Genetic Analysis of Thiobencarb Tolerance in Rice (*Oryza sativa* L.)

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除草劑 Thiobencarb에 대한 벼 耐性의 遺傳

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ABSTRACT

Five parents which showed differential response to thiobencarb and their F_1 hybrids were treated with thiobencarb (S-[(4-chlorophenyl)methyl]diethylcarbamothioate) at 2 and 4 kg ai/ha in order to investigate the inheritance of rice (*Oryza sativa* L.) to the herbicide. In the analysis of diallel crosses for tolerance of rice cultivars to the herbicide, highly significant GCA (general combining ability) and SCA (specific combining ability) effects were observed at both herbicide rates using the parameters of plant height and dry weight ; the GCA effect being greater than the SCA effect. The additive effects appeared to be more prevalent than dominance effects, and partial dominance was recognized in relation to herbicide tolerance in the different rice cultivars. Higher heritabilities in the narrow and broad senses were observed at 4 kg ai/ha. The heritabilities in the narrow sense for plant height and dry weight were 0.726 and 0.743, respectively. IR9660-50-3-1 which showed the highest GCA effects seemed to possess more dominant genes related to herbicide tolerance than the other rice cultivars tested.

Key words : Inheritance, thiobencarb, tolerance, additive effect, dominance effect.

INTRODUCTION

Studies on the inheritance of herbicide tolerance in plants could provide basic knowledge needed to introduce herbicide-tolerant genes into the germplasm and develop a tolerant crop. However, limited information about the inheritance of herbicide tolerance in rice is available.

The inheritance of thiobencarb and molinate tolerance in rice was investigated by Kumagai and Kinoshita (9). They found that additive and dominant factors governed the tolerance and that no epistatic relationship was recognized for the tolerance. There were significant correlations between tolerance to thiobencarb and molinate indicating that a similar gene or genes might be associated with the tolerance to the herbicides. They concluded that multiple factors and/or polygenic inheritance were responsible for the quantitative tolerance to thiobencarb.

According to Sankaran and Mohamed Ali (12), herbicide tolerance of a cultivar depends upon its parents. However, Mohamed Ali and Sankaran (10) observed that tolerance of the progeny to herbicides need not be related to the tolerance of the parents.

This study was conducted to investigate inheritance of thiobencarb tolerance to rice and to estimate the possibility of development of a herbicide-tolerant cultivar.

MATERIALS AND METHODS

In a previous study (14), IR9660-50-3-1 and IR10198-66-2 were found to be tolerant to thiobencarb while IR22, IR31802-48-2-2-2, and IR20656-R-R-R-6-1 were susceptible. These cultivars were used as

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parents in a full diallel set of crosses. The five parents and the 20 F_1 hybrids were tested for tolerance to thiobencarb.

A silty clay soil with pH of 6.5, 1.53% organic carbon, 0.152% total nitrogen, and cation exchange capacity of 40.2 meq/100 g was used for this experiment. Seeds of the parents and their hybrids were soaked for 24 h and incubated for 48 h before sowing. Ten germinated seeds of the parents and the F_1's were planted in plastic trays (32×24×11 cm) filled with soil. Water was introduced into the trays to a depth of 2 cm just before herbicide application. Thiobencarb was applied at 2 and 4 kg ai/ha 6 days after seeding by pouring diluted herbicide into the water at the edges of the trays. The treatments were replicated three times, and untreated controls were provided for comparison. Plant height and dry weight of thirty plants from each treatment were measured 10 days after treatment. Dry weights were determined after oven-drying for 48 h at 80℃. The data were expressed as percent of control.

Combining ability analysis was done to estimate variance for general combining ability and specific combining ability and its effects according to method-1 and model-1 described by Griffing (4). The analyses of variance of diallel tables and components analysis were conducted using the methods of Hayman (6, 7). The graphic analysis based on the variance-covariance analysis was done using the methodology of Jinks (8).

RESULTS AND DISCUSSION

The Response of Parents and F_1 Plants to Thiobencarb

Plant height of the parents ranged from 39.5 to 91.3% compared to the control when thiobencarb was applied at 2 kg ai/ha. Significant differences in response to the herbicide between the tolerant and susceptible cultivar groups were observed. The average plant height of the tolerant group (IR9660-50-3-1 and IR10198-66-2) was 88.0% that of the control; that of the susceptible group (IR22, IR31802-48-2-2-2, and IR20656-R-R-R-6-1) was 46.4%. Similar trends were observed when 4 kg ai/ha was applied (Table 1).

At 2 kg ai/ha, the plant height of the F_1 hybrids ranged from 42.7 to 97.7% (average 73.7%) of the control which is higher than the average for the parents (63.0%). At 4 kg ai/ha, the average plant height of the F_1 hybrids was also higher than that of the parents (Table 1). A similar trend was observed for dry weight (Table 1).

In general, when the susceptible cultivars were crossed with the tolerant ones, plant height and dry weight of the progenies were greater than that of the susceptible parents and, some, especially that of the hybrid between IR9660-50-3-1 and IR31802-48-2-2-2 (B×D) were greater than that of the tolerant parent, suggesting a promising combination for tolerance to the herbicide (Table 1).

Combining Ability Effects

The mean squares of GCA and SCA for plant height and dry weight were highly significant at both herbicide concentrations (Table 2). The mean squares for GCA were higher than those for SCA for both characters at both concentrations, and the difference in mean squares between GCA and SCA was greater at the higher concentration. The relatively higher value for GCA variance suggests that additive gene effects are more prevalent than dominance effects. IR9660-50-3-1 and IR10198-66-2 showed positive GCA effects for plant height and dry weight; IR9660-50-3-1 having the highest positive effects, whereas IR22, IR31802-48-2-2-2, and IR20656-R-R-R-6-1 showed negative effects (Table 3). The SCA effects of the F_1 hybrids differed depending upon the crosses. Crosses with the tolerant cultivars showed higher positive SCA effects at both thiobencarb concentrations.

Gene Action Analysis

The higher genetic component of D than H_1 for plant height indicates that additive effects are more prevalent than dominance effects for both herbicide concen-

Table 1. Plant height and dry weight as a percent of control of 5 parents and 20 F_1 hybrids at two thiobencarb rates.

Genotype	Plant height		Dry weight	
	2 kg[1)]	4 kg[1)]	2 kg[1)]	4 kg[1)]
Susceptible group				
A. IR22	52.9	11.5	71.2	29.7
B. IR31802-48-2-2-2	46.9	10.2	46.7	23.3
C. IR20656-R-R-R-6-1	39.5	7.7	53.1	13.7
Tolerant group				
D. IR9660-50-3-1	91.3	61.0	95.0	70.8
E. IR10198-66-2	84.6	39.6	76.5	41.8
A × B	42.7	18.1	61.5	29.1
B × A	50.9	17.5	56.2	22.9
A × C	59.8	10.2	58.3	13.2
C × A	67.4	11.6	62.4	13.4
A × D	72.9	39.2	69.8	54.7
D × A	76.6	42.6	74.9	57.9
A × E	72.5	32.7	79.3	44.2
E × A	69.0	36.0	76.8	46.1
B × C	57.6	16.6	75.6	26.7
C × B	55.3	12.6	72.4	22.9
B × D	96.1	66.6	109.6	80.5
D × B	97.7	64.9	99.5	70.8
B × E	89.9	29.8	93.1	44.0
E × B	80.3	25.4	90.3	30.5
C × D	75.9	46.1	86.5	55.3
D × C	86.2	50.6	90.0	60.0
C × E	70.5	25.0	81.4	42.4
E × C	81.6	33.2	92.4	47.6
D × E	90.2	66.8	107.7	80.5
E × D	80.4	62.3	92.8	78.4
Overall average	71.5	33.5	78.9	44.0
Parental average	63.0	26.0	68.5	35.9
F_1 hybird average	73.7	35.4	81.5	46.1

[1)] Thiobencarb rate in kg ai/ha.

Table 2. ANOVA of diallel analysis for general (GCA) and specific combining ability (SCA) for plant height and dry weight at two thiobencarb rates[1)].

Source of variation	DF	Mean squares			
		Plant height		Dry weight	
		2 kg[2)]	4 kg[2)]	2 kg[2)]	4 kg[2)]
General combining ability (GCA)	4	1179.900**	2047.580**	1009.230**	2302.810**
Specific combining ability (SCA)	10	190.170**	119.357**	247.064**	162.507**
Reciprocal combining ability	10	28.800ns	8.627ns	27.545ns	19.773ns
GCA/SCA		6.204	17.155	4.085	14.171

[1)]** : significant at the 1% level, ns : non-significant.

[2)] Thiobencarb rate in kg ai/ha.

Table 3. GCA and SCA effects of plant height and dry weight for tolerance to two thiobencarb rates.

Genotype	Plant height		Dry weight	
	2 kg[1]	4 kg[1]	2 kg[1]	4 kg[1]
	GCA effects			
A. IR22	-9.788	-10.406	-10.742	-9.919
B. IR31802-48-2-2-2	-5.118	-6.333	-3.748	-6.622
C. IR20656-R-R-R-6-1	-8.212	-11.380	-6.415	-13.136
D. IR9660-50-3-1	14.321	22.596	13.151	23.947
E. IR10198-66-2	8.798	5.523	7.754	5.730
	SCA effects			
A × B	-9.834	1.000	-5.568	-1.470
A × C	10.058	-0.786	-1.401	-7.674
A × D	-1.324	-4.780	-8.968	-1.774
A × E	0.182	5.726	2.145	5.376
B × C	-1.761	-1.226	5.222	0.529
B × D	16.138	16.013	16.238	14.296
B × E	9.845	-5.080	8.802	-5.904
C × D	3.415	3.610	2.605	2.826
C × E	3.922	1.450	6.602	8.409
D × E	-9.361	2.890	0.385	5.776

[1] Thiobencarb rate in kg ai/ha.

Table 4. Variance components of plant height and dry weight for tolerance to two rates of thiobencarb.

Components	Plant height		Dry weight	
	2 kg[1]	4 kg[1]	2 kg[1]	4 kg[1]
D	490.879	435.570	265.644	393.281
F	-9.388	-358.827	25.290	-443.666
H_1	271.596	116.181	491.017	276.950
H_2	270.592	117.342	341.195	218.301
$(H_1/D)^{1/2}$	0.744	0.516	1.360	0.839
$(H_2/4H_1)$	0.249	0.252	0.174	0.197
KD/KR	0.975	0.113	1.073	0.196
r	-0.824	-0.700	-0.810	-0.922
$\bar{F}_1-\bar{P}$	10.700	9.400	13.000	10.200
h^2N	0.594	0.726	0.457	0.743
h^2B	0.759	0.776	0.649	0.831

[1] Thiobencarb rate in kg ai/ha.

trations (Table 4). For dry weight, the gene effect varied depending upon the herbicide concentration. At 2 kg ai/ha, there were higher dominance effects, whereas at 4 kg ai/ha there were higher additive effects.

Ratios computed from the genetic components provided further information on the degree, order and direction of dominance. Partial dominance was observed for plant height since the $(H_1/D)^{1/2}$ values were 0.744 and 0.516 at 2 kg and 4 kg ai/ha, respectively (Table 4). However, for dry weight, over-dominance was observed at 2 kg ai/ha and partial dominance at 4 kg ai/ha. The $H_2/4H_1$ value for plant height was approximately 0.25 suggesting that the frequency distribution of dominant and recessive genes in the parents was similar. However, for dry weight, the values were 0.174 and 0.197 at 2 kg and 4 kg ai/ha, respectively, showing a different frequency distribution of dominant and recessive genes in parents. This indicates that the frequency distribution of dominant and recessive genes in the parents may vary depending upon the herbicide concentration and the different result between plant height and dry weight might be related to the different gene action.

Higher heritabilities in the narrow and broad senses were observed at 4 kg ai/ha of thiobencarb. The heritabilities in the narrow sense for plant height and dry weight were 0.726 and 0.743, respectively (Table 4).

The Wr-Vr graphs for plant height and dry weight are shown in Figure 1. In the Wr-Vr graph for plant height, the passage of the line of unit slope above the point of origin confirms partial dominance for both concentrations (Fig. 1A and 1B) and for dry weight, passage of the line below the point of origin at 2 kg ai/ha indicates over-dominance (Fig. 1C). IR9660-50-3-1 which was tolerant to thiobencarb seemed to have many dominant genes, but IR31802-48-2-2-2 which was susceptible seemed to have many recessive genes (Fig. 1).

Similar trends in dominance effects and gene action were observed for plant height regardless of the herbicide concentration. However, for dry weight, different results were observed depending upon the herbicide concentration. Great reduction in dry weight of the susceptible parents, IR22 and IR20656-R-R-R-6-1, as the concentration increased from 2 kg to 4 kg ai/ha may be the reason for the different gene action.

Reduction in plant height and dry weight of the susceptible cultivars was greater than that of tolerant cultivars when thiobencarb was applied. Roberts (11) reported that additive effects were present in inheritance of butachlor tolerance in rice, but the traits were largely controlled by dominant genes. Heritability estimates were moderately low. Kumagai and Kinoshita (9) found that additive and dominant

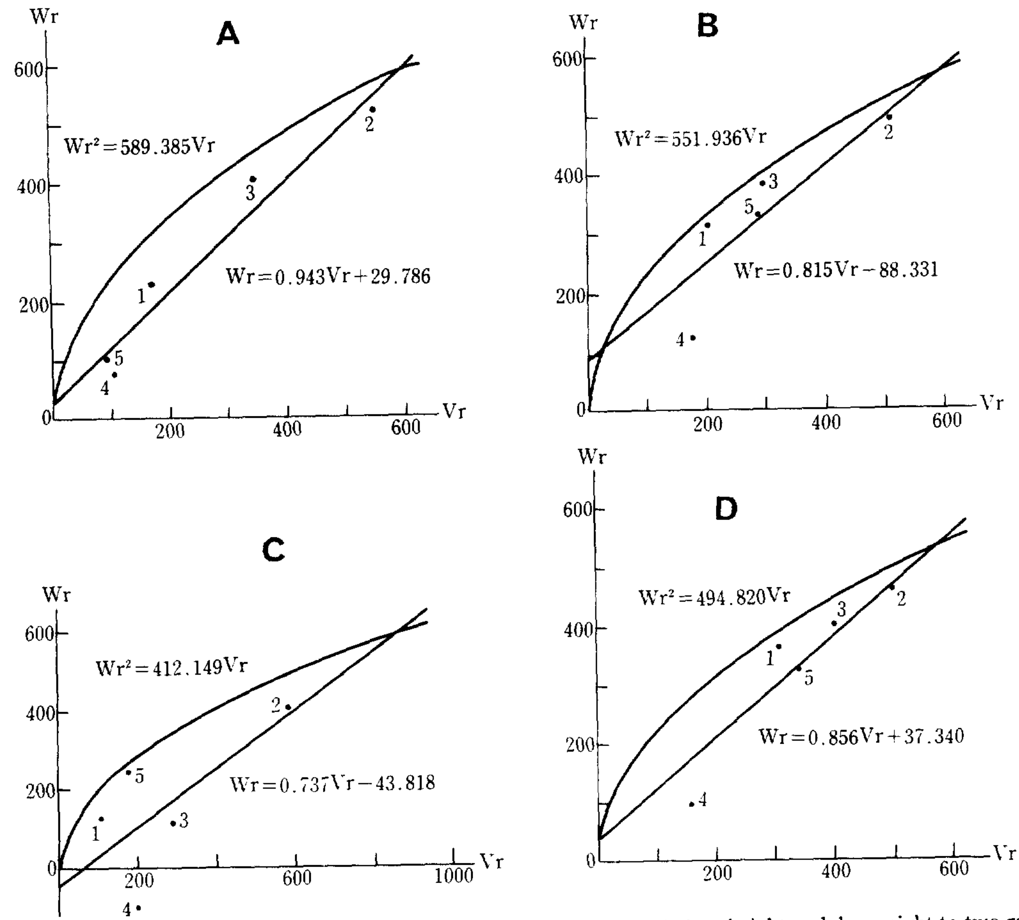

Fig. 1. Relation of covariance (Wr) and variance (Vr) for responses of plant height and dry weight to two rates of thiobencarb. A : plant height at 2 kg ai/ha, B : plant height at 4 kg ai/ha, C : dry weight at 2kg ai/ha, D : dry weight at 4 kg ai/ha. IR22 (1), IR31802-48-2-2-2 (2), IR20656-R-R-R-6-1 (3), IR9660-50-3-1 (4), IR10198-66-2 (5).

factors governed tolerance in the inheritance of thiobencarb and molinate tolerance in rice and that no epistatic relationship was recognized for the tolerance. In their studies, the heritabilities in the narrow and broad senses for the tolerance were 0.290 and 0.456, respectively. Different results obtained in inheritance studies have been attributed to type and concentration of herbicide, characters determined and the cultivars used as parents.

In this study, the response range of the parents and F_1 hybrids to thiobencarb at 4 kg ai/ha was greater than that at 2 kg ai/ha, suggesting that selection of tolerant rice cultivars would be more effective at higher concentration of the herbicide. It is difficult to decide which of the traits such as plant height and dry weight is better for selection of tolerant cultivars but, plant height which showed consistent results at both herbicide concentrations may be a good criterion for determination of herbicide phytotoxicity.

摘　要

除草劑 thiobencarb 處理에 의한 벼 耐性의 遺傳樣式을 조사키 위하여 thiobencarb에 反應을 달리하는 5品種과 이들을 이용하여 二面交雜으로 얻은 F_1 雜種을 대상으로 thiobencarb 2 kg 및 4 kg a.i./ha을 處理하여 二面交雜 分析法으로 조사한 結果를 要約하면 다음과 같다.

Thiobencarb 濃度에 관계없이 草長과 乾物重의 一般組合能力과 特定組合能力에서 共히 有意性이 認定되었으며 一般組合能力이 特定組合能力보다 높게 나타났다. 耐性에 關與하는 遺傳子의 作用은 相加的 效果가 支配的이였으며 耐性이 높은 方向으로의 部分優性도 認定되었다. 狹義 및 廣義의 道傳力은 比較的 높게 나타났는데 特히, 4 kg a:/ha 處理에서 狹義의 遺傳力이 草長에서 0.726 乾物重에서 0.743으로 높은 편이었다. 除草劑 thiobencarb에 耐性을 나타낸 벼 IR9660-50-3-1 系統의 一般組合能力 效果는 耐性이 높은 方向으로 높고 耐性에 關與하는 優性遺傳子를 많이 가진 것으로 推定되었다.

ACKNOWLEDGEMENTS

We thank Dr. J.K. Sohn for critical reading of the manuscript.

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