ALLELOPATHIC POTENTIALS OF A WILD RICE, *ORYZA PERENNIS*(1)

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Abstract: To learn about genotypic variations in allelopathic potential, 24 strains of a wild rice, *Oryza perennis* Moench, collected from tropical Asian and American countries, and two rice cultivars (*O. sativa* L.), were planted at Nankang, and water extracts from their leaves and stems taken at the booting stage were used for bioassay with Chinese cabbage and rice seeds. The extracts were also used for chromatographic analysis to determine the contents of nine phenolic acids. The strains tested markedly differed in root-growth suppression rates in bioassay and contents of phenolic acids, but the two kinds of measurements were largely uncorrelated. The root-growth suppression rate in Chinese cabbage was considered as representing the allelopathic potential better than that in rice. Stepwise regression analysis showed that a combination of several phenolic acids and their interactions could account for the root-growth supprssion rate in Chinese cabbage. The result of bioassay clearly indicates the main direction of differentiation in *O. perennis* strains.

Key words: Allelopathy, competition, neighbor effect, wild rice, *Oryza perennis*, aggressiveness, resistance to aggressiveness, phytotoxic phenolics.

INTRODUCTION

The common wild rice (*Oryza perennis* Moench or *O. rufipogon* Griff.) is distributed throughout the humid tropics; and its Asian race is thought to be the progenitor of cultivated rice, *O. sativa* L. (cf. Oka, 1974, 1988). Germplasms of these species have been collected from different countries of the world and studied with respect to evolutionary aspects of variations by Oka and coworkers (cf. Anon., 1980). The wild populations carry rich genetic variations within as well as between them and exhibit a continuous array ranging from perennial to annual types. Different life-history traits vary in association with this variation (Sano and Morishima, 1982; Oka, 1983). The perennial types grow in deep swamps which retain moisture throughout the year, while the annual types are in temporary swamps which are parched in the dry season. They differ in co-occurring plant species and accordingly in niche preference (Morishima *et al.*, 1984).

When populations of this species were introduced into lowland habitats in Taiwan, their regenerating success depended primarily on competitive interaction with *Leersia hexandra* (Oka, 1984), and the interaction was at least partly by

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allelopathic means (Chou *et al.*, 1984). In cultivated rice, it has also become known that an appreciable amount of phytotoxins is produced during the decomposition of plant residues in submerged soils and plays a role in reducing grain yield in the second (summer) rice crop (Chou and Chiou, 1979).

Measurable differences found among plants in approximately the same environment are largely controlled genetically. The production of allelochemics in tissues can not be an exception although only a few cases have been reported on genotypic differences in allelopathic potential (Putnam and Duke, 1974; Fay and Duke, 1977). In view of the magnificient genetic variations found in the wild and cultivated rice species, the present authors are engaged in a survey of variations in allelopathic potential among rice genotypes. In this paper, the results obtained from 24 wild and 2 cultivated strains are presented in comparison with the data on neighbor effects of the wild strains on certain test-strains in mixed stand.

MATERIALS AND METHODS

Strains Tested

Twenty four strains of *O. perennis* selected from the stock in National Institute of Genetics, Japan, of which 16 were Asian and 8 were American forms, and two *O. sativa* strains provided by the first author, were tested for allelopathic potential. They are listed in Table 1, with the location of collection, habitat, and perenniality index as given by Z_{reg}-Z_{RA}, where Z_{reg} is the standardized score showing the regenerating ability of excised stem segments (Oka and Morishima, 1967) and Z_{RA} is the standardized value of reproductive allocation or the ratio of seed weight to plant dry weight (cf. Morishima *et al.*, 1984).

Plant Materials

The seeds were germinated in middle July, 1984, and the seedlings were transplanted into a paddy field at Nankang in early August, to raise five plants per strain. Two plants per strain were cut at the ground level at the booting stage, and the leaves and stems were air-dried. They were ground, and a 5 g powder per strain was put in 195 ml of distilled water, shaken for 2 hours, and filtered through Whatman 42 paper. The extract obtained was used for both bioassay and chromatographic analysis.

Bioassay

To evaluate the allelopathic potential of the extracts, the bioassay method as described by Chou and Lin (1976) was employed by using the seeds of Chinese cabbage (*Brassica oleraces*, cv. Meifong) and rice (*O. sativa*, cv. Taichung sen 2). Each plot consisting of 10 seeds was sown on a piece of plastic sponge containing distilled water (control) or an extract in a petridish, with 3 replications, and root length was measured 3 days after seed-sowing. The mean root length in an extract was compared with that of the control to obtain the rate of root-length reduction.

Quantitative Analysis of Phenolic Acids

The aqueous extract from each strain was concentrated in vaccum to 50 ml, and the phenolic compounds in it were extracted with ethyl ether three times.

Table 1. Strains Used, Their Origins, Habitats, and Estimates of Perenniality

Strain code	Origin		Habitat	Perenniality[a]
	Country	Province/county		
O. perennis, Asian race				
W106	India	Cuttack, Orissa	Temporary shallow swamp	−1.79
W107	India	Bhuvaneswar	Temporary shallow swamp	−2.37
W120	India	Cuttack, Orissa	Water reservoir	2.61
W122	India	Cuttack, Orissa	Temporary shallow swamp	1.18
W124	India	Gunpur, Orissa	Marsh	2.67
W125	India	Gunpur, Orissa	Marsh	−1.05
W126	India	Gunpur, Orissa	Water reservoir	−0.95
W130	India	Gunpur, Orissa	Water reservoir	−1.78
W133	India	Samalkot, Andhra	Shallow marsh	−0.34
W136	India	East Gôdavry	Shallow marsh	−1.01
W139	India	Trichur, Kerala	Water reservoir	−1.90
W149	India	Raipur, M.P.	Water reservoir (deep)	1.78
W153	India	Canning, W. Bengal	Paddy field (submerged)	−0.46
W168	Thailand	Phimai	Roadside shallow swamp	−0.66
W593	Malaysia	Binjai Render	—	−0.34
W630	Burma	Magwe	Temporary swamp	−2.35
O. perennis, American race				
W036	Cuba	—		−0.62
W612	Brazil	Manaos, Amazonas	Deep water riverside	−0.03
W1185	Surinam	Paramaribo	Deep pond	0.45
W1186	Surinam	Paramaribo	Shallow marsh	0.31
W1187	Brazil	Majoro Is., Para	Swampy pasture	−2.10
W1189	Brazil	Rio Negro, Manaos	Deep water riverside	−1.67
W1192	Brazil	Rio Negro, Manaos	Deep water riverside	0.38
W1196	Columbia	Meta, Viavicencia	Swampy pasture	0.58
O. sativa				
Hsinchu 56		Taiwan	Japonica	
IR 5533		IRRI, Philippines	Indica	

a: Perenniality is shown by Z_{reg}-Z_{RA} (standardized value, of regenerating ability of excised stem segmets minus that of reproductive allocation), the two values being negatively correlated, $r=-0.75$. Smaller (negative) values show annual habit, and larger (positive) values perennial habit. (cf. Morishima *et al.*, 1984)

Then, after being evaporated to dryness, the residus was dissolved in methanol. The methanol solution was passed through a millipore filter and made up to 3 ml solution with spectroscopic methanol (Chou and Young, 1975). The final clean solution and the solutions of nine authentic phenolics, i.e., 1) gallic acid, 2) protocatechuic acid, 3) *p*-hydroxybenzoic acid, 4) vanillic acid, 5) syringic acid, 6) *p*-coumaric acid, 7) *m*-coumaric acid, 8) ferulic acid, and 9) *o*-coumaric acid, prepared in methanol at 5×10^{-4} M as standard, were analyzed quantitatively by using a high-performance liquid chromatograph (LDC Milton Ray Model Constametric I and UV Monitor III, with a Merck reversephase C-18 Column). The wave-length of UV was set at 254 nm, chart speed at 3 mm/min, and flow rate at 2 ml/min. The solvent for separation of these phenolics was water: methanol: acetic acid (80:20:1, V/V/V), using a liquid chromatographic reagent grade.

RESULTS

Comparative allelopathic potential in varieties of wild rice

The phytotoxicities of leaf-stem extracts from respective strains were evaluated by root growth of the tester in the extract as compared with that in distilled water. The root-length reduction rate in extract greatly differed according to the strains giving the extract. The rates obtained from the assay with Chinese cabbage seeds showed a wide range, from a 68% reduction (a Malayan intermediate perennial-annual strain, W593) to an about 5% increase (W126 and W1186, taken as zero, or discarded in computation). The assay with rice seeds gave a narrower range (6 to 35%) of root-length reduction rate.

The Asian strains of *O. perennis* were divided into perennial, annual, and intermediate groups according to their perenniality indices (Table 2A). But, the strain groups thus classified showed no marked difference in the distribution of root-length reduction rate. It was also found that the reduction rate was uncorrelated with perenniality ($r=-0.19$ in Chinese cabbage and $r=-0.05$ in rice). It was noted that the Asian intermediate perennial-annual strains had the widest range of root-length reduction rate in Chinese cabbage. The American wild strains also showed a wide range of variation. The two cultivars tested showed a low rate of root-length reduction (Table 2A).

To estimate the reliability of root suppression rates obtained in respective strains, the original data for root lengths in extracts were subjected to analysis of variance (Table 2B). The result showed that the variance due to strains was

Table 2. Variations in Root-length Reduction Rate Obtained from Bioassay

A: Distributions in Different Strain Groups

	Root-length reduction, %												No. of
	Chinese cabbage								Rice				
Strain group	0	10	20	30	40	50	60	70	10	20	30	40	strains
Wild, Asia													
Perennial[a]			1			2				2	1		3
Intermediate	1[b]		1			2		1	2	1	2		5
Annual		1	1		2	3	1		2	3	2	1	8
Wild, America	1	1	1			3	2		5	2	1		8
Cultivar	1	1								2			2

a: Classification by perenniality index: >1.0: perennial, <−1.0: annual,
1.0 to −1.0: intermediate.

b: This strain (W126) showed a 5% increase of root length. It is not included in Figure 1.

B: Analysis of Variance for Root Length

Source of variation	Degree of freedoom	Mean square	
		Chinese cabbage	Rice
Strain	29[c]	5,969[d]	1,081[d]
Error	60	647.5	396.2
Heritability		0.733	0.369

c: Four more strain of *O. perennis* than those listed in Table 1 were examined, but were omitted from the list as they lacked data for other traits.

d: Significant at 1% level.

highly significant in both Chinese cabbage and rice. However, the heritability of root length in extract as shown by intraclass correlation was much higher in the assay with Chinese cabbage (0.73) than in that with rice (0.37). The root-length suppression rate in Chinese cabbage and that in rice showed a weak and insignificant correlation (r=0.36); when three seemingly unusual entries were excluded, a significant correlation (r=0.48, $P<0.05$) was obtained. Furthermore, as will be mentioned later, the reduction rate in rice showed no relationship with the contents of phenolic acids in the extract. Possibly, the seminal roots of rice are not so sensitive to the plant extract as they have a rich supply of nutrients from the endosperm. Therefore, the result of bioassay with Chinese cabbage was taken as representing the allelopathic potential of the strains tested. The root-growth suppression rates obtained in respective strains with Chinese cabbage are presented in Table 3, with other measurements.

Contents of Phenolic Acids in Extracts

The results of chromatographic analysis in respective strains are presented in Table 3, which indicate that the strains examined greatly differed in the content of each of 9 phenolics. Gallic acid (1) was present in all strains, but its concentration varied greatly. Three others, *p*-hydroxybenzoic (3), vanillic (4), and *p*-coumaric (6) acids were distributed rather ubiquitously, while the rest were distributed more sporadically in different strains. The total amount of these phenolics showed a wide range among the strains, the largest being about 11 times as much as the smallest (Table 3).

The contents of the 9 phenolic acids in 24 *O. perennis* strains were uncorrelated in many combinations, with a few exceptions (Table 4). They also showed no significant correlation with the results of bioassay, with the exception of *o*-coumaric acid (9) correlated with the root-length reduction rate in Chinese cabbage. The total amount of phenolics was uncorrelated with the root-length reduction rates in both Chinese cabbage and rice.

Then, some elaborate statistical techniques were employed to learn more about the interrelation between phenolics content and root-length reduction rate. First, a combination of several phenolics playing a significant role in root suppression was searched for by the stepwise regression analysis. Four phenolics, i. e., (2), (3), (8) and (9) in Table 4 were found to give a multiple correlation of 0.62 ($P<0.01$) to the root suppression rate in Chinese cabbage, the standard partial regression coefficients being 0.23 (2), 0.05 (3), 0.36 (8), and 0.53 (9). Second, the stepwise regression analysis was continued by taking interactions (second-order terms, a^2, $a\times b$, etc.) into account. This gave a few cases of highly significant correlation with the root suppresion rate in Chinese cabbage, the highest being a multiple correlation of 0.84 involving 6 predictors, i. e., $(8)^2$, (1×9), (total), (3×4), and (4×9). It may be suggested that cartain phenolic acids interact to realize allelopathic potential. However, with the root suppression rate in rice, all these attempts were unsuccessful in finding out a significant correlation.

Growth Performance of Wild-rice Strains

The *O. perennis* strains planted at Nankang greatly differed in growth performance. In plant height in October, tallest was W1186 (130 cm) and shortest was W107 (33 cm). The diameter of plant cover also varied from 19 cm (W036) to 48 cm (W126). When the relative biomass was estimated by the product of

Table 3. Measurements for Respective Strains: Root-length Reduction Rate from Bioassay of Extracts with Chinese Cabbage, Contents of 9 Phenolics in The Extract, and Mean Aggressiveness on Test-strains in Mixed Planting

Strain	Root-length reduction,	Content of Phenolics[a], ×10^{-8} M										Aggres-
code	%	1	2	3	4	5	6	7	8	9	Total	siveness
O. perennis, Asian race												
W106	52.8	62	76	10	13	12	141	8	4	7	333	−.045
W107	42.3	53	4	5	46	48	4	13	39	0	212	.090
W120	20.1	51	1	11	7	1	34	25	3	24	157	−.039
W122	52.4	29	0	4	2	0	0	6	0	0	41	.146
W124	53.2	55	3	15	18	15	97	2	3	0	208	.218
W125	18.6	135	18	12	14	8	121	2	0	0	310	.142
W126	0	153	0	9	2	10	42	0	0	0	216	.224
W130	61.0	90	3	20	5	14	0	0	0	0	132	.396
W133	47.8	29	138	15	5	0	0	0	0	0	187	.334
W136	47.0	21	0	13	13	0	26	2	3	24	102	−.016
W139	12.3	157	39	18	26	17	167	4	0	13	441	.074
W149	51.4	237	53	20	15	29	81	2	0	0	437	.019
W153	53.5	39	5	14	7	10	122	0	0	0	197	.305
W168	18.8	55	2	14	15	2	150	0	20	0	258	.148
W593	67.6	64	0	15	11	1	71	4	3	7	176	.476
W630	40.7	66	13	6	31	42	10	8	42	0	218	.108
O. perennis, American race												
W036	55.7	74	29	17	40	23	239	0	0	0	422	.144
W612	22.4	59	1	22	23	1	6	16	3	7	138	.080
W1185	12.4	70	1	37	10	14	91	0	0	0	223	−.107
W1186	0	13	0	4	0	0	59	0	3	0	79	−.048
W1187	61.5	128	12	17	23	8	71	5	0	0	264	.009
W1189	46.5	80	1	11	6	0	39	16	0	7	160	0.026
W1192	53.4	5	1	4	0	3	47	0	3	7	70	.179
W1196	45.2	54	1	12	8	8	111	0	3	0	197	−.063
O. sativa												
Hsinchu 56	6.0	57	0	6	2	1	57	32	0	0	155	
IR5533	1.5	27	2	9	14	1	80	2	3	0	138	

a: The phenolics are: 1: gallic acid, 2: protocatechuic acid, 3: *p*-hygroxybenzoic acid, 4: vanillic acid, 5: syringic acid, 6: *p*-coumaric acid, 7: *m*-coumaric acid, 8: ferulic acid, and 9: *o*-coumaric acid.

Table 4. Correlations between The Reduction Rate of Chinese Cabbage Root Length and Contents of 9 Phenolics in Leaf-Stem Extracts of 24 Wild Rice Strains (*O. perennis*)

Trait	Bioassay[a]	Phenolics								
		1	2	3	4	5	6	7	8	9
1) Gallic acid	−.06									
2) Protocatechuic a.	.12	.09								
3) *p*-Hydroxybenzoic acid	.11	−.02	.74[c]							
4) Vanillic acid	−.05	.24	.27	.06						
5) Syringic acid	−.07	−.16	.21	.03	−.35					
6) *p*-Coumaric acid	−.03	−.36	.58[c]	.68[c]	−.23	.24				
7) *m*-Coumaric acid	−.08	−.05	−.09	−.32	−.11	.51[b]	−.15			
8) Ferulic acid	.29	−.03	−.23	−0.6	−.10	−.14	−.06	−.26		
9) *o*-Coumaric acid	.48[b]	−.10	−.13	−.18	.01	−.26	−.18	−.12	−.03	
Total content	−.03	.25	.66[c]	.44[b]	.88[c]	−.10	.16	−.06	−.19	−.12

a: The results of bioassay with Chinese cabbage; those with rice showed no significant correlation with phenolics.

b, c: Significant at 5% and 1% levels, respectively.

height and diameter, the greatest (W593) was about 5 times as large as the smallest (W107). Among Asian strains, the relative biomass was correlated with the -mean aggressiveness estimated at Mishima (r=0.49, P<0.05), but no such correlation was found among all the strains including the American ones (r=0.01). It seems that a high growth rate is correlated with aggressiveness under a certain condition, as pointed out by Yamagishi *et al.* (1980).

DISCUSSION

The main purpose of the present study was to evaluate the allelopathic potential of extracts from varieties of wild rice as determined by bioassay and contents of phenolic acids in the extracts. All these values greatly differed among genotypes of the wild rice, *O. perennis.* However, search for interrelationships among these measurements has revealed the complexity of variations. Considerations on some of these problems will be presented below.

How to obtain an unbiassed estimate of allelopathic potential of a plant seems to remain undecided. It is known that the allelochemics produced in plant tissues differ in amount according to the growth stage, and are distributed in plant organs differently (Rice, 1984). In the present work, we have not yet compared the differential phytotoxicity among the tissues of rice plants. However, we did find that a wide range of variation in root-growth suppressing effect of leaf-stem extracts from different wild-rice strains, when Chinese cabbage seeds were used for assay. The range observed, from a slight stimulation to 68% reduction, may be compared to those reported by the aforementioned workers who have used a large number of genotypes.

Genotypic variations in allelopathic potential or phytotoxin production have been reported by a few workers. Putnam and Duke (1974) examined more than 500 accessions of *Cucumis sativa* and other *Cucumis* species from different origins, in sand culture with two testers, *Brassica hirta* and *Panicum miliaceum,* and found that the growth of the tester plants differed greatly according to *Cucumis* accessions grown together. Fay and Duke (1977) tested the seeds of some 3,000 introductions of *Avena* species for scopoletin exudation, and assayed some of them excreting much scopoletin with wild mustard (*Brassica kaber*) in sand culture. They recognized a strong suppressing effect of selected accessions on the growth of wild mustard.

The complexity of biochemical genetic variations in plants has become well known with the development of isozyme studies. In *Oryza,* the wild species are known to be much more polymorphic in isozymes than the cultivars (Pai *et al.* 1975; Endo and Morishima, 1983). In the present work, the distribution of nine phenolic acids was found to differ much among *O. perennis* strains. These phenolic acids are byproducts of phenylalanine metabolism, and represent major allelochemics in graminaceous plants (Whittaker and Feeny, 1971). Presumably, a number of genes are concerned with the metabolic processes to produce these phenolic acids, different ones being possessed by different strains.

It will be expected that the higher the content of phenolic acids in the extract, the higher would be its root-growth suppressing effect. However, *o*-coumaric acid only showed a correlation with the result of bioassay with Chinese cabbage. Stepwise regression analysis showed that a combination of four phenolic acids had a significant multiple correlation with the root suppression rate, and when their interactions were taken into account, a high multiple correlation ($r=0.84$) was obtained involving six phenolic acids. It may be suggested that certain phenolic acids interact to suppress plant growth when present at proper concentrations, but some others at different concentrations are ineffective or even promote growth together with plant hormones with similar chemical structures like indole acetic acid. Probably, because of such complexity, the total content of phenolics was not correlated with the root suppression rate.

It is known that allelopathic effects are wide-spread among different groups of plants (Rice, 1984; Whittaker and Feeny, 1971). In general, the interaction between neighboring plants can be partly due to allelopathic effect. The chemical interaction may also be divided into aggressiveness on neighbors and resistance to neighbors, although the variations so far studied are mostly concerned with aggressiveness.

All existing plants that have survived natural selection should be adaptive in their environment. Presumably, if a plant produced a substance that is useless for its life, the waste of resources would make it disadvantageous in natural selection. The allelochemics can no longer be regarded as metabolic waste (Muller, 1970; Whittaker and Feeny, 1971). The complex of phenolic acids as observed in *O. perennis* strains would play a role in their struggle for existance.

The *O. perennis* strains exhibit a range of variation from perennial to annual types, to which variations in many life-history traits are associated (Sano and Morishima, 1982; Oka, 1983). In short, the perennial and annual types assume so-called *K*- and *r*-strategies, respectively. The perennial types occur in swamps retaining moisture throughout the year, which are stable but are crowded. In contrast, the annual types occurs in temporary swaps that are exposed to drought and disturbance in the dry season, but are less crowded (Morishima *et al.*, 1984).

We have found that some of intermediate perennial-annual types had high potentials in both aggressiveness and allelopathy. Such intermediate types occur in habitats with an intermediate water condition, which are characterized by a high degree of disturbance and high species diversity in the community, and the wild rice in such habitates had a low relative biomass or a low dominance (Morishima *et al.*, 1984). In contrast, the perennial types often make a clonal population in which other plant species do not dominate. In view of this trend, the intermediate perennial-annual populations may be regarded as subjected to competitive interaction of co-occurring plants more strongly than the perennial or annual populations. Then, the high allelopathic potential observed in some of them may be taken as adaptation to such competitive habitats.

An intermediate strain from Malayan pennisula, W593, was highest in both allelopathic potential and aggressiveness. This strain is now under observation in an experimental field at Pingtung (southern Taiwan) for regenerating success, with an annual strain, W630 (showing a rather high allelopathic potential and a medium grade of aggressiveness). It was observed that after the first planting in 1985, W593 grew more vigorously and had less weeds than W630. After seed maturity, the herbage of W593, lodging down on the ground, produced a large amount of litter and suppressed the germination of weed seeds almost completely for about six months until their seeds, dispersed and buried, began to germinate. Probably, the litter contained enough phytotoxins to protect the population from weeds. In contrast, W630 produced much less litter and their seed germination was suppressed by weeds in the non-weeded plot.

The intermediate perennial-annual populations contain a large amount of genetic variations and are thought to be the wild progenitor of rice cultivars (Sano *et al.*, 1980). In the present study, they showed a wide range in both allelopathic potential and aggressiveness (Chou and Oka, unpublished data). Putnam and Duke (1974) predicted that wild types would have higher allelopathic potential than cultivars. The two rice cultivars tested presently showed a low allelopathic potential as predicted, while the wild strains varied in a wide range. We will examine the allelopathic potential of wild and cultivated by using more materials including cultivars.

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野生稻品系中之植物相剋潛能

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摘要

採自亞洲熱帶地區及美洲地區的24種野生稻（*Oryza perennis*）及兩種水稻品種（*Oryza sativa*）栽植於中央研究院的農場。在植株長到孕穗期時，其葉之水溶萃取液分別進行生物以分析以檢測其植物相剋潛能，另進行色層分析鑑定其相剋物質。結果顯示，植物相剋作用的潛能因野生稻品系而異。此分化顯與該品系所產生的植物相剋物質有相關關係 。 植物毒性在萵苣上表現的程度顯然高於水稻者，此顯示萵苣對相剋物質較水稻者爲敏感。