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THE BIOLOGY AND GENETICS OF DENSE PANICLE IN TWO CULTIVARS OF RICE, *ORYZA SATIVA* LINN.

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Abstract

A cross was made between two local cultivars of rice: AWGU DWARF-W (a heavy-tillering variety of long maturity) and IJ-86W (a tall, medium maturing variety). A total of 9 panicle parameters were measured on 743 F_2 panicles and the data were subjected to statistical analyses.

Principal Component Analysis showed that one principal component shows positive loading for number of spikelets, number of primary branches, length of primary branches, length and number of secondary branches and panicle length, all of which contribute 52% to the total variability. The second component shows high positive loading for number of secondary branches and mean number of secondary branches while the third component shows high loading for number of primary branches per ciliate ring.

The correlation matrix shows that spikelet number correlates highly positively with length of primary branches, length and number of secondary branches while length of primary branches is highly positively correlated with number and length of secondary branches. Regression analysis with number of spikelets as dependent variable shows that number of secondary branches, length of secondary branches and length of primary branches explain 90%, 78% and 71%, respectively, of the variability. Stepwise regression with spikelet number as dependent variable isolated number of secondary branches, length of primary branches and number of primary branches which resolve into the two number factors considering the high correlation between number and length of primary branches.

Chi-square analysis confirms a 15 normal: 1 dense panicle ratio in the F_2 fitting dihybrid inheritance in which dense panicle is conditioned by homozygous recessive genes at two independent loci. The implication of this result for breeding for yield is discussed.

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Introduction

The inflorescence of rice is a panicle which consists of the central axis divided into nodes. Several branches (1-5) arise alternately or somewhat in whorls at each node of the central axis and these branches in turn produce other branches, all of which carry spikelets.

Many studies have been carried out on the induction of the dense and the lax panicle (Gustafsson,1963; Hsieh, 1962; Kuckuck, 1965; Kawai, 1963;1968). Futsuhara, *et al.* (1979) observed that the panicle density of rice was dependent not only on the number of spikelets and the panicle length but also on the total number and total length of primary and secondary branches, although their effects on the panicle density varied largely according to the cultivars and strains used. Thus they recommended the ratio of total number of spikelets to total length of rachis and primary branches of panicle as the most efficient method to determine the panicle density in rice, at least in so far as the cultivars and strains used in their study were concerned. In the cross between *Soryuto* and the dwarf mutant strain induced from a cultivar, *Akibare*, by X-irradiation, it was found that *Suryuto* carried a single recessive gene responsible for the lax panicle, which was independent of the dwarf gene. Pronounced gene interaction was also observed between the lax panicle gene and the dwarf gene. Similar observations have been made by Narahari (1986) in connection with a dwarfing gene *Tr-5* and the panicle parameters of the cultivar carrying it.

Various kinds of dense panicle mutants have been reported. Gustafsson and Ekman (1967) reported erectoides mutant in barley; Kawai (1968) reported the same mutant in rice. Nagao and Takahashi (1963) reported two genes *Ur* (undulate rachis) and *cl* (clustered spikelets) which demonstrated pleiotropic effects on panicle density, resulting in dense panicle

Futsuhara *et al.* (1979) identified the main patterns of panicle density--panicle density could be due to: 1.increase in number and reduced length of primary branches 2. increase in the number of spikelets and secondary branches 3. increase in the number of spikelets and the primary branches 4. tendency to develop the tertiary branches which are absent on normal branches 5. a remarkable reduction in the total length of primary branches, and 6. depreciation of the lowest primary branches noted in two dense panicle mutants.

Kondo and Futsuhara (1980) performed Principal Components Analysis to elucidate the relationships among 17 characters relating to the panicle density. The first principal component appeared to be a number factor and the second, a length factor. For the dense panicles, however, the first principal component was considered to be a length and number factor. In general, panicle density was negatively correlated with the length of panicle organs.

Chang (1964) reported that clustering spikelets was inherited as a single gene lacking dominace. Dense or compact panicle has also been reported to behave as monogenic dominant over lax or normal panicle. In some other studies (Chang, 1964), lax panicles were reported to be dominant over compact or normal panicles. Ghose *et al.* (1960) reported 9:7 F_2 ratios with the dense panicle being either dominant or recessive. Spreading panicle branches behaved as a recessive to the non-spreading type (Chang, 1964).

Eigushi and Sano (1990) reported a dominant gene complex for seed shattering and panicle spreading. Two genes, *spr1* and *spr2* have been reported so far (RGN 6: p 20); *spr2* could be one of the complementary genes reported by Mitra and Ganguli (1932). Futsuhara *et al.* (1991) reported the incidence of a gene *dn-3,* which in the recessive condition, specifies dense panicle; it is independent of the gene *lax* for lax panicle which is epistatic to *dn-3*.

The objective of this project is to study the biology and genetics of the panicle in two selected local cultivars of rice, *Oryza sativa*.

Materials and Methods

The cultivars used or this study are: AWGU DWARF-W, a heavy tillering, 59.80cm tall land race of late maturity and IJ86-W, a tall (142.34cm), low tillering land race of medium maturity (Table 1). A cross was made between these two cultivars by physical emasculation and the F_1 was advanced to the F_2. A total of 743 F_2 plants were raised. At maturity, the panicles were harvested and labelled independently and the following panicle parameters were measured/calculated for each panicle: number of primary branches per ciliate ring (X3), total number of spikelets (X4), number of primary branches (X5), length of primary branches (X6), mean length of primary branches (X7), number of secondary branches (X8), length of secondary branches (X9), mean length of secondary branches (X10), panicle length (X11). The ratio, total length of secondary branches/total number of primary branches was also calculated. The term, spikelet density, is used here to refer to spikelet number. A total of 40 randomly chosen dense panicle F_2 plants were advanced to the F_3 to confirm fixation of the genes controlling the character.

Spikelet number was counted per panicle, disarticulated ones were counted and grain filling was not taken into consideration. Each panicle was scored for density class because there is no descriptor state for this parameter. Densities of 200, 250 and 300 spikelets, all of which were higher than the mean spikelet numbers for the cultivars and their

Table 1:- Panicle characteristics in the parents and F_1 plants of AWGU DWARF X IJ86-W cross.

	No of 1° branches on ciliate ring	Mean No of spikelets	Mean no of 1° branches	Mean no of 2° branches	Mean length of 1° branches (cm)	Mean length of 2 branches (cm)	Panicle length (cm)
IJ86-W [A]	1	214.70 ±15.65 (180-290)	15.80 ±0.47 (13-18)	36.30 ±2.04 (32-50)	166.48 ±6.16 (131.10-186.50)	98.71 ±4.79 (72.60-125.60)	28.77 ±1.30 (26.00-30.50)
AWGU DWARF WHITE [B]	1	169.80 ±2.41 (160-182)	12.10 ±0.35 (11-14)	28.20 ±0.90 (24-32)	118.01 ±2.44 (107.80-131.10)	75.32 ±2.52 (62.30-86.80)	25.43 ±0.39 (24.3-28.5)
AWGU DWARF WHITE [C] X IJ86-W	1	186 (158-201)	14	26 (24-30)	125.83 ±6.70 (113.00-136.60)	56.07 ±11.80 (38.50-78.50)	27.77 ±1.67 (24.50-30.00)
ANOVA*							
A Vs B		8.9160 (s)	43.230 (s)	14.240 (s)	58.560 (s)	20.206 (s)	16.700 (s)
A Vs C		0.9713 (ns)	4.673 (ns)	6.730 (s)	12.540 (s)	17.104 (s)	0.000 (ns)
B Vs C		4.0196 (ns)	8.407 (s)	1.003 (ns)	1.927 (ns)	6.678 (s)	4.550 (ns)

s = significant
ns = non significant
$p = 0.05$

hybrid were considered in turn as standard for dense panicle. For each standard, the F_2 population was tested for a fit to classical Mendelian ratios. Only the 300 standard fitted a Mendelian ratio and so it was adopted. Detailed observations were made on the panicles during measurement. Chi-square was used to test the segregating ratios for a fit to Mendelian models; correlation, regression and factor analyses were used to analyze the panicle parameters for their interrelationships and their genetic determinism.

Results

Biology of the panicle.

IJ86-W has long panicles (28.771.30cm) bearing a mean of 214.7015.65 spikelets on about 16 primary branches which total about 167cm and about 37 secondary branches totalling about 99cm (Table 1). AWGU DWARF-W has an average panicle of 25.430.39cm. These panicles carry about 170 spikelets on between 11 and 14 primary branches totalling about 75cm (Table 1). The parameters of the panicle of the cross between these cultivars are comparable to those in the parents: mean panicle length is 27.771.67 carrying about 186 spikelets on 14 primary branches totalling about 126cm and 26 secondary branches which add up to about 56cm.

The Analysis of Variance shows that IJ86-W has large values than AWGU DWARF-W for all the panicle parameters. The values for number of secondary branches, length of primary branches, length of secondary branches are significantly larger in IJ86-W than the hybrid; this trend does not however obtain for panicle length, number of primary branches and number of spikelets although the values for IJ86-W are numerically higher than those for AWGU DWARF-W X IJ86-W. AWGU DWARF-W has a significantly larger value than the hybrid for length of secondary branches only. It is important to note that comparisons with the hybrid should take cognizance of the fact that the data on the F_1 is based on two plants (reciprocal crosses).

The spikelet number for the cultivars show that IJ86-W has the highest values (mean = 214.1515.65spikelets) while AWGU DWARF-W had a mean of 169.802.41spikelets and their hybrid had a mean of 186 spikelets. When these figures are compared with the high figures obtained in some segregants, none of these cultivars can be categorised as having a dense panicle.

Statistical analysis of panicle parameters

Table 2 shows the factor loadings of the first three principal components. The principal

Table 2: Factor loadings of the principal components for panicle parameters in the AWGU DWARF X IJ86-W F_2

Variable	Communality Estimates	Principal Components I	II	III	Eigen Value
X3	0.987	0.065	-0.09	0.988	5.154
X4	0.894	0.933	-0.15	0.018	1.155
X5	0.843	0.62	-0.666	-0.119	1.004
X6	0.918	0.934	-0.211	-0.048	0.669
X7	0.8	0.78	0.436	0.042	0.608
X8	0.865	0.924	-0.096	0.033	0.28
X9	0.886	0.932	0.126	0.044	0.077
X10	0.633	0.476	0.637	-0.012	0.034
X11	0.487	0.681	0.123	0.088	0.018
Variable explained by each factor (%)		52	11.6	10	

components show high positive loading for number of spikelets (X4), number of primary branches (X5), length of primary branches (X6), mean length of primary branches (X7), number of secondary branches (X8), length of secondary branches (X9) and panicle length (X11). The parameters X4, X6, X8 and X9 are however outstanding because of their high positive loadings. They are length and number factors and they contribute 52% of total variability. The second component shows high positive loading for X7 and X10 (mean length of secondary branches) while the third component shows high loading for X3 (number of primary branches/ciliate ring) only. Components II and III account for 11.65% and 10%, respectively of total variability. Table 3 shows the correlation matrix for the panicle parameters. Spikelet number (X4)

Table 3: Correlation analysis among panicle parameters in the AWGU DWARF X IJ86-W F_2

	X3	X4	X5	X6	X7	X8	X9	X10	X11
X3		0.0655	0.1522	0.0474	0.0412	0.0673	0.0673	0.0061	-0.0005
X4			0.6026	0.8442*	0.6473	0.9508*	0.8855*	0.3075	0.5213
X5				0.7847*	0.1284	0.5366	0.442	0.0802	0.3448
X6					0.6853	0.8039*	0.7923*	0.352	0.6122
X7						0.6538	0.7326*	0.4655	0.591
X8							0.7329*	0.308	0.5097
X9								0.5081	0.5275
X10									0.2833
X11									

* Significance at P = 0.001

Table 4: Parameters of regression analysis of panicle \ parameters (dependent variable = X4)

Independent Variable	a	b	R^2
X3	179.13	10.82	0.004
X5	-11.96	106.06	0.36
X6	-16.05	1.7	0.71
X7	-54.28	25.47	0.42
X8	53.24	4.46	0.9
X9	87.07	1.63	0.78
X10	122.16	34.48	0.09
X11	-39.29	9.63	0.27

correlates highly positively with length of primary branches (X6), number of secondary branches (X8) and length of secondary branches; length of primary branches is highly positively correlated with number of secondary branches (X8) and length of secondary branches. Table 4 shows the parameters of regression for the panicle parameters with X4 as the dependent variable. Number of secondary branches (X8) explains 90% of variability in the independent variable. The length of secondary branches (X7) explains 78% of the variability in the independent variable while length of primary branches (X6) explain (71%) of the variability. Number of secondary branches is outstanding in its contribution to the spikelet number.

Table 5 shows a summary of stepwise regression for dependent variable X4. This procedure isolates only three parameters: X8, X6 and X5. . These parameters can easily resolve into two: X8 and X5 considering the fact that length and number of primary branches are highly positively correlated. The results of analyses confirm the trend in the 3-D graph (Fig. 2) which shows that high number of primary branches and high secondary branch length : primary branch length ratio correlate with higher spikelet numbers.

Table 5: Summary of stepwise procedure for dependent variable X4.

Independent variable entered	a	b	R^2
X8	53.24	4.46	0.9
X6	24.19	3.61	0.92
X5	19.58	0.94	0.92

Genetics of inheritance of panicle density.

Table 6 shows the Chi-square test for a fit to a 15 normal: 1 dense panicle ratio in the F_2 of the (AWGU DWARF-W X IJ86-W) cross. The data fit the expectation of dihybrid inheritance in which dense panicle is conditioned by homozygous recessive genes at two loci.

Table 6: Test of fit for a 15 normal: 1 dense panicle in the F_2 population of (AWGU DWARF X IJ86-W) F_2.

	Normal	Dense Panicle	Total	P
OBSERVED	691	52	743	
EXPECTED	696.56	46.44		
X^2	0.0444	0.6657		0.1P0.5
ΣX^2		0.7101		

Discussion

The term *panicle density* was defined by Futsuhara *et al.* (1979) as the ratio of total spikelets to total length of rachis and primary branches of the panicle. It has been used here rather loosely to represent the total number of spikelets per panicle. This has been done because the main patterns of panicle density are generally due to increase or decrease in the major panicle members (spikelets, primary branches, secondary branches etc.). Spikelet number remains the ultimate measure of individual plant grain yield.

The panicles in the F_2 show a lot of differences in the expression of the parameters in terms of number and length. Generally, the ciliate ring did not bear many primary branches; infact, they aborted. Some panicles carried the bulk of their spikelets on primary branches; and in such cases, the spikelet number could be reasonably high if the primary branches attained high numbers and consequently, high total lengths. The general picture is that spikelets are borne on secondary branches, in the main, and on the upper half of most primary branches. For dense panicles, the secondary branches are far more numerous than for normal panicles; in some cases, tertiary branches are seen. Fig.1 shows this trend. The 3-D graph in Fig.2 further shows that, even within the dense panicle subpopulation, the total length of the secondary branches measured by the index on the Z-axis and the number of primary branches determine the spikelet number. Low spikelet numbers were generally observed in panicles in which there were a limited number of secondary branches, reduced number of primary branches due to abortion and failure of primary branches at the section proximal to the ciliate ring.

From the general observations in the segregating population, it is clear that spikelet number in the panicle of both cultivars depends on the number and length of both primary and secondary branches. This observation has been validated by the result of the stepwise regression for dependent variable X4 (spikelet number) which isolated number of secondary branches on one hand and number and length of primary branches, both of which have been appropriated as number of primary branches on account of the high positive correlations (0.78) between them, on the other (see Fig. 3). The parameters that depart from the general trend of correlation are: number of primary branches per ciliate ring, mean length of secondary branches and panicle length.

The factor 1 in the factor analysis is the most important factor as it is characterized by high loadings on a group of related variables such as spikelet number, length of primary branches, number of secondary branches and length of secondary branches--all of which are number and length factors as already observed. For all the components, no variable showed high negative loadings. The results of the factor analysis are similar to that obtained by Kondo and Futsuhara (1980).

The inheritance of panicle density fits a 15 normal: 1 dense panicle ratio in this study. All the forty random F_2 plants advanced to the F_3 did not segregate confirming that they had fixed for dense panicle at the F_2. Chang (1964) reported that clustering spikelets was inherited as a single gene lacking dominance. Dense or compact panicle has also been reported to behave as a monogenic dominant over lax or normal panicle. In some other studies (Chang, 1964) lax panicles were reported to be dominant over compact or normal panicles. Ghose *et al.* (1960) reported a 9:7 F_2 ratio with the dense panicle either dominant or recessive. Futsuhara *et al.* (1991) reported the incidence of a gene *dn-3* which, in the recessive condition, specifies dense panicle. Other single genes have been reported for panicle forms (RGN 12, 1995; p. 25-60).

The gene model obtained in this work is significant because it demonstrates that cultivars may carry genes for dense panicle in a 'dormant' state. It is not difficult to see from the analysis of the panicle parameters that number and length of primary branches are inherited from the IJ86-W parent. Although the number of secondary branches is statistically higher in IJ86-W than in AWGU DWARF-W, extensive observation has shown that the nodes on the panicle axis and primary branches in the panicle of AWGU DWARF-W are characteristically congested and this is the character that is observed on all dense panicles. Each cultivar should be in the recessive homozygous condition at one of the loci for primary branch and secondary branch number for their panicles to be normal.

No noticeable effect of the dwarfing gene on panicle density was monitored in this study. About 7% of the dense panicle plants were dwarf and none of them had any spectacular panicle characteristics. Futsuhara *et al.* (1979) observed pronounced gene interaction between the lax panicle gene and the dwarf gene in the strain he studied. Narahari (1986) also implicated such an interaction between gene *TR-5* and panicle density in the cultivar he studied.

Grain yield is central to rice agriculture. The three main components of grain yield are: the number of panicles per unit area, the number of well developed grains per panicle, and grain weight. The genetic manipulation of the panicle based on the knowledge of its basic biology, can improve yield by raising plants in the so-called panicle weight class (plants with heavy but few panicles per plant) or even very high yielding varieties which may fall in the panicle number class (small, light panicles with many panicles per plant). This study has shown that panicle density in the cultivars studied are controlled by two independent genes conditioning number of primary branches and number of secondary branches. Two cultivars that have high values for each of these parameters can be crossed to yield heavy panicles through selection.

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References

Chang, T.T. (1964). Present Knowledge of Rice Genetics and Cytogenetics *IRRI Technical Bulletin* 1 p. 36.

Eiguchi, M. and Y. Sano (1990). A gene complex responsible for seed shattering and panicle spreading found in common wild rices. *Rice Genetics Newsletter* 7: 105-107.

Faluyi, J.O. and Chinyere C. Nwokeocha (1993). Agrobotanical studies of some populations of the *Oryza sativa-Oryza glaberrima* complex of peasant agriculture. *Nigerian Journal of Botany* 6: 1-11.

Futsuhara, Y., S. Kondo, H. Kitano and M. Mii. (1979). Genetical studies on dense and lax panicles in rice. I.Character expression and mode of lax panicle rice. *Japan. J. Breed.* 29(2): 151- 158

Futsuhara, Y., S. Kondo and H. Kitano (1991). Interaction between genes for panicle density in rice. *RGN* 8: 121-122.

Ghose, R.L.M., M.B. Ghatge, and V. Subrahmanyan. (1960). Rice in India 2nd ed. 474 pp. *Indian Council Agric. Res.*, New Delhi.

Gustafsson, A. (1963). Productive mutations induced in barley by ionizing radiations and chemical mutagens. *Hereditas* 50: 211-263.

Gustafsson, A. and G. Ekman (1967). Yield efficiency of the X-ray mutant Svalof's Pallas barley'. *Zuchter* 37: 42-46.

Hsieh, S.C. (1962). Genic analysis in rice. III. Inheritance of mutations induced by irradiations in rice. *Bot. B. Acad. Sinica.* 3: 151-162.

Kawai, T. (1963). Mutations in rice induced by radiation and their significance in rice breeding. I. Mutation by radiophosphorus. *Bull. Nat. Inst. Agr. Sci.* 10: 1-76.

Kawai, T. (1968). Genetic studies on short-grain mutants in rice. *Mutations in Plant Breeding* II. IAEA, Vienna, p. 161-182.

Kondo, S. and Y. Futsuhara (1980). Genetical studies on the panicle in rice. I. Analysis of component characters of panicle density. *Japan. J. Breed.* 30 (4): 335-343.

Kuckuck, H. (1965). The importance of induced mutations in wild and primitive types of cereals for phylogeny and plant breeding. *The use of induced mutations in plant breeding.* Pergamon Press, Rome p. 355-3363.

Mitra, S.K. and P.M. Ganguli. (1932). Some observations on the characters of wild rice hybrids. *Indian J. Agr. Sci.* 2: 271-279.

Nagao, S. and Takahashi (1963). Trial construction of twelve linkage groups in Japanese rice. *J. Fac. Agr.* Hokkaido Univ. 53: 73-13.

Naharari (1986). TR-5 Dwarfing gene in rice. *Rice Genetics* p. 323-332.
RGN 6: Report of the Committee on Gene Symbolization p. 20.
RGN 12: Report of Committee on Gene Symbolization p. 25-60.