

EXPERIMENTAL STUDIES ON THE ORIGIN OF CULTIVATED RICE¹

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ABSTRACT

1) Contributions to the origin of cultivated rice made by the author and his colleagues were briefly reviewed under several headlines.—2) Two parallel series of evolution of cultivated species, the Asian form of *Oryza perennis* to *O. sativa* and *O. breviligulata* to *O. glaberrima*, were pointed out compared.—3) In both the two series, a continuous array of intergrades between wild and cultivated species is found in a particular region. The pattern of character variations among those intermediate plants was considered as indicating the evolutionary path, and the monophyletic origin of the Indica and Japonica types of *O. sativa* was discussed.—4) The conditions of establishment of a weedy form of *O. perennis* found in India were discussed. It was noticed that cultivation by man in itself works as a selective agent for cultivated types.

AN OUTLINE OF OUR INVESTIGATIONS AND BACKGROUND THOUGHTS

THE origin of a crop species can be investigated from two different standpoints, historical or biological. In history, once an event has happened, it is not repeated. In contrast, biologists look into cause-effect relationships that are repeatable at the present time. Thus, the origin of cultivated rice may be an event still in progress at this time (OKA and CHANG 1959).

Cultivated rice species and their wild relatives are diploids and have the same genome (MORINAGA 1964). In this respect, the situation with rice is similar to that with barley. Yet, genes expressing striking morphological differences so far found in rice are rather limited in number and are not so useful for evolutionary studies as are those reported in barley.

In collaboration with DR. H. MORISHIMA and other colleagues, since 1957 the author has been engaged in studies on the origin of cultivated rice under generous financial support from the Rockefeller Foundation. Our general aim was to look into the evolutionary genetics of rice from different angles. Our contributions so far can be classified under the following headings:

1) *Evaluation of relationships between taxa*: When the interrelationships between various wild and cultivated taxa are evaluated, the wild taxon most closely related to a cultivated one may be considered to be the progenitor of the latter. The relationships between taxa can be evaluated on different bases, i.e., (a) comparison of character variations; (b) sterility and other abortive phenomena of the hybrids; (c) ecological and distributional comparisons; and (d) genetic

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relationships in the natural habitat. We have collected materials from different parts of the world and have continued investigations on these problems; many of our reports are related to this heading (reviewed by OKA 1964a). As many different characters were recorded in each strain, numerical taxonomic methods were employed to obtain the overall pattern of variations (MORISHIMA and OKA 1960). An attempt was made to analyze the variation patterns not only from the "phenetic" but also from the "phylogenetic" standpoint (MORISHIMA 1969).

2) *Variations in the breeding systems*: Wide variations in pollinating behavior and in the relative magnitude of seed *vs.* vegetative propagation are found in a wild species (*Oryza perennis* Moench, the progenitor of *O. sativa* L.). Generally, perennial strains having a high potential of vegetative propagation were more allogamous than annuals, and various characters conditioning the breeding systems were intercorrelated (OKA and MORISHIMA 1967). *O. perennis* subsp. *barthii* (African *perennis*) was rhizomatous and partly self-incompatible (CHU, MORISHIMA and OKA 1969b). In tropical Asia, the perennial plants grow in deep swamps which seem to be stable habitats; annual plants grow in temporary swamps (MORISHIMA, OKA and CHANG 1961).

3) *Isolating mechanisms between taxa*: The inviability of young F_1 zygotes (crossing barrier), F_1 weakness, F_1 pollen and embryo sac sterilities, and hybrid breakdown, all being partially in effect, are distributed in this plant group (CHU, MORISHIMA and OKA 1969a). These reproductive barriers are controlled either by complementary or by duplicate genes. (OKA 1957, 1964b; OKA and DOIDA 1962; CHU and OKA 1970a, 1972).

4) *Introgressive hybridization*: Several examples of introgression between wild and cultivated taxa have been reported (OKA and CHANG 1959, 1961). The main direction of gene flow seems to be from cultivated to wild plants as the latter is more allogamous than the former. The observed phenomenon is a "secondary" process which takes place after the establishment of cultivated forms, but it may be inferred that the same forces act in both the "primary" and "secondary" processes. In certain conditions, introgression takes place across isolating barriers (CHU and OKA 1970b). Presumably, there is a balance between isolation and hybridization, as too much hybridization would result in reproductive waste and too much isolation would restrict the exploitation of variability.

5) *Intergrades between wild and cultivated forms*: Continuous series of intergrades between wild and cultivated forms are found in particular geographical regions. They seem to indicate the evolutionary path of cultivated forms as will be mentioned later (OKA and CHANG 1962; MORISHIMA, HINATA and OKA *et al.* 1963).

6) *Genetic variations between and within populations*: Generally, perennial forms contain in their populations more variations and are more heterozygous than annuals, which are more diversified from population to population. The populations of semi-wild forms and primitive cultivars are highly polymorphic possibly because of introgression and disruptive selection, though they are predominantly self-pollinated (MORISHIMA, OKA and CHANG 1961; MORISHIMA and OKA 1970). Perennial wild populations carry a variety of alleles specifying dif-

ferent isozymes, while the allelic differences among *sativa* cultivars are limited indicating a trend to elimination of a part of genetic variability with domestication (CHU 1967; SHAHI, MORISHIMA and OKA 1969a; SHAHI, CHU and OKA 1969b).

7) *Adaptation mechanisms*: Photoperiodic response is latitudinally adjusted (OKA and CHANG 1960). Cultivation by man in itself exerts a selection pressure on the populations of wild plants (OKA and MORISHIMA 1970). Responses to cultural conditions provided by man seem to have progressively developed from wild plants to modern cultivars (OKA and CHANG 1964). On the other hand, wild plants are more plastic in development than cultivated ones, and some of them show a particular pattern of internode elongation that may help to disperse seed. Differences in adaptive strategy are also detected between the taxa (OKA, unpublished).

We have insufficient space to discuss fully all these problems. In this paper, the three topics, wild progenitors, considerations on the evolutionary paths, and domestication are discussed as some problems in these areas have not been studied in plants other than rice.

INQUIRY INTO THE WILD PROGENITORS OF CULTIVATED RICE

There are two cultivated species in the genus *Oryza*, *O. sativa* L. (cosmopolitan) and *O. glaberrima* Steud. (endemic to West Africa). They are apparently closely related to two different wild species, *O. perennis* Moench and *O. breviligulata* Chev. et Roehr (synonymous to *O. stapfii* Roschev.), respectively; *breviligulata*–*glaberrima* series can be distinguished from *perennis*–*sativa* series as the former is characterized by short and tough ligules, smaller number of secondary panicle branches, death at maturity, and other features, and the F_1 plants between the two series are highly pollen-sterile. However, these two wild and two cultivated species are known to have the *A* genome ($n = 12$) in common, and show no significant disturbances in chromosome pairing in their F_1 hybrids (CHU, MORISHIMA and OKA 1969a).

O. perennis is distributed throughout the humid tropics and is a complex of different geographical forms—the Asian, American, African (subsp. *barthii*), and Oceanian (MORISHIMA 1969a). The Asian form is divided further into perennial, intermediate and annual (spontanea) types though the variation is continuous (MORISHIMA, OKA and CHANG 1961). Though the name *perennis* is taxonomically uncertain (TATEOKA 1964), we use this name to represent a group of wild taxa having characters similar to those of *sativa*, and we consider the group of plants as a species in the sense that genes are exchangeable within the group. It then includes *O. rufipogon* Griff. (Asian perennial type), *O. nivara* Sharma and Shastri (Asian annual type), *O. sativa* f. *spontanea* Roschev. (= var. *fatua* Prain; Asian annual type), *O. barthii* A. Chev. (African form), *O. cubensis* Ekman (American form), etc.

The names used by different authors for these *Oryza* species are not consistent; more than 60 latin names have been given to different specimens. In a personal

communication, DR. JACK R. HARLAN suggested to the author the following names for the African taxa:

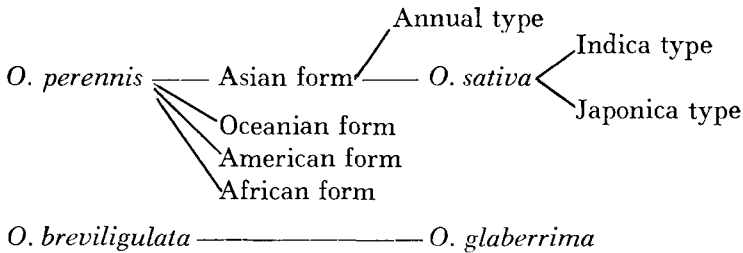
Present author	DR. HARLAN
<i>O. perennis</i> Moench subsp. <i>barthii</i> (A. Chev.)	<i>O. longistaminata</i> Chev. et Roehr.
<i>O. breviligulata</i> Chev. et Roehr.	<i>O. barthii</i> A. Chev.

This change (after CLAYTON 1968) though it may be correct taxonomically, does not seem to remove any confusion.

The Asian form of *perennis* seems to be the wild progenitor of *sativa* on circumstantial evidence: (a) Their hybrids are generally fertile and can be easily propagated (HINATA and OKA 1962); (b) they are often sympatric in tropical Asia (OKA 1964a) and produce hybrid swarms (OKA and CHANG 1961); and (c) no other wild taxa of *Oryza* show such a close relationship to *sativa*.

Strains of Asian *perennis* vary between perennial and annual types. Taxonomists have disputed whether the perennial or the annual type is the ancestor of *sativa*. We have postulated that the perennial type is more likely to be the ancestor because it stores up in its populations larger amount of genetic variability than the annual type, and accordingly, it may have larger evolutionary potential (MORISHIMA, OKA and CHANG 1961). Another indication of the role of the perennial type in the origin of *sativa* may be the wide variation of *sativa* cultivars in the potential for vegetative propagation as shown by the regenerating ability of excised stem segments (OKA and MORISHIMA 1967). This view was supported by the occurrence of intermediate wild-cultivated plants having characters of the perennial type (Figure 1). The occurrence in India of such intermediate plants may be taken as an indication of the origin of *sativa* in India.

For similar reasons, *glaberrima* seems to have been derived from *breviligulata* in West Africa, independent of the origin of *sativa* from Asian *perennis* (MORISHIMA, HINATA and OKA 1963). Accordingly, we have two parallel series of evolution of cultivated rice, as diagrammed below.



Comparing the two series, we find similarities and differences. The similarities are: (1) In both series, the cultivated species are distinguished from the wild ones by the same characters, i.e., absence of natural seed shedding, rapid breakdown of seed dormancy, large grain number per panicle, etc. (2) Hybrid swarms and intermediate wild-cultivated plants occur in certain regions. (3) The wild species have shown in their populations a latent tendency to vary toward cultivated types which has been detected by multivariate analysis of character variations (MORISHIMA, OKA and CHANG 1961; MORISHIMA, HINATA and OKA 1963).

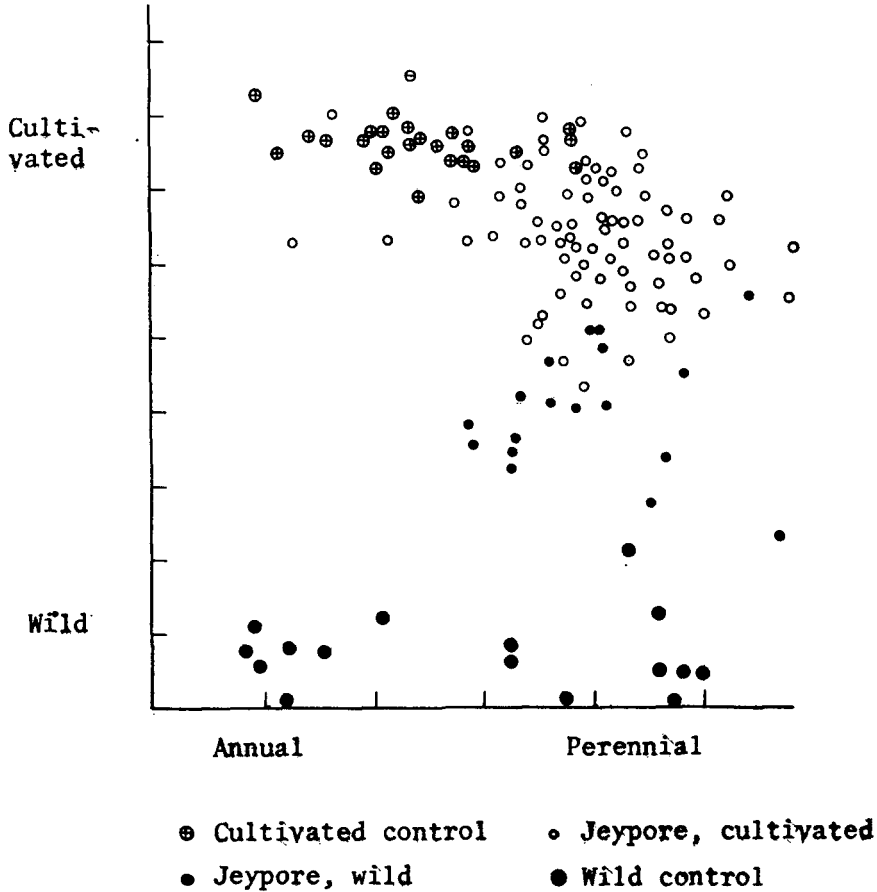


FIGURE 1.—Wild controls, Jeypore strains, and cultivated controls scattered according to the scores given by two discriminant formulas, one (abscissa) for classifying the perennial and annual types of Asian *perennis* and the other (ordinate) for wild and cultivated forms. (From OKA and CHANG 1962.)

Major differences found between the two series are (1) *O. perennis* is distributed throughout the world and its geographical forms show a range from perennial to annual habit, while *O. breviligulata* is endemic to West Africa and is a typically annual grass. (2) Populations of the perennial forms of *perennis* contain more genetic variations than those of *breviligulata* (MORISHIMA, HINATA and OKA 1963). This is also true with peroxidase isozymes (CHU and OKA 1967). (3) Varieties of *sativa* are divided into two groups, the Indica and the Japonica, but such varietal differentiation is not observed in *glaberrima* (MORISHIMA, HINATA and OKA 1962). (4) Distantly related *sativa* varieties show varying degrees of F_1 sterility while *glaberrima* varieties are inter-fertile in most cross combinations. In contrast, F_1 weakness is rare in *sativa* and frequent in *glaberrima* (CHU, MORISHIMA and OKA 1969a). (5) Varietal improvement by modern techniques was carried out in *sativa* but not in *glaberrima*.

CONSIDERATIONS ON THE EVOLUTIONARY PATHS

In both *perennis-sativa* and *breviligulata-glaberrima* series, a continuous array of intergrades between wild and cultivated types is found in a certain region, namely, the Jeypore Tract of India for *sativa* and the inland delta of the Niger for *glaberrima*. According to our present knowledge, rice is the only crop demonstrating such a continuous variation.

The Jeypore Tract is a mountainous region in the western part of Orissa State untouched by modern civilization until recent years. A greater part of this area is under forest, but rice is grown by the native people in their "shifting" farms or terraced paddies. The strains collected from this area were observed by OKA and CHANG (1962) for various plant characters and F_1 -sterility relationships with certain test strains. The pattern of character variations was shown by the scores given by discriminant functions which were constructed with the data taken from certain wild and cultivated strains used as the controls. In Figure 1, the Jeypore and control strains are scattered according to the scores for classifying the perennial from the annual type of Asian *perennis* (abscissa) and for classifying wild (*perennis*) from cultivated (*sativa*) plants (ordinate). The figure shows that the Jeypore strains form a bridge connecting the perennial type of *perennis* with *sativa*. The distribution of the intermediate wild-cultivated plants may be considered as indicating the evolutionary path of *sativa* from the perennial type of Asian *perennis*.

The numerous cultivars of *O. sativa* are largely divided into the Indica and Japonica types which differ in the pattern of character association (cf. OKA 1958). Even the pathogenic races of *Piricularia oryzae* causing the blast disease are similarly divided into two groups by numerical taxonomic analysis of their responses to differential hosts (MORISHIMA 1969b). The Jeypore and control strains are scattered in Figure 2 according to the discriminant scores for distinguishing between the Indica and Japonica types (abscissa) and for distinguishing wild from cultivated plants (ordinate, same as in Figure 1). The distribution of Jeypore strains in the figure suggests that they have become gradually differentiated into the Indica and Japonica types as they were domesticated. This implies that the two *sativa* types are monophyletic.

The progress of Indica-Japonica differentiation can be evaluated by the correlations between characters distinguishing the two types. As shown in Table 1, three characters (potassium chlorate resistance, low-temperature resistance, and apiculus hair length) are strongly intercorrelated among *sativa* cultivars which are divided into two types differing in these characters. In contrast, among *perennis* as well as Jeypore wild strains the three characters are uncorrelated. Among Jeypore strains approaching cultivated type, the correlation coefficients are low but have the same direction signs as are found among *sativa* cultivars. The degree of general agreement among these characters may be shown by the mean of correlation coefficients which is proportional to Kendall's coefficient of concordance.

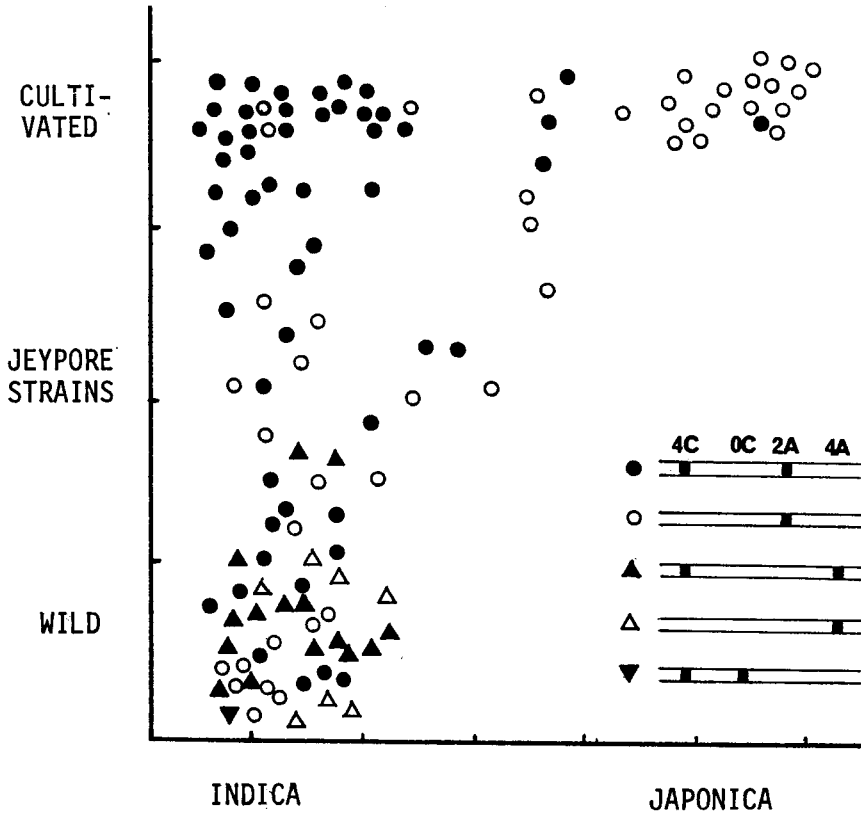


FIGURE 2.—Wild controls Jeypore strains, and cultivated controls scattered according to the scores given by two discriminant formulas, one (abscissa) for classifying the Indica and Japonica types of *sativa* cultivars, and the other (ordinate) for wild and cultivated forms (same as in Figure 1). Alleles for peroxidase isozymes are also shown: 4C — Px_2^{4C} , 0C — Px_1^{0C} , 2A — Px_1^{2A} , and 4A — Px_1^{4A} (the latter three being codominant).

TABLE 1

Correlations between apiculus hair length (*H*), potassium chlorate resistance (*K*), and low-temperature resistance (*L*) in various strain groups

Group	No. of strains	Correlation coefficient			Average (concordance)
		H-K	K-L	L-H	
Asian <i>perennis</i> strains	40	-.04	-.03	-.03	-.03
Jeypore strains, wild	26	-.05	.30	.12	.12
Jeypore strains, cultivated	118	.10	.21	.21	.17
<i>sativa</i> cultivars	120	.68	.59	.64	.64

Further evidence for the monophyletic origin of the two *sativa* types was obtained. Japonica-like progeny lines were derived from a cross between a typical Indica and an Asian *perennis* strain. Similarly, Indica-like progeny lines were obtained from another cross between a typical Japonica and the same *perennis* strain (OKA, unpublished).

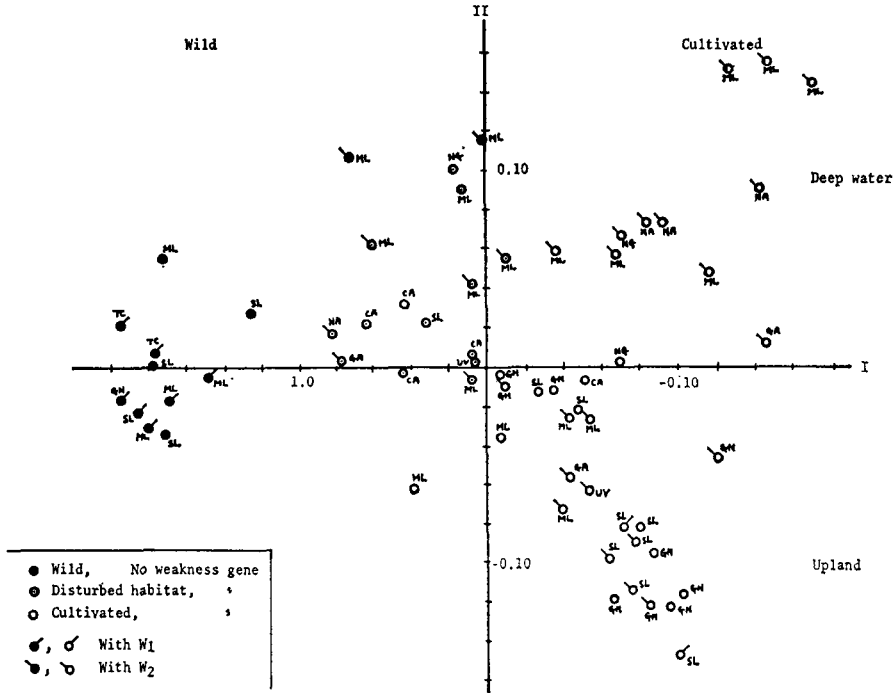


FIGURE 3.—Sixty-five strains of *breviligulata* (wild) and *glaberrima* (cultivated) scattered according to the scores given by the first and second component vectors. Their F_1 weakness genes, W_1 and W_2 , are denoted by σ and δ , respectively. CA: Cameroon, GA: Gambia, GH: Ghana, GN: Guinea, ML: Mali, NA: Nigeria, NG: Niger, SL: Sierra Leone, TC: Tchand, UV: Upper Volta. (From CHU and OKA 1972)

It remains unknown, however, what the internal mechanism of Indica-Japonica differentiation is. Many Asian *perennis* strains produce fertile F_1 hybrids with *sativa* varieties which are intersterile (HINATA and OKA 1962). The F_1 -sterility relationships among *sativa* varieties, however, do not necessarily reflect the pattern of Indica-Japonica differentiation. It seems that the differentiation in certain characters has proceeded ahead of that in sterility relationships (OKA 1964b). The inhibiting factor might be a differential response of primitive cultivars to a yet unknown cultural condition.

In Figure 2 is also shown the distribution of alleles specifying certain peroxidase isozymes. Cultivated as well as intermediate wild-cultivated strains showed only one allelic difference at the Px_2 locus; most Indica varieties had Px_2^{4c} (specifying band 4C) while most Japonicas had Px_2^0 (silent). Asian *perennis* strains had, in addition to these two, three different alleles at the Px_1 locus, and their populations were polymorphic. A similar trend toward restriction of allelic variations with domestication was also found for acid phosphatase isozymes (SHAHI, MORISHIMA and OKA 1969a).

In the inland delta area along the Niger in West Africa, swamps are surrounded by desert. There, *breviligulata* occurs in deep water paddies of *glaber-*

rima, yet natural population of *breviligulata* contain *glaberrima*-like plants. Hybrid swarms between the wild and cultivated species are often found. *O. perennis* subsp. *barthii* and *O. sativa* (introduced from Asia) are also found mix-growing with varying frequencies. This area may be a diversity center of *glaberrima* as pointed out by PORTÈRES (1956).

Strains belonging to the *breviligulata*-*glaberrima* series are scattered in Figure 3 according to the scores given by the first and second component vectors derived from the principal component analysis of correlations among 29 metric characters. It was postulated that the first component represents the variation between wild and cultivated types, and the second component reflects the variation between deep water and upland types (CHU and OKA 1972; the distribution of complementary dominant lethals causing F_1 weakness is also shown in the figure). The pattern of distribution of the strains indicates that wild plants might have been gradually differentiated into deep water and upland types as they were domesticated.

The diversity center of crop plants as early demonstrated by VAVILOV exists as "endemic" or "micro-centers," the latter being evolutionarily active (HARLAN 1963). In view of the presence of hybrid swarms, it seems that "micro-centers" occur in the above mentioned two areas.

THE DYNAMICS OF DOMESTICATION

The side by side derivation of crop and weed forms was advocated by HARLAN (1965). A weed form of *O. perennis* was found in Raipur area, Madhya Pradesh, India (OKA and CHANG 1959). The weedy wild rice grows on the outside fringe of and within paddy fields. Owing to its close resemblance to rice cultivars, the farmers can not weed it out. In badly infested fields, the weedy rice occupies 30 percent or more of the crop stand.

In this area, the annual type of *O. perennis* is abundant in swampy patches, while the perennial type grows in ponds and deep swamps. The weedy rice showed intermediate grades between the annual wild and cultivated plants not only in external characters but also in the degree of seed dormancy and outcrossing rate (OKA and CHANG 1959). They seem to be a product of introgression between the wild and cultivated plants.

The paddy fields are plowed and puddled at the advent of the rainy season in June and rice seed is broadcast. In order to maintain itself, the seed of the weedy rice remains dormant for several months after maturity, and then germinates soon after puddling so as to keep pace with the sprouting seeds of cultivated plants. It is the seed's dormancy that enables it to behave in such a manner. Once the weed germinates, it competes with cultivated plants which generally grow faster than wild ones. It then sheds seeds just before harvest of cultivated rice. The weedy plants are thus selected for their weediness. They would absorb genes from coexisting cultivars and serve as a gene reservoir in the evolution of cultivated rice.

We have pointed out that when wild plants are grown by man, cultivation works in itself as a selective agent (OKA and MORISHIMA 1970). The selection

pressure caused by cultivation or disturbance of the habitat by man has been called "cultivation pressure." Seeding was found to be a powerful selective agent causing cultivation pressure as follows: several *perennis-sativa* hybrid populations were each divided into two plots; in one, the seeds were harvested and sown next spring, while in the other, the naturally shed seeds were allowed to germinate after the remaining plants of the previous generation and weeds of big size had been removed. After three generations, the self-sown plants were found to retain the characters of wild plants, i.e., high rate of seed shedding, long awns, large rachis angle, pronounced seed dormancy, etc., while the hand-sown plants tended to have cultivated characters (Figure 4).

It may be inferred that the first impact of man's activity concerning wild plants might have been collection of grain for food. Seed collecting of *O. perennis* is still done at the present time in some remote areas in India, Africa and South America. As H. G. WELLS (1951) has proposed, the Neolithic men (possibly women), "observing that grain grew at the old camping places, may have consciously scattered grain with the idea of its being returned later." Presumably, the initial cause for plant domestication might have been the discovery of seeding by man. Conscious selection of good plants may be a technique which man has learned in a later phase of civilization.

In rice, domestication seems to be accompanied by autogamy. In the above experiment, plants showing cultivated characters were found to be more homozygous than those showing wild characteristics. Possibly, inbreeding depression and

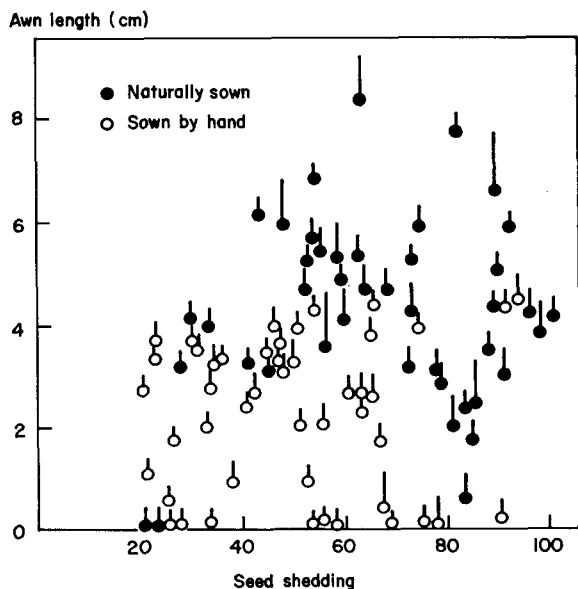


FIGURE 4.—Naturally-sown and hand-sown plants scattered according to percentage of seed shedding and awn length. The length of vertical spicules shows rachis angle. (From OKA and MORISHIMA 1971)

other factors counteracting the natural increasing trend of selfing rate may be removed by domestication.

Another important difference found between wild and cultivated rice plants was that the wild plants were more plastic in development than cultivated ones (OKA, unpublished). Along with genetic heterogeneity of populations, phenotypic plasticity enables the wild plants to cope with varying environmental stresses. On the other hand, the cultivars seemed to have progressively acquired higher responsiveness to weeding, fertilizer application, and other cultural management as they were improved (OKA and CHANG 1964). It may be concluded that the evolution of genotype and environment probably progressed in parallel.

LITERATURE CITED

- CHU, Y. E., 1967 Variations in peroxidase isozymes of *Oryza perennis* and *O. sativa*. Japan. J. Genet. **42**: 233-244.
- CHU, Y. E. and H. I. OKA, 1967 Comparison of variations in peroxidase isozymes between *perennis-sativa* and *breviligulata-glaberrima* series of *Oryza*. Bot. Bull. Acad. Sinica **8** (Special No.): 261-270.
- CHU, Y. E., H. MORISHIMA and H. I. OKA, 1969a Reproductive barriers distributed in cultivated rice species and their wild relatives. Japan. J. Genet. **44**: 207-223. —, 1969b Partial self-incompatibility found in *Oryza perennis* subsp. *barthii*. Japan. J. Genet. **44**: 225-229.
- CHU, Y. E. and H. I. OKA, 1970a The genetic basis of crossing barriers between *Oryza perennis* subsp. *barthii* and its related taxa. Evolution **24**: 135-144. —, 1970b Introgression across isolating barriers in wild and cultivated *Oryza* species. Evolution **24**: 344-355. —, 1972 The distribution and effects of genes causing F₁ weakness in *Oryza breviligulata* and *O. glaberrima*. Genetics **70**: 163-173.
- CLAYTON, W. D., 1968 Studies in *Gramineae*: XVII, West African wild rice. Kew Bulletin **21**: 485-488.
- HARLAN, J. R., 1963 Two kinds of gene centers in *Bothriochloinae*. Am. Nat. **97**: 91-98. —, 1965 The possible role of weed races in the evolution of cultivated plants. Euphytica **14**: 173-176.
- HINATA, K. and H. I. OKA, 1962 A survey of hybrid sterility relationships in the Asian forms of *Oryza perennis* and *O. sativa*. Japan. J. Genet. **37**: 314-328.
- MORINAGA, T., 1964 Cytogenetical investigations on *Oryza* species. Pp. 91-102. In: *Rice Genetics and Cytogenetics*. Edited by R. F. CHANDLER. Elsevier, Amsterdam.
- MORISHIMA, H., 1969a Phenetic similarity and phylogenetic relationships among strains of *Oryza perennis*, estimated by methods of numerical taxonomy. Evolution **23**: 429-443. —, 1969b Differentiation of pathogenic races of *Piricularia oryzae* into two groups, "Indica" and "Japonica." SABRAO Newsletter **1**: 81-94.
- MORISHIMA, H. and H. I. OKA, 1960 The pattern of interspecific variation in the genus *Oryza*: Its quantitative representation by statistical methods. Evolution **14**: 153-165.
- MORISHIMA, H., H. I. OKA and W. T. CHANG, 1961 Directions of differentiation in populations of wild rice, *Oryza perennis* and *O. sativa* f. *spontanea*. Evolution **15**: 326-339.
- MORISHIMA, H., K. HINATA and H. I. OKA, 1962 Comparison between two cultivated rice species, *Oryza sativa* L. and *O. glaberrima* Steud. Japan. J. Breed. **12**: 153-165. —, 1963 Comparison of modes of evolution of cultivated forms from two wild rice species, *Oryza breviligulata* and *O. perennis*. Evolution **17**: 170-181.
- MORISHIMA, H. and H. I. OKA, 1970 A survey of genetic variations in the populations of wild *Oryza* species and their cultivated relatives. Japan. J. Genet. **45**: 371-385.

- OKA, H. I., 1957 Genic analysis for the sterility of hybrids between distantly related varieties of cultivated rice. *J. Genet.* **55**: 397-409. —, 1958 Intervarietal variation and classification of cultivated rice. *Indian J. Genet. and Plant Breed.* **18**: 79-89. —, 1964a Pattern of interspecific relationships and evolutionary dynamics in *Oryza*. Pp. 71.-90. In: *Rice Genetics and Cytogenetics*. Edited by R. F. CHANDLER, Elsevier, Amsterdam. —, 1964b Considerations on the genetic basis of intervarietal sterility in *Oryza sativa*. pp. 158-174. In: *Rice Genetics and Cytogenetics*. Edited by R. F. CHANDLER, Elsevier, Amsterdam.
- OKA, H. I. and W. T. CHANG, 1959 The impact of cultivation on populations of wild rice, *Oryza sativa* f. *spontanea*. *Phyton* **13**: 105-117. —, 1960 Survey of variations in photoperiodic response in wild *Oryza* species. *Bot. Bull. Acad. Sinica* **1**: 1-14. —, 1961 Hybrid swarms between wild and cultivated rice species, *Oryza perennis* and *O. sativa*. *Evolution* **15**: 418-430. —, 1962 Rice varieties intermediate between wild and cultivated forms and the origin of the Japonica type. *Bot. Bull. Acad. Sinica* **3**: 109-131. —, 1964 Evolution of responses to growing conditions in wild and cultivated rice forms. *Bot. Bull. Acad. Sinica* **5**: 120-138.
- OKA, H. I. and Y. DOIDA, 1962 Phylogenetic differentiation of cultivated rice. 20. Analysis of the genetic basis of hybrid breakdown in rice. *Japan. J. Genet.* **37**: 24-35.
- OKA, H. I. and H. MORISHIMA, 1967 Variations in the breeding systems of a wild rice, *Oryza perennis*. *Evolution* **21**: 249-258. —, 1970 The dynamics of plant domestication: Cultivation experiments with wild *Oryza* populations. *Evolution* **25**: 356-364.
- PORTÈRES, R., 1956 Taxonomie agrobotanique de riz cultivés, *O. sativa* L. et *O. glaberrima* Steudel. *J. Agr. Trop. Bot. Appl.* **3**: 342-856.
- SHAHI, B. B., H. MORISHIMA and H. I. OKA, 1969a A survey of variations in peroxidase, acid phosphatase and esterase isozymes of wild and cultivated *Oryza* species. *Japan. J. Genet.* **44**: 303-319.
- SHAHI, B. B., Y. E. CHU and H. I. OKA, 1969b Analysis of genes controlling peroxidase isozymes in *Oryza sativa* and *O. perennis*. *Japan. J. Genet.* **44**: 321-328.
- TATEOKA, T., 1964 Taxonomic studies of the genus *Oryza*. pp. 15-21. In: *Rice Genetics and Cytogenetics*. Edited by R. F. CHANDLER. Elsevier, Amsterdam.
- WELLS, D. G., 1951 *The Outline of History*. (Revised ed.). Cassell, London.