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Ecology of wild rice planted in Taiwan
III. Differences in regenerating strategies among genetic stocks

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Abstract. Variation in the mode of regeneration in a perennial (W120), an annual (W630), and an intermediate perennial-annual type (W593) of common wild rice was tested in lowland fields in semi-natural conditions. The perennial type continued vegetative growth vigorously and increased its population size in a few years. This type also produced a few seedlings. In contrast, the annual type was unsuccessful. Seeds were dispersed and buried in soil, but they did not germinate in the next season. Furthermore, the mother plants died out. Seed germination of this type was sensitive to soil substrates and seemed to be suppressed, at least partly, by an allelopathic effect of field weeds. The intermediate type after maturity covered the field with a thick layer of litter preventing weed growth. In the next season, the seeds germinated to form a new population which included a few mother plants that remained alive vegetatively. Thus, the three genotypes showed markedly different regenerating strategies. Soil-buried seeds of all types survived for years in spite of high moisture content and high temperatures.

Key words: Annual type; Buried seed; Common wild rice; Perennial type; Regeneration; Seed longevity.

Introduction

The common wild rice of Asia (*Oryza rufipogon* Griff.) shows variation from perennial to annual types. These types all differ greatly in breeding systems, life-history traits, and habitat preference. Some of intermediate perennial-annual types are thought to be the progenitor of cultivated rice, *O. sativa* (Sano *et al.*, 1980; Oka, 1988, p.24). The regenerating success of a plant population is controlled by various environmental conditions. In order to learn how the wild rice types differ in the conditions necessary for regenerating success, planting experiments were made using a perennial, an annual and an intermediate type. They were space-planted in lowland fields which had been denuded, tilled and puddled. Populations were observed without particular intervention in comparison with the two hybrid populations planted in the first experiment (Oka, 1991).

It is known that competition with *Leersia hexandra* plays a critical role in the survivability of wild rices planted in Taiwan (Oka, 1984, 1991). The perennial type persisted at different sites and showed a high competitive ability with *Leersia*. In contrast, the annual type failed to survive into the next season. Their seeds did not germinate in the fields covered by weeds. Furthermore the mother plants died after maturity. The intermediate perennial-annual type regenerated by both seeds and vegetative means covering the field with its litter. Thus, quite different modes of regeneration were observed among the three genotypes tested, as are reported in this paper.

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Materials and Methods

Two contrasting types of common wild rice (*Oryza rufipogon*), a perennial type from India (W120, designated as P) and an annual type from Burma (W630, designated as A) were used for the second planting in 1981. Populations T and H tested in the first experiment (planted in 1980) were also newly planted at Taichung and Taoyuan (planted in 1982) where they decayed rapidly.

As mentioned (Oka, 1991), population T is the multiplied progeny of the Taiwan wild rice which became extinct around 1978 (Kiang *et al.*, 1979), and consists of natural hybrids of the original wild rice with cultivars. Population H is derivatives of F_5 bulk seeds from a cross between an Indian annual (W106) and a Philippine perennial (W1294) strain. In addition, an intermediate perennial-annual type from Malaysia (W593, designated as M) was planted together with population A (W630) at Pingtung in 1985 (third experiment), using the field where the first and second planting experiments were over in 1983.

There were five experimental sites, Nankang, Taoyuan (Pate), Taichung (Shisinpa), Chiayi, and Pingtung, as were described previously (Oka, 1984, 1991). The plantings were made in early July, 1981, except for Taoyuan where P, T and H were planted in early April, 1982. About 30 seedlings were planted at 25 × 25 cm spacing with a single plant per hill. At Taichung, a small pond (3 × 3 m, 0.3 m deep) was dug, and populations P, A, T and H were each planted in three rows on the slanted fringe of the pond. At Chiayi, P and A were planted in two rows in the same manner as done for T and H in 1980. At Taichung and Taoyuan, the surrounding area of the new plots was weeded several times to prevent invasion of weeds from outside.

At Pingtung, about 240 seedlings of strains M (W593) and of A (W630) were space-planted in late July, 1985. These were divided into a hand weeded plot (a few times in 1985) and a non-weeded plot. In late February and middle March, 1986, the hand weeded plot of A, which was covered by weeds, was tilled with a hoe. The non-weeded plot of A, which was thickly covered by weeds was also weeded in middle May with a sickle. In the weeded plot for M, weeds were pulled by hand in February and March, 1986.

Throughout these experiments, the density (plant number/unit area) of wild rice and the relative biomass of wild rice and weed species were estimated in the same manner as described in Oka (1991). The estimate of relative biomass was correlated ($r > 0.94$) with the measured value. Dispersed seeds were surveyed at the end of the season with soil samples (10 x 20 cm, 3 cm deep). The soil samples were dried, broken into pieces, and sieved. Complete seeds, broken ones (eaten by animals), and empty ones (infertile) were counted to estimate the number of good seeds per m^2 and the rate of predation by animals. In the third experiment at Pingtung, observations were recorded several times in 1986.

Results

Perennial Type (W120, P)

The perennial type grew vigorously at all sites. At Taichung and Taoyuan where populations T and H were also planted, the T population was suppressed by *Leersia hexandra* and other weeds and decayed. The H population also tended to decline. However population P persisted and increased its covering area. The same trend was also observed at Nankang. At Chiayi and Pingtung where little or no *Leersia* occurred and populations T and H persisted, P increased greatly. The density of plants was not determined because of dense vegetative propagation, but it was estimated to be much more than the initial number from its covering area (Fig. 1; Table 1).

The P plants showed a strong competitive ability against weeds. The total biomass of weeds in P plots

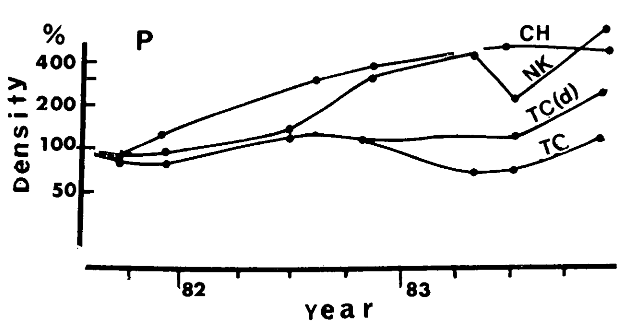

Fig. 1. Density of population P in percent of initially planted number, changing with time at different locations: CH, Chiayi; NK, Nankang; TC, Taichung.; (d), Deepwater side of the pond.

Table 1. *Changes in biomass and density of wild rice, total weed biomass and* **Leersia** *to weeds estimated from second experiment, mean for 10 observations*[a] *in different years and locations*

Population	Season	Wild rice, change/100 days % Biomass[b] ($\sin^{-1}\sqrt{\%}$)	Density[c] (*ln p*)	Total weed biomass[d] (g/m²)	% *Leersia* (exc. Chiayi & Pingtung)[e]
P	Winter	-0.24	0.042	23	8.6
	Summer	-5.75	0.128	93	19.5
T	Winter	-7.56	-0.810	96	25.8
	Summer	-11.05	-1.027	202	34.8
H	Winter	-6.45	-0.645	89	35.9
	Summer	-6.49	-0.590	172	44.1

[a]Nankang (1982), Taichung ('82; '83; '83 deepwater side), Taoyuan ('82; '83), Chiayi ('82; '83), and Pingtung ('82; '83). Data for populations T and H from Taichung and Taoyuan are due to the second planting, but those from other locations are due to the first experiment obtained in corresponding periods.

[b]For 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, then the change in 169 days is -33.1 and expected to be -19.6 in 100 days.

[c]For example, density on 112 days after planting is 82% of the initial number or -0.198 in logarithm and that on 324 days after planting is 59% or -0.528, then the change in 212 days is -0.330 or that in 100 days is -0.156.

[d]Dry matter at the end of season (g/m²).

[e]Data from Chiayi and Pingtung where little or no *Leersia hexandra* occurred were excluded.

Table 2. *Analysis of variance for measurements of wild rice and weeds from second experiment (mean squares are shown)*

Source of variation	df	Wild rice, change/100 days Biomass ($\sin^{-1}\sqrt{\%}$)	Density (*ln p*)	Mean weed biomass (100 g/m²)	df[a]	% *Leersia* ($\sin^{-1}\sqrt{\%}$)
Population						
P: T: H	2	200	5.30**	4.67**	2	1170*
P: (T and H)	1	319*	9.70**	8.95**	1	2201**
Season	1	136	0.01	11.00**	1	591
Population x Season	2	38	0.14	0.14	2	19
Location & Year	9[b]	184*	1.34	8.63**	6	2607**
(Location & Year) x Season	9	285**	1.87*	2.51**	6	179
Other interactions	36	77	0.80	0.296	24	241

[a]Data from Chiayi and Pingtung are excluded.

[b]Listed in Table 1 (footnote a).

*$P < 0.05$; **$P < 0.01$.

was much less than those in T and H plots (Table 1). It was found further that the proportion of *Leersia hexandra* in P plots was less than those in T and H plots (Table 1, except Chiayi and Pingtung). This suggests that the P plants have a competitive ability with *Leersia*. Analysis of variance of the data showed that these differences between P, T and H were significant (Table 2).

The P plants increased mainly by indeterminate cespitose tillering and ratooning from nodes of lodged stems. In addition, seedlings (genets) were also observed. For instance, at Taichung, new plants in the P plot were estimated to be 18.5% in November 1982, of which 16% (1.5% of total) were genets. In 1983, 4.5% of newly occurring plants were genets. At Nankang, 3.3% of new plants in 1982 and 9.3% in 1983 were genets. The survivorship estimated at Taichung in 1982 was 100% for old plants and 85% for new plants. Thus, the perennial type propagates mainly by vegetative means , but there is a small percentage of reproduction by seeds.

Annual Type (W630, A)

The annual plants grew well in the first year and produced many seeds (6,000 /m² or more on the average). A majority of the dispersed seeds were eaten by rodents and small birds in the same manner as was observed in Philippines (Oka, 1976) and Thailand (Sano *et al*., 1984). Yet, the annual type had a lower rate of predation by animals than that of the perennial type (Table 3). The reason may be that more beeds get buried in soil because of the well developed bristles on the awn surface in this type (cf. Oka, 1976). The number of buried good seeds was estimated to be 2,700/m^2 on the average, several times more than the perennial type.

In the next season, however, few of the buried seeds germinated so far as weeds grew on the habitat. The weeds which dominated in the early season of the second year were *Cyperus difformis* at Taichung, *Eleocharis dulcis* at Nankang, *Paspulum conjugatum* at Pingtung. *Leersia hexandra*, the major competitor, became dominant later in the second year. As the mother plants died out at maturity in the first year, the annual population failed to survive.

To account for the non-germination of seeds, germination experiments were carried out using different soils. The results showed that the germination of annual wild-rice seeds was highly sensitive to soil substrates. The soils sampled from beneath the growth of *Leersia hexandra* and *Miscanthus sinensis* (sampled in Mishima) strongly suppressed seed germination, and significantly affected elongation of seminal roots (Table 4). Other weed species probably have similar a

Table 3. *Mean number of buried good seeds and percent predation by animals*

Population	Buried good seeds/m^2		% Predation		Awn bristle length (mm)[c]
	1981-83[a]	1982[b]	1982-83[a]	1982[b]	
P (W120)	546	501	61.8	91.7	0.458
A (W630)		2,728		55.0	0.614
T	301		76.1		0.431
H	738	544	54.4	89.2	0.587

[a]9 Samples from Nankang, Taoyuan, Taichung, Chiayi, and Pingtung.
[b]4 Samples from Nankang, Taichung, Chiayi, and Pingtung.
[c]Awn bristle length is correlated with % buried seeds (Oka, 1976).
T: Taiwan wild rice; H: W106 × W1294, F_5 bulk. ANOV showed that genotypic differences in buried good seeds and percent predation were significant.

Table 4. *Germination rate and seminal root length as affected by substrate soils*

Substrate	% Germination			Seminal root length, mm	
	W630 1984[a]	W630 1986[b]	W106 1984[c]	W630 1986[b]	W106 1984[c]
Control (petri-dish)	35		100		
Paddy soil I	3	44	65	75±4.8	84±5.1
Paddy soil II	20	56	90	66±4.2	114±6.0
Soil from beneath:					
Wild rice I	0		65		83±3.3
Wild rice II	7		45		58±6.3
Leersia hexandra I	0	8	50	60±2.4	75±4.4
Leersia hexandra II	0		25		84±8.1
Miscanthus sinensis	0		40		62±3.9
LSD (5%)					11.4

[a]W630, 1972 seeds stored 0°C (partyle dormant), incubator, 28°C, in 20 days (test at Mishima).
[b]W630, 1985 seeds, buried in soil at Pingtung, greenhouse 25°C~35°C, in 28 days (test at Taichung).
[c]W106, 1963 seeds stored 0°C (dormancy overcome), testing conditions same as a. W106: An Indian annual strain.
Soil substrate: 1984-Soils sampled in late June at Taichung, dried, kept in plastic bags for about 40 days, and put in trays and then moisted for experiment in early August at Mishima. The soil from beneath *Miscanthus* was sampled one week before experiment at Mishima. 1986-Soil samples taken in early June at Taichung, dried and used for experiment in one week.

effect. The inhibition of seed germination may be caused by phytotoxins excreted by these species.

At Pingtung, the A and M plants were tested in natural and weeded plots. Various observations recorded for the two populations are summarized in Table 5. The A plants produced a large number of buried seeds. In February and March of the next season, the weeded plot was tilled shallowly to remove weeds. It produced about 40 seedlings/m^2 in May on the average, and 20% of them were established to attain a 60% cover of the field; this was clear in July. The non-weeded plot was heavily covered by weeds, mainly *Paspulum conjugatum*, and no rice seedlings were found in May. After weeding was made with a sickle, many rice seedlings were observed in June. These were distributed unevenly throughout the plot. With regrowth of the weeds, however, rice seedlings were suppressed and showed poor growth and establishment. This suggests that the regeneration of annual wild rices is difficult unless the field is tilled in the dry season.

Table 5. *Seed production, buried seed number, percent predation by animals, germination in next season, and seedling establishment recorded for populations M and A at Pingtung*

Date	Character	M (W593)			A (W630)			Plot no. for mean
		Natural	Weeded	Mean (±SE)	Natural	Weeded	Mean (±SE)	
1985,								
Nov. 4	Spikelets/plant	1,538	1,475	1,509±138	852	796	825±92	6
	% Weed cover[a]	0	0	0	30	0	(15)	
1986,								
Feb. 27	Seeds dispersed,							
	Total/m^2	5,842	8,550	7,196±1,614	10,575	6,308	8,442±1,395	12
	Buried seeds/m^2	400	392	396±112	1,792	883	1,338±430	12
	% Fertility	77.6	77.1	77.3±2.4	89.3	84.5	87.0±2.05	12
	% Predation	92.5	91.0	91.7±1.9	81.6	77.4	79.4±4.8	12
	% Weed cover[a,c]	4	0		67	57	(62)	12
May 5	Rice seedlings/m^2	8.7	21.3	15.0±3.9	0	44	-	12
	% Weed cover[a]	40	(0)	-	100[b]	(20)	-	
June 13	Rice seedlings/m^2	45.6	32.0	36.4±8.3	74[b]	41	57.6±16.1	12
	Ratoons (total no.)	4	3					6
	% Rice cover	30	20	25	3[b]	30	(16)	12
	% Weed cover[a]	90	40	-	95	80	(87)	
July 21	Established/m^2	4.5	4.4	4.5±0.9	6.2	7.9	7.1±4.5	12
	% Establishment	9.9	13.8	12.2	8.4	19.3	12.3	12
	Tillers/plant	4.1	10.0	6.4±1.1	3.4	10.7	7.4±1.3	32
	Ratooned plants/m^2	0.39	0.29	0.34				6
	% Rice cover	50	100	(75)	1	60	-	
	% Weed cover	25	0	(13)	99	30	-	
Oct. 16	% Rice cover	80	100	90	2	50	-	12
	% Weed cover	13	0	(7)	74	33	53	12
Nov. 20	Seeds dispersed,							
	Total/m^2	6,642	7,067	6,854	1,150	7,158	4,154	12
	Buried seeds/m^2	900	450	675±161	192	500	346±92	12
	% Fertility	77.7	74.9	76.3	84.8	76.5	80.7	12
	% Predation	79.7	91.2	85.4±3.4	82.0	91.2	86.6±3.7	12
	% Rice cover	100	100		0	0		
	% Weed cover[c]	5	0		100	70		

[a] Weeds, mainly *Paspulum conjugatum*
[b] Weeded with a sickle and watered
[c] M plots, covered by rice litter, 100%

Table 6. *Longevity of wild-rice seeds buried in soil (Mean for 11 Asian strains of common wild rice)*

Storage condition	Temperature	% Moisture in seed	Period (month)	% Germination
In water with soil	25°C	ca.30%	12	96±2.6[a]
			30	67±26.2
			34	47±37.1
			40	43±30.0
In moist soil	25°C	28%	30	81±8.4
In moist soil	30-40°C	30%	12	93[b]
In dry soil	30-40°C	19%	12	73[b]
In air (control)	25°C	5%	30	99
			86	99
		13%	30	49±23.9[a]
		16%	9	48±20.2
			12	37±30.4
			16	0

[a]Standard deviation for variation among strains.
[b]Mean for two strains.

Intermediate Perennial-Annual Type (W593, M)

The intermediate type tested at Pingtung employed a unique survival a peculiar strategy. It behaved as an annual type since vegetative remainders from the first tear were only 7% of plants established in the second year. At maturity of the first planting, the plants lodged and a greater part of them died making a thick layer (5 cm or more) of litter. This prevented the weed seeds from germinating. As the litter decomposed, rice seeds germinated in May and seedlings successfully covered the field, even though the density of established plants was not high (Table 5). The weeds did not invade the wild-rice stand much and the underneath was almost empty, suggesting an allelopathic effect of the M plants.

This behavior of the M plants was observed only once in 1986. In late May, the stand of young M plants was observed to grow in varying densities, 7/m^2 (weeded plot) to 30/m^2 (non-weeded plot). The mean density in October was 19/m^2 (weeded) to 52/m^2 (natural), and the plants were distributed unevenly over all the plots. A few A plants wee also found remaining. It seemed that the M plants could regeneration successfully, at least temporarily, at Pingtung where no *Leersia hexandra* occurred.

Longevity of Buried Wild-Rice Seeds

It is a general principle of long-term storage to keep the seeds with a low moisture content at a low temperature. This applies to the wild-rice seeds. They decay rapidly when kept moist in a warm room. However, the wild-rice seeds remained alive for more than three years when kept in moist soil or in water with a spoonful of soil at 25°C (Table 6). Even if stored in dry soil with 11% moisture, the seeds containing 19% moisture were capable of germination for at least one year. Seed dormancy was overcome during the storage in soil. The seeds of rice cultivars kept in these conditions germinated in soil and died soon.

It was found in lettuce seeds that when stored with a high moisture content (above 15%) in aerobic conditions, longevity increased with increasing moisture content up to full hydration as long as the seeds remain dormant (Ibrahim *et al*., 1983). This behavior seems to be found commonly in "orthodox seeds" of different plant species (Roberts and Ellis, 1989). It was inferred that subcellular damage accumulates with increasing moisture content, but repair mechanisms begin to operate when moisture content exceeds a certain limit if enough oxygen is available. In water or in muddly soil, however, oxygen supply is limited. Yet, nearly fully hydrated wild-rice seeds remain alive for years. Wild rice is an aquatic plant, and its seed longevity in anaerobic conditions seems to be due to a different mechanism.

Discussion

The perennial and annual types of the common wild rice are known to differ in breeding systems, various life-history traits, and habitat preference. Moreover the perennial type is thought to be a K-strategist and the annual type as r-strategist (Oka, 1988, p. 32-51). In tropical Asia, the perennial type is distributed in deep swamps which retain water throughout the year, whereas the annual type is found in temporary swamps which are parched in the dry seaon. The present study has shown that they differ markedly in the mode of regeneration.

The perennial type seems to have a wide adaptability in different biotic environments as it has a strong competitive ability with co-existing weeds. Its interaction with *Leersia hexandra* is at least partly allelopathic although the latter seems to have higher phytotoxic effect (Chou *et al.*, 1984). Its vegetative growth is almost indeterminate by both continuous tillering and ratooning from nodes of lodged stems. In addition, it produces seedlings from time to time.

In contrast, the annual type seems to be adapted only to areas where drought in the dry season is severe enough to kill all herbs. It is common in India, but is not found in China and Indonesia where the dry season is not completely dry (Oka, 1988, p. 27). In Thailand, its habitats are not only parched but are also often disturbed by man in the dry season.

Similar differences in regenerating success between the perennial and annual types of wild rice were also reported by Morishima *et al.* (1985) who conducted a planting experiment at Kohama island, Ryukyus. A perennial type (W120) persisted and increased its covering area, but an annual type (W107 from India) disappeared in the second year of planting. Their hybrid and other hybrid populations between perennial wild rices and cultivars declined in a few years, as was observed in the T and H populations. The major competing weed was *Leersia hexandra* as in Taiwan.

An intermediate perennial-annual type from Malaysia (W593) showed a special tactic of competition with weeds, by covering the field with its own litter in the winter season. However, to what extent this strain regenerates successfully in different conditions by this means remains unknown. Its success was observed only in Pingtung where *Leersia hexandra* was absent. The growing plants as well as the litter could have some allelopathic effect on weeds.

An experiment to compare the allelopathic potential among 26 wild-rice strains, by testing the suppressing effect of leaf extract on root elongation of Chinese cabbage seedlings, showed that strain W593 had the strongest allelopathic potential (Chou *et al.,* 1991). Mixed planting experiments of those wild rice strains with three test-strains (cultivar T65, a perennial wild and an annual wild strain) also showed that strain W593 was highest in average aggressiveness to the test-strains although the responses to the test-strains were not correlated well (conducted at Mishima, by Dr. H. Morishima, 1977-1980, unpublished). The suppressing effect on root elongation and the mean aggressiveness values were significantly correlated ($r=0.50$), and several intermediate perennial-annual strains showed high values in both. This suggests that intergenotypic interactions are partly allelopathic, although the data were not published as their repeatability was unknown.

Thus, the present study has shown that the wild rices with different life-histories have quite different strategies of adaptation and recruitment, although they belong to the same species, *Oryza rufipogon*. Probably, the annual type is a derivative from the perennial type for adaptation to habitats with drought stress, as has been suggested in other plant groups (Stebbins, 1958; Whyte, 1972). Indeed, the differentiation can take place in response to a cline of habitat conditions even within the same population, although this needs coadjusted changes in different life-history traits (Morishima *et al.,* 1984). The experiment of population H in Taiwan also has shown this. Yet, in the present study, the three genotypes of the common wild rice tested differed markedly in the mode of regeneration, suggesting that the manner of their differentiation is a complex.

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台灣野生稻之生態
III.不同基因型間再生策略的差異

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三種不同基因型的野生稻(*Oryza rufipogon* Griff.)，一爲多年生型(W120)，一爲一年生型(W630)和一爲介於一年生與多年生之中間型(W593)，分別種植於半自然的試驗田中，以測試其再生策略模式之差異。多年生型野生稻在數年內以無性繁殖的方式逐漸擴大其族群，除了植株生長旺盛外，並有少數幼苗產生。相對的，一年生型野生稻則無法適應當地的環境。其產生的種子經散佈埋藏於土中，並無法於隔季發芽，且母株亦於隔季全部死亡。此種基因型的種子對土壤基質較敏感，考其發芽被抑制的部份原因可能是其他草類產生植物相剋物質而抑制種子的發芽。中間型野生稻在植株成熟後，產生大量乾枯物質舖蓋地表，可避免其他草類的生長。此型野生稻的種子於隔季發芽後，形成一新的族群，其中包括少數以無性繁殖留存下來的母株。因此，這三型野生稻表現了截然不同的再生策略。這三型野生稻的種子，經埋存於高溫，高濕的土壤中過了三年後，仍能存活。