

# THE ANCESTORS OF CULTIVATED RICE AND THEIR EVOLUTION

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We have been engaged in a research project, "Studies on the origin of cultivated rice", which was initiated under a grant of the Rockefeller Foundation in 1957. First, we had to collect material and information on wild species of rice. Study tours, 13 times in total, were made (a list attached to the end of this paper), and the genetic stocks obtained are preserved in our Institute. On the occasion of the XIII International Congress of Genetics (Symposium on origin of cultivated plants), I had a chance to summarize the results of our work on this subject (OKA, 1974). In this paper, I will briefly discuss the problems in an attempt to minimize overlapping.

**TWO PARALLEL SERIES :** There are two distinct species of cultivated rice, *O. sativa* L. and *O. glaberrima* Steud. They may have originated from domestication of the Asian form of *O. perennis* Moench and *O. breviligulata* A. CHEV. et ROEHR., respectively (MORISHIMA *et al.* 1963). Therefore, two parallel series of evolution can be compared, *perennis* to *sativa* and *breviligulata* to *glaberrima*. The two species series distinctly differ in certain botanical characters, and are isolated by a pronounced F<sub>1</sub> sterility and other reproductive barriers. The barriers found within the series are generally less pronounced (CHU *et al.*, 1969), except that *O. perennis* subsp. *barthii* shows a partial crossing barrier with other taxa (CHU and OKA, 1970a). In both series, the wild and cultivated taxa are often sympatric and produce hybrid swarms (OKA and CHANG, 1961 ; CHU and OKA, 1970b).

**LATIN NAMES :** Twenty-two good species are enumerated in the genus *Oryza* (TATEOKA, 1964), whereas more than 60 botanical names have so far been documented. The nomenclature of the ancestral species of cultivated rice is, unfortunately, in confusion. According to CHANG (1967a, b), the Asian forms of *O. perennis* should be called *O. rufipogon* Griff. (perennial type) and *O. nivara* Sharma et Shastry (annual type), even though the variation between the perennial and annual types seems to be continuous (MORISHIMA *et al.* 1961). According to Clayton (1968), the species we call *O. breviligulata* (having short ligules) should be *O. barthii* A. CHEV., and *O. perennis* subsp. *barthii* should be *O. longistaminata* CHEV. et ROEHR. Though these arguments are based on taxonomic convention, changes of species names will add more confusions, particularly for the reader unfamiliar with rice species. The names used in this paper are those recognized at the Symposium on Rice Genetics and Cytogenetics at Los Baños in February 1963 (IRRI 1964) ; we have not changed them in our publications in spite of documentations of new names.

**INTERMEDIATE FORMS :** In both the *perennis-sativa* and *breviligulata-glaberrima* series, intermediate wild-cultivated forms are found in certain areas where genetic diversities are accumulated. Those well known are the Jeypore Tract in India for *perennis-sativa* and the inland delta of the Niger in Mali for *breviligulata-glaberrima*. Possibly, the diversity of a crop species increases in an area where the crop exists with its wild progenitor and a primitive cultural condition has long been maintained stabilizing the agroecosystems. Such an area may have "micro-centers" so named by Harlan (1963), which are evolutionary active. The variation patterns as observed among the intermediate forms may be considered as showing the evolutionary path of cultivated species. Even if the intermediate forms are largely the products of introgression between wild and cultivated species, similar introgression would have played an primary role in the initiating process of cultivated species.

**INDICA AND JAPONICA TYPES :** The varieties of *O. sativa* are divided into the Indica and Japonica types ; the so-called Javanica may be regarded as a tropical type of Japonica (MORINAGA and KURIYAMA 1958). The monophyletic origin of Japonica and Indica types from the Asian *perennis* has been demonstrated by different methods. Among the intermediate wild-cultivated strains from Jeypore Tract, it was found that the Indica-Japonica differentiation proceeded as the plants approached the cultivated species (OKA and CHANG 1962 ; OKA 1974). Also, when a typically Indica cultivar and an Asian *perennis* strain were crossed, in the progenies were found plants with characters of the Japonica type, and when the same *perennis* strain was crossed with a Japonica cultivar, the progeny similarly produced plants with Indica characters (OKA, unpubl.). The evidence suggests that the Asian *perennis* plants have a genetic potentiality enabling such differentiation. However, it remains unknown what selective agent has initiated the varietal differentiation. In Northern Thailand (OKA and CHANG, 1963) and Yunnan Province of China (YU, 1944), Japonica cultivars are often found in the upland fields on hill slopes (shifting), while Indica cultivars are grown in wet fields in the valley ; intermediate Indica-Japonica types were frequently found in such a region (OKA and CHANG 1963), and the wild plants of *O. perennis* are distributed only in the valley. It may be suggested that adaptation to an upland condition could be an initiating agent for the origin of the Japonica type.

In both the Indica and Japonica types of *O. sativa*, geographical variations are striking, as MORINAGA and KURIYAMA (1958) have enumerated several "ecotypes". The varieties vary not only in morphological and agronomic traits, but also in photoperiodic response and other responses. They also show a range from upland to deepwater types. It seems that geographical dispersion has played an important role in varietal differentiation. This leads to the concept of "non-center" as pointed out by Harlan (1971).

In contrast, the varieties of *O. glaberrima* do not seem to be differentiated into types like the Indica and Japonica (MORISHIMA *et al.* 1962). Geographical differentiation of the varieties also seems to be less pronounced possibly because the distributing range, Senegal to Tchad, has similar latitudinal and climatic conditions. They show a range between upland and deepwater types and vary in photoperiodic response in the same manner as *sativa* varieties do. Among strains of *sativa* and Asian *perennis*,  $F_1$ -sterility relationships develop (HINATA and OKA 1962 ; CHU *et al.*, 1969) ; among *glaberrima* and *breviligulata* strains,  $F_1$  weakness is an important reproductive barrier (CHU and OKA, 1971).

**Perennial and annual types :** Among Asian *perennis* strains, the breeding systems vary in a wide range, and the major axis of variation is represented by the continuum between the perennial and annual types (OKA and MORISHIMA 1967). The African form of *O. perennis* (subsp. *barthii*) is perennial (rhizomatous), the American form is intermediate perennial-annual, and the Oceanian form is annual. *O. breviligulata* and *O. glaberrima* are annual species.

Which the progenitor of *O. sativa* was, the perennial or annual type of Asian *perennis*, has been discussed among Indian workers. Sampath and RAO (1951) considered that the perennial type was progenitor and the annual type might be a hybrid derivative between *perennis* and *sativa*. On the other hand, CHATTERJEE (1951) accepted the view of ROSCHEVICZ (1931) that the annual type may be the progenitor of cultivated rice. CHANG (1976a, b) also has the same thought. We have postulated that the perennial type is more likely to be the progenitor on some circumstantial evidence : The intermediate cultivated-wild forms approaching the wild species show characters of the perennial type (OKA and CHANG, 1962 ; Fig. 1a) ; the perennial type has in its populations larger amount of genetic variability and hence may have a higher evolutionary potentiality than the annual type (MORISHIMA *et al.* 1961 ; MORISHIMA and OKA, 1970) ; the autogamous annual type may be in a blind alley of evolution ; and many varieties of *O. sativa* are essentially perennial (OKA and MORISHIMA, 1967).

The general scheme of domestication CHANG (1976b) has considered applicable to rice, wild perennial → wild annual → cultivated annual, does not seem to be the case with *O. sativa* which is itself a perennial plant. Yet, it seems probable that an intermediate perennial-annual form showing perennality and a high seed productivity, whose populations are appreciably heterogeneous, could be the progenitor of *O. sativa*.

**BREEDING SYSTEMS :** We have quantitatively estimated perennality in terms of the percentage of excised stem segments to take root on moistened sand (OKA and MORISHIMA, 1967). Many characters were found to be correlated with the perennality. Positive correlations with perennality were found in the time interval from flower opening to pollen emission, number of pollen grains per anther or anther size, and stigma-style length or the extrusion of stigmas outside the flowers, and the estimate of outcrossing rate. The productivity (seed number per plant), dispersal (shedding and awn development) and maintenance (dormancy) of the seeds were negatively correlated with perennality.

us, the perennial plants tended to be allogamous and the annual plants tended to be autogamous, as considered to be a general trend among higher plants by STEBBINS (1958).

The pattern of variations in reproductive effort as shown by allocation of resources was observed among 30 strains of *O. perennis* (SANO, Y. and H. MORISHIMA, unpubl.). The pattern of variations in 18 characters measured proved that the characters could be classified into two groups of positive correlations, between which the correlations were exclusively negative. One of the character groups appeared to indicate the tendency to vegetative vigor, and the other indicated reproductive activity by seed, as follows :

**Group 1 (vegetative)**

Culm length  
 Panicle length  
 Tillering angle  
 Regenerating ability of excised stem segments  
 Leaf and stem weight/total weight  
 Leaf and stem weight/seed number  
 Competitive ability in growth  
 Anther weight/spikelet  
 Anther weight/seed number  
 Outcrossing rate

**Group 2 (reproductive)**

Seed weight/total plant weight  
 Panicle number/tiller number  
 Spikelet number/plant  
 Panicle number/plant  
 Seed fertility  
 Awn development index  
 Awn weight/seed weight  
 Seed dormancy index

Thus, the data proved a variation of *perennis* strains between the so-called *r*- and *K*-strategists, as GADGIL and SOLBRIG (1972) have discussed. The estimate of reproductive effort by seed weight/total plant weight (including root, dry matter) was negatively correlated with anther weight per spikelet (at flowering, dry matter) which indicated pollen production and outcrossing (Fig. 2a). It was also negatively correlated with competitive ability in vegetative growth (percent loss of dry weight due to mix-planting of a tester strain ; Fig. 2b) ; nevertheless, *sativa* cultivars showed a high reproductive effort and a high competitive ability. The low reproductive effort of the perennial type of Asian *perennis* might have been gradually increased with domestication (Fig. 1b).

The perennial type grows in deep swamps which seems to be relatively stable, while the annual type is found in temporary swamps which are parched in the dry season and often disturbed by man when located nearby rice fields. It seems that the annual type has evolved from the perennial type by acquiring adaptability to unstable habitats, possibly in parallel with the evolution of cultivated species. However, the weedy annual form, which grows in rice fields together with cultivated plants, would be a hybrid derivative between *perennis* and *sativa* (OKA and CHANG, 1959).

**ADAPTIVE MECHANISMS :** The perennial-annual continuum shows variations in adaptive mechanisms, only a part of which have been elucidated (OKA, 1976). The annual type had higher infant mortality, but lower mortality of the plants once established, than the perennial type. Though the implication of this difference remains unexplained, the survival rate was significantly correlated with phenotypic plasticity in each stage of growth. This suggests that the strains differ in the developmental stage at which greater plasticity is expressed, and plasticity is due to adaptive changes in growth of the plants responding to environmental stresses (Fig. 3).

Further, in the number of seeds buried in the soil and its percentage to total seeds, the perennial (low) and annual (high) types showed a wide range (OKA, 1976). The bristles on the surface of glumes and awns were found to play a role in the movement of the seeds into soil to protect them from animal predation (Fig. 3d). Thus, various traits were intercorrelated to make up different adaptive strategies. More survey and analysis are needed to have an integrate understanding of the variations, particularly on how the adaptive mechanisms are modified with domestication.

When populations of *O. perennis* containing some genes of cultivated species are cultivated (the seed is harvested and sown), plants with cultivated characters increased in a few generations resulting in a significant difference from those left for natural seeding (OKA and MORISHIMA, 1971). This suggests that seeding by man has exerted a selection pressure on wild plants in the origin of cultivated species.

The natural populations of Asian *perennis* contain various genes, some of which are common to those of *O. sativa*. For instance, observing isozymic variations, we found that the *perennis* populations had at least 5 alleles at

two loci for peroxidase (PAI *et al.* 1973), and 12 alleles at three loci for acid phosphatase (PAI *et al.* 1975). In addition to these structural genes, variations supposedly in regulatory genes conditioning the intensity of peroxidase bands were found in the wild species (PAI *et al.*, 1973). In contrast, *sativa* cultivars have shown allelic differences only in a part of the loci ; two peroxidase alleles at a locus and two acid phosphatase alleles at another locus linked with the former were found among the cultivars, and the allelic differences represented the Indica and Japonica types. In this respect, domestication seems to have been a convergent process of genic variations. On the other hand, genic substitutions exhibiting various agronomic characters of cultivated rice should have taken place in the process of domestication.

**CONCLUSIONS :** The origin of rice has been a subject discussed by many workers. Among recent contributions, the reviews by NAYAR (1973), SAMPATH (1973), and CHANG (1976a, b) may be of considerable importance. NAYAR placed emphasis on cytogenetic researches and developed his speculations. SAMPATH extended bold hypotheses on species relationships stimulating our interest in the problems. CHANG has reviewed a wide range of references in an attempt to provide a concise overall view. As he claims, the various contributions in the past have been discipline-oriented and do not provide an integrate picture of botanical and historical knowledges. Yet, it may be doubted whether or not all published views are acceptable for the purpose of integration in case when some are subjective speculations not based on reliable data.

History is a science of incidence in the past which is essentially non-repeatable, while repeatable cause-effect relationships are sought for in biological studies. It is not an easy task to correctly use the past and present tense in a logical thinking. More archeological data are wanted to locate the time and place of origin of rice. The excavation conducted in Thailand is expected to throw a light (c.f. SOLHEIM, 1972). There also remain many unknowns in the study of evolutionary dynamics, *e.g.*, the adaptive mechanisms, the interrelation between adaptive and random (or historical) processes, etc. The most important might be to explore new problems which attract the interest of young scientists.

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## TRIPS FOR COLLECTION OF RICE SPECIES (1957-1964)

1. India 1957 (West Bengal, Orissa Madhya Pradesh, Andhra, Madras, Kerala, and Ceylon). - H. I. OKA, T. TATEOKA and T. NARISE, Oct. 1 - Dec. 28. Rep. mimeo.
2. Thailand 1958 (Central, North and Northeast regions). - H. I. OKA, Nov. 20 - Dec. 22 (from Taipei). Rep. mimeo.
3. Malaya 1959 (Malayan Peninsula and Java). - I. HIRAYOSHI, Jan. 7 - Mar. 11. No. rep.
4. Africa 1959 (Senegal, Gambia, Sierra Leone, Guinea, Mali, Ghana, Nigeria, Sudan, Ethiopia, and Kenya). - K. FURUSATO, Oct. 4 - Jan. 25, 1960. No Report.
5. Northern India 1959 (Sikkim and Assam). - H. KIHARA and S. NAKAO, Oct. 7 - Dec. 11. No. rep.
6. Burma 1959 (Southern to Northern regions). - K. KATSUYA, Oct. 4 - Dec. 8. No. rep.
7. Latin America 1960 (Cuba, Guatemala, Costa Rica, Guiana, Surinam, Amazon basin, and Colombia). - H. I. OKA, Oct. 25 - Feb. 19, 1961. Rep. mimeo.
8. Philippines (a) and New Guinea (b) 1961 (a : Luzon, Mindanao, and Palawan ; b : Papua and Dutch New Guinea). T.C. KATAYAMA, Jan. 21 - Mar. 27. Rep. mimeo.
9. Philippines 1963 (Mindanao, Negros, Panay, Mindoro, Palawan, Samar, Leyte, Luzon, etc.). T. TATEOKA and J. V. PANCHO, Jan. 20 - Mar. 11 ; H. I. OKA and W. T. CHANG, Jan. 26-28 (from Manila). Rep. mimeo.
10. Borneo 1963 (North Borneo, Brunei, Sarawak, Kalimantan, and Java). T.C. KATAYAMA, Mar. 16 - May 23. Rep. mimeo.
11. West Africa 1963 (Sierra Leone, Guinea, Mali, Liberia, Ivory Coast, Upper Volta, Niger, Dahomey, Nigeria, Cameroon, and Tchad). - H. I. OKA and W. T. CHANG\*, Oct. 16 - Jan. 31, 1964. Rep. mimeo.
12. Madagascar 1964 (Kenya, Uganda, Tanzania, and Madagascar). T. TATEOKA, May 1 - Aug. 1. Rep. mimeo.
13. Amazon 1964 (Manaos area). G. TAKENAKA, May 15 - 25 (from Sao Paulo). No. rep.

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\* Dr. Wen-Tsai CHANG, Professor, Taiwan Prov. College of Agriculture, passed at Yagoua, Cameroon, on December 14, 1963, after a car accident.

*Oryza* genetic stocks collected in National Institute of Genetics, Japan.

Species	Trip													Other sources	Total	
	1	2	3	4	5	6	7	8a	8b	9	10	11	12			13
<i>sativa</i>	301	110	224	29	326	48	27	88	21		63	61			2,676	3,974
<i>perennis</i> <sup>1</sup>																
Asia	57	23	37		49	17			1	1	4				14	203
America							16							6	7	29
Africa				22								39	11		4	76
Oceania								2							4	6
<i>glaberrima</i>				9								77			184	270
<i>breviligulata</i>				44								33			9	86
<i>australiensis</i>															3	3
<i>officinalis</i>	3	2	3		8	1				14	37				9	77
<i>minuta</i>								10		18					6	34
<i>eichingeri</i> <sup>2</sup>				1									13		1	15
<i>punctata</i>				1								3	4		3	8
<i>latifolia</i> <sup>3</sup>							14								16	30
<i>grandiglumis</i>							2							2	3	7
<i>meyeriana</i> <sup>4</sup>	3	2				2		6		1	1				5	20
<i>ridlevi</i>	1		4								1					6
<i>longiglumis</i>									16							16
<i>brachyantha</i>				2								7			1	10
<i>perrieri</i>													1			1
<i>tisseranti</i>												1				1
<i>coarctata</i>	1															1

1. *O. perennis* complex. The African form is subsp. *barthii*.
2. *O. eichingeri* and *O. punctata* are not easily distinguishable.
3. *O. alta* is included in *O. latifolia* as they are indistinguishable.
4. *O. granulata* is synonymous. *O. abromeitiana* is included.



**Comments on Dr. Oka's paper entitled  
"The ancestors of cultivated rice and their evolution" :**

**T.T. Chang**

With all due respect for Dr. OKA'S intensive study of the Asian and the African cultivated rices and his views on their progenitors, may I add a few remarks based on my studies and field travel. Perhaps we should exercise caution in the tendency to rely on small collections of existing rice germ plasm to analyze evolutionary trends in the distant past.

As a generalist, I propose to draw on pertinent evidence from several fields of study outside biosystematics in order to get a fresh insight into the complicated and controversial subject. If we begin with my postulate on the Gondwanaland origin of the genus (*Euphytica* 25 : 425-441, 1976), we can readily endorse the parallel evolution of the two cultivated species in Africa and in South-Southeast Asia, as well as the pan-tropical distribution of the wild relatives of *O. sativa* in South America and Australia. We can also recognize the close fit between genomic composition and the Gondwanaland components (*Int. Rice Res. Newslett.* 1(2) : 4, 1976). I may add that the Gondwanaland postulate is no longer a hypothesis ; it is well supported by studies in plate tectonics, the newest branch of the earth sciences.

If we could avoid using "*O. perennis*" as the common progenitor of the two cultivated species, we would eliminate most difficulties that we have encountered in designations and interpretations.

By comparing the topography, latitudinal spread of the ancestral species, diversity in climate, movement of people, population density, availability of iron tools and draft animals in Africa and Asia, we may readily understand the greater extent of genetic diversification in *O. sativa* than in *O. glaberrima*.

I agree with Dr. OKA that we need more help from archaeological findings. On the other hand, the fracture and drift of the Gondwanaland components probably began as early as the early Cretaceous period (slightly more than 100 million years ago) – we would then need to search beyond those relics which only dated back to several millennia.