Analysis of Genetic Variation in Plant Type of Rice.

VI. Intervarietal Variations in Growth Pattern obtained from the International Rice Adaptation Experiment¹

Hiroko MORISHIMA and H. I. OKA
National Institute of Genetics, Misima

Synopsis Intervarietal variations in growth pattern were investigated using the data from the International Rice Adaptation Experiment (JIBP/UM). Two trends of variation, early- vs. late-vigor type and sustained- vs. dash-vigor type, were detected, and their contributions to grain production were examined.

The basic concept of statistical genetics, Phenotype=Genotype+Environment, seems to be too mechanical to elucidate the dynamics of phenotype determination; when a geneticist is confined to this thought, he has no room to seek for collaboration of physiologists. Growth is a function of time, and quantitative characters depend on sequential events that take place during growth. Genotype+Environment do not instantly make up phenotypes. In an attempt to look into the dynamic aspect of genetic variations, we have shown that logistic growth curves obtained from data on dry-matter weight were genetically controlled; in our previous paper (Oka *et al.* 1970), the F₇ lines derived from Peta x I-geo-tse varied between so-called early-vigor and late-vigor (then called "sustained vigor") types, the former producing more spikelets while the latter filling the spikelets with more grain. To look more closely into the variations in growth curve, the data from the International Rice Adaptation Experiment (JIBP/UM), particularly those from the Sizuoka Agricultural Experiment Station, were examined. The results are reported in this paper.

Materials and Methods

The International Rice Adaptation Experiment (I.R.A.E.; Phase A) was carried out from 1968 to 1970 at 19 stations in 14 countries

of the world using about 45 rice varieties of different origins. It was continued for two more years (1971 and 1972; Phase B) at 7 stations in 4 countries using 10 selected varieties. The purpose of this experiment was primarily to estimate the general adaptabilities of rice varieties (Matsuo *et al.* 1972), and the results will be published elsewhere (Adaptability in plants with special reference to crop yield, in press). Of the data, those obtained at Sizuoka Agricultural Experiment Station (35°N, Japan) in Phase A (for 29 varieties listed in Table 1) and those from 5 stations in Phase B (Niigata, Saitama, Saga, and Miyazaki in Japan, and Beaumont, Texas, USA) for 10 varieties (Table 2) were used for the present study, as these included records of dry-matter weight measured four times during the growing period and at maturity (the data from Taipei and Cuttack were not used as the sampling dates of dry-matter weights were not properly recorded).

The experimental conditions at Sizuoka were as follows: Seedlings raised in ordinary seed beds for 43 days were transplanted on the 8th or 9th of June with three plants per hill spaced at 30×20 cm (16.67 hills/m²). A split plot design with two replications was adopted to test the varieties (subplots) at two fertilizer levels (main plots) which were lower than the ordinary standard (in kg/ha):

1968: No fertilizer and 38-38-38 NPK (basic dressing),

1969: No fertilizer and 48-48-48 NPK (basic dressing),

1970: 48-48-48 NPK (basic only) and the

1. Contribution from National Institute of Genetics, Japan, no. 1021

Received July 13, 1974

Table 1. Abstract of data for growth pattern (I.R.A.E.; Sizuoka, Japan; Mean for 1968, 1969 and 1970)

Variety	Growth rate (g/day/m ²)				No. of days			Type	Yield (kg/a)
	R ₋₂₅	R ₀	R ₁₀	R _{max}	Head.	Max-H	Max-1/2		
6 Rafaello (Italy)	11	19	14	23	62	8	20	L, D	47
7 Vialone nano	10	16	9	21	59	10	20	D	40
8 Fujiminori (Japan)	12	18	11	24	61	7	19	L, D	43
9 Koshihikari (♂)	13	18	11	21	66	9	23	L	49
11 Norin 41 (♂)	11	15	10	19	63	8	23		47
14 Panbira (Pakistan)	16	13	7	22	71	14	21	D	35
16 Hsinghchu 56 (Taiwan)	16	13	9	18	81	16	28	S	48
17 Taichung(n) 1 (♂)	13	14	10	18	72	12	25		49
18 Taichung 65 (♂)	14	12	10	16	78	11	33	S	47
19 Taichung 176 (♂)	15	14	10	18	81	15	33	S	51
20 Tainan 3 (♂)	18	13	9	19	78	18	33	E, S	54
22 Bluebelle 9544 (USA)	20	5	3	21	78	27	21	E, D	36
24 Calrose 8988 (♂)	14	13	10	18	73	11	26		47
25 Hybrid 170/15 (Egypt)	18	11	8	19	90	25	32	E, S	53
26 68-1 (France)	7	16	11	19	54	5	20	L	41
30 Romeo (Italy)	10	17	12	21	61	6	22	L	45
31 Honenwase (Japan)	11	17	10	20	63	8	20	L	44
32 Hoyoku (♂)	17	12	8	18	84	19	28	E, S	47
33 Kinmaze (♂)	19	16	12	20	79	13	27		50
34 Manryo (♂)	15	18	12	21	71	10	23	L	52
36 Norin 22 (♂)	18	13	8	20	77	18	23	E	49
37 Norin 29 (♂)	19	13	8	23	73	17	24	E, D	52
41 Jin Heung (Korea)	15	13	8	18	70	13	24		47
42 Palkweng (♂)	17	18	8	20	74	16	23		45
45 Blue bonnet (USA)	17	14	6	21	82	17	23	E	40
46 Dawn 9534 (♂)	16	12	8	18	73	15	26		41
48 Nato 8998 (♂)	16	14	9	20	72	14	23		42
49 Star bonnet (♂)	16	12	8	22	75	16	23	E, D	37
50 Zenith 7787 (♂)	14	15	10	18	76	12	26		52

Type E-Early vigor; L-Late vigor; S-Sustained vigor; D-Dash vigor

Table 2. Abstract of data for growth pattern from International Rice Adaptation Experiment, Phase B (Mean for Niigata, Saitama, Saga, Miyazaki, and Beaumont in 1971 and 1972)

Variety	Growth rate (g/day/m ²)				No. of days			Grain yield g/m ²
	R ₋₂₅	R ₀	R ₁₀	R _{max}	Head.	Max-H	1/2-1/2	
6 Rafaello (Italy)	8.4	19.3	13.4	22.5	90.6	6.8	58.8	317
9 Koshihikari (Japan)	9.5	23.0	15.4	25.1	88.9	5.6	58.9	355
13 Paltal (Korea)	10.2	21.0	16.0	22.3	96.4	6.1	67.1	389
14 Panbira (Pakistan)	15.5	18.4	11.4	25.4	94.4	16.5	60.1	372
15 IR 8 (Philippines)	14.1	14.6	10.6	19.7	118.5	22.5	85.6	396
17 Taichung(n) 1 (Taiwan)	12.5	17.2	12.0	21.7	101.1	14.6	70.0	447
20 Tainan 3 (Taiwan)	12.4	20.1	15.8	23.0	102.6	8.1	69.8	407
21 Belle patna (USA)	11.4	17.8	11.4	23.3	95.1	10.8	58.9	303
22 Blue belle (USA)	12.7	16.2	10.2	21.6	97.6	15.3	62.9	302
37 Norin 29 (Japan)	12.7	18.5	13.7	22.4	96.2	12.6	69.2	356

same basic dressing plus a top dressing of 32-32-32 NPK 20-25 days before heading. Similar experimental conditons were adopted

in the B Phase experiments except that direct seeding was made at Beaumont. The fertilizer levels were 0 and 50 N (kg/ha) with standard amounts of P₂O₅ and K₂O at each station.

For measuring dry-matter weight, six hills per plot were sampled at the time of transplanting, 45 days after that, at heading, 25 days after heading, and at maturity in Sizuoka (Phase A), and ten hills per plot were sampled at about 40 and 20 days before heading, at heading, 15 days after heading and at maturity in Phase B. The samples were oven-dried at about 95°C and weighed to estimate dry matter per m². Grain yield (g/m²), number of days to heading, panicle number (per m²), panicle length, culm length, 1000 grain weight, etc. were measured by ordinary methods.

From the dry-matter data for each variety in each replication, a logistic equation was computed by using the "Pearl-Reed" function (cf. GROSENBAUGH 1965), $y = A/(1 + ae^{-bt - ct^2})$, where y is the dry-matter weight at time t (number of days from seeding), A is that at maturity, and a , b , and c are values determining relative growth rate. From the equation, crop growth rates (dy/dt , g/day/m²) were computed and other parametric values characterizing growth curve were estimated, *i.e.*, the growth rates 25 days before heading (R_{-25}), at heading (R_0), and 10 days after heading (R_{10}), maximum growth rate (R_{max}), number of days from the time of maximum growth to heading (Max-H), and number of days from the time of maximum growth to the time at which growth rate is reduced to half of the maximum or duration of high growth rate is reduced to half of the maximum or duration of high growth rate ($M-1/2$; in Phase B, $1/2-1/2$ was used which is the number of days from the time at which $1/2$ maximum rate is attained to that at which growth rate is reduced to $1/2$ maximum).

Results

The results obtained from the Sizuoka experiment are mainly described. Those from five stations in Phase B are presented without detailed explanations as they were essentially the same as those from Sizuoka.

1) Intervarietal variations in growth curve

The parametric values characterizing growth curve obtained in each variety at Sizuoka (mean for 2 fertilizer levels, 3 years, and 2 replications) are given in Table 1, and those

from Phase B experiments are in Table 2.

The values varied in considerable ranges, and variance analysis for each value proved that varietal differences were highly significant in most of them (Tables 3 and 4). This indicates that the growth pattern as shown by these values is genotypically controlled, even though the values were subjected to environmental modification and had relatively low heritabilities (Table 3).

Intervarietal correlations between those parametric values indicate the trend of variations in growth curve. In general, the growth rate reaches the maximum at a certain stage and then declines, but the developmental stage at which the maximum growth rate is attained differs according to varietal genotypes. The positive correlation between R_{-25} and Max-H days ($r=0.88\sim0.83$) and their negative correlations with R_0 and R_{10} indicate that varieties which had a high growth rate in the panicle-differentiation stage (25 days before heading) attained the maximum growth rate many days before heading and then had a low growth rate at and after heading (Table 5).

Another trend of variation in growth curve is represented by the strong negative correlation between R_{max} and Max-H (or $1/2-1/2$) days ($r=-0.67\sim-0.77$, Table 5). This indicates that varieties with a high maximum growth rate tend to have a short duration of high growth rate.

The occurrence of these two variation trends among rice varieties was also demonstrated by the principal component analysis of the intervarietal correlations (Table 5). As shown in Fig. 1, the rotation to simple structure of loadings on the first and second component vectors showed that Max-H, R_{-25} , R_0 and R_{10} values could represent the variation in the time of maximum growth rate. We have pointed out earlier (OKA *et al.* 1970) that F_7 lines from a varietal cross varied between the "early-vigor" and "late-vigor" (then called "sustained vigor") types, the former showing maximum growth rate around the time of floral initiation while the latter showing it around the time of heading. The above-mentioned variation apparently indicates the range between early- and late-vigor types among the tested varieties.

Table 3. Variance analysis of parametric values showing growth pattern obtained at Sizuka (converted into log₁₀)

Variation due to	d.f.	Mean square (in log ₁₀ × 10 ⁴)								
		R ₋₂₅	R ₀	R ₁₀	R _{max}	Max-H	Max-1/2	Grain yield	A	B ⁷⁾
Replication ¹⁾	3	35	332*	290	247*	485	93	29	214	55
Variety	28	489**	392**	521*	103	1238**	276**	138**	692**	1027**
Environment ²⁾ ,	5	1823**	901**	524**	1286**	1579**	904**	1022**	1532**	594
Year ³⁾	2	68	379*	8	292*	851*	1240**	573**	158	518
Ferti ⁴⁾	2	2468**	452*	145	1343**	2080**	49	1238**	1510**	1139**
Top dress ⁵⁾	1	120	400	677*	57	328	2	207**	412	158
Variety × Env.	140	133	120	157	78	228	79	11	245	419
V. × Year ³⁾	56	319**	258**	350**	141**	529**	176**	1516**	416	815
V. × Ferti ⁴⁾	56	249**	859**	145	172**	538**	136**	2698**	1304**	760
V. × Top d. ⁵⁾	28	173**	226**	147	117*	183	148**	1053**	354	646
Error	171	91	107	154	77	190	70	12	305	612
Heritability % ⁶⁾		17	15	16	2	27	16	26	10	8

** Significant at 1% level, * at 5% level

1) 2 replications in each of 3 years, not corresponding one another

2) Environments: (a) 1968 no fertilizer, (b) 1968 basic dressing, (c) 1969 no fertilizer, (d) 1969 basic dressing, (e) 1970 basic dressing, (f) 1970 basic+top dress.

3) Year: Differences between (a) and (c) and between (b) and (d)

4) Fertilizer: Differences between (a) and (b) and between (c) and (d)

5) Top dressing: Difference between (e) and (f)

6) $h^2 = \sigma_{\text{var}}^2 / (\sigma_{\text{var}}^2 + \sigma_{\text{env}}^2 + \sigma_{\text{var} \times \text{env}}^2 + \sigma_{\text{error}}^2)$; each variance component was obtained according to the random model.

7) A & B: Grain weight due to growth after (A) and before (B) heading in % of total dry weight at maturity. More explanations in text.

Table 4. Variance analysis of parametric values showing growth pattern obtained from I.R.A.E., Phase B

Variation due to	d.f.	Mean square					
		Growth rate (g/day/m ²)				No. of days	
		R ₋₂₅	R ₀	R ₁₀	R _{max}	Max-H	1/2-1/2
Location (L)	4	515.7**	649.9**	525.1**	363.3**	1377.7**	685.5**
Year (Y)	1	154.4**	220.3**	12.3	198.1**	635.0**	1033.6**
Fertilizer (F)	1	2395.3**	1064.4**	112.9**	3867.8**	1346.9**	35.4
Interactions ¹⁾	13	32.5	159.2**	106.3**	177.4**	186.5**	161.2**
Error (a) ²⁾	20	18.3	15.4	15.7	13.3	31.8	31.7
Variety (V)	9	183.4**	228.9**	189.5**	109.3**	428.2**	992.7**
V × L	36	77.5**	59.5**	67.0**	47.1**	136.8**	141.2**
V × Y	9	11.0	22.9	30.5*	49.4**	90.1**	27.6
V × F	9	21.4	7.9	19.3	33.1*	16.0	77.7*
Interactions ³⁾	117	18.8	57.4**	46.6**	76.3**	113.0**	81.8**
Error (b)	180	37.3	16.0	14.0	14.5	28.6	31.0
LSD (5%) for varieties		4.34	2.85	2.66	2.71	3.81	3.96

** Significant at 1% level, * at 5% level

1) L × Y, L × F, Y × F, and L × Y × F

2) 2 replications at each location; varieties were considered as sub-plots.

3) V × L × Y, V × L × F, V × Y × F, and V × L × Y × F

The second variation trend was represented by the axis connecting Max-1/2 days and R_{max} value in Fig. 1, which appeared to be nearly independent of the first axis. This variation indicates that the varieties ranged

between two contrasting types, one with a long duration of relatively low growth rate, and the other with a high maximum growth rate which declines rapidly. These two types may be called "sustained vigor" and "dash

Table 5. Intervarietal correlation between parametric values showing growth pattern and their principal components;
Below diagonal: 29 varieties at Sizuoka,
Above diagonal: 10 varieties in I. R. A. E., Phase B

Value	R ₋₂₅	R ₀	R ₁₀	R _{max}	Max-H	1/2-1/2	Phase B	
							I (66)	II (20)
R ₋₂₅		-.61	-.56	-.10	.83**	.44	.74	-.41
R ₀	-.60**		.88**	.69*	-.89**	-.54	-.96	.04
R ₁₀	-.65**	.81**		.34	-.82**	-.16	-.80	.43
R _{max}	-.03**	.33	.05		-.48	-.77**	-.67	-.68
Max-H	.88**	-.78**	-.81**	-.11		.62	.97	-.19
Max-1/2	.41*	-.39*	-.07	-.67**	.41		.70	.60
Component, Sizuoka,								
I (59)	.85	-.89	-.83	-.33	.95	.54		
II (25)	-.20	.02	.39	-.86	-.19	.74		

** Significant at 1% level, * at 5% level

I & II-1st and 2nd components; (%) shows contribution to the total multi-dimensional variance.

Fig. 1. Principal component analysis of correlations among values showing growth pattern and rotation to simple structure.
(I. R. A. E., Sizuoka, 29 varieties, 1968-1970)

vigor" types, respectively.

For measuring varietal characteristics along the variation axis between early- and late-vigor types, a linear combination of four variates, $X_{EL} = R_{-25} - 1.52 R_0 - 2.03 R_{10} + 0.71 (\text{Max-H})$, was obtained from the rotated axis in Fig. 1 (by dividing the loading on each variate by its standard deviation). This was quite close to the first component vector obtained from the principal component analysis of correlations among these four variates ($R_{-25} - 1.18 R_0 - 1.51 R_{10} + 0.61 \text{Max-H}$). The difference between R_{-25} and R_{10} values ($R_{dif} = R_{-25} - R_{10}$) was also used for the same purpose since X_{EL} and R_{dif}

were highly intercorrelated ($r = 0.97$, Table 7).

For measuring the variation between sustained- and dash-vigor types, $X_{SD} = (\text{Max-H}) - 2.43 R_{max}$ was obtained from the rotated vector in Fig. 1. The Max-1/2 value itself was also used for the same purpose as X_{SD} and Max-1/2 values were highly intercorrelated ($r = 0.91$). The same computations as mentioned above were carried out with the data from Phase B experiments, and the X_{EL} , R_{dif} , and X_{SD} values were obtained in each of the 10 varieties used.

It may be asserted that, as shown by significant varietal variances of the parametric values representing growth curve (Tables 3 and 4), the early *vs.* late as well as sustained *vs.* dash vigor types are genotypically controlled. There might be gene complexes governing these variation trends in growth.

2) Interrelationships between growth pattern and yielding potential

Correlations of the growth parameters with grain yield and other agronomic characters found among the tested varieties are given in Table 6. In general, the early- *vs.* late-vigor variation was uncorrelated with grain yield, though the growth rate 10 days after heading (R_{10}) was positively correlated with yield ($r = 0.42$ in Sizuoka data) indicating that late vigor takes a part in grain production. The days to heading was strongly correlated with X_{EL} and R_{dif} values ($r = 0.74$ and 0.77 , respectively) indicating that early-maturing varieties

Table 6. Correlations between scores showing vigor-types and agronomic characters

Vigor-type score	Grain yield	Days to heading	Panicle number	Panicle length	Culm length	1000 grain weight
29 varieties at Sizuoka :						
R ₋₂₅ -R ₁₀ (Early : Late)	-.08	.77**	-.00	.50**	.25	
Max-1/2 (Sustain : Dash)	.57**	.73**	.20	.09	.12	
10 varieties in Phase B :						
R ₋₂₅ -R ₁₀ (Early : Late)	.03	.51	-.17	.70*	.10	-.43
1/2-1/2 (Sustain : Dash)	.59	.94**	.51	.04	-.67**	.44

** Significant at 1% level, * at 5 level

tended to be late-vigor types. It was also that early-vigor types tended to have long panicles ($r=0.50$). Culm length and panicle number were uncorrelated with the early- vs. late-vigor variation.

On the other hand, the sustained- vs. dash-vigor variation shown by X_{SD} or Max-1/2 value was correlated with grain yield indicating that sustained vigor increases grain production ($r=0.57\sim0.59$, Table 6). This correlation was consistently observed even between the Max-1/2 days at Sizuoka and the mean yield for 14 different environments (Phase A; $r=0.48$). The X_{SD} or Max-1/2 value was strongly correlated with the days to heading ($r=0.73\sim0.94$) indicating that late-maturing varieties generally had a long duration of high growth rate, but it was uncorrelated with other agronomic characters.

In our previous paper (Oka *et al.* 1970), we have asserted that early vigor contributes to the production of panicles (shown by total panicle length per m^2) which was considered as representing the amount of containers for rice grain or "demand" for grain production, and late vigor contributes to filling the container with grain or "supply" (shown by grain weight per unit panicle length).

The F_7 lines tested were then classified into three groups, two in which either the "demand" or the "supply" was a limiting factor in grain production, and one in which the two factors were balanced.

In the present study, the capacity of containers (denoted by P) was estimated as panicle number/ $m^2 \times$ spikelet number/panicle $\times$ spikelet length $\times$ spikelet width $\times 0.523$ (assuming a spikelet to be an ellipsoid with 1 mm latent thickness). The P value varied from 391 to

290 cm^3/m^2 among the 29 varieties tested at Sizuoka. The degree of filling the container (denoted by Q) was represented by grain weight/ m^2 divided by P, which ranged between 2.0 and 1.0 g/cm^2 among the varieties. The P value was uncorrelated with grain yield, but the Q value was strongly correlated with grain yield ($r=0.75$, Table 7).

The X_{EL} or R_{dif} value showing the early- vs. late vigor variation gave no significant correlation with the P and Q values. However, when the variation in days to heading (ranging from 54 to 90 days) which was positively correlated with X_{EL} or R_{dif} was fixed by the use of partial correlation, the X_{EL} or R_{dif} value showed a positive correlation with P ($r=0.37$ or 0.41) and a negative correlation with Q ($r=-0.57$ or -0.54 , Table 7) indicating that early vigor increases containers and late vigor promotes filling the containers. This implies that our previous assertion holds good among different varieties with similar growth durations. Partial correlations fixing the days to heading also revealed that late-vigor types tended to give a high yield among varieties with similar growth durations ($r=-0.54$ between X_{EL} and yield, Table 7).

The mode of grain production was examined further by dividing grain yield into two portions, one due to growth after heading (A) and the other due to growth before heading (B), both shown in percent of total dry weight at maturity; letting the increment of dry matter after heading be a , dry-matter weight at maturity be w and grain weight be g , $A=a/w$ and $B=(g-a)/w$. Then, $A+B=g/w$ or so-called harvest index.

It was then found that the X_{EL} or R_{dif} value was correlated negatively with A ($r=-0.86$

Table 7. Correlations among grain yield, yield-component factors and scores showing vigor-types obtained at Sizuoka;

Below diagonal: Intervarietal correlations ($n=29$)

Above diagonal: Partial correlations fixing the days to heading

Character	Y	H	P	Q	A	B	R _{diff}	X _{EL}	X _{SD}
Grain yield (Y)			-.29	.75**	.47*	-.17	-.48**	-.54**	.37*
Days to head. (H)	.28								
"Container" (P)	-.28	-.02			-.22	.15	.41*	.37*	-.11
"Filling" (Q)	.75*	.17	-.83**		.42*	-.23	-.54**	-.57**	.29
Grain, after heading (A)	.21	-.58**	-.17	.24			-.82**	-.79**	.65**
Grain, before heading (B)	-.08	.27	.13	-.17	-.70**		.70**	.7.**	-.47*
R ₋₂₅ -R ₁₀ (R _{diff})	-.08	.77**	.24	-.21	-.87**	.63**			-.55**
X _{EL}	-.14	.74**	.23	-.25	-.86**	.65**	.97**		-.33
X _{SD}	.44*	.60**	-.10	.33	.08	-.20	.18	.26	

** Significant at 1% level, * at 5% level

or -0.87, Table 7) and positively with B ($r=0.65$ or 0.63). These correlations indicate that the grain production in late-vigor types depends largely on carbohydrate synthesis after heading, while that in early-vigor types depends more upon translocation of carbohydrates synthesized before heading. On the other hand, the X_{SD} value showing the sustained-*vs.* dash-vigor variation was almost uncorrelated with the P, Q, A, and B values (Table 7). It was directly correlated with grain yield as already mentioned. Sustained-vigor types generally have given higher grain yield than dash-vigor types possibly because sustained vigor keeps up a balance between the "demand and supply" factors, while dash vigor may result in unbalance between the two factors.

To observe the interrelation between the changing pattern of growth rate and grain yield more closely, the growth rates in the period from 35 days before to 20 days after heading were computed at 5-day intervals in each variety and were standardized (by using intervarietal standard deviations). It was then found that the growth rate was oscillating. As shown in Fig. 2, however, best-yielding five varieties tended to keep up a high growth rate throughout the period, whereas worst-yielding five varieties displayed oscillation more clearly being either early-vigor or late-vigor types. This serves as another indication of the role of long-continued vigor in grain production and suggests the significance of stability in growth rate.

3) Modification of growth pattern caused by fertilizer application

A fertilizer treatment involved in the International Rice Adaptation Experiment enabled us to observe the effects of fertilizers on the values representing growth curve. In general, as shown in Fig. 3, fertilizers modified the growth curve toward early-vigor type. However, this response differed according to genotypes as shown by significant variety-fertilizer interactional variances (Table 3). Estimating this response by the difference in R_{diff} value (R₋₂₅-R₁₀, in g/day/m²) between fertilized and unfertilized plots, the 29 varieties tested at Sizuoka ranged from 15.5 (Fujiminori, changing toward early vigor) to -7.0 (Norin 29, toward late vigor) with a mean of 5.5

Fig. 2. Oscillating pattern of growth rate for high and low yielding varieties, shown in the values standardized by mean and standard deviation obtained from 29 varieties. (I.R.A.E., Sizuoka, 1969)

Fig. 3. Daily dry-matter increase curves of the three varieties tested at two fertilizer levels. (I.R.A.E., Sizuoka, 1969)

Table 8. Correlations among the magnitudes of changes due to fertilizer application (Sizuoka data)

Value	Year	Max-H	R _{dif}	R _{max}	Max-1/2
R ₋₂₅ -R ₁₀ (R _{dif})	1968	.83**			
	69	.80**			
	70	.70**			
Max-1/2 days	1968	.15	-.08	-.88**	
	69	-.02	-.14	-.69**	
	70	-.03	-.14	-.93**	
Grain, after hrading (A)	1968	-.78**	-.77**	-.39*	.30
	69	-.71**	-.57**	-.13	.02
	70	-.56**	-.69	-.62**	.65**
Grain, before heading (B)	1968	.68**	.68**	.43*	-.33
	69	.88**	.78**	.05	.06
	70	.47*	.54**	.57**	-.64**
Grain yield	1968	.33	.26	.39	-.01
	69	-.27	-.34	.00	.25
	70	-.05	.09	.18	-.11

** Significant at 1% level, * at 5% level

1968 0-0-0 : 38-38-38 NPK (basic dressing, kg/ha)

1969 0-0-0 : 48-48-48 NPK (〃)

1970 48-48-48 (basic) : 80-80-80 (basic+top)

(standard deviation for varietal means being 4.7).

Fertilizers either extended or shortened the duration of high growth rate as shown by Max-1/2 days. The 29 varieties ranged from 9 days (Koshihikari, extended) to -8 days (Star bonnet, shortened) with a mean of 0.5 (± 4.4) days (Fig. 3).

Correlations among the magnitudes of change in these values were examined with the Sizuoka data in each year, as the fertilizer treatment differed year by year (Table 8). The results showed that the extension of Max-H days due to fertilizer application was highly correlated with the increase in R_{dif} indicating varietal variation in the change toward early-*vs.* late-vigor type, and that the changes in these two values were correlated negatively with that in A and positively with that in B value. Also the change in Max-1/2 days was strongly negatively correlated with that in R_{max} indicating varietal variation in the change toward sustained-*vs.* dash-vigor type. Thus, the pattern of correlations was similar to that found among varietal means of these values. This implies that the effect of fertilizers on growth pattern can be represented by the changes in the two variation trends, early-*vs.* late-vigor and sustained-*vs.* dash-vigor.

Varieties which in response to fertilizers do not change toward early-vigor type much and tend to extend the duration of high growth rate are expected to have a good fertilizer response in grain production. However, the fertilizer effects on R_{dif}(early-*vs.* late-vigor) and Max-1/2 (sustained-*vs.* dash-vigor) values showed no significant correlations with the fertilizer response in grain yield which was shown by the difference between fertilized and unfertilized plots (Table 8). It was also found that the changes in

values representing growth curve and in grain yield due to fertilizer application were uncorrelated with their varietal means.

It should be noted that the nitrogen level in the present experiment was too low to measure fertilizer responses. Beside this, the dry-matter weight data from which logistic equations were computed involved much error variance which was larger than that for grain yield; this is recognized in Table 3 in which the variances of different values can be compared as they are on a logarithmic scale. Further investigations are needed for working out how varietal differences in the fertilizer response of growth pattern are related to grain yield and its fertilizer response.

Further, it is observed from Tables 3 and the variety-year and variety-location interactions have attained significance in certain values representing growth curve. This suggests that the varieties differ in developmental plasticity. Varietal differences in stability-plasticity relationship will be discussed elsewhere.

Discussion

A conclusion drawn from the present study is that there are two major trends of variation in growth curve, one represented by the developmental stage at which growth rate becomes maximum (early *vs.* late vigor) and the other high growth rate (sustained *vs.* dash vigor). Apparently, these variations are at least partly under the control of varietal genotypes.

Growth is exponential at the beginning and gradually becomes restricted by both internal and external factors. Growth rate then reaches its maximum at a certain developmental stage and declines. It is also a conclusion from the present study that the pattern of sequential changes of growth rate during the growing period, called "growth pattern", plays an important role in the expression of yield performance.

As discussed by YOSHIDA (1972), grain yield depends upon the capacity of containers and the extent of their filling with grain, which can be regarded as representing "sink" or "demand" and "source" or "supply" for grain production, respectively. The capacity of containers may be shown by panicle number per

unit area $\times$ spikelet number per panicle $\times$ spikelet size, and the extent of filling by grain weight per unit size of containers. We have following knowledges on these yield components: 1) Panicle number depends on tiller number and is determined in the tillering stage. The number and size of spikelets are determined in panicle-development stage (MATSUSHIMA 1966). 2) All these characters are genotypically controlled, but panicle number is most and spikelet size is least responsive to outer conditions. The extent to which genetically prescribed potentiality is expressed may depend on the activity of growth at the time of determination of each character. 3) The extent of filling the spikelets with grain largely depends on the growth after heading, but partly on the translocation of carbohydrates assimilated before heading (TANAKA 1965, p. 424).

The crop growth rate at a time is determined by assimilation rate minus respiration rate or net assimilation rate, which depends on leaf area index, light transmission rate, root activity, and other physiological conditions while these physiological traits change with growth. Even though crop growth rate is an overall expression of "supply" or "source", it is known that "source" is at least partly conditioned by "sink" (KING *et al.* 1967). The internal mechanisms regulating growth rate are a complex. Yet it was observed that growth rate was rather regularly oscillating. Oscillating growth was also observed in the pattern of internode elongation (OKA and MORISHIMA 1968).

In the light of the present study, it seems that sequential regulation of growth rate determines the "sink" and "source" relations in grain production. Possibly, rapid growth in a stage results in suspension of growth in the next stage, while different organs are formed and different provisions for grain production are made in the succession of stages. There might be an internal mechanism which enables the plants to save energy for the development in subsequent stages. Such regulating ability might be genetically controlled giving rise to different "vigor types" as worked out in the present study.

Summary

Variations in logistic growth curve among rice varieties were investigated using dry-matter weight data from the International Rice Adaptation Experiment. Two major trends of variation were detected, one represented by the developmental stage at which growth rate becomes maximum (variation between early- and late-vigor types), and the other represented by the durability of high growth rate (between sustained- and dash-vigor types). These variations were found to be controlled by varietal genotypes. Early vigor contributes to the production of many spikelets, while late vigor contributes to the growth after heading and filling the spikelets with grain. Sustained-vigor types gave more grain yield than dash-vigor types. The pattern of changes in these vigor types due to fertilizer application also appeared to be varietal characteristics.

Acknowledgement

We express our sincere thanks to Dr. T. Matsuo and other colleagues who have worked together with us in the research program under J.I.B.P. for their kind cooperations and

encouragements. Tranks are also due to Professor A. TANAKA of the Hokkaido University for his reading of the manuscript.

Literature Cited

- GROSENBAUGH, L. R. 1965. Generalization and re-parameterization of some sigmoid and other non-linear functions. *Biometrics* 21: 708~714
- KING, R. W., I. F. WARDLAR and L. T. EVANS 1967. Effect of assimilate utilization on photosynthetic rate in wheat. *Planta* 77: 261~276
- MATSUO, T., F. KIKUCHI and K. KUMAGAI 1972. Studies on the adaptability of rice, I. Comparative studies on the adaptability of rice varieties tested under different conditions in temperate zone. *Japan. J. Breed.* 22: 83~91
- MATSUSHIMA, S. 1966. *Crop Science in Rice*. Fuji Publ., Tokyo. 365 pp.
- OKA, H. I. and H. MORISHIMA 1968. Analysis of genetic variations in plant type of rice. IV. General growth rate, oscillating growth and allometric pattern. *Japan. J. Genet.* 43: 191~201
- OKA, H. I., H. MORISHIMA, T. T. CHANG and O. TAGUMPAY 1970. *Ditto*. V. Early vs. sustained vigor types in growth and their bearing on yielding potential. *Theo. & Appl. Genet. (Der Züchter)* 40: 50~55
- TANAKA, A. 1965. Plant characters related to nitrogen response in rice. *In* The Mineral Nutrition of the Rice Plant (Ed. R. F. Chandler), Johns Hopkins, Baltimore, p. 419~435
- YOSHIDA, S. 1972. Physiological aspects of grain yield. *Ann. Rev. Plant Physiol.* 23: 437~464

稲における草型の遺伝的変異

VI. 国際稲適応性試験から得られた成長型の品種間変異

森島啓子・岡 彦一

(国立遺伝学研究所)

本研究の出発点は、序論に述べたように、成長は時間の関数であり「表現型=遺伝子型+環境」という統計遺伝学の基本的観念は収量決定のダイナミックスを理解するには機械的すぎることである。この見地から私達は品種間雑種 F_7 系統の成長曲線の変異を分析し、その遺伝的支配と収量要因との関係を報告した(OKA *et al.* 1970)。本報告は、この点をもっと詳しく検討するため、JIBP/UM 班(班長松尾孝嶺)における適応性研究の一環として、国際稲適応性試験(I. R. A. E.; MATSUO *et al.* 1972)の成績の一部を分析した結果である。

収量と通常の生産形質の他に、生育途中(4回測定)の乾物重とそれぞれの測定月日ならびに成熟時乾物重が記載されたデータは1968~70年(Phase A)にお

ける静岡農試(29品種)および1971~72年(Phase B)における新潟、埼玉、佐賀、宮崎、Beaumont(テキサス)各農試の成績(10品種)から得られた。それぞれ2反復、2肥料条件の品種試験である。各区、各品種の乾物重のデータをPearl-Reed(二次)のロジスティック方程式にあてはめ、成長曲線の特徴を示す数値として出穂前25日、出穂当日および出穂10日後の成長率(それぞれ R_{-25} 、および R_0)、最大成長率(R_{10})、最大成長率を示す日から出穂までの日数(R_{max})、最大成長率を示す日から成長率がその半になるまでの日数(Max-H)、などを求めた(表1, 2)。これらの変異の調査から次の結論が得られた。

1) 上記の成長曲線を示す種々の数値の品種間差異は

統計的に有意であって、これらの数値に代表される成長の型は遺伝的支配を受けている（表 3, 4）。

2) これらの数値の品種間相関とその主成分分析から、2 種の互いにはほぼ独立の変異の方向が指摘される。その 1 つは最大成長率を示す発育時期の差であってこれについて供試品種は 早期強勢 (early vigor) 型と 晩期強勢 (late vigor) 型との間に変異する。他は高い成長率の持続性であって長期持続 (sustained vigor) 型と短期強勢 (dash vigor) 型との間の変異を示す（表 5, 図 1）。

3) 早期強勢は多数の顕花を作るのに役立つ穀粒の容器を増加する。晩期強勢は登熟を増進する。晩期強勢型では穀粒生産は出穂後の炭酸同化によるが、早期強勢型では出穂前の同化産物の移行がかなりの部分を占める。（表 7）。

4) 長期持続型は 短期強勢型より 収量が多い（表 6,

7）。花芽分化から成熟までの期間の成長率（標準化した値）の変動を調べると、収量の高い品種は変動が小さく低収の品種は変動が大きかったが、このことも持続型成長の穀粒生産に対する貢献を示している（図 2）。

5) 施肥は成長の型を概して早期強勢の方向に変えるがその程度は品種によって異なる。また品種によって施肥が成長持続性を増進するものと低減するものがある（表 8, 図 3）。施肥による成長型の変化様式は品種の遺伝的特性である。しかし国際稲適応性試験の施肥水準は普通の標準より低かったので、穀粒生産における肥料反応性と成長型の変化様式との関係は今後の研究に残された。また場所や年による成長型の変化程度も品種の特性であることが判ったが、発育可変性と収量安定性の問題は別の論文で考察する。