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THE EXTINCTION OF WILD RICE (*ORYZA PERENNIS FORMOSANA*) IN TAIWAN[1]

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ABSTRACT

We document the near extinction of Taiwan wild rice (*Oryza perennis formosana*) and suggest with evidence three possible causes for its disappearance; namely, hybridization with cultivated rice, changes in water management, and pollution of water by heavy application of chemical fertilizer. Taiwan wild rice contains a large amount of genetic variability and may be a very valuable genetic resource for rice crop improvement. We suggest that this genetic resource should be preserved, and that the study of the impact of changes in agricultural practice in Taiwan on ecological systems should be initiated.

INTRODUCTION

Modern human activities have brought very rapid changes in environmental conditions that have caused the disappearance of many plant and animal species. One aspect of these that has caused especial concern is the loss of relatives (and primitive varieties) of crop plants since such relatives are potential sources of genetic variability useful in crop improvement (Frankel and Bennett, 1970). This paper documents the near extinction of Taiwan wild rice, *Oryza perennis formosana*, and suggests possible reasons for its disappearance. This disappearance was in fact first noted by one of us (Wu, 1978) at the beginning of a study of Taiwan wild rice explicitly with regard to its potentially useful agronomic trait, seed dormancy.

HISTORICAL AND TAXONOMIC STATUS

Taiwan wild rice was first studied by Hara (1942) who noted that in the 1920's and 30's it grew abundantly in a large number of irrigation ponds and ditches around Sinchu and Taoyuan highland areas in northwestern Taiwan. This area was revisited in 1957 during a general study of wild rice by Oka and Chang (1961) but only three populations were found, each less than one thousand plants. In 1976, one of us, Wu, visited the sites studied by Oka and Chang but only found a small population of around seventy plants at Patu village, at the site reported by Oka and Chang. This population appeared on the edge of the pond on mud which had been brought up from dredging operations. Twenty three plants were sampled as tillers (without destroying the existing individuals) and were maintained in the field and greenhouse at the Institute of Botany, Academia

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Sinica. This small population had disappeared when we visited the site in October 1977. The data obtained from subsequent studies of the sampled plants and their progeny labeled "1976 sample" are reported here. Several individuals of this population were also transplanted to the edge of an adjoining drainage stream: one of these individuals still survived in February 1978, which disappeared but a young plant was found in April 1978 at the edge of a stream behind a pig farm building. Dr. H. I. Oka, who had visited the Patu village area in 1957, revisited the site with us in early 1978, confirming that in our search for wild rice we had indeed examined those sites studied by Oka and Chang (1961) nearly twenty years previously.

To see whether there were still wild rice seeds in the pond and stream beds where wild rice used to grow, in the spring of 1978 we took 40 samples of mud using a cylindrical core 15 cm in diameter and 15 cm deep from the Patu village site. It was impracticable to identify rice seeds directly from the mud, so attempts were made to germinate the buried seed. The soil samples were divided into two parts: one part was spread thinly in flats without pretreatment, whereas the other part was air dried, again moistened and then spread in the flats. After 2 weeks, one seedling of wild rice was observed from the predried sample. Many seedlings of *Leersia hexandra* sprouted from all samples and treatments.

The herbaria at the Botany Department, National Taiwan University, and the Institute of Botany, Academia Sinica, were checked for specimens of wild rice. Table 1 summarizes the findings which confirm the formerly greater abundance and wider distribution of wild rice in Taiwan. In the 1920's and 30's there were many collections, including one from Kaohsiung in the southern part of Taiwan. By 1940, collection numbers had dwindled and subsequent to this date all were from the Patu village area. In addition to such numerical evidence, notes accompanying the specimens indicated a far greater abundance of wild rice in former times. For example, on one specimen collected in the Patu village area in 1934 by S. Suzuki we note the remark "abundantly growing in wild areas, ponds and ditches".

Table 1. Records of Taiwan wild rice collections in the herbaria of the National Taiwan University and the Institute of Botany, Academia Sinica.

Year	1920	1930	1940	1950	1960	1970
# Collections	6	4	1	0	1	0
# Specimens	9	7	1	0	4	0

Note: The earliest collection 1923, the latest 1961.

In conclusion it is very likely that naturally occurring populations of wild rice in Taiwan are no longer represented by adult individuals although buried seed may exist. Certainly naturally occurring populations are on the verge of extinction.

There has been some discussion about the precise taxonomic status of Taiwan wild rice. Gotoh and Okura (1933) found the chromosomal number of Taiwan wild rice 2n = 24, and named it *Oryza formosana*, Masamune et Suzuki. Based on cytogenetic studies on hybrid rice, Morinaga (1940) labeled Taiwan wild rice *Oryza sativa* f. *spontanea* or *O. sativa* var. *fatua*. Hara (1942) suggested that Taiwan wild rice should be named *O. sativa* L.f. *spontanea* because he did not find distinct cytological and genetic differences between Taiwan wild rice and *O. sativa* L. Oka (1956) used *Oryza sativa spontanea* in his report on Taiwan wild rice. However, in 1961 Oka and Chang reclassified Taiwan wild rice as *Oryza perennis* based on the presence of rhizomes. The uncertain taxonomic status of Taiwan wild rice is also reflected in classification of herbarium specimens which we examined. Collections made in 1920 – 30 *Oryza sativa* was used, in 1940 *O. formosana,* Masamune et Suzuki, and in 1960 *O. perennis* Moench. *Oryza perennis* Moench has been suggested as the wild progenitor of cultivated rice *O. sativa* L. (Oka and Morishima, 1971; Oka, 1974). Combining Oka and Chang (1961) with the unique characteristics of Taiwan wild rice because of its geographical isolation from other wild rice types and of Taiwan's unique climate, we name *Oryza perennis formosana* for Taiwan wild rice.

CAUSES OF THE EXTINCTION OF WILD RICE

Based on observational and circumstantial evidence, we would argue that hybridization with cultivated rice, changes in water management, and heavy application of chemical fertilizer are the major causes for the decline of Taiwan wild rice.

Hybridization

Wild rice, unlike cultivated rice, is capable of a considerable degree of outcrossing: the degree of outcrossing was estimated to be 30.7% by Oka (1956). Moreover, it can hybridize easily with cultivated rice (Oka and Chang, 1961) and in nature gene flow is unidirectional from cultivars to the wild rice, because cultivars are predominantly selfing. The nature of the hybrid progeny will depend on whether the cultivated variety is of the *indica* or *japonica* type and to some extent, on the specific cultivar used. Since wild rice is more closely related to the *indica* type, the F_1 progeny from crosses with *indica* will have a relatively higher fertility than those from crosses with *japonica* (Chu *et al.*, 1969; Hinata and Oka, 1962).

The wild rice seeds collected at Patu village in 1929 and grown in Japan (Hara, 1942) all showed the typical wild rice morphological characteristics such as purple stems and leaf sheaths, red seed coat, decumbent growth habit, and long awns (Hara, 1942). These traits are known to be genetically controlled (Hara, 1942; Miu, 1964). However in the 1976 sample some of the plants showed traits typical of cultivated rice (Table 2). Moreover, in this sample there was large variation in certain quantitative traits as well as segregation for these traits in the selfed progeny. Awn length, which was also measured by Oka and Chang (1961) for a 1957 sample, shows a progressive decrease from 1929 to 1976. Seed set and pollen fertility of the 1976 sample were compared with that in the 1929 and 1957 collections (Table 3). The average percent good seed set decreased greatly from 1929 to 1976, and there was variation in seed set among clones. Similarly, pollen fertility decreased drastically from 1957 to 1976 and there was a corresponding increase in the variance.

Such changes in the characteristics of Taiwan wild rice are undoubtedly due to introgression following hybridization with cultivated varieties. Although the wild rice sampled in 1929, 1957 and 1976 was studied in three separate investigations and therefore grown under different conditions, it is unlikely that the large differences observed are due to growing conditions since the characters studied all have a strong genetic component and all the changes are in the direction predicted by the effects of introgression with cultivated forms. Such introgression has had effects at two levels. Firstly, characteristics of cultivated rice have been introduced into the wild rice. This would have the effect of lowering chances of survival of the hybrid progeny of wild rice since they would no longer have the full suite of characters essential for their survival in the wild. Secondly, any hybrids that do survive will have a lowered pollen and seed fertility. The lowered pollen fertility would in turn increase the chance of cross pollination with viable pollen of the cultivated varieties.

Such introgression must have been occurring for many hundreds of years, ever since rice cultivation started in Taiwan. It is therefore pertinent to ask why the intensity of its effects has

Table 2. Comparison of morphological traits of Taiwan wild rice sampled in different years and those of the cultivated rice Taichung 65.

	Awn length (cm)		Flag leaf width (cm)	Coloration			Growth habit
				Stem	Sheath	Seed coat	
1929[1]	mean	5.80	0.80	purple	purple	red	prostrate
1957[2]	mean range	4.48 2.0–6.0	–	–	–	–	–
1976[3]	mean range	4.17 0.0–5.9	1.00 0.65–1.52	17 purple 6 green	19 purple 4 green	13 red* 4 white	13 upright 10 prostrate
T–65[4]	awnless		1.58 1.5–1.8	light green	green	white	upright

1. Hara, 1942 (wild rice).
2. Oka and Chang, 1961 (wild rice).
3. Data taken from the cloned material grown in 31 cm pots in an open area (wild rice).
4. Grown from seed in 31 cm pots (cultivar).
* No seed was available from 6 plants.

Table 3. Seed set, pollen fertility and regeneration of Taiwan wild rice collected in different years (in %).

	N	Good seed		Good pollen		Regeneration[2]	Source
		Average	Range	Average	Range		
1929	–	80.0	–	–	–	–	Hara, 1942
1957	28	–	–	96.0	80.0–100	71.7	Oka & Chang, 1961
1976[1]	23	50.9	7.0–84.1	61.4	27.8–90.0	52.2	

1. Data taken from the cloned material grown in 31 cm pots in an open area.
2. Excised stems planted in flats with shallow water for estimating regeneration ability.

increased over the past fifty years. There are several reasons. Firstly, the extent of cultivation of rice has increased, particularly in the second crop; it is at this time (October) that the heading of cultivated and wild rice coincide. Secondly, the abundance of wild rice has probably been reduced for other reasons, outlined in the following sections. Thirdly, there has been a tremendous increase in the use of *japonica* varieties since the introduction of Taichung 65 (*japonica*) in 1930: introgression from these varieties will create a much greater level of sterility and inviability than introgression from the *indica* varieties. The latter were the types almost exclusively grown before and at the beginning of this century.

Table 4. Analysis of variance of percent good seed of Taiwan wild rice collected in 1976[1].

Source of variation	df	SS	MS	F
Among genotypes	22	2.171	0.099	3.81**
Within genotypes	46	1.176	0.026	

1. Data taken from cloned material grown in 31 cm pots in an open area.

Changes in water management

Throughout the world, and undoubtedly also in Taiwan, the natural habitats of wild rice are marshy, low-lying areas, characterised by fluctuating water levels which permit periods of seedling establishment. In the past in Taiwan, most such areas have been destroyed and converted to paddy fields, a process that has continued well into this century. The Taoyuan and Sinchu regions are on relatively high ground and have been dependent largely on direct rainfall rather than river systems for rice paddy irrigation. Moreover, rainfall in this area is very uneven from month to month and from year to year, with prolonged dry periods occurring particularly in the fall (Table 5). Because of such unevenly distributed rainfall, farmers have in the past used ponds to store water for irrigation during dry periods. These ponds have therefore been characterised by fluctuating water levels and have formed an excellent refuge for wild rice, following conversion of much of the wet marshy areas into paddy.

Table 5. Monthly precipitation in mm from 1938 to 1947 in Sinchu area, Taiwan[1].

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1941	217	178	309	301	102	693	120	202	33	19	81	121
1942	72	110	48	101	217	341	192	271	127	7	15	20
1943	37	181	142	194	72	206	318	111	32	1	28	33
1944	13	106	207	265	494	535	54	277	31	6	43	100
1945	77	372	49	72	516	246	29	215	131	28	1	31
mean[2]	65	127	182	200	283	403	156	181	96	28	31	40

1. From Agrometeorological Bulletin by Taiwan Weather Bureau, Agrometeorological Section.
2. Average precipitation of ten years from 1938 to 1947.

A fluctuating water level is essential for the germination of wild rice, since the seeds remain dormant if submerged in water; they will only germinate after exposure to air and drying. In the laboratory, seed submerged in water at room temperature remained dormant for more than 8 months with little loss of viability, and dormancy could be readily broken by allowing the seeds to dry for a period. A similar observation made under field conditions at Patu village has already been mentioned. The 1976 sample came from seeds which had germinated on mud which had been dredged up from the pond. Early collections of wild rice in the herbaria also showed variations in the decumbent habit, length of internodes, rooting at nodes, and rhizome formation, suggesting collection from a wide range of water levels.

Since 1964, irrigation in the Taoyuan area has been stable and abundant because of construction of the Shimen dam and reservoir. This stable water supply had two impacts on the wild rice populations. Firstly, since water levels were kept constant, new plants could not be recruited from the seed pool since the seeds were constantly submerged in water. Secondly, the remaining habitats of wild rice and the irrigation ponds were destroyed since they were no longer needed. For example, at Patu three neighbouring ponds where the wild rice used to grow were modified. A factory now sits on one of them, one has been drained dry, and the third was dredged deep for raising fish and its edge area filled to build a pig farm.

Fertilizer application

The intensive agricultural practice in Taiwan involves the application of a large quantity of chemical fertilizer to replenish plant nutrients in soil. The records show the amount of chemical fertilizer allocated for rice increased rapidly in the past 30 years (Table 6). For example, the amount

Table 6. Average quantity of chemical fertilizer allocated for the rice crop in Taiwan (Kg/hectare)[1].

Year	Nitrogen	Phosphate	Potassium
1949	23.34	7.82	–
1954	83.39	29.24	11.97
1959	89.04	34.35	21.88
1964	139.95	44.22	38.60
1969	156.59	27.58	33.98
1974	133.76	33.62	41.66
1976	145.74	41.87	52.26

1. From Taiwan Food Statistics Book by Food Bureau, Taiwan Provincial Government.

of nitrogen application increased more than six times in the 15 years from 1949 to 1964. This heavy fertilizer application leads to pollution of waterways and ponds because more than 25% of the chemical fertilizer applied to rice paddy fields flows into streams and ponds (Prof. K. H. Hung, personal communication). Such fertilizer application can therefore shift the balance of the aquatic ecosystem due to differential response of species to major nutrients. We observed that an aquatic grass, *Leersia hexandra,* grows very densely above the water surface, and its stems and runners often form a 1 to 2 feet thick layer covering the soil under water. Its lush growth in habitats occupied previously by wild rice suggests that it has likely outcompeted wild rice by virtue of a superior response to nutrient enrichment of the water.

To test the hypothesis that *Leersia hexandra* has outcompeted wild rice by its superior responses to water polluted by fertilizer, the effects of *L. hexandra* on the growth and survival of wild rice were examined in an experimental field. On March 21, 1977, 4 replicates of 23 genotypes of wild rice sampled in 1976 were planted by single tillers in the field. (The plantation originally was not designed for a study of the effects of *L. hexandra* on survival of wild rice). The field was left without disturbance. On May 30, 1978 the plantation was thickly covered by weeds. The major weeds were *Leersia hexandra, Murdania Keisak* and *Alternanthera philoxeroides,* and some minor components were *Echinochloa crusgalli* Var. *formosensis, Cyperus haspen* and *Panicum repens. Leersia hexandra* covered thickly more than one quarter of the plantation at one corner. There were very few other species growing among *Leersia.* The mortality of wild rice growing in the *L. hexandra* area was 52.2% (12/23), and that in the non-*Leersia* area was 26.1% (6/23) and 13.0% (3/23) respectively, in two of the replicates. The fourth replicate was covered partly by *Leersia* and partly by other weeds, and the mortality of wild rice was 30.4% (7/23). The fourth replicate was excluded from comparison because of the partial cover of *Leersia.* The mortality of wild rice growing with *Leersia* was significantly higher than that growing in the non-*Leersia* weeds area. The fresh weight above the ground of both weeds and surviving wild rice was compared. The average fresh weight of wild rice growing in *L. hexandra* and in non-*Leersia* weeds was 155.5 g/plant and 557.5 g/plant respectively; the difference was highly significant (Table 7a). The mean fresh weight of *L. hexandra* and non-*Leersia* weeds was 440.7 g/0.25m^2 and 603.6 g/0.25m^2 respectively; these are highly significantly different (Table 7b). The stand of *L. hexandra* was tall (60 – 70cm) and thick. The major non-*Leersia* weed *Murdania Keisak,* which is succulent and prostrate (20 – 30cm tall), contributed most of the fresh weight of the non-*Leersia* weeds. The plantation was

Table 7a. Analysis of variance of fresh weight of Taiwan wild rice growing with *Leersia* and non-*Leersia* weeds.

Source of Variation	df	SS	MS	F
Between Groups	1	1147126.4	1147126.4	25.63**
Within Groups	29	1297847.8	44753.4	
Total	30	2444974.2		

Table 7b. Analysis of variance of fresh weight of *Leersia hexandra* and other weeds.

Source of Variation	df	SS	MS	F
Between Groups	1	225914	225914	375.13**
Within Groups	26	185658	602.23	
Total	27	411572		

surrounded by a rice paddy and was lower than the rice paddy on three sides. Water from the rice paddy continuously flowed into the plantation and accumulated in a depressed corner where *Leersia* flourished. Although we did not analyze the water from the rice paddy, it can be assumed to have contained high nitrogen and other nutrients since heavy chemical fertilizer was used in the surrounding rice paddy. The observations seem to support the hypothesis that *Leersia* can exclude wild rice where water is polluted by chemical fertilizer.

There is a possibility that other factors such as pollution with pesticide residues may have been important in the survival of wild rice. However, there is no direct evidence to support this suggestion.

DISCUSSION AND CONCLUSIONS

This paper has provided clear cut evidence that Taiwan wild rice is on the verge of extinction, and has identified three factors, namely hybridization, water management, and fertilizer pollution, as being likely causes of such extinction. It is obviously difficult to measure the relative roles of these, particularly post facto; however, an essential ingredient to the process of extinction may be that these factors interact in a synergistic way. For example, the effects of hybridization are made more severe by population decline due to other causes. Clearly the effects of factors not investigated may also have been important. It is only by a thorough and broad examination of the ecosystem effects of changes in agricultural management that a clearer understanding of the relevant forces can be obtained. The data on the effects of hybridization, in themselves, provide a unique illustration of how this process can promote the extinction of a wild relative of a crop plant. This process has, for example, been postulated as being important in the extinction of wild corn (Mangelsdorf *et al.*, 1964) although its importance has been disputed. In Taiwan, it would be interesting to trace the dynamics of this process in more detail, particularly to assess the relative roles of the increase in cultivation of the second crop, the increase in use of *japonica* varieties (and therefore hybrid sterility), and the decline in numbers of the wild rice. This would help define more clearly what pre-conditions are required for extinction by hybridization to be a relevant factor in other crops.

The extinction and loss of any group of plants or animals is a source of serious concern from both an aesthetic and practical standpoint. The case of Taiwan wild rice is by no means unique; many other wild rice species have receded from cultivated areas and some of them are becoming extinct (Chang, 1976). Our own studies on seed germination (Wu, 1978), protein content (Wu and Lin, 1978), and electrophoretic variation show that Taiwan wild rice stores a large amount of genetic variability which may be valuable for crop improvement (see also Oka and Chang, 1961). Therefore, there seems to be great value in preserving this genetic resource and even restoring the species to its natural habitat.

The realization that Taiwan wild rice was on the verge of extinction was a timely one, but essentially accidental. Clearly there has been inadequate monitoring of the impact of the dramatic changes in agricultural practice in Taiwan on ecological systems. There is also a parallel with the DDT situation. Not until there was alarm among ornithologists about the decline in abundance of rare bird species, were the far reaching effects of DDT investigated and brought to light. Until we have a baseline body of information on natural and semi-natural ecosystems, such changes are likely to go undetected. In Taiwan such baseline ecological studies are nearly non-existent. We feel that the present paper provides a strong argument for initiating more such studies.

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