

Ecology of wild rice planted in Taiwan

II. Comparison of two populations with different genotypes

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Abstract. Two wild-rice (*Oryza rufipogon*) populations, the Taiwan wild rice (T) and an F₅ population from an annual x perennial cross (H), were compared. They showed differences in behavior when tested under semi-natural conditions. Both declined similarly when subjected to competition with *Leersia hexandra*, but population H was somewhat more tolerant to *Leersia* than T and slowed down the growth of *Leersia* slightly. Although both had similar regenerating scores of excised stem segments showing perenniality, population H was recruited mainly by ramets and T mainly by genets. This seemed to bring about differences in demographic characteristics as represented by transition coefficients, and in the mode of clumping of plants. Furthermore, population H showed genetic changes toward higher perenniality as a result of selection, but population T did not. The absorption of cultivar genes by population T could be a subsidiary cause of its extinction.

Key words: Competition; Demographic pattern; Genets; Perenniality; Ramets; Response to selection; Spatial distribution.

Introduction

In the preceding paper (Oka, 1991), the responses of two wild-rice (*Oryza rufipogon* Griff.) populations to different biotic environments in Taiwan were dealt with on the basis of their mean measurements. Of the two populations, one (called population T) was progenies of Taiwan wild rice which became extinct recently, and the other (called population H) started from F₅ bulk seeds of a cross, an Indian annual strain (W106) x a Philippine (Mindanao) perennial strain (W1294). The T population was a natural hybrid between the original wild rice and cultivars (Oka and Chang, 1961), and its contamination with cultivar genes was supposed to be a factor promoting its extinction (Kiang *et al.*, 1979). To reexamine this point, the H population not containing cultivar genes was tested in comparison with T for

their survival in different environmental conditions. The two populations showed similar behaviors but significant differences, as are reported in this paper.

Materials and Methods

The T population planted was derived from seeds multiplied in a greenhouse of National Institute of Genetics, Mishima, Japan. The original seeds came from about 20 plants of three populations (called A, B and C) each in a natural stream running through rice fields in Pate village, Taoyuan Municipality, which were collected by Dr. W. T. Chang in 1958. The plants in the original habitats showed characters of wild rice like high seed shedding, positive phenol reaction (black hulls), apiculus coloration, and long awns, but their selfed progenies segregated for these characters indicating the hybridity of the original plants with rice cultivars (Oka and Chang, 1961). The occurrence of plants with negative phenol reaction suggests that the donors of cultivar genes have been Taichung 65 and

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other Japonica types which were extended after 1930 in this area.

The H population was derived from an F_5 bulk seed between two *O. rufipogon* strains, W106 (an Indian annual type) and W1294 (a perennial type from Mindanao, Philippines). The hybrid population consisting of 150 or more plants in each generation, were raised at Mishima in an automatic shortday field without deliberate selection. Seeds dispersed on the ground were gathered for the next seeding. The population segregated for various characters differing between the parents, but was little contaminated by cultivar genes.

The seeds of the two populations were sown in trays at Taichung in late July, 1980, and seedlings were transplanted at five locations: Nankang; Pate, Taoyuan; Shisinpa, Taichung; Chiayi; and Pingtung, as mentioned in the preceding paper (Oka, 1991). At Nankang, a part of the plots was dug down so as to keep water about 10 cm deeper. Also, weeding was made by hand in a part of the plots once a year in 1980, 1981 and 1982; at Taichung, in September 1980. Each plot was tilled, denuded, puddled and irrigated, and 100 to 800 seedlings of each of the two populations were trans-

planted with a single plant per hill at a 20×30 cm spacing. At Chiayi, planting was made in two rows along the fringe of an irrigation ditch slanted a priori, at a 20 cm spacing. Thereafter, no intervention was made in principle.

At Taichung where the wild rices declined rapidly, second planting was made in early July, 1981. A small pond (3×3 m, 0.3 m deep) was dug, and ratoons from the first experiment were planted on the slanted fringe of the pond, with about 30 plants of populations T and H in three rows (together with other strains which will be reported elsewhere). At Taoyuan where the wild rices also decayed rapidly, second planting was made in April 1982. But the plants were depressed again by *Leersia hexandra* similarly as in the first planting. The data from this experiment will not be presented except for inclusion of a part in analysis of variance (given in Table 2).

The experimental plots were visited at an interval of about two months to take records, but the data for biomass and density (plant number) were recorded in June-July and November (December for 1980). The methods of estimating biomass of rice and weeds were

Table 1. Mean estimates of changes in relative biomass ($\sin^{-1}\sqrt{\%}$) and density relative to initially planted number ($1n p$) of wild-rice populations per 100 days, mean weed biomass (g/m^2 , dry matter at the end of season) and growth rate of *Leersia hexandra* ($\text{g}/\text{m}^2/100$ days)

Location	Season ^a	No. of years		Change in 100 days				Mean weed biomass (g/m^2)		<i>Leersia</i> biomass change	
		T	H	Biomass ^b		Density ^c		T	H	T	H
Nankang ^d	Winter	2	3	0.0	-1.8	-0.42	-0.29	329	282	31	11
	Summer	2	4	-24.9	-7.6	-1.33	-0.31	296	314	123	81
Pate,	Winter	1	1	-19.6	-18.7	-0.72	-1.02	191	191	81	81
Taoyuan	Summer	2	2	-20.6	-15.3	-1.78	-0.29	242	254	143	158
Shisinpa,	Winter	2	2	-1.8	-15.5	-0.66	-0.72	808	842	22	44
	Taichung	Summer	2	2	-40.5	-38.7	-1.45	-1.29	570	495	509
Chiayi	Winter	3	3	2.5	4.4	-0.09	-0.10	34	20	0	0
	Summer	4	4	-4.1	-5.9	-0.16	0.01	25	18	15	0
Pingtung	Winter	3	3	-10.5	-4.8	-0.04	-0.19	89	34	0	0
	Summer	4	4	5.5	4.1	-0.86	0.04	84	26	0	0

^aWinter - November to July; Summer - July to November.

^bFor example, % biomass on 130 days after planting was 94% or 75.8 in $\sin^{-1}\sqrt{\%}$ and that on 299 days after planting was 46% or 42.7 in $\sin^{-1}\sqrt{\%}$. Then, the decrease was 33.1 in 169 days or -19.6 per 100 days.

^cFor example, density on 112 days after planting was 82% of the initial number or -0.198 in logarithm, and that on 324 days after planting was 59% or -0.528. Then, the change in density was $-0.528 - (-0.198) = -0.330$ in 212 days, or -0.156 per 100 days. Minus sign shows decrease.

^dMean for shallow and deep-water parts of experimental plots.

described previous papers (Oka, 1984, 1991). The density of wild rice was shown by the percentage of plant number in each plot to the initially planted number.

For estimating the rate of changes, since the November to July period and July to November period differed in the number of days and the date of visit of the experimental site also differed each by each, the date of observation was represented by the number of days from initial planting and the rate of change was shown by the change per 100 days. Each estimate recorded at a date was converted into $\sin^{-1}\sqrt{\%}$ for percent biomass and into natural logarithm for density, and from the difference (d) between two records with an interval of n days, the change per 100 days was estimated as $100d/n$ (cf. Table 1, footnote).

Starting from the second year (1981), plant recruitment was an object of observation. A plant occurring apart from an old stubble was considered new, and was designated with a small bamboo stick. Whether it was a ramet (vegetative sprout) or a genet (seedling) was judged by its outward appearance and relation to its nearest old plant. When a new plant grew several months, it became indistinguishable from old ones.

For estimating the number of buried seeds and rate of predation by animals, several soil samples (10×20 cm, 3 cm deep) were taken from each plot at the end of the season, dried, smashed to pieces and sieved to count the numbers of complete and broken seeds.

Results

Depression of Wild-rice Populations in Response to Growing Weeds

The mean rates of changes in relative biomass and density per 100 days of wild rices are summarized in Table 1, together with total weed biomass (g/m^2) and growth rate ($\text{g}/\text{m}^2/100$ days) of *Leersia hexandra*. The pattern of changes in density with time is depicted in Fig. 1. Populations T and H both declined rapidly at Taoyuan and Taichung, more slowly at Nankang, and persisted for four years at Chiayi and Pingtung. In general, decline was more rapid in summer than in winter, and the rate of reduction in relative biomass and density were greater in population T than in H. The growth rate of *Leersia hexandra* was greater in summer than in winter, and on the average greater with population T than with H. No *Leersia* occurred at Pingtung.

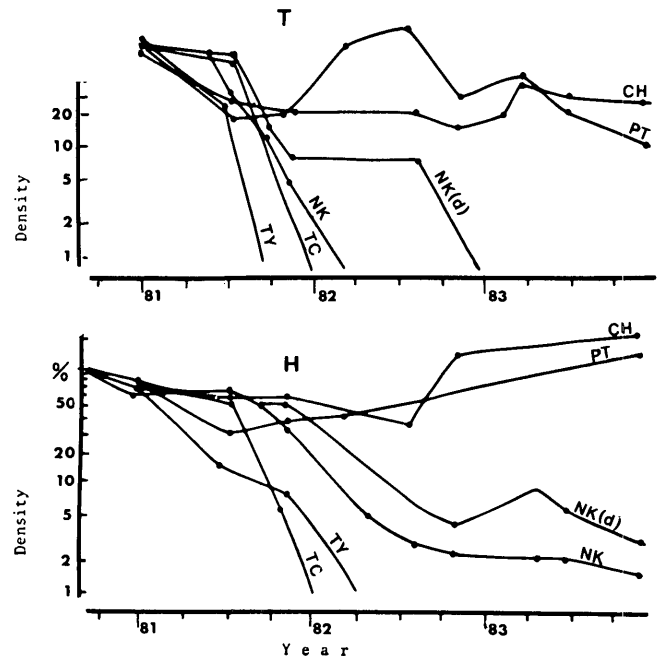


Fig. 1. Density of wild rice in percent of initially planted number, changing with time at different locations: NK—Nankang, (d)—Deepwater side, TY—Pate, Taoyuan, TC—Shisinpa, Taichung, CH—Chiayi, PT—Pingtung.

At Chiayi, *Leersia* appeared in October 1982, but did not grow vigorously.

Analysis of variance of these data showed that the differences between populations T and H were significant (Table 2). Population H was more resistant to weeds and showed a lower growth rate of co-occurring *Leersia* than population T. The data suggest that the mode of interaction between wild rice and weeds differs according to the genotype of wild rice.

Mode of Plant Recruitment

In both populations T and H, starting from the second year of planting, a part of initial plants gradually decayed and were replaced by new plants, although the birth or death of very young plants hidden under weeds could not be recorded precisely. The rate of recruitment or population turnover was described by the percentage of newly occurring plants recorded until November of a year to the total surviving plants. It tended to become high with time (Table 3a).

In population T, almost all new plants appeared to be seedlings (genets), while in population H, many of new plants were vegetative sprouts (ramets). In the second planting at Taichung, however, it was found that

Table 2. Analysis of variance of changes in biomass and density of wild-rice populations in 100 days and measurements of weeds

Source of variation	df	Biomass change (sin ⁻¹ %)	Density change (ln p)	Weed biomass (100g/m ²)	df ^a	<i>Leersia</i> biomass change ^b
Population, T:H	1	173	2.69**	13.04**	1	492*
Season	1	564**	7.53**	29.89**	1	9087**
Population x Season	1	362*	3.66**	0.77	1	451*
Location & Year ^c	22	398**	0.71**	13.28**	15	1074**
(Loca. & Year) x Season	22	191**	0.69**	3.61**	15	1075**
Other interactions	44	63	0.28	0.98	30	100

^a Data for Chiayi and Pingtung where *Leersia* was rare or absent were excluded.

^b Dry-matter estimate in g/m², change per 100 days.

^c Nankang 1981, '82, '83, (weeded part) '81, '82 '83, (deepwater part) '81, '82, and '83. Taoyuan 1981, (2nd planting) '82, and '83. Taichung 1981, (weeded part) '81, (2nd planting) '82, '83, and (deepwater part) '83. Chiayi 1981, '82, and '83. Pingtung 1981, '81, and '83.

*P<0.05, ** P<0.01.

Table 3. Population turnover and survivorship

a) Percentage of newly occurring plants to total existing plants in November, classified into genets (g) and ramets (r) partly by guess-estimation

Location	Population T						Population H					
	1981		1982		1983		1981		1982		1983	
	g	r	g	r	g	r	g	r	g	r	g	r
Nankang	20	1	67				2	11	5	19		
"Deep plot	6		35				3	18	7	31		
Taichung	61*							67*				
"2nd exp.			42	10	99*				2	12	93*	7*
Chiayi	9		37		41		4	17	9	37	7	28
Pingtung	70		79		43		1	27	6	25	5	60

*Population declined and was close to extinction.

b) Percent survival per year estimated for old (occurring in the preceding year) and new (occurring in the given year) plants

Location	Population T						Population H					
	1981		1982		1983		1981		1982		1983	
	Old	New	Old	New	Old	New	Old	New	Old	New	Old	New
Nankang (mean)	10	47	15	19			67	19	13	55		
Taichung	4	6					3	15				
"2nd exp.			57	28	0	71			80	57	0	-
Chiayi	36*	16	55	17	93	58	46	50	17	68		
Pingtung	8*	23	32	74	19	31	31	35*				

*About 27% of old plants at Chiayi, and 33% at Pingtung died of yellow dwarf virus.

stems of T plants lodged in the pond produced ratoons from the nodes.

As mentioned, both populations are hybrids and one of the parents is a wild rice of perennial type. When estimated by the regenerating ability of excised stem segments (rooting of stem cuts at maturity, put in

moist sand for 4 days, scored zero for no rooting, and scored 3 for very high rooting; cf. Oka and Morishima, 1967), there was no significant difference between populations T and H in the initially planted material, namely, 1.65 ± 0.09 ($n=77$) for T and 1.76 ± 0.096 ($n=84$) for H (standard errors are shown). Thus, both were moder-

ately perennial and capable of vegetative propagation. It remains unexplained why such a difference in the mode of recruitment has come about between the two populations, T mainly by genets and H mainly by ramets. The H plants increased mainly by cespitose growth of tillers and incidentally by ratooning from lodged stems. The T plants showed a lower degree of cespitose growth. Possibly, their possession of cultivar genes has restricted indeterminate vegetative growth. On the other hand, the seeds of T plants with cultivar genes would have a lower degree of dormancy than those of H plants and germinated easily bringing about many seedlings. The seeds of H plants would have more pronounced dormancy.

The survivorship of old (remaining from the preceding year) and new (occurring in a given year) plants was also estimated so far as possible. It fluctuated widely, and no significant difference was detected between the two populations were significant.

although on the average H plants appeared to have higher survivorship than T plants in both old and new classes (Table 3b).

The mean number of seeds produced per plant,

recorded in the first planting at Nankang (December 1980, 22 plants for both T and H) was 77 ± 13.3 for T and 83 ± 17.8 for H, and the estimate of reproductive allocation (%) was 28.8 ± 2.8 for T and 25.0 ± 1.4 for H plants. Similar values were obtained also at Taichung. Population H showed a larger number of buried good seeds ($505/m^2$ on the average for 5 locations in 1980–1983) and a lower rate of predation by animals (58%) than population T ($182/m^2$, 77%). The differences between the two populations were significant.

Demographic Aspects

A population of wild rice in a habitat may be regarded as consisting of individuals at three age classes, *i. e.*, mature plants (M, capable of reproduction), juvenile plants (J, from genets or ramets, incapable of reproduction), and seeds (S, buried in soil). The densities of plants at the three age classes will change from time to time.

The columns showing densities of the three age classes in December 1980, July 1981, December 1981, and December 1982 were estimated from field records (Table 4, as means when observations were repeated,

Table 4. Columns showing age structure of populations T and H (number/ m^2)

Location/ plant stage (Interval)	Population T				Population H			
	Dec. 1980	July 1981	Dec. 1981	Dec. 1982	Dec. 1980	July 1981	Dec. 1981	Dec. 1982
	(1)	(2)	(3)		(1)	(2)	(3)	
Nankang,								
Mature (M)	13.3	7.32	1.61	0.39	11.7	10.1	8.31	1.27
Juvenile (J)	0	0.67	0.66	0.30	0	2.73	0.47	0.38
Seed (S)	113	99	58	17	306	101	389	400
Taichung,								
Mature (M)	11.0	5.81	0.37		11.1	5.89	0.34	
Juvenile (J)	0	5.10	0.67		0	1.35	1.13	
Seed (S)	160	73	17 ^b		547	51	34	
Chiayi,								
Mature (M)	7.81	2.70 ^a	2.82	1.16	8.48	3.86	5.27	3.59
Juvenile (J)	0	0.51	0.13	0.89	0	2.18	1.41	2.44
Seed (S)	162	83	749	217	660	67	393	650
Pingtung,								
Mature (M)	15.9	1.74 ^a	2.57	0.83	16.1	4.91	7.23	5.01
Juvenile (J)	0	6.70	1.33	2.08	0	3.90	1.05	4.75
Seed (S)	262	167	424	733	777	133	1327	1353

^aDamaged by yellow-dwarf virus disease.

^bEstimated from indirect sources.

excluding Taoyuan where wild rices declined rapidly). The matrix of transition coefficients between two columns and transition formulas were modeled as follows (cf. Silvertown, 1982, p. 8-11):

Transition coefficient

- a_{mm} – Survivorship of mature plants
 a_{jm} – Survival and growth of juvenile plants
 a_{mj} – Sprouting of new plants from a mature plant
 a_{sj} – Seed germination and seedling survival
 a_{ms} – Seeds per plant minus loss due to animal predation
 a_{ss} – Survival of seeds in soil

Transition matrix

$$\begin{vmatrix} a_{mm} & a_{jm} & 0 \\ a_{mj} & 0 & a_{sj} \\ a_{ms} & 0 & a_{ss} \end{vmatrix} \times \begin{vmatrix} M_1 \\ J_1 \\ S_1 \end{vmatrix} = \begin{vmatrix} M_2 \\ J_2 \\ S_2 \end{vmatrix}$$

Transition formula

$$\begin{aligned} M_2 &= M_1 a_{mm} + J_1 a_{jm} \\ J_2 &= M_1 a_{mj} + S_1 a_{sj} \\ S_2 &= M_1 a_{ms} + S_1 a_{ss} \end{aligned}$$

The transition coefficients were estimated from various records taken from the field and were adjusted by iteration so as to give M_2 , J_2 and S_2 in conformity with field records. It was assumed that $a_{mj} = 0$ for population T which showed few vegetative sprouts. The transition coefficients thus obtained for three time

Table 5. Estimates of transition coefficients for three time intervals (1: Dec. 1980-July 1981; 2: July 1981-Dec. 1981; 3: Dec. 1981-Dec. 1982)

Location/ interval	Population T ($a_{mj} = 0$)					Population H						
	a_{mm}	a_{jm}	a_{sj}	a_{ms}	a_{ss}	a_{mm}	a_{jm}	a_{mj}	a_{sj}	a_{ms}	a_{ss}	
Nankang,												
1	0.551	0.206	0.0059	(0) ^a	0.885	0.866	0.085	0.188	0.0017	(0) ^a	0.327	
2	0.377	0.577	0.0066	3.82	0.300	0.765	0.205	0.022	0.0025	36.8	0.166	
3	0.162	0.196	0.0052	5.30	0.147	0.145	0.172	0.036	0.0002	37.2	0.232	
Taichung,												
1	0.528	0.287	0.0320	(0) ^a	0.456	0.531	0.181	0.090	0.0064	(0) ^a	0.093	
2	0.023	0.046	0.0092	0	0.239	0.034	0.104	0.145	0.0044	4.68	0.137	
Chiayi,												
1	0.346	0.254	0.0031	(0) ^a	0.512	0.455	0.672	0.206	0.0006	(0) ^a	0.102	
2	0.896	0.785	0.0016	259.5	0.582	0.999	0.647	0.295	0.0041	98.9	0.168	
3	0.392	0.416	0.0012	38.5	0.145	0.578	0.388	0.374	0.0012	104.3	0.254	
Pingtung,												
1	0.110	0.340	0.0260	(0) ^a	0.637	0.305	0.350	0.194	0.0010	(0) ^a	0.171	
2	0.154	0.344	0.0080	175.7	0.500	0.862	0.769	0.164	0.0015	265.8	0.170	
3	0.134	0.365	0.0049	238.2	0.284	0.598	0.653	0.443	0.0012	119.1	0.185	

^aAssumed to be zero as no seeds are produced by July.

Table 6. Correlation between transition coefficients and between those and the growth rate ($g/m^2/100$ days) of *Leersia hexandra* (shown by L). (above diagonal - population H, $df = 9$; below diagonal - H and T, $df = 20$)

Trans. coef.	a_{mm}	a_{jm}	a_{mj}	a_{sj}	a_{ms}	a_{ss}	L
a_{mm}		0.42	0.25	0.08	0.61	0.24	-0.59
a_{jm}	0.51*		0.55	-0.29	0.87*	-0.29	-0.48
a_{mj}	—	—		-0.20	0.30	0.19	-0.20
a_{sj}	-0.23	-0.19	—		-0.30	-0.46	0.42
a_{ms}	0.44	0.66**	—	-0.24		0.04	-0.57
a_{ss}	-0.00	-0.06	—	0.41	0.04		-0.25
L	-0.45*	-0.47*	—	0.12	-0.50*	-0.18	

* $P < 0.05$, ** $P < 0.01$.

“—” As a_{mj} was assumed to be zero in population T, its mean for T and H was not obtained for correlation computation.

intervals are given in Table 5, which showed wide variations according to time and location. Generally, a_{sj} was quite low suggesting a low probability of seed germination and seedling establishment. On the average, population T had larger values of a_{sj} and a_{ss} than population H, while H had larger values of a_{mm} than T. When a population declined (*e. g.*, Taichung, time interval 2), various coefficients for survival and recruitment were reduced although a_{ss} remained unaffected. In view of the wide fluctuation of transition coefficients, however, it seems difficult to predict the fate of a population in the future on the basis of transition matrix.

Correlations between different transition coefficients were investigated (Table 6). The result showed that a_{jm} and a_{ms} were correlated. When the data for populations T and H were pooled to increase degrees of freedom, a_{mm} and a_{jm} also were found to be correlated. As mentioned, an agent conditioning wild-rice populations is the growth of *Leersia hexandra*. Its growth rate ($\text{g}/\text{m}^2/100$ days) was estimated for each time interval at each location, and its correlations with transition coefficients were also computed (Table 6). It was found that a_{mm} , a_{jm} and a_{ms} were affected by *Leersia* significantly.

Spatial Distribution of Wild Rices

The initial planting in experimental plots was made evenly at a certain spacing with a plant per hill. As the plants were depressed by weeds, the surviving plants tended to form clumps. Some wild-rice plants were dispersed outside the plots and grew transgressing the plot border. In 1983, at Nankang and Taichung (second planting), the spatial distribution of plants was surveyed as follows: When the interval between two neighboring plants was greater than 0.5 m, they were

considered to belong to different clumps or groups. When no wild rice occurs in a 1×1 m area, the area was taken as zero. Thus, the number of subplots with zero, one to several plants were counted (Table 7).

The data obtained were tested for their fitness to binomial, Poisson and negative binomial distributions. The distribution data for populations T and H both did not fit binomial at all, and fitted negative binomial distribution well. To the Poisson distribution, population T showed fitness suggesting that its distribution was nearly random, while population H did not fit suggesting its non-randomness of distribution. From negative binomial distributions fitted, clumping index, $I = \text{mean}/k$ was computed (*cf.* Pielou, 1969, the measurement of aggregation). Population H showed a much larger I value than population T. Thus, the pattern of aggregation differed between populations T and H. Probably, the high rate of clumping in population H is due to its regeneration by vegetative sprouting.

Changes in Population Structure Due to Selection

Both populations T and H were hybrids, as mentioned. To examine their selectional changes due to experimental planting, the seeds initially planted (1980) and those from plants propagated for three years (1982, mixture of seeds from different locations) were planted in a uniform condition at Taichung and tested for some characters.

The result showed that the regenerating score of excised stem segments increased significantly in population H, indicating that recruitment by vegetative means resulted in selection for higher vegetatively propagating ability (Table 8). This was confirmed by testing the seeds in Mishima again. The 1980 seeds showed a mean regenerating score of 1.65, and the 1983

Table 7. Trend to clumping of surviving plants in 1983 (pooled data from Nankang and Taichung, second planting)

Population	Plants/group ^a						Chi-square		df	k	I^c
	0 ^b	1	2	3	4	5	Poisson	Negative binomial			
T	81	19	3	1	0	0	2.2	0.19	103	1.663	0.162
H	52	17	8	1	3	1	49.9**	0.32	81	0.702	0.920

** $P < 0.01$

^aWhen the interval between two neighboring plants was greater than 0.5m, the two plants were considered to belong to different groups or clumps.

^bNumber of 1 m^2 areas in which no wild-rice plant occurs.

^cClumping index $I = \text{Mean}/k$, k is given by negative binomial formula. (Pielou, 1969, The measurement of aggregation)

Table 8. Some characters and isozymes compared between populations initially planted (1980) and naturally recruited for two (1982) or three (1983) years (mean for seed samples from different locations)

a) Character values (measured at Taichung)

Population	Year	No. of plants	Regenerating score ^a of stem segments	Anther length (mm)
T	1980	77	1.65±0.79	3.1±0.45
	1982	29	1.72±0.69	3.2±0.23
	<i>t</i>		0.4 ^{ns}	0.3 ^{ns}
H	1980	84	1.76±0.58	2.7±0.51
	1982	40	2.22±0.67	3.3±0.50
	<i>t</i>		2.9**	4.3**

^a Stem, segments with a node (above the first or second elongated internode) are excised at seed maturity and put in moist sand to observe rooting in 4 days. Score 0-no rooting, 3-full rooting, several roots 2 cm or longer (Oka and Morishima, 1967).

b) Population H, allele frequencies at 3 loci (observed at Mishima)

Year	No. of plants	<i>Pox-1</i>		<i>Acp-1</i>		<i>Sdh-1</i>		H	\hat{F}
		2A	4A	-4	+9	1	3		
1980(F _s)	21	0.55	0.45	0.50	0.50	0.60	0.40	0.49	0.33
1983	102	0.24	0.76	0.33	0.67	0.35	0.65	0.41	0.47
Homogeneity chi-square			**		**		**		

**Significant at 1% level.

H - Average gene diversity: $\frac{1}{n} \sum_j (1 - \sum_i x_{ij}^2)$

(x_{ij} : Frequency of allele *i* at locus *j*)

\hat{F} - Fixation index: $\frac{1}{n} \sum_j (1 - h_j / (1 - \sum_i x_{ij}^2))$

2A, 4A, etc. - Alleles identified at each locus.

seeds had a mean score of 2.04, the difference being significant statistically. But population T showed no such difference between the 1980 and 1982 or 1983 seeds. Anther length is another character distinguishing between the perennial and annual types of the common wild rice (Morishima *et al.*, 1984). It increased significantly in population H but showed no significant change in population T. These data suggest that population H was selected toward a perennial type through field recruitment for two or three years.

With the seeds brought to Mishima, isozymes in seedling plumules or mature leaves were examined by starch-gel electrophoresis. Population T was polymorphic at several loci, *i. e.*, *Est-2* (esterase, allele 0>2>1), *Est-9* (allele 1>2), *Cat-1* (catalase, allele 2>1), *Pgi-1* (phosphoglucose isomerase, allele 2>1), *Pgi-2* (allele 1>2), and *Sdh-1* (shikimate dehydrogenase, allele 2>3>1). However, plants from the 1980 and 1983 seeds showed no significant difference in allele frequencies. They showed a relatively high average gene diversity

(H=0.25) and a high fixation index reflecting their predominant selfing (\hat{F} =0.89). Generally, the pattern of isozyme variations was close to that of Japonica cultivars.

In population H, the parents W106 (annual) and W1294 (perennial) showed allelic differences at six isozyme loci, as follows:

(W106-W1294)

<i>Acp-1</i>	-4	+9	acid phosphatase;
<i>Est-2</i>	1	0	esterase;
<i>Pox-2</i>	0	4C	peroxidase;
<i>Amp-3</i>	2	1	aminopeptidase;
<i>Pox-1</i>	2A	4A	peroxidase;
<i>Sdh-1</i>	1	3	shikimate dehydrogenase

The 1980 and 1983 seeds showed significant differences in allelic frequency at three loci, *Acp-1* (chromosome 12), *Pox-1* (chr. 5) and *Sdh-1* (chr. 12), as shown in Table 8b. As to *Pox-1*, allele 4A is known to be associated with regenerating score of excised stem segments and other traits which characterize the perennial

type of wild rice (Morishima, 1991). As mentioned, population H was recruited mainly by vegetative sprouting. Through this process, plants with a high ramet-producing ability would have been selected, which had many genes from the perennial parent. In contrast, population T recruited mainly by seedling showed no such selectional changes.

Discussion

Comparison of ecological characters between populations segregating for different genes have been little reported in the literature. In the present experiment, populations T and H showed similar regenerating scores of excised stem segments in the initially planted material, but population T was recruited mainly by genets while population H mainly by ramets. Why such a behavioral difference has come about is unknown. The two populations seem to differ in the ability of cespitose growth of tillers and in the germinability of seeds in relation to dormancy. Probably, these differences would be expressed under the pressure of competition with weeds to result in the observed differences.

The initial objective of this experiment was to look into the causes of extinction of the T population at Pate, Taoyuan. The main cause was found to be the competition with *Leersia* which became vigorous as the result of silting up of the habitat due to a change in water regime. If water is kept at a depth of more than 10 cm and drained in spring to allow buried seeds to germinate, the wild rice may co-exist with *Leersia*.

In addition, Kiang *et al.* (1979) suggested that hybridization with cultivars could have promoted extinction. Population H was tested together with T to check this point. Slight but significant differences in the mode of interaction with *Leersia* were then found. The growth rate of *Leersia* with population T was in many cases greater than that with population H. This serves as an example of competitive interaction differing according to population genotype. As the result, population H was more durable than T in some habitats. A difference in the mode of aggregation of plants was also detected. When depressed by weeds, the T plants were distributed nearly at random, while the H plants showed clumping.

Furthermore, population H showed genetic changes toward higher perenniality as the result of

selection, but population T did not. In population H, plants with genes from the perennial parent increased against those with genes from the annual parent. If natural recruitment was continued for more years, a population of perennial habit adapted to the conditions in Taiwan could be selected.

It may be suggested that the absorption of cultivar genes could be a cause of extinction of the Taiwan wild rice as it reduced vegetatively propagating ability and seed dormancy, but the main cause would be silt sedimentation in the habitat which promoted *Leersia hexandra* to occupy the land. The third planting experiment of the T plants was initiated in 1990 in one of the original habitats at Pate, Taoyuan, using the seeds which appeared to be less contaminated by cultivar genes. Planting was made in a small pond dug beside the stream and bordered so as to prevent silting up.

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台灣野生稻之生態

II. 二個族群間不同基因型之比較

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本篇報告是利用二個野生稻 (*Oryza rufipogon*) 族群為材料進行比較。台灣野生稻族群 (T)、一年生及多年生交配而得之 F₂ 族群 (H) 兩者在半自然狀態下呈現不同的習性。兩者在與李氏禾 (*Leersia hexandra*) 競爭時具有相似之衰退現象，但 H 族群對 *Leersia* 之忍受性相對地高於 T 族群，甚至些微地抑制了 *Leersia* 之生長。具多年生之莖部截斷後，二個族群雖具類似的再生能力，但 H 族群是由芽體 (ramet) 復甦但 T 族群則是藉幼苗體 (genet)。此點造成植物群集生態上之差異，及族群數量學上遷移係數所顯示之特性差異。由於選拔的結果，H 族群呈現有遺傳之變異而漸趨於多年生；但 T 族群則否。栽培品種基因導入 T 族群，可能是造成該族群擴展的原因之一。