation in southwest China is no way different.

"Today one can find in the hills of Yunnan and Kweichow provinces (China) where the sinica ("keng") rices were grown at elevations above 1800 m., a mixture of sinica and *indica* rices growing at medium elevations and exclusively *indica* ("hsien") rices at altitudes below 1000 m" [17, 55]. The *japonica*-like types which were domesticated in southwest China spread west towards along the sub-Himalayan belt upto Nepal (and even to northern India?) and south-ward upto Myanmar and Indochina. According to Watabe *et al.* [56], these *japonica*-like types had much more distribution in southern Indochina in first millenium A. D. Within the area of distribution of *japonica*-like types, the only area where *O. nivara* occurs frequently is southwest China. It is, therefore, highly probable that the *japonica* -like cultivars were domesticated in southwest China.

The hill rices of mainland southeast Asia ("hrmsea") are morphologically similar to *bulu* and *gundil* types of Indonesia though the Indonesian types are late in maturity, have a long vegetative phase and are adapted to irrigated agriculture. Genetically, the *japonica* and *javanica* are closer to each other and produce fairly fertile hybrids when intercrossed [57, 58]. Based on isoenzyme studies, Glaszmann [59] put the *japonica*, "hrmsea" and the *javanica* in the same cluster. According to Glaszmann and Arraudeau [36], the morphological characters of the cultivars of Japan, Korea and China and that of Indonesia, form two extremes of a geographical cline and the cultivars of the mountainous areas of southeast Asia and the Himalayas, occupy an intermediate position. It is, therefore, probable that the hill regions of the mainland southeast Asia represent another centre (or a subcentre?) of genetic diversity of *O. nivara* and the hill rices of mainland southeast Asia ("hrmsea") originated from *O. nivara* of that region.

As discussed already, the populations of *O. nivara* are often genetically differentiated [42]. This differentiation increases with increase in spatial separation of their populations and is expressed as sterility of their F1. The genetic differentition that already existed in the original populations of *O. nivara* of southeast India and southwest China has been carried over to the domesticated rice (*O. sativa*) and is reflected as sterility in the inter-ecotypic hybrids e.g. in *japonica* x *indica* hybrids. The "seihr" types of southeast India, the *japonica* -like types of southwest China and the "hrmsea" types of central Indochina represent three basic stocks of *O. Sativa* that have directly evolved from the annual wild species (*O. nivara*) of their respective regions in Asia.

ORIGIN OF ECOTYPES

The photoperiod-insensitive rice cultivars that are grown in bunded fields during monsoon (July-October) and mature in 100 to 120 days are collectively known as *aus* types in Bengal. In fact, cultivars similar to *aus* are widely cultivated in whole of southeastern, northeastern and eastern India although they are called by different names in different states. Ecogenetically, they are one and the same group that has been termed as *aus* in rice literature [32]. The *aus* cultivars are genetically superior to "seihr" types in their yield attributes and better responsive to agronomic practices. The *aus* ecotype seems to have directly evolved from the upland rice ("seihr") of southeast India. Traditionally, *aus* are grown under rainfed conditions only as the whole of eastern India used to receive sufficient rain so much so that no irrigation facilities were ever developed in this region. Its cultivation spread from southeast to other parts of India.

The *japonica*-like types were carried from southwest China, to eastern and northern China where they developed into *keng* types [60]. These types had better yield attributes, were better amenable to agronomic manipulations and suited to irrigated conditions.

The migration of early man from upland to lowland areas of river deltas must have been a later event in the history of rice cultivation [14, 61]. If so, the primitive cultivars of rice evolved from *O. nivara* were carried by man to new habitats closer to that of *O. nivara*, resulting in the introgression of *rufipogon* genes into sativa cultivars. The *aman* types of rice cultivars appear to be the result of introgression of *rufipogon* genes into *sativa* cultivars. The *aman* types are photoperiod-sensitive, late in maturity, adapted to wetland rice cultivation and have traditionally been more productive than *aus* types. Besides the grains are slender and accepted as more palatable. In fact, the variation in size and shape is much greater in *aman* rices. The lower Gangetic valley was probably the meeting ground where *rufipogon* genes got introgressed into *aus* and, as a result, *aman* types were developed. Endowed with the new traits, the rice plant was capable of spreading over wetland, an ecosystem that was abundantly available in south and southeast Asia and had hardly ever been exploited earlier by any crop plant. However, for exploitation of this new ecosystem, draught animals (oxen) for ploughing the fields and iron for the ploughs were pre- requisites. It is inferred that this could not have happened before the advent of Aryans into the lower Gangetic valley i.e. before the middle of the second millenium B. C. According to Watabe and his associates [60, 62-63], the Indians carried *aman* types to Indochina sometime in the 9th century A.D. The *tjereh* types of Indonesia could have developed from the *aman* types of India which were carried to Indonesia by Indians during that period.

Though the *shali* types have many similarities with the *aman* types, the former do show affinity with the *japonoca* types with regard to their morphological and physiological characters as discussed already. In the inter-ecotypic hybrids reported by Tripathy [50], the *shali* types showed greater fertility with *japonica* than with aman. It is, therefore, interpreted that *shali* types are the product of introgression of *rufipogon* characters into *japonica*-like forms of that region. In this context, it is noteworthy that *O. rufipogon* and *shali* cultivars of *O. Sativa* are sympatric in the Brahmaputra valley and hence the introgression of *rufipogon* genes into *japonica*-like cultivars is highly probable.

The migration of hill rices of mainland southeast Asia ("hrmsea") from that region to Indonesia (with introgression of genes of *O. rufipogon*?) could be the only plausible explanation for the physiological and ecological adaptation of *javanica* types to the irrigated as well as for the high fertility observed in *javanica* x *nivara* hybrids [42].

Whereas the primary ecotypes (*aus* and *japonica*) of *O. Sativa* have retained the photoperiod-insensitivity of the annual wild species (*O. nivara*) and man has successfully exploited this trait to develop genotypes suitable for rice cultivation in different seasons of a year, the secondary ecotypes (*aman, tjereh* and *shali*) have acquired photoperiod-sensitivity, adaptation to lowland and even to greater depths of water. Man has successfully exploited these secondary traits of rice plant to spread its cultivation to lowland ecosystems available over vast stretches of land in south and southeast Asia. A diagrammatic presentation of the origin of various ecotypes has been provided in Figure 2.

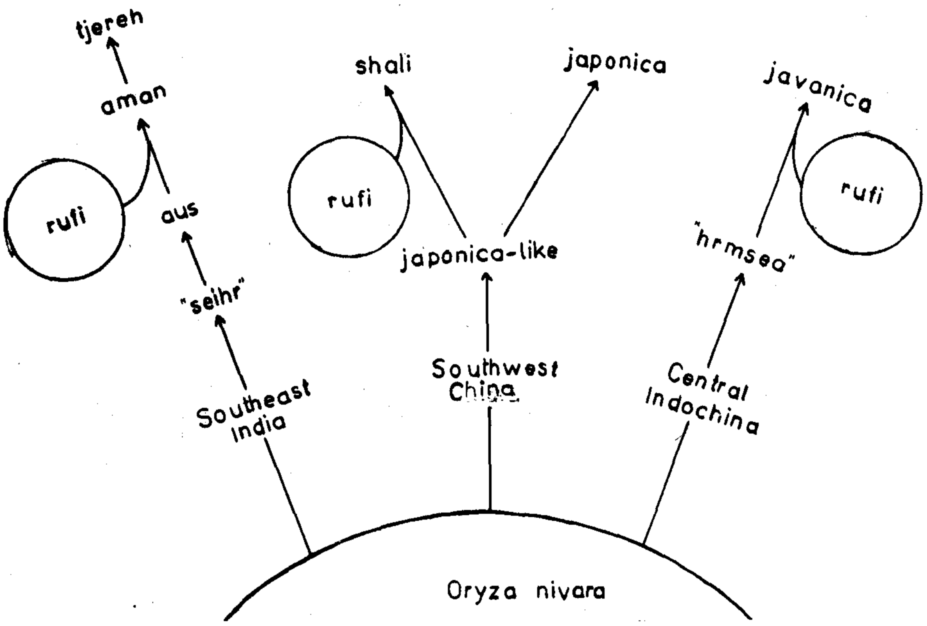

Fig. 2. Origin of ecotypes of *O. sativa*

SUPPORTING EVIDENCES

Our hypothesis that the Asian cultivated rice (*O. sativa*) had not only a polyphyletic (two species of Oryza have played key roles in its origin) but also a polytopic origin (rice originated simultaneously and independently at plural sites) does not contradict the findings of other disciplines. The archaeological excavations indicate the presence and role of rice in the food economy of early man of 5000 B.C. in China as well as in India. It suggests that rice might have been simultaneously domesticated at many sites. Anthropologically, the total area from western coast of India to eastern coast of south China and Vietnam was inhabited by Proto-Australoids *i.e.* people speaking Austric group of languages. It is, therefore, probable with the domestication of rice, these Proto-Australoids [64] have been responsible for origin of "seihr" types in southeast India, *japonica* -like types in southwest China and "hrmsea" types in southeast Asia. However, rice may have played only a marginal role in the food economy but not in their staple diet [61, 65].

Watabe and his associates [60,62-63, 66-67] extensively surveyed the rice grains found in the ancient bricks at historical sites of India, Burma, Thailand, Laos, Cambodia and Vietnam. An analysis of the size and shape of rice grains from these sites, revealed, not only the type of rice varieties cultivated by the people of those areas during different periods of history but also transitions in the type of grains cultivated in those areas for the last several centuries. Summarising their findings, Watabe [60] has remarked, "In Indochina, there were two routes of dispersal of cultivated rice in early times, one followed the Mekong River from Laos to the South. The strains of rice transmitted along this route show the characteristic features of the *japonica* or *japonica*-like grain type. This type of rice is considered to have been first cultivated in Indochina. The second route was from India over the Bay of Bengal to the coastal areas of Indochina. The grain type migrated through this route is clearly of the *indica* or aman type. This group was transmitted to Indochina at a later date than the *japonica* or *japonica*-like group. The authors have named the former "Mekong descent group" and the latter "Bengal descent group".

The development of three basic ecotypes of *O. Sativa* from three different populations of *O. nivara* in different regions is not only associated with their genetic differentiation but also with their ecological and physiological differentiation. Tsunoda [68] has rightly remarked "I infer that the *japonica* is an ecospecies which was established in the Sub-Tropical Hardleaf Evergreen Forest region grown under a watered condition to avoid the cold, that the *javanica* was established in the Tropical Rain Forest region primarily under rainfed upland conditions benefitting from the warm climate and the rain fall throughout the year, and that the *indica* is an ecospecies which was established in the Monsoon Moist Deciduous Forest region grown under high temperatures to summer monsoon rains on the uplands and monsoon rains and flood waters in lowlands forming ecotypes such as early *aus* and late *aman*".

The proposition made in this paper is in accordance with the observations made and conclusions drawn by Watabe [60] and Tsunoda [68]. It is also in accordance with the historical and philological evidences on rice in India and China although any detailed discussion on these aspects will be outside the scope of this paper.

APPENDIX I

Nomenclature of some *Oryza* species

1. *O. barthii* A. Cheval

The annual wild species of Africa having genomic constitution AA. The rice workers have known this species as *O. breviligulata* A. Cheval. et Roehr. which is now treated as a synonym of *O. barthii*. It may be noted that the binomial *O. barthii* was wrongly used for the perennial wild species (*O. longistaminata*) almost by all the rice biosystematists until Clayton [69] clarified the situation.

2. *O. glaberrima* Steud.

The African cultivated species. The variation available in the two cultivated species is strikingly parallel. The hybrid between the two species is highly sterile. Majority of rice researchers hold the view that the two cultivated species originated independently from two different progenitor. According to Porteres [70], Oka [10] and Chang [13], *O. glaberrima* has originated from the annual wild, *O. barthii*.

3. *O. glumaepatula* Steud.

The American perennial species having genomic constitution AA., it is widely distributed in tropical America from Cuba and Mexico to Paraguay. It is also known as *O. cubensis* Ekman which is a *nomen nudum*. It has also been referred to as *O. perennis* subsp. cubensis [23]. Some taxonomists group it with the Asian perennial *O. nivara* [19, 20]. Whereas the Asian species is a runner, the American species is semi-erect. Subgenomically, they are different [71].

4. *O. longistaminata* A. Chaval. et Roehr.

The perennial wild species of Africa having genomic constitution AA. It was referred to as *O. perennis* subsp. *barthii* by those who treated the three perennial wild species (*glumaepetula, longistaminata* and *rufipogon*) of America, Africa and Asia respectively as single species. It was wrongly identified as *O. barthii* by all rice biosystematists until Clayton [69] pointed out the mistake.

5. *O. minuta* J.S. Presl. ex C.B. Presl.

It is a tetraploid (2n = 48) wild species having genomic constitution BBCC. Its distribution is restricted to the Philippines only. Morphologically, it closely resembles *O. officinalis* (genome CC)

6. *O. nivara* Sharma et Shastry

The annual wild species of Asia having genomic constitution AA. and is closely related to the Asian cultivated species, *O. sativa*. In past, it was known as *O. fatua* Koenig which is a nomen nudum. It was also identified as *O. Sativa* var fatua following Prain [26] or as *O. Sativa* var sponatanea following Roschevicz [3] which also include their naturally occurring hybrids. Tateoka [19] included this annual species in the perennial wild species *O. rufipogon*. Chang [13, 17] and Vaughan [20] recognise it as a distinct species. Senaratna [72] and Sampath [7, 73] have identified wrongly this species as *O. nivara* Griff.

7. *O. officinalis* Wall. ex Watt

The diploid species having genomic constitution CC. Recently, Dhua [74] has suggested that its genome should be DD. It is widely distributed in south and southeast Asia and grows in partial shade of forests near running streams, moist grounds and rarely in shallow ditches. The F_1 between *O. Sativa* and *O. officinalis* is completely sterile. Morphologically, it resembles tetraploid *O. minuta* [genome BBCC] which is restricted to the Philippines only.

8. *O. nivara* Griff.

The diploid perennial wild species of Asia having genomic constitution AA and is closely related to the annual wild (*O. nivara*) and the cultivated (*O. sativa*) of Asia. It was identified as *O. perennis* Moench by most of rice biosystematists from 1951 to 1962 following Chatterjee [22], until Bor [29], Tateoka [19] and Sharma and Shastry [28, 30] clarified the position. It has also been referred as *O. perennis* subsp. *balunga* [33] or as *O. balunga* [15]. According to Tateoka [19], *O. nivara* (*sensu lato*) also includes *O. nivara* and *O. glumaepetula*.

9. *O. Sativa* L.

The Asian cultivated species is a diploid having genomic constitution AA. It has been grown in south and southeast Asia and south China since prehistoric times. Subsequently, its cultivation spread to northern China, Korea and Japan. It is now cultivated all over the rice-growing areas of the world including tropical west Africa i.e. the homeland of *O. glaberrima.*

10. *Porteresia coarctata* (Roxb.) Tateoka

It was known as *Oryza coarctata* Roxburgh by most of rice researchers until Tateoka [75] removed it from the genus *Oryza* and created a new genus *Porteresia* to accommodate this single species. Sharma and Shastry [76] provided additional evidences for its removal from genus *Oryza*. It is a tetraploid (2n = 48) and Its genome has not been worked out so far. It grows in the tidal swamps of rivers in south Asia.

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