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GENETIC STUDIES IN RICE (*ORYZA SATIVA* L.). INHERITANCE AND LINKAGE RELATIONSHIP OF LEAF ANGLES

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ABSTRACT

Inheritance and linkage relationships of leaf angles, i.e. angles of leaf attachment and openness and flag leaf angle were studied in a cross between two upland cultivars of rice, namely, D 6-2-2 (drooping leaf) and HY-256 Purple (acute leaf angles). Acute leaf angle was a dominant trait under the control of 4–5 nonallelic mutually interacting genes. The joint segregation pattern revealed the existence of common pleiotropic genes with similar and differential action between each of these angle characters coupled with linkage between only antiinhibitory genes. Nature of inheritance and interrelationship of these leaf angles are discussed and, based on the genetic hypotheses, genotypic constitution of each parent proposed.

Key words: *Oryza sativa*, rice, inheritance, pleiotropy, linkage, leaf angles.

The literature on linkage groups in *indica* rice was summarised by Misro et al. [1] and Goud and Nadaf [2, 3]. This paved the way for a better understanding of the linkage groups in rice. In rice, though genetics of traits has been studied since 1908, the linkage maps are far from complete. The present investigation has been taken up to continue the construction of linkage maps in rice.

MATERIALS AND METHODS

Investigation on the inheritance of leaf angle was taken up in a cross between two upland cultivars, viz. D 6-2-2 (green variety with wide/drooping leaf angles) and HY-256 Purple (purple variety with acute leaf angles). The F_2 consisted of 2458 plants.

Three types of leaf angles are distinguished in rice [4]. The first two types are related to the leaf blade (first leaf below the flag) and are called "angle of attachment" and "angle of openness." The third type is related to the flag leaf, hence called "flag leaf angle." The leaf

angles were recorded at flowering stage using a protractor [5] and subsequently classified [4]. Angle up to 30° was considered as acute (erect), and above 30° as wide (horizontal) in case of angle of leaf attachment and flag leaf angle. In respect of angle of leaf openness, the angle up to 30° was considered as acute (erect), and above 30° as drooping or descending.

The recombination values were computed according to Kolhe [6].

RESULTS AND DISCUSSION

The phenotypes of the parents, F_1 and F_2 ratios are presented in Table 1.

Table 1. Inheritance of leaf angle in the cross between strains D 6-2-2 x HY-256 Purple of rice

Character	Parent phenotype		F_1	Ratio tested	O/E	F_2 frequency		χ^2	P
	D 6-2-2	HY-256 Purple				acute	wide or drooping		
Angle of leaf attachment	Wide	Acute	Acute	702 : 322	O	1667.00	791.00	0.616	0.50–0.30
					E	1685.07	772.93		
Angle of leaf openness	Drooping	Acute	Acute	702 : 322	O	1673.0	785.00	0.275	0.70–0.50
					E	1685.07	772.93		
Flag leaf angle	Wide	Acute	Acute	195 : 61	O	1880.00	578.00	0.133	0.80–0.70
					E	1872.30	585.70		

Inheritance studies. Acute/erect leaf angles were dominant in this study, in contrast to the single report [7] published on this aspect, where it was stated to be controlled by one recessive gene. Chang and Bardenas [4], however, concluded that inheritance of leaf angle was more complex. In the present investigation, the segregation patterns for acute to wide angle/drooping or descending leaf showed that they are not simple in their inheritance. On critical examination, genetic hypotheses were formulated and confirmed through χ^2 analyses.

The results (Table 1) show that angle of leaf attachment segregated in the pentagenic ratio of 702 acute : 322 wide angles, which was explained by the hypothesis of three complementary duplicate genes, where any two of them together would complement to cause acute angle of attachment, along with one inhibitory gene and one anti-inhibitory gene. Angle of leaf openness also segregated in the pentagenic ratio of 702 acute : 322 wide/drooping or descending which could be explained by a similar hypothesis as for angle of leaf attachment. However, flag leaf angle segregated into 195 acute : 61 wide, which indicated that two duplicate genes along with an inhibitory gene and anti-inhibitory gene control this character.

Table 2. Joint segregation of angle of leaf attachment (702:322) angle of leaf openness (702:322) and flag leaf angle (195:61) in F_2 generation

Character pair and F_2 ratio	Basis of expectation	Expected ratio	Genes involved in linkage	Per cent recombination	O/E	Phenotypic frequncies				χ^2	P
						AB	Ab	aB	ab		
					O	1270.0	397.0	403.0	388.0		
Angle of leaf attachment	Independence	492804:226044: 226044:103684	—	—	E	1155.2	529.9	529.9	243.0	161.6	< 0.001
(702 : 322) vs	Three genes common	9126:2106:2106: 3046	—	—	E	1369.1	315.9	315.9	457.0	62.4	< 0.001
Angle of leaf openness (702 : 322)	Linkage	—	Ai-Ala–Ai-Alo	16.46	E	1304.0	381.0	381.0	391.9	2.89	0.50–0.30
					O	1523.0	144.0	357.0	434.0		
Angle of leaf attachment	Independence	136890:42822: 62790:7642	—	—	E	1283.5	401.5	588.8	184.2	640.0	< 0.001
(702 : 322) vs	Two genes common	9126:2106: 3354:1798		—	E	1369.1	315.9	503.2	269.2	253.4	< 0.001
Flag leaf angle (195 : 61)	Linkage	—	Ai-Ala–Ai-Fla	9.88	E	1532.8	152.2	339.5	437.5	1.4	0.80–0.70
					O	1520.0	153.0	360.0	425.0		
Angle of leaf openness	Independence	136890:42822: 62790: 7642	--	—	E	1283.5	401.5	588.8	184.2	601.2	< 0.001
(702 : 322) vs	Two genes common	9126:2106: 3354:1798	—	—	E	1369.1	315.9	503.2	269.7	230.8	< 0.001
Flag leaf angle (195 : 61)	Linkage	—	Ai-Alo–Ai-Fla	11.33	E	1525.4	159.7	346.9	426.0	0.8	0.90–0.80

Combined segregation. Table 2 shows the joint segregation pattern of leaf angles which revealed the existence of common pleiotropic genes between each of these angle characters coupled with linkage between only anti-inhibitory genes. The three leaf angles formed a triangle of pleiotropic effects (Fig. 1), and it was established that the angles of leaf attachment and leaf openness have three common genes, Ala1, Ala2 and Ala3, which act similarly as complementary duplicate genes for determining acute angle. Two of these three genes also cause acute angle of flag leaf behaving differentially, only as duplicate genes.

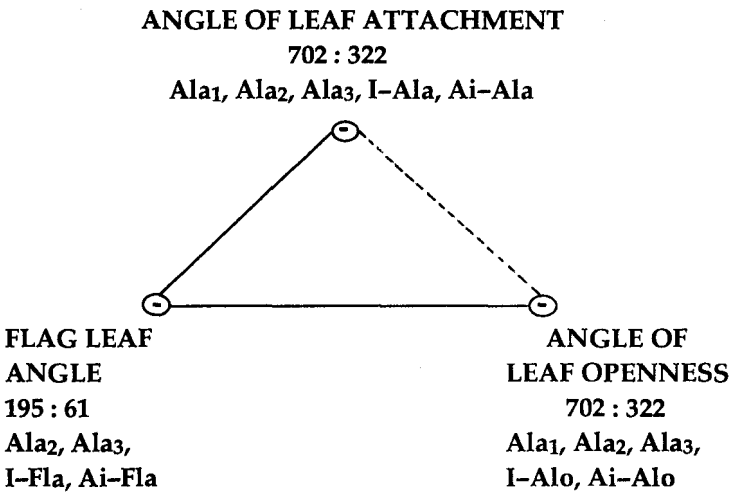

Fig. 1. Pleiotropic nature of genes involved in the expression of leaf angles. ——— Two genes common. - - - - Three genes common.

All the three genes of anti-inhibitory nature, which control leaf angles, namely, angle of attachment (Ai-Ala), angle of leaf openness (Ai-Alo), and flag leaf angle (Ai-Fla) are linked in the following sequence: Ai-Ala — Ai-Fla — Ai-Alo (Fig. 2). The genes Ai-Ala and Ai-Alo maps at the extreme ends with a distance of 16.4 map units. Since these three genes were not studied earlier and showed independent assortment with all other genes for pigmentation and morphological characters under investigation [8], this group does not form part of any of the 12 linkage groups so far constructed and

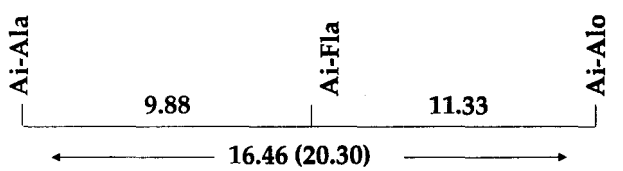

Fig. 2. Linkage map showing the relative positions of three genes. Crossover values are given in percentage. The crossover value modified by applying the Kosambi [9] formula is given in parentheses.

remains a miscellaneous group. Based on the above hypothesis of leaf angles, the genotypic constitution of each parent was derived as:

Character	D 6-2-2	HY-256 Purple
Angle of leaf attachment	ala1 ala1 ala2 ala2 ala3ala3 i-Ala i-Ala ai-Ala ai-Ala	Ala1 Ala1 Ala2 Ala2 Ala3 Ala3 I-Ala I-Ala Ai-Ala Ai-Ala
Angle of leaf openness	ala1 ala1 ala2 ala2 ala3 ala3 i-Alo i-Alo ai-Alo ai-Alo	Ala1 Ala1 Ala2 Ala2 Ala3 Ala3 I-Alo I-Alo Ai-Alo Ai-Alo
Flag leaf angle	ala1 ala1 ala2 ala2 i-Fla i-Fla ai-Fla ai-Fla	Ala1 Ala1 Ala2 Ala2 I-Fla I-Fla Ai-Fla Ai-Fla

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