

WILD PROGENITORS OF CULTIVATED RICE AND THEIR POPULATION DYNAMICS

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The common wild rice of Asia shows a perennial-annual continuum and wide variations in life history traits suggesting r - vs. K -selection. It also shows a trend of association of $KC10_3$ resistance and low temperature resistance among populations as is found among indica and japonica rice cultivars. The populations contain various isozyme alleles, and the most frequent genotypes are those found in intermediate indica-japonica cultivars. The genetic structure of populations reflects differences in breeding systems. When experimental populations raised from juvenile plants collected in natural habitats were examined, intermediate perennial-annual populations were mostly polymorphic. An example is presented showing that an intermediate population is ready to respond to environmental heterogeneity both spatially and temporally. These observations support our previous hypothesis that the intermediate perennial-annual type of wild rice is most likely to be the immediate progenitor of rice cultivars.

The common wild rice or the *Oryza perennis* complex is distributed throughout the humid tropics and is comprised of four major geographical forms: Asian, American, African, and Oceanian (8). It is generally accepted that *O. sativa* L. has been domesticated from the Asian form of this species complex (= *O. rufipogon* Griff.) in Asia, while *O. glaberrima* Steud. in Africa stems from *O. breviligulata* Chev. et Rheor (10). With my colleagues, I have continued investigations on the wild and cultivated rices concerning character variations, isozymes, breeding systems, F_1 sterility relationships, isolating mechanisms, introgression, population structure, and adaptive strategies, as partly reviewed by Oka (18) and Morishima (9). The main direction of differentiation in the Asian common wild rices is represented by that between the perennial and annual types (13). The two types also differ in many traits and habitat preferences and in adaptive strategy (26).

Whether the perennial or the annual type of wild rice is the ancestor of cultivars has been an unsettled issue. Chatterjee (3), Ramiah and Ghose (23), and Chang (1, 2) considered the annual type to be the ancestor in view of character similarities. Sampath and Rao (25), Richharia (24), and Oka (17, 18) considered the perennial type to be the ancestor. *O. sativa* is essentially a perennial plant, and a continuous array of grada-

tions between the perennial types and cultivars has been found in the semi-wild material from Jeypore Tract, India (19). Recently, we put forward another hypothesis that an intermediate perennial-annual type was more likely to be the progenitor in view of its high evolutionary potentiality and fairly high reproductive effort (27).

As to the site of incipient domestication, Chang (1, 2) considered a broad area extending over the foothills of the Himalayas and its associated mountain ranges; this broad area is comparable to Harlan's (6) noncenter concept. As to the time of origin, the eldest remains of rice grains or hulls have been excavated in India (Naharaga, Uttar Pradesh), China (Ho-Mu-Do, Xhejiang), and Thailand (Non Nok Tha), all being 6,500 to 7,500 years old. This suggests diffused origins of rice domestication (7).

DIFFERENTIATION OF ASIAN WILD RICE POPULATIONS

Compared with the perennial type, the annual type is characterized by a low regenerating ability, high reproductive allocation of resources, early flowering time, awn development, high selfing rate, and tolerance to drought and submergence (26). The annual types grow in relatively shallow, temporary swamps that are parched in the dry season, while the perennial types grow in deeper swamps having a more stable water condition. The mode of association of life history traits with habitat conditions indicates that the annual types are *r* strategists and the perennial types *K* strategists (4).

Wild strains from various localities of Asia are scattered according to anther length, representing outcrossing rate and percent reproductive allocation (Fig. 1). The two values are intercorrelated (20) and show a wide range of variation among strains for each locality, although Chinese strains are largely of perennial types having a low reproductive allocation. Strains with medium values in these traits can be regarded as intermediate perennial-annual types. Some of them showing traces of characteristics of a cultigen could have resulted from introgression between wild and cultivated plants. The intermediate types are relatively infrequent and often found in strongly disturbed habitats, suggesting that they are disturbance tolerant. They also contain a large amount of genetic variation in their populations and can be differentiated into perennial and annual types in response to microenvironmental conditions (14, 27).

Reproductive allocation (%)

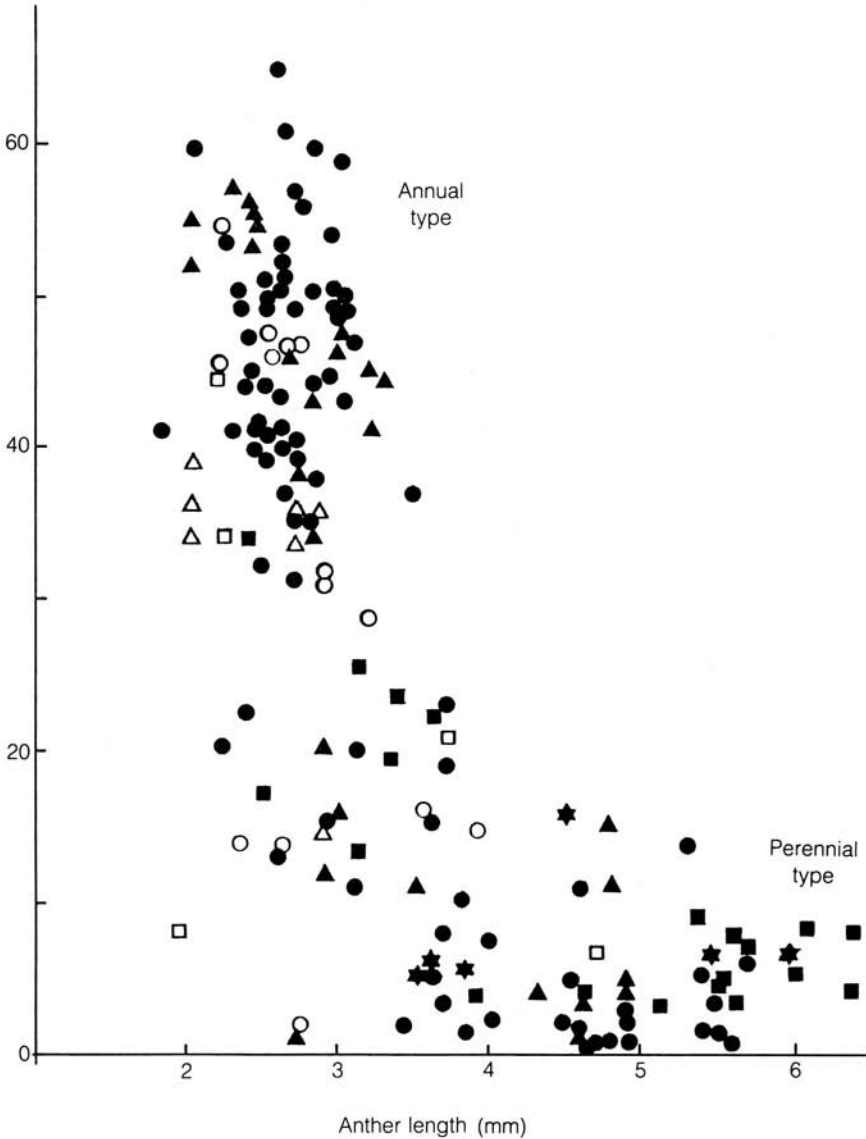


Fig. 1. Asian wild rice strains scattered by anther length and reproductive allocation. Solid symbols represent the strains showing high seed shedding and open symbols show low seed shedding. ▲ = India; ● = Thailand, Burma, Malaysia; ■ = China; ★ = Malayan archipelago.

In reproductive effort or seed productivity and selfing rate, wild annual types are more similar to cultigens than perennial types. In vegetative regenerating ability, seed dormancy, and awn development, wild perennial types are more similar to cultigens than the annual types. In view of the trend of evolution generally recognized in higher plants, it may be inferred that the perennial type is primitive and the annual type and cultigen have shared the evolutionary process to increase seed productivity. However, domestication has brought about other characteristics like uniform seed germination due to reduced dormancy, contemporary tillering and uniform seed maturity, and reduced seed shedding in addition to seed productivity, most probably in response to selection due to seeding and harvesting by man, which we have called cultivation pressure (21).

One may question which of the perennial and annual types is more similar to a cultigen in alleles for isozymes. Based on a multivariate analysis of data for 20 loci, Second (29) pointed out that the perennial and annual types could not be distinguished clearly. In our data, the perennial and annual types showed a difference in the frequency of alleles at *Sdh-1*, *Pox-1*, and some loci; at *Sdh-1*, allele 1 was predominant in the annual and allele 3 in the perennial types, while allele 2 was predominant among cultivars (J.C. Glaszmann, pers. comm.). At *Pox-1*, allele 2A was predominant in annual and cultivars, and both 2A and 4A in perennial types. Whether or not allozymic variations are associated with adaptive traits is under observation. In general, the wild populations are more polymorphic than cultivars and carry alleles that are not found among cultivars. Yet, it does not seem possible, at present, to detect the wild progenitors of cultivars on the basis of isozymic genotypes.

INDICA-JAPONICA DIFFERENTIATION IN WILD RICES

Rice cultivars are differentiated into the indica and japonica types, which are distinguishable by different patterns of character association or by correlations of diagnostic characters (12, 16). In wild rices, no significant correlations of diagnostic characters were found among strains from India and Thailand, so that the indica-japonica differentiation was not detectable (18, 22). Using a wider range of materials, we have recently found a tendency to such differentiation shown by a correlation between KClO_3 resistance and cold resistance (Fig. 2a). Most wild strains were sensitive to both KClO_3 and low temperature and were indica-like, but some of them, particularly those from China, were relatively resistant to both and were japonica-like in this sense.

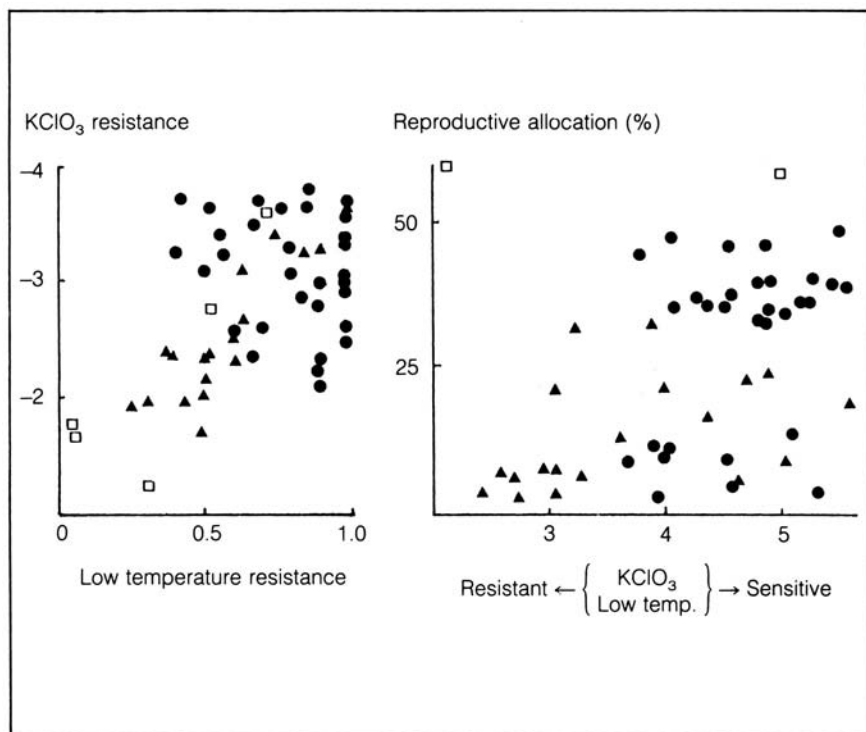


Fig. 2. Asian wild rice strains scattered (a) by resistance to low temperature and to KClO₃ and (b) by a score representing both resistance ($-K + 1.94 L$) and reproductive allocation. ● = India and Thailand, ▲ = China, □ = cultivated strains.

The wild strains were also scattered by an index obtained by combining the measurements of KClO₃ resistance and cold resistance and percent reproductive allocation (Fig. 2b). Strains with low reproductive allocation or perennial types were closer to japonica in the index value than those with high allocation or annual types, which tended to be scattered toward the indica type.

A survey of allozyme variations in wild and cultivated strains by Second (28) showed a certain trend of variation among rice cultivars that correspond to the indica-japonica differentiation. We are also engaged in this work; when examined with three diagnostic loci, *Cat-1*, *Pgi-1*, and *Acp-1*, 14 genotypes were recognized among cultivated strains. Two genotypes were most frequent and represented the indica and japonica types in cultivars (Fig. 3). The third most frequent genotype, which was a recombinant type, formed a group distributed mainly in the hilly areas of tropical Asia. When compared with the result of multivariate analysis of character values, varieties having those allozyme genotypes were inter-

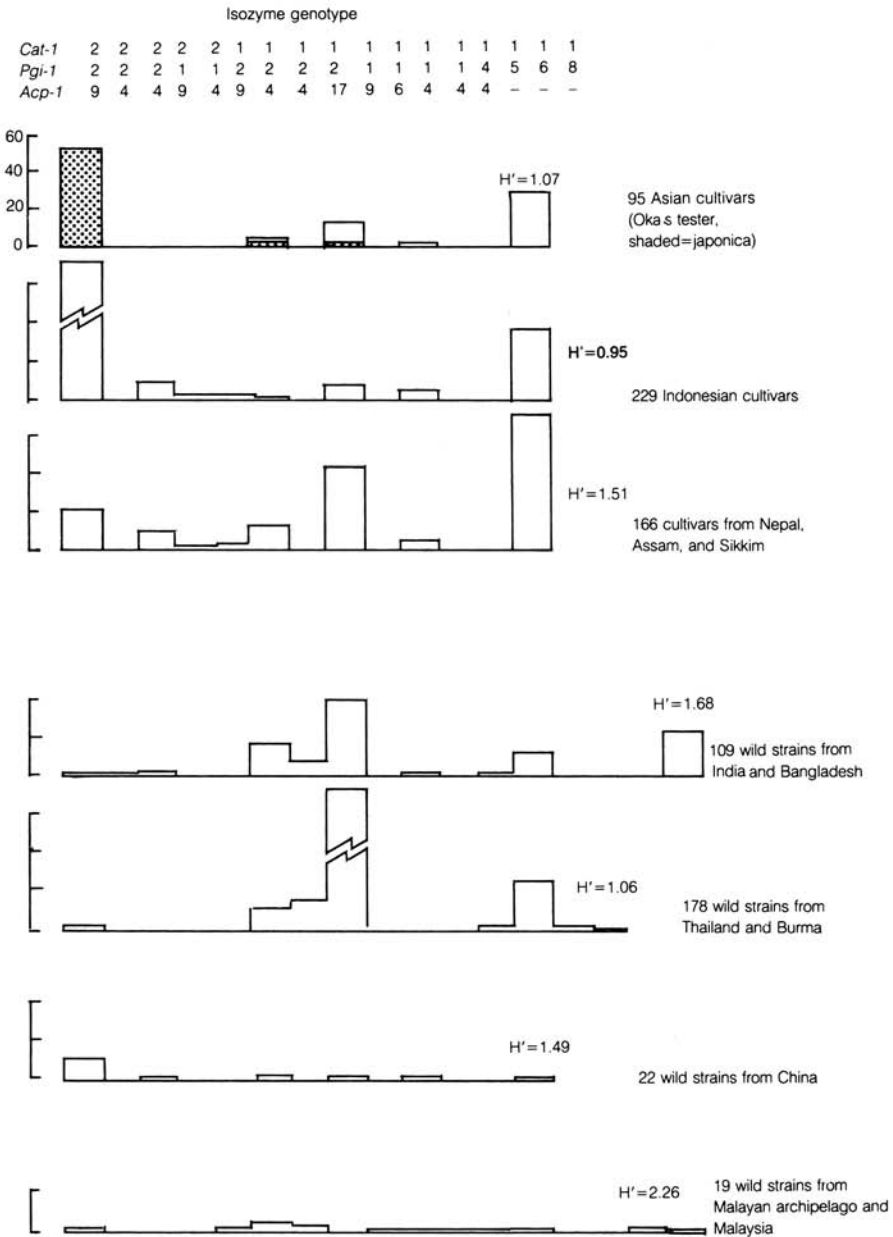


Fig. 3. Distributions of 17 isozyme genotypes for *Cat-1*, *Pgi-1*, and *Acp-1*, whose alleles differ in frequency between the indica and japonica types, among Asian rice cultivars and wild rice strains from different localities. $H' = -\sum x_i \ln x_i$, in which x_i represents frequency of the i -th genotype.

mediate indica-japonica types, although most of them were classified as indicas.

The wild strains showed a wider range of genotypic variation. Among them, the intermediate indica-japonica genotypes were most predominant. Among Chinese strains, the genotypes representing japonica were relatively frequent, as pointed out by Second (29). Allozyme similarity has often been used to assess phylogenetic relationships. In rice, however, the allozyme genotypes are various and their frequencies are subjected to sampling error and other conditions. It may be concluded that the genotypes representing intermediate indica-japonica cultivars are frequent among Asian wild rice strains.

GENETIC STRUCTURE OF WILD RICE POPULATIONS

Inter- and intrapopulational diversities were assessed on the basis of variations in isozymes and character values by using plants raised from seeds collected in their natural habitats. Generally, perennial populations were more polymorphic than annual populations in both isozymes and visual characters (Table 1). In contrast, interpopulational diversity was much higher among annual populations than among perennial ones. Intermediate perennial-annual populations were in an intermediate state. This pattern reflects the differences in breeding systems (11).

However, the data thus obtained represent the genetic diversity released by seed propagation, which is infrequent in perennial populations. To assess the realized or actual genetic diversity, we have raised experi-

Table 1. Genetic diversity and other parameter values estimated within and between wild rice populations.

Type	Average for <i>Pox-1</i> and <i>Acp-1</i>					Average for 6 characters		
	No. of populations	H_S^a	G_{ST}^b	Fixation index	Heterozygote %	No. of populations	C_S^c	C_{ST}^d
Perennial	24	.290	.532	.083	23.0	9	114	83
Intermediate	12	.117	.688	.427	9.1	7	77	63
Annual	14	.092	.670	.914	1.4	10	48	81

^a H_S = average gene diversity within population.

^b C_{ST} = relative magnitude of gene differentiation among population (15).

^c C_S = intrapopulation genetic variance shown by $\ln X \times 10^3$.

^d C_{ST} = relative magnitude of interpopulational generic variance to total genetic variance (%).

mental populations from juvenile plants collected in natural habitats in addition to those from seeds and have compared them (Table 2). In seed-derived populations, the average gene diversity for 10 isozyme loci was higher in the perennial and intermediate types than in annual types. In the juvenile-derived populations, however, there was no such difference between perennial and annual populations, and intermediate perennial-annual populations showed the highest diversity. The low genetic diversity in perennial populations indicates clonal propagation of a few competitive plants. The high diversity in intermediate populations may be attributed to their propagation by both seed and ratooning (27).

The difference in gene diversity between seed- and juvenile-derived populations differed according to the loci (Table 2). At *Sdh-1*, *Pgd-2*, and *Pox-1*, seed-derived populations seemed to be more polymorphic than corresponding juvenile-derived ones, but no marked differences were found at other loci. The fact that the perennial and annual types differed in allelic frequency at *Sdh-1* and *Pox-1* suggests that selectional mortality is involved in the demographic process of populations.

Table 2. Gene diversities at 10 isozyme loci observed in seed (S)- and juvenile (J)-derived populations, sampled at 6 sites in Thailand.^a

Site	Annual type						Intermediate type				Perennial type	
	NE-2		NE-3		NE-4		NE-1		CP-20		NE-88	
	S	J	S	J	S	J	S	J	S	J	S	J
Plants examined (no.)	33	7	18	78	26	118	64	14	71	9	10	24
Gene diversity ^b												
<i>Acp-1</i>	.000	.000	.000	.000	.076	.076	.295	.495	.661	.661	.500	.000
<i>Est-2</i>	.058	.240	.000	.000	.163	.170	.059	.500	.397	.466	.492	—
<i>Est-Ca</i>	.000	.000	.058	.000	.000	.000	.095	.000	.058	.000	.000	.000
<i>Pgd-1</i>	.226	.130	.448	.226	.496	.499	.113	.332	.379	.180	.320	.076
<i>Pgd-2</i>	.163	.000	.095	.058	.195	.000	.490	.000	.257	.168	.420	.000
<i>Pgi-1</i>	.196	.086	.466	.000	.000	.000	.435	.442	.255	.375	.000	.000
<i>Pgi-2</i>	.080	.086	.436	.108	.000	.080	.376	.526	.243	.643	.000	.076
<i>Pox-1</i>	.000	.000	.195	.000	.000	.000	.498	.000	.255	.500	.500	.499
<i>Pox-2</i>	.000	.000	.000	.036	.000	.262	.000	.000	.000	.095	.000	.000
<i>Sdh-1</i>	.467	.000	.265	.000	.166	.019	.498	.000	.382	.000	.180	.000
Average	.199	.054	.196	.043	.110	.111	.286	.230	.289	.313	.242	.112

^a Data from P. Barbier (unpublished data).

^b $h = 1 - \sum p_i^2$

OBSERVATIONS OF AN INTERMEDIATE PERENNIAL-ANNUAL POPULATION

In an attempt to look into the population biology and genetic changes of wild rice populations, we have continued monitoring several fixed sites in Thailand. An example is a population at site NE-1 near Saraburi that covers a roadside ditch and adjacent waste land. At our first visit in December 1977, seemingly intermediate perennial-annual plants scattered in a parched ditch were found to be an annual type by examining their seed-derived progeny. In December 1980 and May 1981, however, perennial-like plants dominated this site. A close observation in December 1983 revealed that different types were distributed, forming patches or subpopulations, some being persistent but others being more rapidly changing or short-lived (Table 3).

Examining seven subpopulations, we have learned the following:

- The plants in shallow water (December) were of annual type, propagating by seeds and having a low regenerating ability of excised stem segments and long awns, while those growing in deeper water were of perennial type, propagating by ratooning only and having a high regenerating ability and shorter awns.
- The regenerating ability of seed-derived plants was generally lower than that of juvenile-derived plants when plants sampled from the same patches were compared.

Table 3. Heterogeneity of subpopulations with different microenvironments in regenerating ability measurement, awn length, and allelic frequency from site NE-1 near Saraburi, Thailand.

Sub-population	Water depth Dec.83-Aug.84 (cm)	Plants/ m ^{2a}	Regenerating ability ^{b,c}	Awn length ^c (cm)	Frequency of ^c		Observation in 1985
					<i>Sdh-1</i> ¹	<i>Pox-1</i> ^{2A}	
A	0 – 25	—	0.2	11.0	100	100	Habitat destroyed
C	3 – 27	1760S	– (0.2)	10.4(8.1)	100(100)	100(100)	Extinct
F	27 – 55	0	0.6	7.1	86	100	
B	4 – 30	—	1.5	7.0	17	0	Persistent
D	16 – 50	412R	2.0 (2.4)	6.4 (6.1)	0 (0)	0 (0)	"
E	40 – 55	392R	0.0 (15)	7.4 (7.4)	55 (0)	33 (0)	"
G	25 – 64	304R	1.2 (1.9)	6.9 (6.8)	14 (0)	0 (0)	"

^aDensity of seedlings (S) and ratooned shoots (R) observed in June 1984.

^bRegenerating ability of stem cuts examined at Misima.

^cData obtained on plants raised from seed are shown. Those in parenthesis are due to plants raised from juveniles collected in the natural habitat and grown under the same condition.

- The perennial and annual types were fixed for different alleles at *Sdh-1* and *Pox-1*, but the perennial plants released some variants in their seed-derived progeny.
- All annual subpopulations observed in 1983 disappeared before January 1985 because of strong disturbance of the habitats by man, while perennial subpopulations persisted.

CONCLUSION

The intermediate population seemed to be a mixture of different perennial and annual types and readily responsive to selection imposed by environmental changes. The subpopulations can follow up environmental heterogeneity, both spatially and temporally, and can be differentiated into different perennial and annual types. They have high evolutionary potential. Even if this population is a product of hybridization between perennial and annual types, the evolutionary process is essentially due to differentiation-hybridization cycles (5).

Sano et al (27) considered that intermediate perennial-annual populations could be the immediate wild progenitor of *O. sativa*. This view is supported by the present observations, because it was found that:

- such intermediate populations carry a large amount of genetic variations, particularly when tested with juvenile-derived plants,
- they are highly evolutionarily flexible, and,
- some of the plants have a fairly high seed productivity and a perenniality as is found in *O. sativa* cultivars.

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