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Genetic Analysis of Traits Associated with Panicle and Flag Leaf in Tropical Japonica Rice

Jae Ki Chang*, Byeong Geun Oh*, Ho Yeong Kim*, Sang Jong Lim*, Soon Chul Kim*, and Jae Keun Sohn**

ABSTRACT

Diallel analysis was conducted with F1's derived from crossing in all combinations without reciprocals among six rice varieties; three tropical japonica and three temperate japonica varieties, with different traits associated with panicle and flag leaf. Epistasis was observed in the number of primary branches (PB) per panicle and of spikelets per panicle, while flag leaf length, flag leaf color, PB length and neck node thickness were explained with the additive-dominance model. The estimated genetic mode of flag leaf length and PB length was a positive complete dominance model with high heritability, and that of flag leaf color and neck node thickness was an incomplete dominance model. In particular, tropical japonica varieties with low-tillering and heavy-panicle appear to have higher number of dominant genes for flag leaf length and PB length than temperate japonica varieties.

Key words : rice, tropical japonica, diallel analysis, flag leaf, panicle.

Low-tillering and heavy-panicle type have been proposed as an ideotype that would support a significant increase in rice yield potential, particularly for direct-seeding establishment by many rice breeders and physiologists. According to the goal of International Rice Research Institute's strategic plan, the new plant type can give a 30～50% higher yield potential than the current semidwarf varieties in tropical environments during the dry season (Khush, 1995). Many efforts to improve local varieties with this plant type have been made in Korea.

To reduce the time for commercialization of this plant type, it is necessary to undertake studies of rice germplasm with low-tillering and heavy-panicle type. A previous study (Chang et al., 1997) using tropical japonica germplasms with low tillering and heavy panicle investigated the genetic mode of panicle number per hill and panicle length. Tropical japonica varieties carried higher number of dominant genes for panicle length and panicle number, and breeding values (additive effects) were predominate over dominance effect with high heritability and no epistasis.

Study on the morphology of the rice panicle mainly concentrated on qualitative genetics and physiology. Murai & Iizawa (1994) reported that single genes associated with morphology of panicle had influences upon expression of other characters related to the panicle. The effects of Ur-1 (Undulate rachis), Dn-1 (Dense panicle), Cl (Clustered spikelets), lax (lax panicle) and sp (short panicle) were defined : Ur-1 increased the number of spikelets per panicle and the number of secondary branches per primary branch (PB), Dn-1 increased the number of secondary branches per PB and the number of spikelets per panicle but decreased PB length, and lax and sp decreased the number of spikelets per panicle. The number of spikelets per panicle was highly correlated with neck node thickness rather than with the number of vascular bundle (Son et al., 1997) and the neck node thickness was positively correlated with dry wind damage tolerance (Lee et al., 1997).

Among the components of the number of spikelets per panicle, the number of PB per panicle was the highest realized heritability, and exceeded the heritability for the number of spikelets per panicle. Genetic correlations indicated that the number of PB per panicle was positively and strongly associated with the number of spikelets and was not positively correlated with the number of spikelets on secondary branches per secondary branches (Kato, 1997). Hashimoto et al. (1983) claimed that spikelets on the upper PB are developmentally more stable and harder to degenerate under unfavorable environments. Rice spikelets on PB generally produce fully filled grains, in contrast to spikelets on secondary branches. The result indicated that characters related to PB were important to produce filled grain or high density grains and high yield.

In measuring leaf color, SPAD 501 was used because many researchers reported that the chlorophyll meter SPAD 501 was more efficient than other methods, and values were highly correlated with leaf nitrogen and chlorophyll content (Furuya, 1987 ; Takebe & Yoneyama, 1989).

In this study, we investigated the difference among characters associated with the panicle and flag leaf of tropical japonica and temperate japonica, and performed genetic analysis of these characters using 6×6 half diallel crosses.

* National Yeongnam Agricultural Experiment Station, Milyang 627-130, Korea.
**College of Agriculture, Kyungpook National University, Taegu 702-701, Korea.
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MATERIALS AND METHODS

Six parents were crossed in all possible non-reciprocal pairs resulting in 15 crosses in 1995. The parents were three temperate japonica varieties with high tillering and three low tillering tropical japonica varieties. The three temperate japonica varieties were Milyang 95 (Korea), Milyang 99 (Korea), and Hitomebore (Japan), and the three tropical japonica varieties were Hapcheon 1 (China), Shennung 89-366 (China), and IR65598-112-2 (IRRI). These two types of japonica rice were significantly different not only in tillering ability but also in morphology of panicle and flag leaf. Temperate japonica parents generally showed a larger number and shorter panicles, and smaller leaves than tropical japonica parents (Table 1).

The six parents and their fifteen F1 hybrids were sown on April 22, 1996. Seedlings grown in a protected semi-irrigated rice nursery were transplanted to a paddy field on May 22 with a single plant per hill spaced at 30×15 cm. The amount of fertilizers applied by dressing was N ; 110 kg, P_2O_5 ; 70 kg and K_2O ; 80 kg per ha. The randomized block design with two replications was employed.

At full heading, flag leaf color of 45 plants per plot was measured using SPAD 501 (Minolta). Flag leaf length, the number of spikelets per panicle, the number of PB per panicle, PB length and neck node thickness were measured on the tallest culm per hill from 15 plants per plot at maturity.

Genetic analyses were carried out based on Hayman's (1954 a, b) and Jones's (1965) methods.

RESULTS AND DISCUSSION

Analysis of variance

Mean values of the parents and the F1's for six panicle and flag leaf associated characters are presented in Table 1. Tropical japonica varieties with low-tillering and heavy-panicle were larger than temperate japonica varieties with high tillering in six characters ; flag leaf length, flag leaf color, PB length, the number of PB per panicle, spikelets per panicle and neck node thickness, especially sink size.

Morishima et al. (1967) reported that a genetic plant type is defined as a panicle number type and a panicle length type. The panicle number type has a larger number of shorter panicles and smaller leaves than the panicle

Table 1. Mean values and range of six parents and their F_1 plants for traits associated with panicle and flag leaf in 6×6 half diallel crosses.

Parents and crosses	Flag leaf		Primary branches per panicle		No. of spikelets per panicle	Thickness of neck node (cm)
	Length (cm)	Color†	Length (mm)	Number		
1. Hapcheon 1	37	48	91	17.4	284	2.2
2. Shennung89-366	37	51	103	16.7	249	2.2
3. IR65598-112-2	45	55	128	18.1	543	3.2
4. Milyang 95	34	39	92	10.5	151	1.5
5. Milyang 99	27	42	77	10.6	103	1.4
6. Hitomebore	31	42	91	10.9	131	1.3
1 × 2	35	52	102	16.7	270	2.1
1 × 3	41	48	101	17.2	337	2.5
1 × 4	36	43	94	14.6	245	1.9
1 × 5	33	42	84	14.1	199	1.7
1 × 6	34	46	93	13.8	203	1.5
2 × 3	45	49	114	18.4	380	2.6
2 × 4	36	43	93	13.6	199	1.8
2 × 5	36	47	103	13.8	173	1.7
2 × 6	34	48	99	12.3	175	1.5
3 × 4	48	41	127	18.1	348	2.6
3 × 5	43	43	122	17.2	273	2.3
3 × 6	47	47	129	14.5	251	2.2
4 × 5	33	40	82	11.4	132	1.5
4 × 6	39	39	91	11.3	150	1.4
5 × 6	34	39	81	11.1	117	1.3
Range of parents	27~45	39~55	77~128	10.5~18.1	103~543	1.3~3.2

† Flag leaf color was measured by chlorophyll meter, SPAD 501 (Minolta) at full heading stage, and high SPAD value means dark green.

length type. The materials in this study fit this genetic plant type, that is, tropical japonica varieties with low tillering heavy panicle were the panicle length type in a viewpoint of this genetic plant type.

An analysis of variance was carried out according to Jones's formula (1965) as shown in Table 2. Item a (additive genetic effect) showed highly significant for all characters, and item b (non-additive genetic effect) was the same aspect. This indicated that additive and non-additive gene effects are all involved in these characters. The mean square of an item was remarkably larger than that of the b item for all characters, suggesting that the additive effects of the genes explain most of the total genetic variation.

Test of hypotheses

To test the hypotheses of independent distribution of genes among the parents and independent action of non-allelic genes, two kinds of tests; one by the heterogeneity of Wr-Vr and the other by the regression coefficient of Wr on Vr, were conducted (Table 3).

The heterogeneity of Wr-Vr for flag leaf length, flag leaf color, PB length, and neck node thickness was not significant, showing that the hypothesis of the additive-dominance model was satisfied. In the relationship between Vr and Wr for these four characters, coefficient of the regression of Wr on Vr (b) was significantly different from zero, but not from unit slope, suggesting the absence of epistasis. But two characters, the number of PB and spikelets per panicle were significantly different in the heterogeneity of Wr-Vr, indicating invalidity in the estimation of genetic parameters.

The additive-dominance model explained 92%, 98%, 98%, and 99% of the variation of flag leaf length, flag leaf color, PB length, and number of PB per panicle and

Table 2. Mean square values for traits associated with panicle and flag leaf of F_1 plants in half diallel crosses between six rice varieties.

Source of variation	df	Mean square: Flag leaf Length	Flag leaf Color	Primary branches per panicle Length	Primary branches per panicle Number	No. of spikelets per panicle	Thickness of neck node
Replication	1	1.04^{ns}	0.57^{ns}	8.57^{ns}	0.38^{ns}	27.43^{ns}	0.005^{ns}
Genotype	20	62.12**	41.25**	500.10**	15.60**	22286.56**	0.555**
a†	5	192.95**	137.87**	1578.0**	55.70**	85026.77**	2.141**
b‡	15	18.51**	9.05**	140.79**	2.24**	1373.16**	0.026**
Error	20	5.47	0.84	12.99	0.22	37.55	0.003

† a ; additive genetic effect.
‡ b ; non-additive genetic effect.
*,** Significant at the 5% and 1%, respectively.

Table 3. Test of hypothesis for traits associated with panicle and flag leaf in the F_1's of 6×6 half diallel analysis.

Item		Flag leaf Length	Flag leaf Color	Primary branches per panicle Length	Primary branches per panicle Number	No. of spikelets per panicle	Thickness of neck node
Heterogeneity of Wr+Vr (F-value)		2.72ns	13.69**	25.87**	15.62**	62.80**	11.03**
Heterogeneity of Wr-Vr (F-value)		0.73^{ns}	1.11^{ns}	3.12^{ns}	12.35**	6.12*	2.30^{ns}
Regression of coefficeint of Wr on Vr		0.84	1.02	0.90	–	–	1.02
t-test of b on the null-hypothesis	b=0	3.25*	15.07**	4.60**	–	–	10.41**
	b=1	0.60^{ns}	0.31^{ns}	0.52^{ns}	–	–	0.17^{ns}

*,** : Significant at the 5% and 1%, respectively.

neck node thickness.

Analysis of genetic parameters

For the four characters which satisfied the hypotheses, the variance components and genetic parameters were obtained (Table 4, Fig. 1).

Highly significant additive components of genetic variation (D) in all characters revealed that expressions of these characters were under the control of additive gene effects, and the dominance components of variation were non-significant except in flag leaf color. The variance components due to additive effects were larger than those due to dominance effects for two characters, flag leaf color, and neck node thickness.

In flag leaf length and PB length, the expression $\sqrt{(H_1/D)}$ which represented the degree of dominance (weighted estimate) was nearly at 1, and the regression line of Wr on Vr graph cut the Wr-axis near the origin with no significant difference, indicating that the average degree of dominance level was in the nearly complete dominance range. In flag leaf color and neck node thickness, expression of $\sqrt{(H_1/D)}$ was 0.72 and 0.32, respectively, and the constants of regression line of Wr on Vr graph were significantly different from $H=d$ and $H=0$, indicating that the average degree of dominance level was in the incomplete dominance range. The estimated values of narrow-sense heritability were quite high (77%, 83%, 76%, and 96% in flag leaf length, flag leaf color, PB length, and neck node thickness), due to the major contribution of additive gene effects to genetic variations. The direction of dominant effects from Wr+Vr on Vr graph and 2 (F(s)mean-P.mean), in flag leaf length and PB length were positive while it was ambiguous in the other characters.

Three tropical japonica varieties formed a group towards the point of origin while three temperate japonica varieties occupied the position distant from the origin on the Wr/Vr graph of flag leaf length and PB length. This indicated that three tropical japonica varieties possessed higher numbers of dominant alleles for flag leaf length and PB length than the other three temperate japonica. Dominant alleles governed the maximum expression of these characters. In flag leaf color, Milyang 95 carried the maximum number of dominant alleles while IR65598-112-2 possessed the maximum number of recessives. Hitomebore carried the maximum number of dominant alleles for thickness of necknode while Milyang 95 on the other hand, possessed maximum number of recessives.

The present experiment showed that the genetic mode in flag leaf length and PB length involved the positive co-

Table 4. The variance components and genetic parameters for traits associated with panicle and flag leaf in the F_1's of 6×6 half diallel crosses.

Genetic components and their ratio	Flag leaf length	Flag leaf color	Length of primary branches per panicle	Thickness of neck node
D	35.8** ± 6.40	37.4** ±1.12	293** ± 50.7	0.54** ±0.009
F	−7.0 ±15.64	8.6* ±2.75	−115 ±123.8	0.02 ±0.022
H_1	31.8 ±16.25	19.0** ±2.85	270 ±128.7	0.06 ±0.023
H_2	20.9 ±14.52	13.0** ±2.55	247 ±114.0	0.04 ±0.021
E	2.7 ± 2.42	0.4 ±0.42	6.5 ±19.16	0.001 ±0.003
Heritability				
$h_{(B)}$	0.92	0.98	0.98	0.99
$h_{(N)}$	0.77	0.83	0.76	0.96
No. of genes concerned (effective factors)				
h^2/H_2	1.68	0.68	0.24	0.19
$\sqrt{(\max P. - \min P.)/4D}$	0.36	0.33	0.21	0.94
Direction of dominance				
2 ($F_{(s)}$mean-P.mean)	6.05	−3.05	7.89	−0.09
Regression of Wr+Vr on Yr	−3.01*	1.63	−8.69	0.00
Average degree of dominance				
$\sqrt{(H_1/D)}$	0.94	0.72	0.96	0.32
Constant of Wr / Vr graph	3.03	4.15*	20.49	0.11**
Distribution of dominant and recessive genes among parents				
$H_2/4H_1$	0.16	0.17	0.23	0.17
kD/kR	0.10	1.00	1.00	1.19

*,** Significant at the 5% and 1%, respectively.

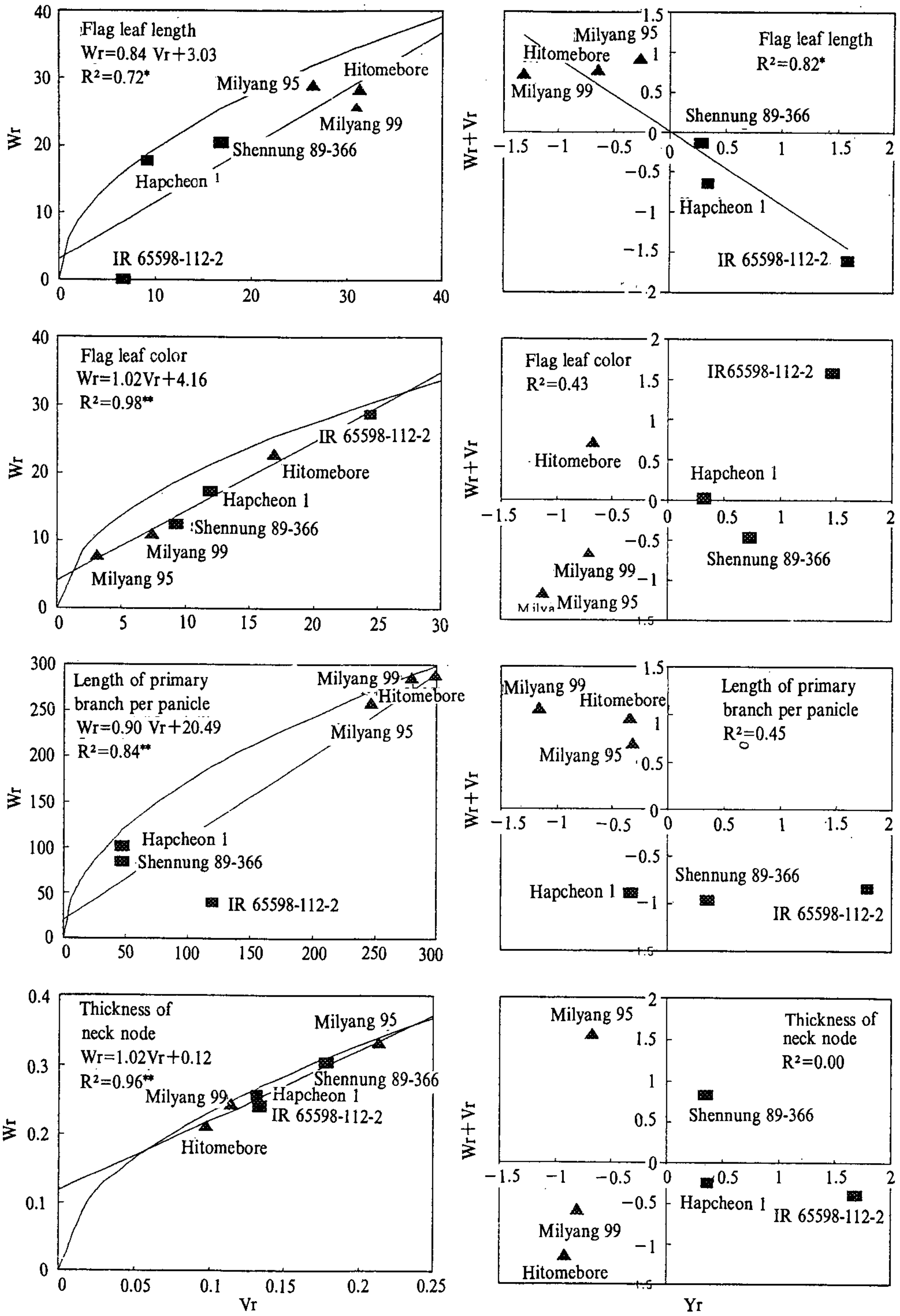

Fig. 1. Wr / Vr and Wr+Vr / Yr graph for traits associated with panicle and flag leaf in the F_1's of 6×6 half diallel crosses.

(■ : Tropical japonica variety, ▲ : Temperate japonica variety)

mplete dominance with no epistasis and high heritability, and flag leaf color and neck node thickness were incomplete dominance due to the additive genetic effect and high heritability estimated at 83% and 96% with no epistasis. In particular tropical japonica varieties with low-tillering and heavy-panicle carried higher number of dominant alleles for flag leaf length and PB length.

Flag leaf length was accepted the hypotheses of diallel analysis in this study, but Murai et al. (1987) reported presence of epistatis. However, additive gene effects predominated over the dominance effects in two studies showed similar trend.

SPAD values were highly correlated with leaf nitrogen and chlorophyll contents especially at the panicle-formation and full heading stage (Furuya, 1987 ; Takebe & Yoneyama, 1989). Okamoto & Horino (1994) showed that varietal differences of nitrogen content of rice are closely correlated with varietal differences in leaf color, and environmental variations of nitrogen contents of milled rice were highly correlated with SPAD values in almost all varieties.

Among the components of the number of spikelets per panicle, the number of PB per panicle had the highest realized heritability which exceeded the heritability for the number of spikelets per panicle. The genetic correlations indicated that the number of PB per panicle was positively and strongly associated with the number of spikelets and was not positively correlated with the number of spikelets on secondary branches per secondary branches (Kato, 1997). Murai & Iizawa (1994) investigated the effects of Ur-1 (Undulate rachis), Dn-1 (Dense panicle), Cl (Clustered spikelets), lax (lax panicle), and sp (short panicle) on morphology of panicle and reported that Ur-1 increased the number of spikelets per panicle and the number of secondary branches per PB. Dn-1 increased the number of secondary branches per PB and the number of spikelets per panicle but decreased the length of PB, and lax and sp decreased the number of spikelets per panicle.

Several traits of tropical japonica varieties seemed available in temperate japonica breeding program; long flag leaf, dark green flag leaf, long PB, and thick neck node. Tropical japonica varieties seemed to possess higher numbers of positive dominant genes for flag leaf length and PB length. The presence of additive gene action and high heritability in four characters suggested that the selection would be effective in earlier generations for flag leaf length, flag leaf color, PB length, and neck node thickness.

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