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Ecology of wild rice planted in Taiwan
I. Sequential distribution of species and their interactions in weed communities

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Abstract. To learn about the conditions necessary for recovering the wild-rice (*Oryza rufipogon*) populations in Taiwan which became extinct around 1978, abandoned lowland fields selected at several locations were denuded and puddled, wild-rice seedlings were space-planted, and were observed without particular intervention for four years. The distribution of weed species developing in the field, including the wild rice, was exclusively lognormal, suggesting that species interactions are multiplicative. The component species of each community changed rapidly with secondary succession, and their interactions appeared to be diffused in general. But the fate of introduced wild-rice populations depended on the competition with a particular grass species, *Leersia hexandra.*

Key words: Competition; *Leersia hexandra*; Lognormal distribution; *Oryza rufipogon*; Weed community; Wild rice.

Introduction

The populations of wild rice (*Oryza rufipogon* Griff.) which had existed in Taoyuan municipality, Taiwan, became extinct around 1978 (Kiang *et al.*, 1979). To learn about the cause of extinction and the conditions necessary for restoration, experiments were conducted. Abandoned lowland fields selected at several locations in Taiwan were denuded, puddled, planted with seedlings of the wild rice, and were observed without particular intervention for four years. The rise and fall of the introduced wild-rice populations and co-occurring weed species were recorded, mainly in terms of estimates of relative biomass and density. Analysis of the data for weed species showed that their distribution was lognormal (Oka and Liu, 1984). It was also found that the wild-rice populations declined or persisted as conditioned mainly by the growth thickness of a competing grass, *Leersia hexandra* (Oka, 1984). However, the sequential distribution of species was computed excluding the wild rice, and the interrelations between species were examined only partly. To look more closely into the interaction between wild rice and the community to which it belongs, the data were recomputed, as are reported in this paper.

Materials and Methods

The experimental sites were five, *i.e.*, Nankang (25°02'N, an abandoned rice field, on the campus of Academia Sinica), Pate, Taoyuan (24°56'N, a marshy strip along a stream, one of the orignial habitats of Taiwan wild rice), Shisinpa, Taichung (24°05'N, an abandoned lowland field), Chiayi (23°30'N, an irrigation ditch in the farm of Chiayi Institute of Agriculture), and Pingtung (22°41'N, a lowland field used for

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depositing rice straw, in Kaohsiung Distr. Agric. Improvement Station). In this paper, the data recorded at Nankang, Taichung and Pingtung are mainly dealt with, where the introduced wild rice showed quite different behaviors. These experimental sites, each having two plots 8 to 70 m^2 in size, were denuded, tilled and puddled in August 1980, and were planted with wild-rice seedlings. No fertilizers were applied.

Two wild-rice populations were tested at each site, one raised from multiplied seeds of Taiwan wild rice which had been natural hybrids between the wild rice and cultivars (Oka and Chang, 1961), and the other from F_5 bulk seeds of a cross between an annual (W106, India) and a perennial (W1294, Philippines) strain. They showed similar behaviors. In this paper, their mean measurements are dealt with, and their differences will be reported elsewhere (2nd paper of this series).

The wild-rice plants were observed for number (density), height (cm) and stem number at 2 to 3 month intervals, and the dry weight of each plant (g) was estimated as height × stem number × 0.0203. This estimate and measured dry weight were highly correlated ($r=0.98\sim0.94$). The biomass (g/m^2) was obtained from this and plant number. Each of weed species was recorded with regard to standing height (cm) and percent cover (visual judgement), and its biomass (dry weight, g/m^2) was estimated as height × % cover × 0.0485. This is comparable to "multiplied dominance ratio" proposed by Numata (1979), and gave a high correlation ($r=0.95$) with the dry weight measured by cutting quadrats (0.5 × 0.5 m, several replicates each time). The multiplier, 0.0485 was adopted for different weed species similarly although it had a standard error of 0.0053.

From the data recorded at each observation on each site or location, the relative importance of each species was computed as the proportion (p) of its biomass estimate to the total dry weight estimate per unit area (m^2). The computation procedures for sequential distribution of species is essentially the same as described by Oka and Liu (1984), but will be re-presented briefly together with the results.

Results

Lognormal Distribution of Species

Weed species identified were 62 in total, of which 30 occurring with a frequency exceeding 10% were listed by Oka (1984). The mode of their sequential distribu-

Table 1. *An example of computation of sequential distribution of species, with vegetation data at Nankang, November 1983*

Species[a] rank	Biomass proportion (p)	$Y=-\ln p$	$Z=\frac{Y_i-\bar{Y}}{\sigma}$	Cumula. normal distr. (F)	Cumula. empirical distr. (S)	$\lvert$ Dif. $\rvert$ F_i-S_i	$\lvert$ Dif. $\rvert$ F_i-S_{i-1}
1	0.4406	0.820	-1.737	0.041	0.083	0.042	0.041
2	0.2648	1.729	-1.432	0.076	0.167	0.091	0.007
3 (rice)	0.1560	1.858	-1.116	0.132	0.250	0.118	0.035
4	0.0373	3.289	-0.260	0.397	0.333	0.064	0.147
5	0.0320	3.442	-0.169	0.433	0.417	0.016	0.100
6	0.0187	3.979	0.152	0.560	0.500	0.060	0.143
7	0.0178	4.029	0.182	0.572	0.583	0.011	0.072
8	0.0124	4.390	0.398	0.655	0.667	0.012	0.072
9	0.0064	5.067	0.803	0.789	0.750	0.039	0.122
10	0.0062	5.083	0.813	0.792	0.875	0.083	0.042
11	0.0062	5.083	0.813	0.792	0.875	0.083	0.083
12	0.0018	6.320	1.552	0.940	1.000	0.060	0.065
Total	1.0	$\bar{Y}=3.724$ $\sigma=1.672$		$R_F^2=0.988$	$R_S^2=0.944$	Max.dif.=0.147 P>0.20	

[a] Species: 1-*Leersia hexandra* Sw.; 2-*Panicum repens* L.; 3-*Oryza rufipogon* (mean for 2 populations); 4-*Dimeria ornithopoda* Trin.; 5-*Commelina diffusa* Burm.; 6-*Ishaenum aristatum* L.; 7-*Polygonum hydropiper* L.; 8-*Ipomoea cairica* Sw.; 9-*Ludwigia octovalvis* Raven.; 10-*Paspalum conjugatum* Berg.; 11-*Ipomoea aquatica* Forsk.; 12-*Ageratum houstonianum* Min.

tion was lognormal exclusively (Oka and Liu, 1984). To examine if the lognormality remains unchanged after incorporation of the introduced wild rice, the data from 17 observations of vegetations at Nankang, Taichung and Pingtung were analyzed. As an example, the compution procedures for the data recorded at Nankang in 1983 are shown in Table 1.

The proportion of biomass (p) obtained for each species was arranged in descenting order and was converted into natural logarithm ($-ln\ p = Y$). Then, the regressions of Y values were computed on species rank (or "cumulative empirical frequency", designated as S distribution) and on the cumulative normal frequency which was derived from Z values, $Z_i = (Y_i - \bar{Y})/\sigma$ (designated as F distribution). The regression of Y on species rank gave a coefficient of determination, 0.944 (shown by R_s^2 in Table 1), and that on cumulative normal frequency gave 0.988 (shown by R_f^2). The former regression shows the fitness of the observed distribution to a geometric series discovered first by Motomura (1932), and the regression coefficient, $b = 0.451$ shows the rate of decrease of biomass in the geometric series according to the rank, $p_{i+1}/p_i = e^{-0.451} = 0.637$. Evidently, the regression on species rank is equivalent to that on cumulative empirical frequency (0.083... 1.0; the regression coefficient on this is 0.451 × 12=5.416. On this point, the description by Oka and Liu is erroneous). A higher coefficient of determination, 0.988 from the regression on cumulative normal frequency indicates a better fitness of the data to a lognormal distribution. The difference in coefficient of determination, $R_f^2 - R_s^2 = 0.044$, may be regarded as a curvilinearity term associated with the lognormal distribution.

On the other hand, the Lilliefors test for normal distribution (Conover, 1971, p. 302-306) showed that the maximum difference between the cumulative normal (F) and cumulative empirical (S) frequencies, 0.147 was not significant ($P > 0.2$). From the standpoint of this nonparametric test, the fitness of the data to a geometric series means that to a lognormal series. This was con-

Table 2. *Distribution of wild rice and weed species in communities*

Location	Time	No. of species	Attribute of distribution				Wild rice % biomass
			$1-R_s^2$	$R_f^2-R_s^2$	p_{i+1}/p_i	H'/H'_{max}	
Nankang	Dec. '80	13	0.037	0.029	0.533	0.527	27.4
	July '81	14	0.053	0.039	0.586	0.722	22.4
	Nov. '81	13	0.061	0.046	0.559	0.743	14.6
	July '82	10	0.026	0.020	0.473	0.593	10.0
	Nov. '82	10	0.090	0.040	0.558	0.401	3.0
	June '83	12	0.019	0.011	0.562	0.604	16.9
	Nov. '83	12	0.057	0.045	0.637	0.621	15.6
Taichung	Dec. '80	16	0.015	0.0	0.698	0.683	36.1
	July '81	20	0.028	0.014	0.704	0.635	30.1
	Nov. '81	14	0.060	0.040	0.560	0.392	0.2
	July '82	7	0.146	0.106	0.562	0.524	0.0
Pingtung	July '81	8	0.111	0.081	0.461	0.309	84.6
	Nov. '81	11	0.150	0.099	0.498	0.107	95.4
	July '82	9	0.093	0.064	0.586	0.487	72.6
	Nov. '82	5	0.066	0.059	0.229	0.199	92.9
	June '83	8	0.047	0.035	0.424	0.405	74.5
	Nov. '83	5	0.093	0.091	0.360	0.571	71.5
Mean		11.0	0.068	0.048	0.529	0.501	39.3

$1-R_s^2$: Partial variance due to deviation from regression on species rank.

$R_f^2-R_s^2$: Increase in coefficient of determination by adoption of cumulative normal distribution.

p_{i+1}/p_i: p_i stands for the proportion of biomass of i-th species to total biomass. This ratio represents e^{-b} or $ln^{-1}\ b$ where b is the regression coefficient of $ln\ p_i$ on species rank. It then represents the slope of regression on species rank.

H'/H'_{max}: $H' = -\Sigma p_i ln\ p_i$; $H'_{max} = ln$ (no. of species). This ratio represents equitability. (Krebs 1985, p. 522) firmed also by Shiou and Wu (1987) who studied weed species in ratooned rice fields.

By using the above-mentioned method, 17 sets of relative biomass data from Nankang, Taichung and Pingtung, each converted into natural logarithms, were examined. The observed distributions fitted geometric series well and fitted cumulative normal series better. The deviation from the former, 1-R_s^2 ranged from 0.015 to 0.150 (Table 2) and that from the latter (1-R_f^2) ranged from 0.006 to 0.051. The 1-R_s^2 value was strongly correlated ($r=0.95$) with the curvilinearity term (R_f^2-R_s^2) indicating that the deviation from geometric series was in a larger part due to the curvilinearity associated with lognormal distribution. The Lilliefors test also showed that the maximum difference between the F and S distributions was expectable with a probability greater than 0.05 in all cases. These results are well comparable to those obtained excluding wild rice (Oka and Liu, 1984) and confirm that the sequential distribution of species can be approximated by a geometric series and represented better by a lognormal distribution. The introduced wild rice has been a component of communities.

Successional Changes in Community Structure

The rank of the introduced wild rice fluctuated along the regression line at Nankang, declined rapidly at Taichung, and persisted at the top at Pingtung. The co-occurring weeds also altered their ranks (Table 3). In general, perennial grass species increased with secondary succession, while the component species of communities changed rapidly. The index of similarity in species composition (Krebs, 1985) was largely below 0.5 between seasons at the same site, and was lower between locations at the same time (Table 4).

To examine if the component species of communities have particular trends of association and dissociation, two-way contingency chi-squares were computed in 78 combinations of 13 weed species which occurred with a relative frequency higher than 20% in 25 observations (*Leersia hexandra, Panicum repens, Cynodon dactylon, Echinochloa crus-galli, Kyllinga*

Table 3. *Rank of species and perennial grass biomass changing with seasons*

Site & species	Time of observation						
	1980	1981		1982		1983	
	Dec.	July	Nov.	July	Nov.	July	Nov.
Nankang							
Oryza rufipogon (wild rice)	2	1	4	3	4	2	3
Leersia hexandra	14	4	3	1	1	1	1
Panicum repens	4	2	1	4	5	4	2
Eleocharis dulcis (Trin.)	1	-	-	5	-	3	-
% perennial grass[a]	5	28	73	93	82	74	87
Taichung[b]							
Oryza rufipogon (wild rice)	1	2	8	-			
Leersia hexandra	12	1	1	1			
Panicum repens	10	3	3	3			
Cyperus pilosus (Vahl.)	-	6	2	-			
% perennial grass[a]	7	74	79	84			
Pingtung							
Oryza rufipogon (wild rice)	1	1	1	1	1	1	1
Echinochloa crus-galli	2	3	6	4	4	-	-
Cynodon dactylon (Pers.)	8	-	4	3	2	-	3
Paspalum conjugatum (Berg.)	-	-	2	5	6	4	5
% perennial grass[a]	7	6	21	37	68	77	32

[a] Excluding *O. rufipogon* (wild rice) biomass.

[b] Observation was discontinued in November 1982 since all wild rices disappeared by July.

"-", Shows absence.

Table 4. *Index of similarlity between weed communities*

Index of similarlity=$2c/(a+b)$, where a and b are the number of species present in two communities to be compared and c is the number of species occurring in both. (Krebs 1985, p. 447)

Location	1980 Dec.	1981 July	1981 Nov.	1982 July	1982 Nov.	1983 July	1983 Nov.
Between seasons:							
Nankang		0.43	0.96	0.35	0.50	0.55	0.33
Taichung		0.27	0.35	0.29	-	-	-
Pingtung		0.35	0.32	0.50	0.80	0.57	0.46
Between locations:							
Nankang-Taichung	0.41	0.35	0.30	0.35	-	-	-
Taichung-Pingtung	0.33	0.17	0.48	0.13	-	-	-
Nankang-Pingtung	0.17	0.36	0.33	0.11	0.38	0.20	0.35

"-", Shows no data since wild rices disappeared at Taichung by July 1982 and observation was discontinued.

brevifolia, Fimbristylis miliacea, Alternanthera philoxeroides, Al. sessilis, Commelina diffusa, Eclipta prostrata, Ludwigia octovalvis, Monochoria vaginalis, and *Polygonum hydropiper*). The pattern of combinations of these species appeared to be largely at random. Chi-square values were significant at the 5% level in 11 species combinations, but none at the 1% level. A trend to repulsion was noticed between *Polygonum hydropiper* and *Althernanthera sessilis,* as well as between *Echinochloa crus-galli* and *Commelina diffusa.* It may be suggested that the interactions between these weed species are diffused.

Nevertheless, the lognormality of species distribution has remained unchanged throughout succession. This suggests that the interactions between species are exclusively multiplicative, as discussed by Oka and Liu (1984). Probably, this applies to the distribution of species in various other cases.

Several attributes showing community structure were examined as to their interrelations. The slope of regression on species rank, p_{i+1}/p_i ranged from 0.70 to 0.23 (Table 2). The information content shown by the Shannon-Wiener function, $H' = -\Sigma p_i \ln p_i$, was computed in each community, and equitability was estimated by H'/H'_{max} where $H'_{max} = \ln S$ (S being the number of species; Krebs, 1985, p. 522). The equitability estimate ranged from 0.11 to 0.74, and was correlated with the p_{i+1}/p_i value. Percent biomass of wild rice was correlated negatively with both p_{i+1}/p_i and H'/H'_{max}. Percent biomass of most dominant species, p_i was correlated with the deviation from geometric series ($1-R_s^2$) and all other attributes either positively or negatively (Table 5). However, when differences between locations were excluded and correlations were computed with differences due to succession at the same sites (df = 13), significant correlations were reduced to a few. The p_i value was correlated with $1-R_s^2$ and p_{i+1}/p_i values. Percent biomass of wild rice showed no significant correlation with these attributes when differences between locations were excluded.

Successional Changes in Wild-Rice Biomass

When wild-rice populations declined, the rate of decline was generally higher in the period from July to November (corresponding to the second or summer crop season of rice in Taiwan) than in the period from December to June (corresponding to the first or winter

Table 5. *Correlations between some attributes of communities*

Above diagonal-among communities at the same location (Nankang 7, Taichung 4, and Pingtung 6; df=13); Below diagonal-among all communities (df=15).

Attribute[a]	1	2	3	4	5
1. % wild-rice biomass		-0.45	0.26	0.09	-0.47
2. $1-R_s^2$	0.25		0.04	-0.38	0.53*
3. p_{i+1}/p_i	-0.54*	-0.26		0.30	0.84**
4. H'/H'_{max}	-0.56*	-0.57*	0.58*		-0.35
5. p_i (most dominant species, % biomass)	0.52*	0.68**	-0.61**	-0.91**	

[a] Explanations in Table 2 footnote.

$^*P<0.05$; $^{**}P<0.01$.

crop season), and in the summer period changes in biomass and density (plant number) were correlated ($r=0.50$). The growth of weeds was also more vigorous in summer than in winter. This agrees with the general trend of plant mortality to be high at the time of rapid growth (White and Harper, 1970).

To look into the effect of successional changes on introduced wild rice, multiple regressions of the relative biomass of wild rice (Y) were computed on seven attributes of weed communities (X_1 to X_7) or a part of them. The seven attributes were percent biomass of perennial species (X_1), equitability (H'/H'_{max}, X_2), percent biomass of grass species (X_3), that of sedge species (X_4), that of dicot species (X_5), and those of two species which appeared to be in intense competition with wild rice, *Leersia hexandra* (X_6) and *Panicum repens* (X_7). The data used were 15 sets: Nankang (Dec. 1980; July '81; Nov. '81; July '82), Pate, Taoyuan (Dec. '80; July '81; Nov. '81), Taichung (Dec. '80; July '81; Nov. '81; July '82), Chiayi (Dec. '80), and Pingtung (Dec. '80; Nov. '82), and all percentages were converted into $\sin^{-1}\sqrt{\%}$ values. To evaluate the relative importance of X variables, standard partial regressions were computed (Table 6). The multiple regression of Y on all X values gave a coefficient of determination as high as 0.93, although only the partial regression of *Leersia* biomass (X_6) was significant. When *Leersia* and *Panicum* only were taken as X variables, the regressions on both were significant. But when these two (X_6 and X_7) were excluded, the multiple regressions on other attributes (X_1 to X_5) gave low coefficients of determination and were insignificant, while the simple correlation of Y with X_6 was significant. This indicates that the introduced wild-rice populations are conditioned by the competition with *Leersia hexandra* particularly.

Table 6. *Standard partial regression coefficients of percent biomass of wild rice on 7 variables showing community characteristics*

Variable	Standard regression coefficient df=7	df=11	df=12	df=12	df=13
X_1 % perennial	0.075		-0.653		
X_2 Equitability (%)	0.052		-0.189		
X_3 % grass	0.565	1.601			
X_4 % sedge	0.012	1.181			
X_5 % dicot	0.266	0.991			
X_6 % *Leersia*	-0.970**			-0.650**	-0.809**
X_7 % *Panicum*	-0.256			-0.447**	
R^2: Coef. of determination	0.933**	0.198	0.294	0.829**	0.654**

**P<0.01

Discussion

The present study has shown that the introduced wild rice behaves as a component of developing weed communities as it is incorporated into the lognormal distribution together with other weed species. The interactions among co-existing plant species are multiplicative and diffused in general. But the competition between the wild rice and *Leersia hexandra* is of particular significance, the domination of the latter being critical in depressing the regenerating success of the former.

Analysing interspecific interaction by removing particular species from communities, Silander and Antonovics (1982) reported that the interactions were diffused in many cases, but were specific between two particular species in a few cases. The present experiment is an addition of a particular species to weed communities developing after clearance, which is unsuccessful in many cases (Caver and Harper, 1967).

Probably, *Leersia hexandra* comes into intense competition with the introduced wild rice as their niches overlap. Their interaction seems to be at least partly allelopathic (Chou *et al.,* 1984). Yet, an experiment (unpublished) has shown that the wild rice can survive the competition with *Leersia* if water depth is kept more than 10 cm. This suggests that the extinction of wild rice in its original habitat, Pate village, Taoyuan, is mainly due to the increase of *Leersia hexandra* which resulted from a change in water regime and silt deposit on the habitat after the completion of an irrigation system following the construction of Shimen dam in 1964.

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台灣野生稻之生態
I. 種之序列分佈及其與野草社會之相互關係

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本項研究選用幾於 1978 年間遭致滅絕命運的野生稻(*Oryza rufipogon*)爲材料，希望能獲知回復其族群之條件需求。將幾處荒廢的水田加以除草、整地後播下野生稻幼苗，四年間除進行觀察外，不再施加特殊的處理。野草及野生稻在田間之生長分佈皆呈指數性地增加，此意味種類間之相互關係具有相乘性。至於個別社會之組成種類則隨次級消長而迅速改變，其相互關係漸擴展至全體。所導入之野生稻族群之繁衍與否取決於其與 *Leersia hexandra* 草種之競爭性。