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Diallel analysis of tiller number at different growth stages in rice (*Oryza sativa* L.)

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Summary. The genetics of tiller number at different development stages in rice was studied in a 6 × 6 diallel cross set involving six indica rice varieties in which a large difference of phenotypes existed. Estimates of genetic parameters following Hayman's method showed significant additive and nonadditive gene action, and the latter appeared to be solely due to dominance. High tillering ability was inherited as a partial dominant character conditioned by two or more blocks of genes, and var 'H1459' had more dominant genes, whereas 'Zhu-Yun-Luo' had more recessive ones. Combining ability analysis by Griffing's method also indicated significance of both additive and nonadditive effects, but the former was more important than the latter. 'H1459' and 'Bi-Yu-Zao-Luo' were good general combiners, and their hybrids 'H1459' × 'Le-Yi' and 'Zhu-Yun-Luo' × 'Bi-Yu-Zao-Luo' were better crosses for combining an optimum tiller number with high percentage of productive tiller. An identical polygenic system appeared to be responsible for the genetic control of both tiller number at the different growth stages and the terminal character, productive tiller number. However, with growth of the plant, relative contributions of nonadditive gene action and environmental factors to the variation decreased, while those of additive gene action increased. Selection for high tillering ability, therefore, should be exercised at peak tillering or later stages.

Key words: *Oryza sativa* L. – Inheritance – Tiller number – Combining ability – Gene effects

Introduction

The number of productive tillers per plant plays an important role in the formation of grain yield in rice. At the advanced stage of the crop, there are considerably fewer productive tillers than what have been formed, the difference being the result of an early mortality of young tillers due to several reasons. Pavilov (1971) considered the death of young tillers as lost capital.

The genetic studies reported so far have largely focused on terminal characters, such as productive tiller number at the advanced growth stage (Ahmad et al. 1986; Li 1977; Murai and Kinoshita 1986; Perera et al. 1986; Sinha et al. 1985; Subbaraman and Rangasamy 1989; Wu 1968). According to the theory of developmental genetics, genes are expressed selectively at different growth stages following a certain sequence of time and place. Kheiralla and Whittington (1962) reported that in tomato the genetic variance components for some quantitative characters, such as plant height, varied with the developmental stages. Some other reports have supported this result and the conclusion that, the genetic model from the final character could not fully reflect the real actions of genes during the development of the character (Peat and Whittington 1965; Wu 1987). It is necessary, therefore, to understand gene action at different development stages. In the research reported here diallel analysis was used to study the inheritance of tiller number at different development stages of rice.

Materials and methods

The following varieties were selected, representing various levels of tillering ability: 1, 'H1459'; 2, 'Le-Yi'; 3, 'Zhu-Yun-Luo'; 4, 'Bi-Yu-Zao-Luo'; 5, 'Ai-Mei-Zao 3'; 6, 'Wen-Xuan-Qing'. All possible single crosses were made among them. The six parents

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and their 30 F_1 hybrids were sown on April 5, 1988. Seedlings cultured in the nursery were transplanted to the paddy field on May 5, with a single plant per hill spaced at 15 × 20 cm. The experiment was laid out in a randomized complete block design with three replications. Each plot was surrounded by two rows of guard plants of purple leaf rice. Normal cultural practices were adopted.

Commencing on the 20th day after transplantation of the seedling, observations on tiller number were made at 10-day intervals, i.e., May 25, June 4, June 14 and June 24. Maximum tiller number (MTN) was observed at the peak tillering stage, and productive tiller number (PTN) was observed at the maturity stage. Eight plants, excluding the border ones, were sampled from each plot for measurement of tiller number, and the average score of each plot was used in the statistical analysis.

Statistical analysis

Analysis of variance was computed to have a general test of significance. Hayman's diallel analysis procedure (Hayman 1954a, b; Mather and Jinks 1982) was used to compute variance (Vr) and covariance (Wr) in the analysis of the F_1 data; subsequently the Vr, Wr graphs were constructed. The significance of some genetic parameters was tested by the jackknife resampling method (Miller 1974) in which the k-th pseudo value was produced by omitting the k-th parent and its relevant hybrids.

Combining ability was analyzed following method 1, model I (fixed effects for genotypes) of Griffing (1956). The relative importance of general combining ability (gca) and specific combining ability (sca) was studied by calculating the ratios of sums of squares, SSgca/(SSgca + SSsca), as suggested by Auld et al. (1983). The correlation of gca effects of parents and of sca effects of hybrids between each two characters was analyzed.

Results

Performance of the parents and of the F_1s

For all characters studied, analysis of variance showed highly significant differences among the genotypes (parents and the F_1, data not shown). At different growth stages, 'H1459' showed the highest tiller number and 'Le-Yi' had the lowest (Fig. 1). Six parents could be divided into two groups by their tillering ability: the one with higher tiller number included 'H1459', 'Ai-Mei-Zao 3' and 'Bi-Yu-Zao-Luo'; the other with lower tiller number included 'Wen-Xuan-Qing', 'Zhu-Yun-Luo' and 'Le-Yi'.

In Fig. 1 the periodic observation points could represent different tillering stages. May 25 (5/25) could be considered as the initial stage; tiller growth started to increase rapidly on June 4 (6/4), and reached its peak about June 14 (6/14). Subsequently tiller growth stopped and began to decline as a result of the death of some tillers. Consequently, the final tiller number (PTN) was much lower than both MTN and the tiller number (TN) observed on both 6/14 and 6/24. A large difference in the percentage of productive tiller number (PPTN) was found between parents on the basis of the slope of their lines between MTN and PTN. Therefore, the parents used in this study could be taken to be representative of different tillering characterizations.

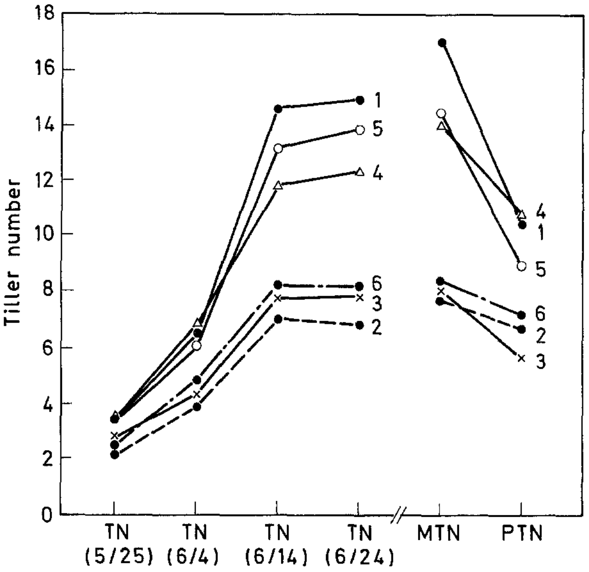

Fig. 1. The number of tillers at different growth stages in six diallel parents of rice. *TN* Tiller number (month/day); *MTN* maximum tiller number; *PTN* productive tiller number. The names of the parents: *1* H1459, *2* Le-Yi, *3* Zhu-Yun-Luo, *4* Bi-Yu-Zao-Luo, *5* Ai-Mei-Zao 3, *6* Wen-Xuan-Qing

Table 1. Tests of hypotheses for tiller number at the different growth stages in rice

Character[a]	Heterogeneity of Wr-Vr (F value)	t-test of b on the null-hypothesis	
		b = 0	b = 1
TN (5/25)	2.54	0.32	0.62
TN (6/4)	1.70	0.31	1.25
TN (6/14)	1.32	8.47**	2.07×10^{-2}
TN (6/24)	1.06	26.92**	1.30
MTN	1.95	4.35*	1.05
PTN	0.96	16.57**	0.50
PPTN	0.91	2.19	5.26**

* and ** significant at the 5% and 1% levels, respectively

[a] TN, Tiller number (M/D); MTN, maximum tiller number; PTN, productive tiller number; PPTN, percentage of productive tiller number

Tests of hypotheses

It is necessary for advanced analyses to ascertain that each character satisfies the hypotheses assumed by Hayman (1954b). Two kinds of tests, one by the heterogeneity of Wr-Vr and the other by the regression coefficient of Wr on Vr, were conducted to ascertain the three hypotheses: i.e., no multiple allelism, independent distribution of genes among the parents and independent action of nonallelic genes. The results of the tests are shown in Table 1. The heterogeneity among the six arrays was not significant for any character. Regression coefficients were not significant for TN (5/25), TN (6/4) and PPTN. Further,

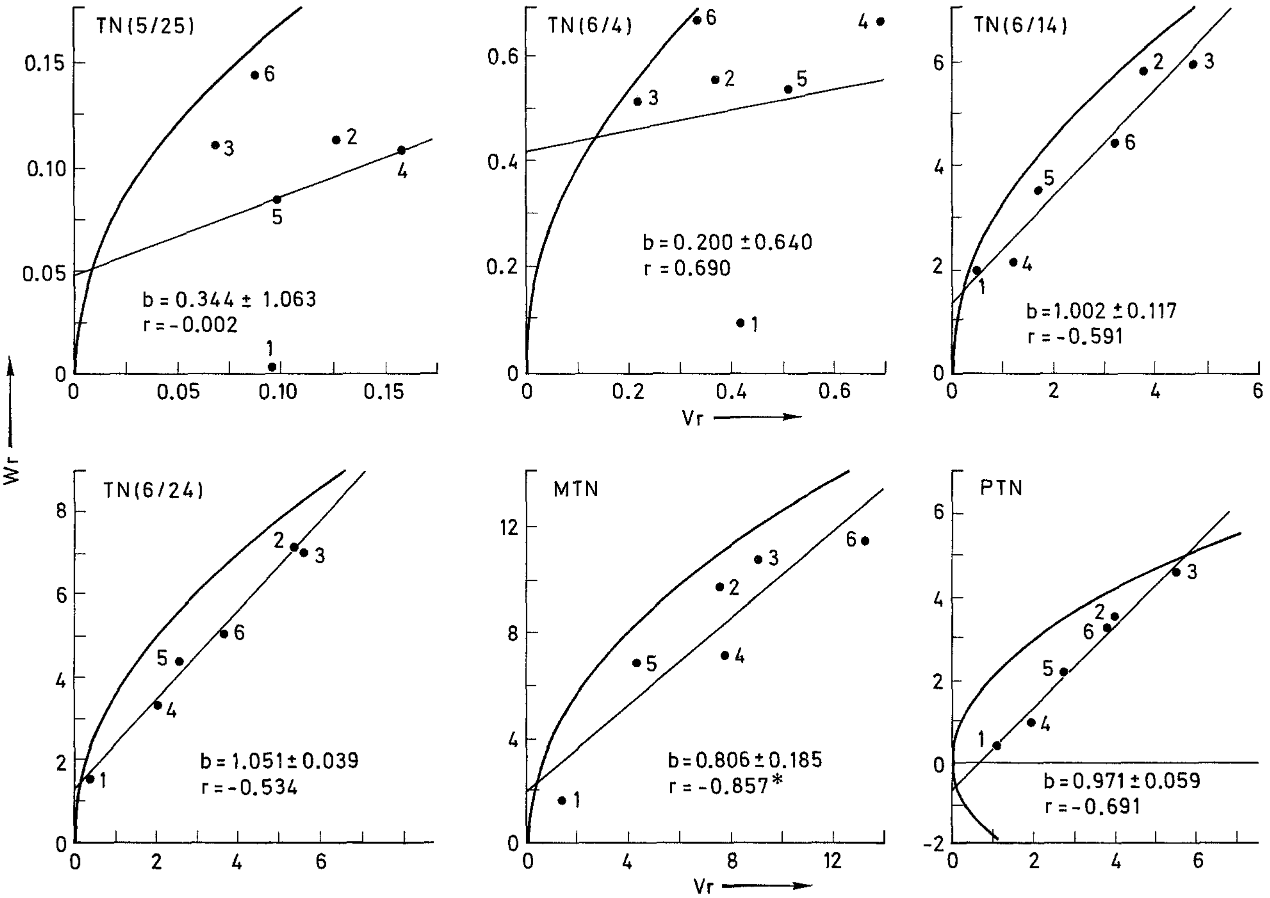

Fig. 2. Relationship between Wr and Vr in tiller number at the different growth stages of rice. For the names of the characters, see Table 1; for the names of the parents, see Fig. 1

the regression coefficient deviated significantly from 1 for PPTN. Therefore, this character failed to satisfy some of the hypotheses and was left out of further analyses. TN (5/25) and TN (6/4) were not significant for any test value, indicating that at the early stages the influence of environmental factors was predominant relative to that of the genetic factors. The other four characters were regarded to have satisfied the hypotheses.

Graphic analysis

The variance and covariance (Vr, Wr) graphs of the tiller number at the different stages are shown in Fig. 2. The position of Vr, Wr on the line revealed the relative proportions of dominant and recessive genes in the parents. In the present study, parent 1 ('H1459') occupied a position near the point of origin, suggesting the predominance of dominant genes. Parent 3 ('Zhu-Yun-Luo'), located at a position away from the point of origin, indicated a relative excess of recessive genes. These results became more clear for tiller number at advanced stages, and a consistent order of the relative proportions among parents was obtained as parent 1, 4, 5, 6, 2, 3 for TN (6/14), TN (6/24) and PTN. For all characters exclusive of TN (6/4), relatively high negative correlations between the values of parents and Wr + Vr indicated the dominance of positive genes. As the regression lines passed above the point of origin except for PTN, partial dominance in the inheritance of tiller number was indicated at these growth stages. In PTN, however, overdominance might be involved. As shown by the significant test of regression coefficients, the parents occupied closer positions of Vr, Wr on the lines and showed a more remarkably linear relationship with the coming of the advanced stage.

Analysis by variance components

The estimated genetic components of variation for tiller number at different stages is presented in Table 2. Additive genetic variance (D) and environmental variance (E) were highly significant for all characters. The three components of dominance (H_1, H_2 and h^2) were significant for tiller number at the peak tillering and later stages.

Table 2. Estimates of genetic components of variation for tiller number at the different growth stages in a six-parent diallel cross of rice

Notation[a]	Character					
	The tiller number on				MTN	PTN
	5/25	6/4	6/14	6/24		
D	0.20**	1.04**	9.09**	10.86**	14.20**	3.44**
F	0.10	0.37	3.18**	3.63*	−1.96	−2.31
H_1	0.15	–[b]	1.95*	3.50**	8.56*	4.86**
H_2	0.15	0.11	1.51*	2.90**	7.00*	4.59
h^2	0.00	0.15	5.00**	6.30**	15.52**	11.18**
E	0.08**	0.44**	0.95**	0.97**	1.84**	0.79**

* and ** significant at the 5% and 1% levels, respectively

[a] D, Component of variation due to additive gene effects; *F*, mean of covariance of additive and dominance effects over the arrays; H_1, component of variation due to dominant gene effects; H_2, $H_1\ [1-(u-v)^2]$ where u and v are the proportion of positive and negative genes in the parents and where $u+v=1$; h^2, dominance effect (as the algebraic sum over all loci in heterozygous phase in all crosses); E, component of variation due to environmental effects

[b] –: Illogical minus value. For names of characters, see Table 1

Table 3. Estimates (upper figure) and jackknife estimators (lower figure) of genetic parameters for tiller number at the different stages in rice

Notation	Character[f]					
	The tiller number observed on				MTN	PTN
	5/25	6/4	6/14	6/24		
$(H_1/D^{1/2}$ [a]	0.88	–	0.46	0.57	0.78	1.12
	1.17	–	0.48	0.48	0.61	0.87**
$H_2/(4H_1)$ [b]	0.25	–	0.19	0.21	0.20	0.24
	0.37**	–	0.45	0.15	0.16**	0.25**
h^2_B [c]	0.52	0.41	0.79	0.83	0.85	0.84
	0.53	0.31	0.77**	0.82**	0.87**	0.84**
h^2_N [d]	0.29	0.37	0.71	0.70	0.71	0.61
	0.15	0.24	0.77**	0.74	0.85**	0.72**
h^2/H_2 [e]	0.01	1.42	3.32	2.17	2.22	2.44
	–	8.65**	–	4.05**	4.06**	4.33**

* and ** significant at the 5% and 1% levels, respectively

[a] Mean degree of dominance over loci

[b] Ratio of genes with positive and negative effects in the parents

[c] Heritability, broad sense

[d] Heritability, narrow sense

[e] Number of groups of genes which control the trait and exhibit dominance

[f] –: Illogical minus value. For MTN and PTN, see Table 1

Table 4. Combining ability for tiller number at the different growth stages in rice

Character	Mean square due to[a]				SSgca
	gca (*df*=5)	sca (*df*=15)	RE (*df*=15)	Error (*df*=70)	SSgca+SSsca (%)
TN (5/25)	0.36**	0.15**	0.16**	0.01	43.6
TN (6/4)	2.10**	0.50	0.45	0.35	58.5
TN (6/14)	20.02**	1.70*	1.50	0.85	79.7
TN (6/24)	24.46**	2.42**	1.49	0.97	77.1
MTN	55.03**	5.33**	5.66**	1.75	77.5
PTN	18.84**	3.09**	2.51**	0.81	67.1

* and ** significant at the 5% and 1% levels, respectively

[a] RE, Reciprocal effect. For other abbreviations see Table 1

These results indicated the importance of both additive and nonadditive types of gene action in the inheritance of tiller number at the late stages. In order to compare the relative contributions of variance components, ratios of D, H_1 and E to their sum, $D+H_1+E$, were calculated for each character: the proportional value $D/(D+H_1+E)$ varied from 45.9% in TN (5/25) to 75.8% in TN(6/14), $H_1/(D+H_1+E)$ from 16.3% in TN(6/14) to 35.8% in TN(5/25), and $E/(D+H_1+E)$ from 6.3% in TN(6/24) to 18.3% in TN(5/25). This indicates that the contribution of additive genes increased while that of nonadditive genes decreased with the growth of tillers. For the final character (PTN), however, additive gene action was at the intermediate level. The significance of *F* values for both TN (6/14) and TN (6/24) suggested gene asymmetry.

Ratios computed from the genetic components provided information on the degree, order and direction of dominance. For the characters studied, except PTN, average dominance $(H_1/D)^{1/2}$ was within the range of incomplete dominance and was in agreement with the conclusion drawn from the graphic analysis; but for PTN, overdominance was confirmed by its $(H_1/D)^{1/2}$ being larger than unity. The low values of $H_2/(4H_1)$ (less than 0.25) suggested unequal mean allelic frequencies at the loci influencing the tiller number at most stages. Upon growth of the plant, estimates of heritability (the upper figure in Table 3) were increased from 0.41 (6/4) to 0.85 (MTN) for h^2_B and from 0.29 (5/25) to 0.71 (MTN) for h^2_N, respectively. Highly significant values (the lower figure), indicated by t-tests based on the jackknife method, showed the great importance of additive gene action in high tillering ability at the peak tillering and later stages. The ratios for h^2/H_2 suggested the involvement of two or more groups of genes having dominance at these stages, but lower ratios were obtained at the early stages.

Combining ability analysis

The analysis of variance for combining ability is given in Table 4. Although the variances for both gca and sca

Table 5. General combining ability effects for tiller number at the different growth stages in 6 × 6 diallel of rice

Character	Parent					
	1	2	3	4	5	6
TN (5/25)	0.12	−0.29**	0.02	0.15	0.12	−0.12
TN (6/4)	0.25	−0.53**	−0.33*	0.54*	0.29	−0.22
TN (6/14)	1.72**	−1.71**	−0.38	0.74**	0.73**	−1.10**
TN (6/24)	1.89**	−1.88**	−0.36	0.76**	0.87**	−1.28**
MTN	3.39**	−2.70**	−1.06**	1.37**	0.08	−1.09**
PTN	1.58**	−1.42**	−0.82**	1.37**	0.17	−0.87**

* and ** significant at the 1% and 1% levels, respectively
For abbreviations, see Table 1; parent names see Fig. 1

Table 6. Specific combining ability effects for tiller number at the different growth stages in 6 × 6 diallel of rice

Cross	Character					
	The tiller number on				MTN	PTN
	5/25	6/4	6/14	6/24		
1 × 2	0.54**	0.84*	1.08	1.86**	1.72*	1.98**
1 × 3	−0.15	−0.20	0.03	−0.09	0.36	−0.33
1 × 4	−0.40*	−0.82*	−0.76	−0.74	0.91	−0.07
1 × 5	−0.48**	−0.90	−0.46	−0.81	−1.00	−0.29
1 × 6	0.16	0.21	0.62	0.63	1.36	1.43**
2 × 3	−0.10	0.03	0.11	0.05	0.21	−0.41
2 × 4	−0.37*	−0.60	−0.02	−0.31	−1.42	−0.63
2 × 5	0.02	−0.00	0.10	−0.26	0.17	−0.12
2 × 6	−0.13	−0.30	−0.06	0.05	−0.26	−0.43
3 × 4	0.24	0.25	1.37*	1.34*	0.24	1.55**
3 × 5	0.06	−0.07	0.69	1.09	1.59*	1.24*
3 × 6	0.06	0.07	0.79	0.88	1.00	0.52
4 × 5	0.11	0.41	0.14	0.51	0.15	1.02
4 × 6	0.15	0.13	0.47	0.43	2.47**	0.12
5 × 6	−0.05	0.01	−0.58	−0.70	−1.41	−0.46

* and ** significant at the 5% and 1% levels, respectively
For abbreviations, see Table 1; parent names, see Fig. 1

Table 7. Correlations between gca effects of parents (upper diagonal) and between sca effects of crosses (lower diagonal) for tiller number at the different growth stages in rice

Character[a]	Tiller number on				MTN	PTN
	5/25	6/4	6/14	6/24		
TN (5/25)		0.881*	0.921**	0.921**	0.822*	0.848*
TN (6/4)	0.963**		0.857*	0.846*	0.809	0.913*
TN (6/14)	0.811**	0.718**		0.999**	0.950**	0.935**
TN (6/24)	0.872**	0.791**	0.944**		0.938**	0.921**
MTN	0.603*	0.482	0.555*	0.631*		0.961**
PTN	0.800**	0.701**	0.794**	0.875**	0.592*	

* and ** significant at the 5% and 1% levels, respetively
[a] For names of characters, see Table 1

were significant for all characters and reciprocal effect significant for some of them, relatively higher values for gca variance suggested the preponderance of additive gene effects as compared to dominance and reciprocal effects. The ratios involving the sums of squares SSgca/(SSgca + SSsca) confirmed that additive gene effects were more important than nonadditive effects. Furthermore, the ratios at the early tillering stages were much lower than those at the peak tillering and maturity stages. These results were in agreement with those obtained by Hayman analysis.

The perusal of Table 5 indicated that parents 'H1459' and 'Bi-Yu-Zao-Luo' with higher tiller number showed high gca effects, whereas parents 'Le-Yi' and 'Wen-Xu-an-Qing' with lower tiller number showed low gca effects; these were consistent at all growth stages. Among the hybrids involving high tillering crosses, 1 × 2 and 3 × 4 showed higher sca effects for strong tillering ability at all stages (Table 6).

Correlation analysis revealed the highly positve relationship of both gca and of sca effects among characters – the only exception being between MTN and TN(6/4) (Table 7); this reflected conformity in gene action at the different tillering stages.

Discussion

The terminal character PTN is the product of MTN and PPTN. In the present study, the results clearly indicated a large difference in tiller number among six diallel parents (Fig. 1). A large number of tillers died during the growing period, and mortality increased progressively as the plant matured. In the six parents PPTN varied from 61.9% ('H1459') to 87.9% ('Le-Yi'). As a result, the terminal character did not really indicate tillering potential. For example, 'H1459' had the highest MTN but had a lower PTN than 'Bi-Yu-Zao-Luo', even though the latter had a much lower MTN than the former. Evans and Wardlaw (1976) noted that as many as two-thirds of the tillers in cereals could be lost to mortality, which is clearly a wasteful drain of plant energy that would have otherwise gone into productivity. In view of this fact, we agree with Kulshrestha and Chowdhury (1987), i.e., it seems more promising to select those plants with relatively fewer tillers, most of which would survive to produce grains.

At the early stages tiller number was more easily mimicked by non-inheritable factors. Thus, the genetic difference between parents could not be reliably detected by analysis of variance. The relatively lower and unstable estimates of gene effects and genetic parameters were obtained at these stages. As the plant matured, the genetic difference became more remarkable. Consequently, the genetic parameters at the peak tillering and later stages should reflect more fully the inheritance of tillering ability.

Several authors report the application of diallel analysis to the final tiller number (PTN) of rice. Murai and Kinoshita (1986) and Sinha et al. (1985) considered additive gene effect to be more important than nonadditive gene effect. But Li (1977) indicated an equal importance of additive and dominant gene effects. Using triple test cross analysis, Ahmad et al. (1986) showed predominant additive gene action without the influence of nonadditive gene action, whereas Perera et al. (1986) have suggested that both number of tillers at maturity and number of panicles per plant are controlled by genes with additive, dominance, and epistatic effects of the duplicate types and that at least some of these genes are linked in the repulsion phase. These reports reveal the complexity of the inheritance of tiller number. In the present study, the fulfillment of assumption for Hayman's analysis indicated that a relatively simple genetic model was involved. High tillering ability was inherited as a partial dominant character conditioned by two or more blocks of genes. Additive gene action was more important than nonadditive gene action, which was also supported by Griffing's combining ability analysis.

By combining the methods of growth analysis with quantitative genetic analysis, Kheiralla and Whittington (1962) showed that in tomato the additive and dominance components of genetic variances for quantitative characters such as plant height vary with developmental stages. Wu (1987) revealed that the genetic models for three quantitative characters in maize show distinct changes with their growth stages, which can be considered to be the result of actions of different gene loci at each stage. In the present study we also found that the estimates of genetic parameters for tiller number changed during growth of the plants. However, the genetic model did not change qualitatively. With advancing developmental stages the contribution of both nonadditive gene effect and environmental factors to the variation decreased while that of additive gene effect increased. From these results the conclusion could be drawn that an identical polygenic system is responsible for the genetic control of tiller number at the different development stages. Even so, extreme caution should be taken in making generalizations based on a genetic analysis made at only one point in time. In order to find the appropriate stage(s) for selection, it is still necessary to make a genetic study at the different stages, especially for the quantitative characters that are easily influenced by noninheritable factors. As for tillering ability, as indicated by this study, selection should be more effective at the late stages than at the early stages.

The jackknife method for estimating sampling variance was used in this study to derive the standard deviations of the estimates of some genetic parameters. It provides compensation for Hayman's diallel analysis. Using this method we found that the estimates of heritability progressively increased, reaching a highly significant level, with plant growth, although they were not significant at the early tillering stages.

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