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Analysis of Genetic Variations in Plant Type of Rice

V. Early vs. Sustained Vigor Types in Growth and their Bearing on Yielding Potential

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Summary. To examine genetic variation in the growth curve parameters and their contribution to factors determining grain yield, 40 randomly chosen F_7 lines of a cross between two contrasting rice varieties were measured for dry matter weight and for other yielding characters during the growing period. From the dry weight data, growth curves were computed using linear and quadratic (Pearl-Reed) logistic equations, and various values derived from them were compared among lines. The results showed that: 1) The growth curves of the lines varied genetically between the "early-vigor" and "sustained-vigor" types. 2) Total panicle length per unit area, representing the potentiality for carbohydrates to be produced in grains, seemed to depend on the growth rate at floral initiation, and panicle weight per unit length, representing the rate of carbohydrate supply to the panicles, seemed to depend on the growth rate at heading. These two values were negatively correlated. 3) "Early-vigor" types tended to produce more panicles but had a low rate of carbohydrate supply than "sustained-vigor" types. Either "potentiality" or "supply" was a limiting factor in grain production, depending upon the pattern of growth being either "early-vigor" or "sustained-vigor" type.

In their studies on competition among rice varieties, Jennings and Aquino (1968) showed that a strong competitor could be distinguished from a weak one by their growth rate about 60 days after germination. Their data suggested that the high growth rate of the strong competitors at that early stage was associated with a low growth rate at heading time and a low yield under intensive culture.

To estimate the genetic variation in growth curve parameters and to examine their relationships with yield characters, 40 F_7 lines randomly sampled from the progeny of a cross between the two rice varieties (*Oryza sativa* L., Indica type) 'Peta' and 'I-g-t' were grown and observed by the co-authors Chang and Tagumpay at The International Rice Research Institute. The data were analyzed by the co-authors Oka and Morishima. The results indicated that the growth pattern is genetically controlled and can have an important bearing on the yielding potential.

Materials and Methods

The F_7 lines observed were the progenies of F_3 lines used by the present authors for studies on genetic variation in plant type (Morishima et al. 1967a, b). 'Peta' is a tall variety of Indonesian origin, while 'I-g-t' is a semi-dwarf variety from Taiwan having a recessive gene controlling short stature (Chang et al. 1965). The former is weakly sensitive, while the latter is insensitive, to photoperiod. At Los Baños, Philippines (lat. 14° 10′ N) both varieties behave essentially as insensitive to photoperiod as do all of their hybrid derivatives.

Twenty tall and 20 short F_7 lines, randomly chosen, were grown in the 1968 dry season (seeded on December 20, 1967) at The International Rice Research Institute. Three-week old seedlings were transplanted at 20 × 30 cm spacing, with a single plant per hill (16.67 plants per m²). The fertilizers applied were a basal dressing and a top dressing (3 weeks after planting) of 30-0-0 NPK (kg/ha). Each line was planted in six rows each of 26 plants. Data were taken from the plants in the inner four rows. The two height groups were each subdivided into two blocks, each block containing 10 F_7 and 2 parental plots. Since the fertilizer dose was low and the plants were grown in the sunny, dry season, the tall lines did not lodge seriously.

During the growing period, 20 randomly chosen plants per plot were cut at the soil surface on the 41st, 61st, and 91st day after seeding for measuring dry matter weight. The sampled hills were immediately replaced by plants of the same age. The mean heading date was recorded for each plot. At maturity, 20 plants per plot were used for measuring grain yield and dry straw weight, and the other 20 plants were measured on a single-plant basis for plant height, panicle number per plant, mean weight of single panicles, and mean panicle length. The plot means for these characters were used for computation.

Data from the eight parental plots (four of 'Peta' and four of 'I-g-t') were used for estimating error variances. For estimating heritabilities, the error mean squares were subtracted from the between line mean squares to obtain genetic variances. Genetic covariances were also computed by the same method to estimate genetic correlations.

Computations were made on the following items:

(a) Estimates of growth curve parameters — For each line, growth curves were computed from dry matter weight on the 61st and 91st day and at maturity. A linear logistic equation was fitted to the values on the 61st and 91st day and at maturity. A quadratic (Pearl-Reed) logistic equation was also fitted to the same data, assuming that 99% of the final dry weight was attained 25 days after heading. Since no measurement of dry weight after heading was available, this assumption was necessary to let the growth curves approach the final dry weight in about one month after heading. The equations used were:

$$\log_e (A/y - 1) = \log_e a - b\,t\,,$$

or

$$dy/dt = y\,(1 - y/A)\,b \ldots \text{(linear)}\,,$$

and

$$\log_e (A/y - 1) = \log_e a - b_1\,t - b_2\,t^2\,,$$

or

$$dy/dt = y\,(1 - y/A)\,(b_1 + 2\,b_2\,t) \ldots \text{(quadratic)}\,,$$

where y is the dry weight at time t, A is the final dry weight at maturity (grain + straw), and a, b, etc. are parameters showing growth rate. From the linear and quadratic equations obtained for each line, daily growth rates (dy/dt in g/day/m^2) were computed separately and were averaged to estimate the maximum growth rate and other values given in Table 1.

Further, from the dry weight on the 41st and 61st day, growth rate was computed using an exponential function, $\log_e y = r\,t + \log_e y_0$, or $dy/dt = r\,y$, assuming that growth before the 61st day was not affected by mutual shading.

(b) Yield characters. — The values for the characters listed in Table 1 were computed for each line. For obtaining the grain yield of a line, an estimate from mean weight of single panicles × panicle number per square meter (m^2) and the actual dry weight of grains were averaged. This estimate of grain yield divided by panicle number per m^2 then represented single panicle weight. Total panicle length per unit area (P) was given by mean panicle length × panicle number per m^2, and panicle weight per unit length (Q) was given by single panicle weight/mean panicle length (in g/m). The ratio of grain yield to total dry weight at maturity was taken as the harvest index (R).

Results

1. Variations in growth pattern of F_7 lines

From the various values showing the growth pattern obtained for each line, the group means, within-group between-line mean squares and the corresponding heritabilities were computed (Table 1). Since there was no replication for the F_7 lines, the significance of between-line variances could be judged only from the variances of parental plots or from the heritability values. A heritability higher than 74% would imply an F value higher than 3.9, which represents the 5% level of significance when the degrees of freedom are considered to be 19 for the between-line variance and 6 for the error variance.

The data in Table 1 show that various growth parameters had mostly heritability estimates higher than 74% within the tall or the short line group, or in both. This indicates that the growth curves of the F_7 lines differed genetically. The tall parent, 'Peta', had a higher growth rate at floral initiation (taken to be 30 days before heading) but a lower growth rate at heading than the short parent, 'I-g-t' (Table 1). The maximum growth rate of Peta (18.8 days before heading) appeared at a much earlier stage than that of I-g-t (6.5 days before heading). But the tall and short lines do not show such differences in group mean. It may thus be inferred that the major gene controlling height does not exert pleiotropic effects on the growth pattern, while the parental varieties differ in other genes controlling growth.

A comparison of the growth curves of two lines is presented in Fig. 1. In general, growth rate gradually increased after the initiation of tillering and later declined. Within both the tall and the short groups, lines differed in maximum growth rate as well as in the developmental stage at which this rate was attained. In the figure, line T36 (tall) showed its maximum growth at an earlier stage than S18 (short).

Phenotypic correlations found among various growth parameters are given in Table 2. As the correlation coefficients found in the tall and the short line groups were quite similar, their means obtained after z transformation are given in the table. The table shows that many of the values were significantly correlated either positively or negatively. Phenotypic and genotypic correlations were generally similar.

Table 1. *Parental and line group means, between-line mean squares and heritabilities for growth and yield characters*

Character	Tall group				Short group			
	Peta mean	Line mean	M.S.	h^2 (%)	Igt mean	Line mean	M.S.	h^2 (%)
Growth pattern								
A) Days to heading	112.0	108.3	19.36	97	97.5	110.3	49.46	96
B) Exponential growth rate (% of y)	9.15	9.07	2.29	77	8.35	7.84	2.17	76
C) Maximum growth rate (g/day/m^2)	34.7	34.0	8.73	39	22.1	28.2	11.31	53
D) Days from maximum rate to heading	18.8	12.0	10.37	67	6.5	13.6	36.47	80
F) Growth rate at floral initiation (dy/dt, g/day/m^2)	28.6	19.3	16.56	94	7.4	18.3	34.18	97
H) Growth rate at heading (g/day/m^2)	17.8	24.7	12.99	49	20.5	19.5	21.58	74
I) Weight increment after heading (% of A)	13.8	23.2	24.80	78	32.0	22.7	86.12	80
Yield character								
L) Panicle length (cm)	26.8	27.6	2.32	83	21.9	23.6	2.49	84
W) Single panicle weight (g)	2.96	2.57	0.163	90	1.74	2.03	0.110	95
N) Panicle number per plant	12.0	12.5	2.65	65	14.0	15.0	5.82	84
P) Total panicle length (m/m^2)	52.2	57.7	47.78	71	51.2	58.0	38.56	72
Q) Panicle weight per unit length (g/m)	11.05	8.94	1.246	78	7.95	8.72	1.097	83
R) Harvest index (%)	36.7	33.7	1.66	76	44.5	38.2	12.47	82
Y) Grain yield (g/m^2)	577	511	2641	58	407	503	3146	63

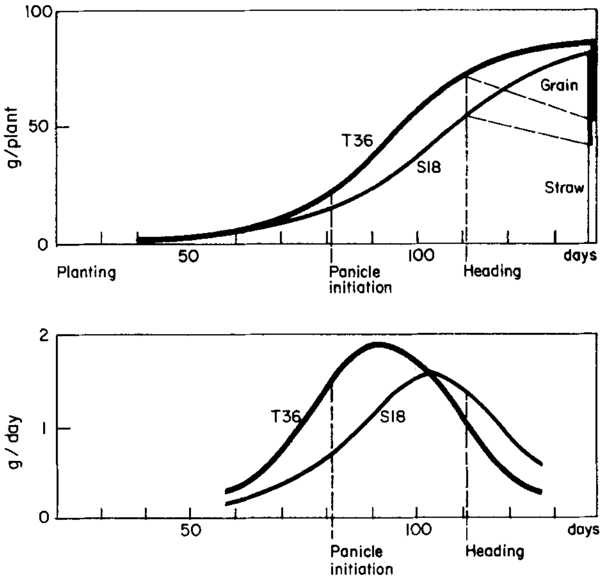

Fig. 1. Comparison of growth pattern between two F_7 lines having the same maturity. T36 had a higher growth rate at floral (panicle) initiation and a lower growth rate at heading than S18. The grain yield per plant was 28 g in T36 and 33 g in S18

The growth rate at floral initiation (F) and that at heading (H) were negatively correlated ($r = -0.59$). This is due to that, as the example in Fig. 1 shows, the F_7 lines vary between those showing maximum growth rate at an early stage and others showing it at a later stage. Such lines may be called the "early-vigor" and "late-vigor" types, respectively. 'Peta' is an "early-vigor" type, while 'I-g-t' is a "late-vigor" type.

Under the conditions of the present experiment, the maximum growth rate was positively correlated with the growth rate at floral initiation ($r = 0.63$), indicating that "early-vigor" types had higher maximum rate than "late-vigor" types. As expected, the weight increment after heading was highly correlated with the growth rate at heading ($r = 0.78$), but was negatively correlated with the growth rate at floral initiation ($r = -0.88$). The "late-vigor" type can have a larger increment of body weight in the ripening stage than the "early-vigor" type and actually showed a sustained type of vigor following heading. Correlations of the number of days to heading with other values also showed that early-maturing lines tended to be "sustained-vigor" types.

2. *Yield characters and their correlations with growth pattern*

Most yield characters had high heritability values, indicating that the F_7 lines were genetically different (Table 1). As previously mentioned, the product of single panicle weight and panicle number per unit area (m^2) was used for estimating grain yield. The product of total panicle length per unit area and panicle weight per unit length also gives the estimate of grain yield. Total panicle length per unit area represents the potentiality for grain production, assuming a similar density of spikelet distribution and similar spikelet size. It then shows the requirement for carbohydrates by the panicles. The panicle weight per unit length represents the rate of carbohydrate supply to the panicles. These two values may be regarded as potentiality (or demand) and supply factors limiting grain production.

As is usually found, panicle number per plant was negatively correlated with panicle length ($r = -0.43$) and with single panicle weight ($r = -0.74$). As expected, total panicle length and panicle weight per unit length were also negatively correlated ($r = -0.59$). Between-line (phenotypic) and corresponding genotypic correlations of these yield characters with growth parameters are summarized in Table 3. Since the tall and short line groups had similar correlations, their means obtained after z transformation are given in the table. Table 3 shows that panicle length, single panicle weight and panicle number per plant were not correlated with growth-curve characters except for a significant correlation of single panicle weight with maximum growth rate ($r = 0.47$). But, total panicle length was significantly correlated with the growth rate at floral initiation ($r = 0.42$) and with the number of days between maximum growth and heading ($r = 0.34$), and panicle weight per unit length (g/m) was significantly correlated with the growth rate at heading ($r = 0.46$). These

Table 2. *Between-line and genetic correlations among values indicating growth pattern*

Value	*A*	*B*	*C*	*D*	*F*	*H*	*I*
A) Days to heading	ph g	−.41	.72	.63	.78	−.26	−.58
B) Exponential growth rate	−.32*	—	−.42	−.41	−.47	.18	.39
C) Maximum growth rate	.47**	−.29	—	.87	.87	−.39	−.95
D) Days from maximum rate to heading	.66**	−.37*	.40*	—	.93	−.72	(−1.0)
F) Growth rate at floral initiation	.77**	−.38*	.63**	.93**	—	−.61	−.95
H) Growth rate at heading	−.30	.23	.11	−.78**	−.59**	—	.69
I) Weight increment after heading	−.56**	.37*	−.41*	−.97**	−.88**	.78**	—

Below the diagonal (ph) — Between-line correlations within line groups. Above the diagonal (g) — Genetic correlation Mean of correlation coefficients within tall and short groups, obtained by z transformation, is given.

* Significant at 5% level; ** significant at 1% level.

Table 3. *Correlations between yield characters and values indicating growth pattern*

Growth pattern character		Panicle length	Single panicle weight	Panicle number p. plant	Total panicle length	Panicle wt. p. unit length	Harvest index
A) Days to heading	ph	.29	.21	.21	.39*	.12	−.45**
	g	.30	.23	.33	.51	.16	−.51
B) Exponential growth rate	ph	−.10	−.07	−.11	−.15	−.02	.26
	g	−.05	−.15	−.34	−.42	.02	.22
C) Maximum growth rate	ph	.34	.47**	.09	.31	.39*	−.29
	g	.48	.59	−.13	.24	.40	−.36
D) Days from maximum rate to heading	ph	.18	.01	.17	.34*	−.17	−.33*
	g	.19	−.03	−.01	.63	−.23	−.41
F) Growth rate at floral initiation	ph	.03	.17	.20	.42**	−.02	−.43**
	g	.04	.12	.33	.42	−.07	−.40
H) Growth rate at heading	ph	.01	.31	−.10	−.13	.46**	.15
	g	.01	.40	−.36	−.47	.63	.20
I) Weight increment after heading	ph	−.08	.11	−.23	−.35*	.25	.34*
	g	−.15	.14	−.59	−.67	.36	.48

ph — Phenotypic correlation between lines; g — Genetic correlation
Mean of correlation coefficients within tall and short line groups, obtained by *z* transformation, is given.
* Significant at 5% level; ** significant at 1% level.

correlations were recognized not only phenotypically but also genetically.

These correlations imply that when growth rate reaches the maximum around floral initiation, a large amount of panicle material in terms of length may be produced; if it takes place at heading, the panicles will be satisfactorily filled with grains. The "early-vigor" types had higher growth rate at floral initiation and lower growth rate at heading than the "late-" or "sustained-vigor" types. It then follows that the "early-vigor" types could produce more panicle material and would require more carbohydrates but have a lower rate of carbohydrate supply than the "sustained-vigor" types.

The product of total panicle length per unit area and panicle weight per unit length represents the grain yield. Accordingly, the growth rates both at floral initiation and at heading were correlated with grain yield (Table 4, right column). Harvest index was negatively correlated with the growth rate at floral initiation ($r = -0.43$; Table 3). The exponential growth rate measured at an early stage showed no significant correlations with yield characters (Table 3).

3. Limiting factors in grain production

In some lines insufficient panicle production may be a factor limiting grain production, while in others it may be insufficient carbohydrate supply to the panicles. To look into this relation, the four values, growth rate at floral initiation (F) and at heading (H), total panicle length (P), and panicle weight per unit length (Q), were each transformed into probit for comparing them with one another. The 40 F_7 lines under observation were then divided into three groups, $P > Q$ ("potentiality or demand factor" being by more than one probit larger than "supply factor"), $P \div Q$ (difference between the two values being less than one probit), and $P < Q$ ("potentiality factor" being by more than one probit smaller than "supply factor"). Correlations of the growth rates at floral initiation and at heading with grain yield in these three line groups are given in Table 4.

In the $P > Q$ group, the growth rate at heading was correlated with yield ($r = 0.36$) but that at floral initiation was not ($r = 0.08$). In contrast, in the $P < Q$ group, the growth rate at floral initiation was correlated with yield ($r = 0.45$) but that at

Table 4. *Correlations of the growth rates at floral initiation and at heading with grain yield, and of total panicle length and panicle weight per unit length with grain yield, in line groups classified by those values*

Factor	Correlation with yield in classified group						Whole lines
	$P > Q$	$P \div Q$	$P < Q$	$F > H$	$F \div H$	$F < H$	
No. of lines	13	14	13	14	13	13	40
Growth rate in probit,							
at floral initiation (F)	.08	.70	.36				.43
at heading (H)	.45	.45	.04				.34
Yield factor in probit,							
Total panicle length (Potentiality factor: P)				.04	.05	.56	.37
Panicle weight per unit length (Supply factor: Q)				.55	.66	.55	.52

heading was not ($r = 0.04$). Although the number of lines in each group was too small to determine the significance of correlations, this correlation pattern indicates that in lines having a large demand for carbohydrate deposit but a small supply, yield may depend on growth rate at heading, while in lines having a small demand but a large supply, yield may depend on growth rate at floral initiation. In other words, either the demand for carbohydrate deposit or the supply rate may be a limiting factor in grain production, and this relation differs according to the pattern of growth being either of "early-vigor" or "sustained (late)-vigor" types.

Similarly, the 40 lines under observation were divided into $F > F$, $F \doteqdot H$, and $F < H$ groups comparing the growth rates (in probit) at floral initiation and at heading with·each other. In the $F > H$ and $F \doteqdot H$ groups, panicle weight per unit length, but not total panicle length, was correlated with grain yield (Table 4). In the $F < H$ group, the two values were both correlated with yield and may also be considered as limiting factors in grain production. In the $P \doteqdot Q$ as well as in $F \doteqdot H$ groups, the "potentiality" and "supply" factors may be considered to be balanced.

Discussion

The yielding capacity of grain crops has been studied by geneticists dealing mainly with morphological yield characters and by plant physiologists dealing with photosynthesis, respiration and mineral nutrition. Since grain yield is the final result of many interacting factors, studies on the performance of individual factors can not contribute much to an understanding of the internal mechanisms of yield determination. As Nelder (1963) has remarked, this leads to the necessity of investigation of growth pattern and developmental paths.

In his studies on yield determination in rice, Matsushima (1966, p. 298) considered that panicle number per plant and spikelet number per panicle determine the volume of the vessel or container that has to be filled with starch, and fertility and mean grain weight determine the actual content of the vessel. When we consider the total panicle length per unit area as the capacity for carbohydrate deposit, the panicle weight per unit length would indicate the rate of carbohydrate supply. These correspond to Matsushima's vessel and actual content, respectively, though they are different from the "demand-dependent" and "supply-dependent" characters as discussed by Nelder (1963).

Matsushima (1966, p. 26—33, 112—117, and 174 to 182) demonstrated that panicle number per plant and spikelet number per panicle were determined at the active tillering stage and the flower-organ differentiation stage, respectively. The size of the "vessel" is thus determined at the floral initiation stage. He also showed that fertility and mean grain weight or the "actual content" were determined at around the heading stage.

The authors found in the present study that the observed lines ranged from an "early-vigor" to a "sustained-vigor" type, and that panicle production was dependent on the growth rate at panicle initiation and grain production on that at heading. Since the early-vigor types tended to decline at heading time, the growth rate at panicle initiation and that at heading were negatively correlated. Although Matsushima (1966) did not discuss it critically, the "vessel" and "actual content" were conditioned by the pattern of growth.

As grain yield is the product of "potentiality" and "supply rate", high yield is realized when both factors have high values and are well balanced. When an unbalance takes place, one of them can act as a limiting factor as we have demonstrated. Which one of them restricts the yield may depend upon the pattern of growth being either of "early-vigor" or "sustained-vigor" type.

The general tendency of "early-vigor" varietal types to show a decline in later stages was demonstrated by Tanaka et al. (1964). Their extensive studies in nutritional physiology showed that early vigor is due to a high initial rate of nitrogen uptake giving rise to luxurious vegetative growth, which leads to mutual shading of the leaves, loss of carbohydrates by respiration, death of lower leaves and lodging. This type of growth may bring about a high competitive ability as shown by Jennings and Aquino (1968), and may be favored by natural selection.

When the plants are spaced widely, vigor shown during early stages of growth can be maintained until maturity (Tanaka et al. 1964). However, at economical planting densities, the growth rate begins to decline as soon as excessive leaves are produced.

This relationship differs according to the plant type and various internal conditions. The growth pattern depends primarily on the turning point of a decline in growth rate. It may be conditioned by the response of plant organs to crowding and mutual shading. The independence of exponential growth rate of other growth parameters may be an indication of this relationship. Presumably, internal characters such as intrinsic growth rate, nitrogen absorbing rate, leaf structure, and reaction to the effects of crowding are determined by genes, bringing about genetic variation in the growth curve as found in the present work.

To observe the effect of nitrogen on the shape of the growth curve, the data obtained by Jennings and de Jesus (1968) for three rice varieties grown at 0 N and 100 N (kg/ha) levels were re-analyzed using a cubic Pearl-Reed function. The results are given in Fig. 2, which shows that the growth curve is shifted towards an "early-vigor" type by nitrogen application. It was also found that in tropical native varieties such as "MTU-15" (indica), the application

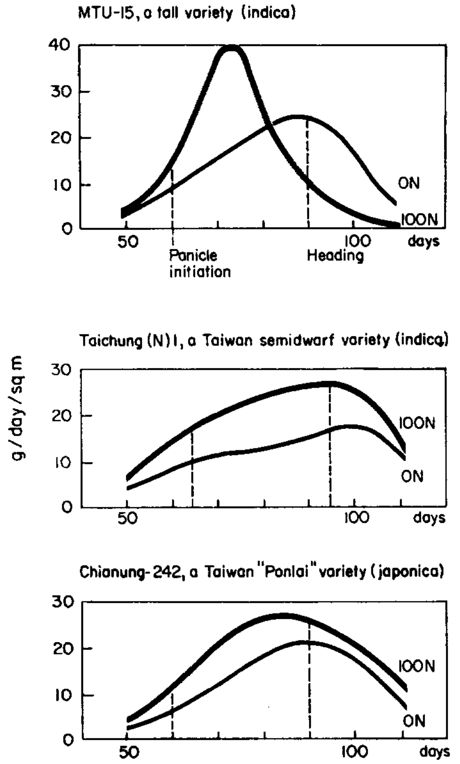

Fig. 2. Daily drymatter increase curves of three rice varieties tested at two nitrogen levels, 0 N and 100 N (kg/ha). Computed from data obtained by Dr. P. R. Jennings in the 1966 dry season, using a Pearl-Reed function

of 100 N may cause drastic acceleration of growth and subsequent rapid decline, whereas improved plant type varieties such as "T.N. 1" and "Ch. 242" showed a gradual increase in growth rate persisting through heading in response to 100 N. Accordingly, it may be said that "sustained-vigor" types generally have lower initial nitrogen uptake than "early-vigor" types, and can be better adapted to intensive culture at high nitrogen levels.

Zusammenfassung

Zur Untersuchung der genetischen Variation der Parameter von Wachstumskurven und ihres Beitrages zu den Faktoren, die den Kornertrag bestimmen, wurden 40 zufällig ausgewählte F_7-Linien einer Kreuzung zwischen 2 unterschiedlichen Reissorten hinsichtlich des Trockenmasse-Gewichts und anderer Ertragsmerkmale während der Wachstumsperiode gemessen. Aus den Trockengewichts-Daten wurden mit Hilfe linearer und quadratischer (Pearl-Reed) logistischer Gleichungen Wachstumskurven berechnet und die verschiedenen, hieraus abgeleiteten Werte zwischen den Linien verglichen. Die Ergebnisse zeigen:

1. Die Wachstumskurven der Linien variieren genetisch zwischen den „Frühwuchs-" und den „Dauerwuchs-"Typen.

2. Die gesamte Panicellänge pro Flächeneinheit, die das Potential der Erzeugung von Kohlenhydraten in den Körnern repräsentiert, scheint von der Wachstumsrate während der Blüteninitiation abzuhängen. Das Panicelgewicht pro Längeneinheit, das die Rate der Kohlenhydratversorgung der Panicel repräsentiert, scheint von der Wachstumsrate während des Ährenschiebens abzuhängen. Diese beiden Werte sind negativ miteinander korreliert.

3. Die „Frühwuchs-"Typen tendierten dazu, mehr Panicel auszubilden, hatten aber eine niedrigere Rate der Kohlenhydratversorgung als die „Dauerwuchs-" Typen. In Abhängigkeit vom Wachstumsmuster erwies sich entweder das „Potential" oder die „Versorgung" als begrenzender Faktor der Kornproduktion, je nachdem, ob es zu einem „Frühwuchs-" oder zu einem „Dauerwuchs-"Typ führte.

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