GENETIC BASES, CLASSIFICATION AND ORIGIN OF REPRODUCTIVE BARRIERS IN *ORYZA* SPECIES[1]

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Abstract

Reproductive isolation barriers can be classified on different bases, namely, according to the developmental stage at which abortion takes place, and according to the genetic basis of the abortive phenomenon. The former classification seems to be useful for understanding the physiological features of reproductive barriers, while the latter may help us to understand speciation patterns. According to the genetic basis, reproductive barriers in plants can be broadly classified into chromosomal, genic and cytoplasmic categories.

Species of the genus *Oryza* can be divided into "Sativa", "Officinalis" and "miscellaneous" groups. "Sativa group" carrying the A genome comprises two cultivated species, *O. sativa* and *O. glaberrima*, and two wild species, *O. perennis* and *O. breviligulata*. Further, *O. perennis* is differentiated into four geographical races or forms, Asian, American, African (subsp. *barthii*) and Oceanian.

Various reproductive barriers were found between the taxa commonly having the A genome, as follows:

1) Barrier to cross-fertilization: *O. sativa* and *O. glaberrima* may be partly isolated by a particular crossing barrier which brings about differential cross-fertilities in back-crosses possibly controlled by genotype-cytoplasm interaction.

2) Inviability of young F_1 zygotes: *O. perennis* subsp. *barthii*, is isolated from its wild and cultivated relatives by an F_1 inviability barrier which is controlled by a set of complementary dominant lethals.

3) F_1 vegetative weakness: This was found between varieties of *O. sativa* and also between strains of *O. glaberrima* and *O. breviligulata*. The latter case was found to be controlled by a set of two complementary dominant lethals which disturbed tissue differentiation in the adventitious root.

4) Gametophytic hybrid sterility: This is commonly found in various cross-combinations between and within species, and the case in *O. sativa* is known to be controlled by duplicate gametic lethals.

5) Sporophytic hybrid sterility: This was found between strains of *O. sativa*. It appeared to be controlled by duplicate genes of sporophytic effect, the development of gametes being interrupted in plants having their recessive combinations.

6) Hybrid breakdown: This may be commonly distributed in various *Oryza* species. In certain cases in *O. ativa*, it was found to be controlled by a set of complementary recessive lethals.

It was discussed that the reproductive barriers found in *Oryza* might have developed largely due to geographical separation, but those isolating *O. perennis* subsp. *barthii* from its sympatric relatives could be partly due to selection.

The role of genetic variation and selection in evolution is well known since Darwin. However, as we know today, isolation or "restriction of gene exchange between Mendelian populations" (Stebbins 1958a p. 147) is necessary for species differentiation. This was pointed out first by Romones (1910) and numerous contributions to this problem have been published as reviewed by Dobzhansky (1951) as well as by Stebbins (1950, 1958a).

Isolation is achieved by vicinism and geographical distance on the one hand, and by various physiological factors conditioning mating and the development of hybrid on the other. Distantly related taxa may seldom mate. But if crossfertilization is made, the hybrid shows abortive phenomena at various phases of development (Chu *et al.* 1969a; Vickery 1959, 1964, 1966). A reproductive barrier may be in many cases an outcome of racial differentiation caused by geographical disjunction and other evolutionary factors. But, it may be selected for when isolation is advantageous, and when it is established in a sympatric population of related forms, the isolated forms may be set on their respective evolutionary paths. Therefore, the barriers should be investigated from two different angles, one observing the present status of differentiation between existing taxa, and the other acknowledging the cause of differentiation and evolutionary dynamics. When the barriers are due to developmental abortions of hybrids, we may be interested in how the taxa differ in the system of genetic control of development.

I. Classification of reproductive barriers based on genetic basis.

Dobzhansky (1951, p. 181) proposed to divide isolating barriers into geographical or spatial and reproductive categories; the latter was classified according to the mating process of parents and the developmental stages at which abortion takes place into ecological, seasonal or temporal, sexual or psychological, mechanical, and gametic crossing barriers, hybrid inviability, hybrid sterility and hybrid breakdown.

This classification is useful for understanding the overall picture and for distinguishing the physiological bases, but it does not reflect the underlying genetic factors. Developmental abortions of hybrids may occur at different stages controlled by various genetic factors, which are broadly classified into chromosomal, genic and cytoplasmic categories. Further, the life cycle of a plant consists of its existence as sporophyte and as gametophyte. It should be kept in mind that sterility is abortion of the gametophyte, but according to its genetic basis it is classified into gametophytic (haplontic) and sporophytic (diplontic) categories, the former being mainly due to gametophytic, and the latter to sporophytic genotypes (Stebbins 1958a, p. 165-178). From this concept, we can classify various reproductive barriers as follows:

a) Parental difference in chromosome number: Many plant species are polyploids, while some may be secondarily balanced polyploids. When plants differing in ploidy are crossed, the F_1 hybrids are sterile primarily because of irregular chromosomal assortment. In crosses between polyploid species having the same chromosome number, lack of preferential homogenetic pairing may also give rise to disturbances in chromosomal assortment.

b) Parental difference in chromosomal structure: This results in failure of normal meiotic pairing and gametogensis. But it is known that pairing is controlled not only by structural homology, but also by particular genes. Cases of genic control of asynapsis have been found as reviewed by Gaul (1954). following the first discovery by Peto (1938). Riley (1960) found that preferential pairing in polyploid wheat was controlled by a gene located in chromosome 5B.

c) Segmental substitution of chromosomes: Inversion and translocation are found in many organisms. The heterozygotes show certain meiotic irregularities and are semi-sterile.

d) Substitution of small chromosomal segments: Segmental differentiation of chromosomes have been found in various species hybrids. The number of chiasmata is often reduced in such hybrids (Rees 1961; Rees and Tompson 1956, 1958; Jones and Rees 1964; Gottschalk and Pietrini 1965; Chu et al. 1969a). They are sometimes called "cryptic structural hybrids", as no cytological irregularities are found in meiosis though there is circumstantial evidence for structural hybridity.

e) Substitution of genes controlling the development of gametes: This was demonstrated by Oka (1957b, etc.) in hybrids between distantly related varieties of Oryza sativa. Gametes carrying double recessive combinations of duplicate genes controlling their development deteriorate resulting in gametophytic or haplontic sterility, as will be discussed later. It should be noticed that "small chromosomal rearrangements could be expected to segregate in the same way as genes and to show linkage relationaships" (Stebbins 1958, p. 178).

f) Substitution of complementary lethal genes: When the parents grow normally but the F_1 zygotes are aberrant, the genetic basis of the abortion may be complementary. Complementary lethal genes controlling sporophytic abortion have been reported in Gossypium ("corky", "crinkled" and "crumpled", Stephens 1946, 1950), as well as in Triticum ("necrosis", "chlorosis", etc., Tsunewaki 1960; Tsunewaki and Kihara 1962; Hermsen 1957, 1962, 1963a, 1963b, 1967; Nishikawa 1953, 1962; etc.).

Similarly, when a certain combination of complementary genes physiologically affects some tissue in flower organs and interrupt gametogenesis, spor-

ophytic or diplontic sterility results (Oka 1957a). Further, the F_1 sterility in *Phlox* was considered polygenic (Levin and Smith 1966). It may be inferred, though not proved, that the deterioration of gametes in hybrids is in some case due to an interaction between sporophytic and gametophytic genotypes.

g) Gene-cytoplasm interaction: Many cases of genotype-cytoplasm interaction causing hybrid abortions have been reported, mainly from differences between reciprocal crosses, as reviewed by Stebbins (1958a).

h) Zygote-maternal tissue interaction: The death of young embryos was found in some plant hybrids as reported by Greenshield (1954) and Weaver (1957, 1958). Some such cases were considered to be due to an interaction between zygote and maternal tissue genotypes (Blakeslee 1954; Mclean 1946, etc.). This phenomenon was called "somatoplastic sterility" by Brink and Cooper (1939, 1941), Cooper and Brink (1940, 1945) and Gooper (1951). In other cases, endosperm-maternal tissue incompatibility was considered to interrupt the development of F_1 seed (Hakansson 1952; Oakes 1966; Stokes 1955). In this case, viable F_1 plants can be obtained by employing the technique of embryo culture.

II. Reproductive barriers found in *Oryza* species.

Since the early days, the taxonomy of the Genus *Oryza* has attracted the interest of researchers (Prodoehl 1922; Roschevicz 1931; Chatterjee 1948; Sampath 1961, 1962), through many problems remain unsolved. In 1964, the symposium on "Rice Genetics and Cytogenetics" was held at the International Rice Research Institute, Philippines. In the symposium, a scheme to standarize classification of *Oryza* was agreed as shown in Table 1. Morishima and Oka (1960) reported that from a numerical analysis of variations in 42 characters, the genus could be divided into three groups named "Sativa", "Officinalis" and "miscellaneonus". "Sativa group" includes all species with the A genome, and "Officinalis group" includes diploid and tetraploid species carrying the C genome. This classification thus supports the results of genome analysis (Kihara 1959, 1963; Kihara and Nezu 1960; Morinaga 1959) and cytogenetic studies (Li *et al.* 1961, 1962, 1963a, 1963b, 1965, 1966; Morinaga 1941, 1943; Morinaga and Kuriyama 1960 Morinage *et al.* 1962; Okura 1937; Wuu *et al.* 1963). Genome A is carried by two cultivated species *Oryza sativa* and *O. glaberrima*, and two wild species *O. perennis* and *O. breviligulata*. Futher, *O. perennis* is differentiated into four geographical races or forms, Asian, African, American, and Oceanian.

On the other hand, in view of the secondary pairing of meitotic chromosomes, the diploid species of *Oryza* have been postulated to be secondary balanced polyploids (Chu 1967a; Hu 1957, 1958, 1960, 1962; Nandi 1936; Sakai

Table 1. Species of the genus *Oryza*

Group	Species	Chromosome no. (2n)	Genome	Distribution
Sativa group	*sativa* L.			
	Indica type	24	A	Asia
	Japonica type	24	A	Asia
	perennis Mcench			
	Asian form			
	Annual type f. *spontaneu* Roschev	24	A	Asia
	perennial type	24	A	Asia
	African form (Subsp. *barthii* A. Chev.)	24	A	Africa
	American form (Subsp. *cubensis* Ekman)	24	A	South America
	Ocean'an form	24	A	Ocean'a
	glaberrima Steud. *	24	A	West Africa
	breviligulata A. Chev. et Roehr.	24	A	West Africa
Officinalis group	*officinalis* Wall. ex Watt	24	C	South and Southest Asia, New Guinea
	eichingeri A. Peter	24, 48	BC	East and Central Africa
	malampuzhaensis Krish. et Chand.	48	BC	India
	minuta J.S. Presl ex C. B. presl	48	BC	Southeast Asia
	punctata Kotschy ex steud	24, 48	BC	Africa
	alta Swallen	48	CD	Central and South America

grandiglumis (Doell) Prod.	48	CD	South America
latifolia Desv.	48	CD	Central and South America
angustifolia C. E. Hubbard	—	—	Africa
australiensis Domin	24	E	Australia
brachyantha A. Chev. et Roehr.	24	F	West and Central Africa
coarctata Roxb.	48	—	Burma, India and Pakistan
granulata Nees et. Arn. ex Hook f.	24	—	South and Southeast Asia
longiglumis Jansen	48	—	New Guinea
meyeriana (Zoll. et Mor. ex Steud.) Baill	24	—	Southeast Asia
perrieri A. Camus	24	—	Malagasy
ridleyi Hook f.	48	—	Southeast Asia
schlechteri Pilger	—	—	New Guinea
subulata Ness	24	—	South America
tisseranti A. Chev.	24	—	Central Africa

Others

1935). This may account for the presence of duplicate genes for F_1 sterility and other characters (Chu *et al* 1970a; Oka 1964b).

Hybrids between different taxa of *Oryza* have been investigated with respect to crossability, chromosome pairing in F_1 pollen mother cells and the sterility of F_1 plants. Further, some more detailed studies were reported regarding the developmental abortions of F_1 plant and its genetic basis (Amemiya and Akemine 1960, 1963; Chu and Oka 1971; Chu *et al*. 1969a). On the other hand, natural hybrid swarms among species with the A genome were observed (Chu 1967b; Chu and Oka 1967, 1970b; Morishima *et al*. 1961, 1963; Oka and Chang 1959, 1961, 1962, 1964). Some hybrid swarms were borne as escapes from isolating barriers. They were found to serve as a mediator in gene exchange among different species and to release various forms. We have found the following reproductive barriers in this plant group.

1) Barrier to cross-fertilization: This may be found in crosses between remote species (Nezu *et al*. 1960; Morinaga 1964; Morinaga *et al*. 1960a, 1960b; Morinaga and Kuriyama 1960). Species crosses generally show a low rate of success, but whether it is due to failure of fertilization or to the death of F_1 zygotes is in many cases unknown. The F_1 plants among *O. australiensis* and *O. paraguaiensis*, *O. alta*, *O. minuta* and *O. sativa* as well as between *O. brachy-antha* on one hand and *O. paraguaiensis*, *O. minuta* and *O. sativa* on the other were obtained by Li *et al*. (1961, 1962, 1963a 1963b) from more than 3,000 cross-pollinations for each combinations, by the use of embryo-culture technique. There were few studies on the genetic basic of cross-fertilization barrier except for a recent report by the present author (Chu 1968). *O. stativa* and *O. glaberrima* seems to be partially isolated by a cross-fertilization barrier. The F_1 plants of *O. sativa* × *O. glaberrima* could be more successfully pollinated by *sativa* than by *glaberrima* parent, while the *O. glaberrima* × *O. sativa* F_1 plants gave better seed set when pollinated by *glaberrima* than by *sativa* parent. The same trend for cross-fertilities to differ according to the direction of cross was also found in B_1, B_2 and B_3 generations. This cross-fertility barrier might be controlled by genotype-cytoplasm interaction.

2) Inviability of young F_1 zygotes: This is frequent in species crosses though there have been no published reports. The report by the present author may be the first one in *Oryza* (Chu and Oka 1970a). The African subspecies of *Oryza perennis* Moench, called *barthii* (considered by Tateoka (1963) to be of species rank and was called *O. barthii*), does not easily produce viable F_1 seeds when crossed with its wild and cultivated relatives (other forms of *perennis*, *O. sativa* L., *O. breviligulata* Chev et Roehr., and *O. glaberrima* Steud.). When *barthii* is used as the pollen parent, the F_1 embryos and endosperms begin to deteriorate about six days after fertilization, resultiting in shrunken

and inviable F_1 seeds. When *barthii* is used as the maternal parent, the F_1 seeds deteriorate about three days after fertilization. In both directions of cross, tissue, differentiation in the zygotes was disturbed. The chance to obtain viable F_1 seeds was in both less than 5%. The results of crossing experiments using exceptionally obtained F_1 plants indicated that the crossing barrier was controlled by a set of complementary dominant lethals with an imperfect penetrance. These genes interrupted differentiation of organ primordia possibly affecting the development of endosperms primarily.

     3) F_1 weakness in the vegetative stage: This may be taken as a case of F_1 inviability though the symptom is expressed after a period of growth.

     In rice, this has been firstly reported by Oka (1957a) in *O. sativa*. The F_1 plants, though their germination and growth in the seedling stage were normal, stopped to grow showing chlorosis after the seedlings had developed 3 to 4 leaves. They died later unless protected in a favorable environment. The two genes controlling this F_1 weakness were complementary dominant lethals. Amemiya and Akemine (1960, 1963) found the second case of F_1 weakness also between varieties of *O. sativa*. The F_1 plants between a strain from Jamaica and a variety of Norin group died in their seedling stage. The prominant features of this lethality lie with a peculiar growth inhibition of the hybrid root. This F_1 weakness was due to a set of "root-growth inhibiting complementary lethal genes".

     The third case of F_1 weakness was found between strains of *O. glaberrima* (cultivated) and *O. breviligulata* (wild) by Chu and Oka (1971). The weakness was found to be due to a disturbance in tissue differentiation of the adventitious roots. The undifferentiated tissues of induced calluses derived from weak plants grew as well as those from normal plants. From the segregation pattern of normal and weak plants, a set of complementary weakness genes, $W_1 W_2$, was found to control the F_1 weakness.

     4)   Gametophytic hybrid sterility: a) Chromosomal aspect—The mode of chromosome pairing in the F_1 plants between *Oryza* species has been observed by many workers as reviewed by Moringa (1964), and six different genomes named A to F were classified (Chandler (Ed) 1964, p. 253-4). The cultivated species and their wild relatives having the A genome show no significant disturbance in chromosome pairing in their F_1 hybrids (Gotoh and Okura 1935; Jones and Longley 1941; Morinaga and Kruiyama 1956 and 1957; Nezu et al. 1960; Chu et al. 1969a: Hsieh and Oka 1958), with a few exceptions (Yeh and Henderson 1961 and 1962).

     b)   Genic aspect—The F_1 plants between distantly related varieties of *O. sativa* are infertile in varying degrees as reported by many workers (Ting 1933; Terao and Mizushima 1939; Hinata and Oka 1962; Oka 1958 etc; Morin-

aga 1954 etc; Katsuo and Mizushima 1958; Nagamatsu and Omura 1960; Kitamura 1962; Chandler (Ed)—1964, p. 147-189). But some strains of the Asian form of *O. perennis* produce fertile F_1 hybrids with inter-sterile *sativa* varieties (Hinata and Oka 1962). This sterility was found to be due to sets of duplicate gametic lethals called "gametic-development genes" by Oka (1957b, 1964a). The various strain-groups of wild and cultivated rice species are isolated by F_1 sterility though they often show a less pronounced embryosac sterility. Based on the relationship between pollen and embryosac sterilities, the F_1 hybrids examined could be divided itno two groups, one in which embryosac and pollen fertilities were correlated as reported by Terao and Mizushima (1939), and the other in which pollen fertility was near zero while embryosac fertility was apparently higher (Chu *et al.* 1969a). After the formation of embryosac tetrads, various deteriorative phenomena were found to come about (Chu *et al.* 1969a).

c) Cytoplasmic aspect—A few cases of reciprocal differences in F_1 fertility were reported in an Asian *perennis* (Katsuo and Mizushima 1958) and a *sativa* strain (Kitamura 1962). It seems that the incidence of cytoplasmic F_1 sterility is sporadical in Oryza. Recently a detailed genetic analysis was made by using isogenic lines (Shinjyo and Omura 1966; Shinjyo 1969). The male sterile cytoplasm and its fertility restoration gene were found from an Indica variety, and both of them were put in isogenic lines with the genetic background of Taichung 65. When a plant with sterile cytoplasm was homozygous for the restoration genes, it was completely fertile, when heterozygous it was 50% fertile, and when it was a recessive homozygote, completely sterile. Plant with normal cytoplasm were male-fertile regardless of the genotype for restoration gene. The restoration gene was thus found to be of gametophytic type. The embryosacs were not affected by the cytoplasm.

5) Sporophytic hybrid sterility: This was also found between varieties of *O. sativa* (Oka and Doida 1962; Oka 1964b). Partly sterile segregants occurred in the F_2 from fertile F_1 plants, and true-breeding semi-sterile lines were obtained in later generations. This sterility was found to be due to duplicate genes with sporophytic effect, the development of gametes being interrupted in plants with their recessive combinations. The parental strains were considered to have $A_1 A_2 a_1 a_2$ or $a_1 a_2 A_1 A_2$ (called "Duplicatefertility genes)". It was assumed that $a_1 a_1 a_2 a_2$, $A_1 a_1 a_2 a_2$ and $a_1 a_1 A_2 a_2$ plants have a low fertility. Possibly, this phenomenon may be commonly distributed in various wild and cultivated rice species.

6) Hybrid breakdown: This was suggested by Oka (1964b, p. 165-7) in relation to sporophytic hybrid sterility. When distantly related varieties are crossed, it is often found that some F_2 plants show poor growth. Segregation

of weak F_2 plants was found to be due to a set of complementary recessive lethals, A_1 A_1 a_2 a_2 in P_1 and a_1 a_1 A_2 A_2 in P_2. In this case, plants with more than two A's (A_1 A_1, A_2 A_2 or A_1 A_2) were considered to normally grow. The genetic basis of this weakness is similar to that of above-mentioned sporophytic hybrid sterility. This phenomenon may be commonly distributed in *Oryza* species though not yet investigated much.

Summarizing up the whole picture in *Oryza*, we find that the various reproductive barriers are in many cases incomplete and quantitative in effect. The capacity for hybridization also varies among different groups as shown by Oka and Morishima (1967). It is suggested that hybridization and isolation might be in a balance (Chu and Oka 1970b).

III. Origin of isolating barriers.

In the early days, Goldshmidt (1940, 1952) as well as Lamprecht (1941, 1945, 1948) considered that a single mutation could bring*about morphological differences and reproductive barriers to distinguish a newly arised form. Muller (1942, 1950), Dobzhansky (1951, p. 206–2111), and Stebbins (1950, p. 236–250) demonstrated on accoumulated evidence that speciation was a gradual process guided by natural selection for many genes.

The mode of development of a reproductive barrier may differ according to allopatric and sympatric populations. Dealing with allopatric populations, Rensch (1933) and Mayr (1947) suggested that gene frequencies in different populations would change in different directions due to selection and genetic drift, resulting in differences in the system of genetic control of development.

Oryza perennis is distributed throughout the tropical countries of the world and comprises many varieties or forms with different propagation habits. They can be divided into four main geographical groups or subspecies (Table 2), which could be distinguished by character-association patterns though not by single characters.

The breeding system is an important factor in determining the genetic structure and evolutionary dynamics of a population. As shown by Oka and Morishima (1967) and Chu *et al.* (1969b), the geographical groups differ in the breeding systems. The African strains are rhizomatous and partialy self-inompatibility, and the Amazonian strains can be propagated by tiller separation in water, while *sativa, glaberrima* and *breviligulata* strains propagate by seed. Various reproductive barriers are found among them as mentioned above. This pattern of differentiation in characters, breeding systems and in reproductive barriers may be regarded as resulting from geographical disjunction and adaptation to different environments.

Smith and Daly (1959) reported that repeated selections for long and short

Table 2. *Reproductive barriers found in Oryza species with the A genome*

Stage of developmental abortion	Genetic basis	Cross-combination	Reference
Cross-sterility in back-crosses	Genotype-cytoplasm interaction	*glaberrima* and *sativa*	Chu 1968
Inviability of young F_1 zygote	Complementary dominant lethals	*perennis* subsp. *barthii* and other forms with the A genome	Chu and Oka 1970a
F_1 vegitative weakness	Complementary dominant lethals	Between *sativa* varieties	Oka 1957a
	Complementary dominant lethals	Among *sativa* varieties	Amemiya and Akemine 1960, 1963
	Complementary dominant lethals	Among and within *glaberrima* and *trevilgulata* species	Chu and Oka 1971
F_1 pollen sterility	Duplicate gametic dominant lethals	Among *sativa* varieties	Oka 1967b, 1964
	Unknown	Among and within species	Oka 1964a, Chu *et al.* 1969a
F_1 embryosac sterility	Genotype-cytoplasm interaction	Among *sativa* varieties	Shinjyo and Omura 1966 Shinjyo 1969
	Unknow	Among and within species	Terao and Mizusima 1939 Chu *et al.* 1969a
F_2 hybrid breakdown	Complementary recessive lethals	Among *sativa* varieties	Oka 1957a
F_2 sterlity	Duplicate sporophytic recessive lethals	Among *sativa* varieties	Oka and Doida 1962 Oka 1964b

corolla tubes in *Nicotiana rustica* resulted in the formation of a crossing bar-
riers. Ehrman (1964) also reported that when two strains of *Drosophila* were
cultured in different conditions for four and a half years a mating barrier
resulted. It seems that in a certain allopatric condition, reproductive barriers
can be rapidly established.

In contrast, Huxley (1942) as well as Allee *et al.* (1949) assumed that
reproductive barriers could arise without inital geographical isolation. But
Mayr (1947) and Clay (1949) pointed out that the insect species considered
sympatric by the above authors were allopatric in view of their limite migrat-
ing ability.

Fisher (1930) early asserted that for a Mendelian population to be divided
into two and to become isolated by a reproductive barrier, a temporary geo-
praphical isolation would be needed. Then, natural selection could intensify
the development of a barrier. This thought was lately supported by Sturtevan
(1938), Dobzhansky (1940) and Stebbins (1958b).

When a partial barrier is formed in a sympatric population, whether or
not the barrier itself can be selected owing to its reproductive advantage has
been a disputable question.

Ae (1959) gave an example of the role of geographical isolation showing
that hybrids between two species of *Colias* rapidly increased when a forest
separating them was removed. Whether in the future the two species will
form a hybrid swarm, or become isolated by a sexual barrier, may be a
problem to be investigated as the author has pointed out. Stephens (1964,
1950) has shown that *Gossypium hirsutum* and *G. barbadense*, which are isolated
by a strong tendency to F_3 breakdown, have developed an F_1 weakness barrier
("corky", "crinkled", and "crumpled") in the localities where they were
sympatric. This may be due to selection of complementary lethal genes.
Grant (1966a, 1966b) also pointed out that in *Gilia*, species growing sympatric-
ally in California were isolated by a crossing barrier, but those separated by
a long distance were not. Levin and Kerster (1967) gave a similar example
for two *phlox* species from observations of the frequency of white flowers in
the population of one species sympatric with the other "congener" species.
These researches indicate that reproductive barriers can be intensified in
sympatric populations as the result of natrual selection, possibly when selec-
tion favors higher reproductive rate.

In *Oryza*, the cultivated species, *sativa* and *glaverrima*, and their respective
wild relatives, *perennis* (*barthii*) and *breviligulata*, often grow sympatrically
in Africa (Oka and Chang 1964). It was found that *barthii* had more pro-
nounced barriers with its sympatric forms than with other froms from Asia
and America. Namely, the complementary lethals controlling the crossing

barrier seemed to have higher penetrance with sympatric than with allopatric forms. Also the incidence of F_1 weakness was higher between sympatric than between allopatric forms. These differences between sympatric and allopatric forms may suggest selection for the reproductive barriers.

Production of non-reproductable progeny must be disadvantageous. Let us supposed that hybrids between two species are frequently produced by natural crossing. If the F_1 plants are vigorous in vegetative growth but complete sterile, they occupy an area in the habitat competing with their parents. The parental populations maintain themselves under the impact of natural selection. Therefore, when a barrier which takes effect at earlier developmental stage occurs, it may be selected. Koopman (1950) reported that when *Drosophila pseudoobscura* and *D. persimilis* were mix-reared in a cage, the mating barrier between them was intensified; the two species were isolated by the deterioration of testis in hybrid males. The mating barrier may save them from producing sterile males.

Further, genes for reproductive barriers may be selected due to their linkage with other genes conditioning favarable characters. Oka (1968) has reported that the sterility genes between Indica and Japonica groups of *Oryza sativa* were cross-linked with certation genes. Sterility genes may thus be maintained at a higher frequency than expected.

On the other hand, it was suggested by Oka (1964b, p. 173) that the partial F_1 sterility between *sativa* varieties could not be more than an outcome of varietal differentiation which might be attributable to adaptation to different environments; examining the intermediate wild-cultivated forms from Jeypore Tract, India, he found that differentiation in characters could proceed ahead of that in F_1 sterility relationship.

O. sativa is predominantly self-pollinated, while its wild progenitors are partly or highly cross-pollinated (Oka and Morishima 1967; Chu *et al.* 1969b). Selfing must be in itself a reproductive barrier. When plants become self-pollinated, various forms will be released, and selection for isolating mechanisms may no longer work.

According to Stebbins (1958a, p. 187–8), "it is rather unusal that isolating mechanisms develop in a long-lived plant". But we found that *O. perennis* subs. *barthii*, a long-lived plant with rhyzomes, had a complex of partial barriers which could have been selected. Generally, perennial habit is correlated with allogamy as has been found among *perennis* strains (Oka and Morishima 1967). As *barthii* has a high capacity of hybridization, when it grows together with other forms, excessive hybridization resulting in reproductive waste may favorably be counter-balanced by reproductive isolation.

Considering the overall picture, we may infer that the origin of an isolat-

ing barrier is due to geographical separation, at least temporarily set up, but its development and establishment in a sympatric population may depend on natural selection. Environmental factors and adaptation to different environments may also influence barrier formation. The various factors as mentioned above may concurrently interact to bring about a pattern of combination of different kinds of barriers.

Acknowlegments

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