Studies on Competition in Plants and Animals

XI. Competitive Ability and Density Response in Barley

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Synopsis. The relationship between competitive ability and density response was investigated with twelve barley varieties. Characters investigated were dry plant weight, seed yield, plant height, number of culms and number of ears. The result showed that the two were independent, suggesting that they should be controlled by different genes.

Introduction

Increase in density in a plant population brings about two botanical consequences: One is a general retardation of plant growth due to shortage of space and resources, and the other is interaction between plants due to their adjacent stand. Interaction between plants comprises competition within the same genotype and competition between different genotypes.

Competition within the same genotype may occur between individuals of the same clone or isogenic strain. They are isogenic but can vary in growth rate owing to environmental or chance variation. It may then happen that a plant germinating a little earlier than others has a competitive superiority over its sib-plants. Such competition, if it happens, may favour some and disfavour other individuals, but it may have little to do with the genetics of the population. Thus, intragenotypic competition, if any, will be of little interest to geneticists.

Retardation of growth due to density increase in a plant population or the density response, on the one hand, and intergenotypic competition, on the other, however, attract the attention of geneticists. It is expected that a developing population of a plant species will be subject to pressures of natural selection for either, intergenotypic competitive ability and density response.

It then becomes a matter of interest to find whether or not density response and competitive ability are related with each other. This paper describes the results of our experiments with twelve barley cultivars, which were carried out in order to answer the question.

Materials and Methods

The present study consists of two experiments: spacing experiment conducted in 1961 and competition experiment of 1962. Twelve cultivars of barley used in the experiments are Aizu No.7 (AZ), Golden Saitama No.1 (GS), Ise-hadaka (TH), Jōshū Shiro-

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hadaka (JH), Kōgen-mugi (KG), Kuro-mugi (KM), Sakigake (SK), Seto-hadaka (SH), Shizuoka Shiro Six-rowed (SZ), Suifu (SF), Tochigi Bōzu (TC) and Yane-hadaka (YH).

The spacing experiment included five levels of spacing: $2 \times 2 \text{ cm}^2$, $4 \times 4 \text{ cm}^2$, $8 \times 8 \text{ cm}^2$, $16 \times 16 \text{ cm}^2$ and $32 \times 32 \text{ cm}^2$ per plant. The experiment was conducted by the split-plot method with three replications. The twelve cultivars assigned to the main-plots, while the densities to the sub-plots. Number of plants planted in each sub-plot was from 80 in the $32 \times 32 \text{ cm}^2$ plot to 800 in the $2 \times 2 \text{ cm}^2$ plot. Fifty to sixty plants selected at random from the harvest of each sub-plot after discarding the border plants were investigated. Examined were dry plant weight (grams), seed yield (grams), plant height (centimeters), number of culms and number of ears on an individual plant basis.

The competition experiment was conducted in the subsequent year, 1962, with the same twelve cultivars, each in pure-stand and in mixture with a common test-variety "Aka-shin-riki". The experiment was conducted by the split-plot method with four replications. Twelve cultivars were assigned to main-plots, each being divided into sub-plots of pure-stand and the mixture. The planting was made singly spaced at 12 cm distance in rows 60 cm apart. The mixture was produced by alternate planting of the test variety and the cultivar to be tested for its competitive ability.

Competitive ability was measured by the difference between

Figure 1. Response of twelve barley varieties to plant density: Culm number.

Figure 2. Response of twelve barley varieties to plant density: Ear number,

Figure 3. Response of twelve barley varieties to plant density: Seed yield.

Figure 4. Response of twelve barley varieties to plant density: Plant weight.

the performance in the mixture and that in pure-stand. The number of plants examined in each sub-plot was 25 in pure-stand and 11 in the mixture. Examined were dry weight (grams), seed yield (grams), number of culms, number of ears, plant height (centimeters) and ear length (centimeters) on an individual plant basis.

Experimental Results

(A) Spacing experiment

In all examined characters except for plant height, the effect of spacing was found to be statistically significant. The response of 12 cultivars to plant density in respect of culm number, ear number, seed yield and plant weight is presented in Figures 1 to 4.

It is found from Figures 1 and 2 that culm number and ear number per plant increase linearly as the density decreases. Figure 3 shows that the increase in seed yield was linear up to $16 \times 16 \text{ cm}^2$ in every cultivar, but further decrease in density seems to bring about a halt in the increase at least in a few cultivars (SK, AZ and TC), while some others are still showing linear increase even at wider spacing than $16 \times 16 \text{ cm}^2$. The pattern of response in plant weight appears to be more or less intermediate between culm or ear number and seed yield (Fig. 4). This is quite possible

Table 1. Density response, expressed in terms of linear regression coefficients, in plant weight, number of culms, number of ears and seed yield of twelve cultivars of barley

Variety		Density response (linear regression coefficient)			
		Plant weight	Culm number	Ear number	Seed yield
Shizuoka Shiro 6-rowed	SZ	1.383 ± .145	.355 ± .039	.557 ± .044	.238 ± .022
Golden Saitama No. 1	GS	1.288 ± .424	.402 ± .182	.344 ± .062	.330 ± .087
Yane-hadaka	YH	.876 ± .189	.267 ± .064	.352 ± .036	.224 ± .023
Jōshū Shiro-hadaka	JH	.834 ± .247	.354 ± .070	.240 ± .031	.272 ± .026
Kuro-mugi	KM	.823 ± .256	.302 ± .083	.325 ± .051	.272 ± .036
Ise-hadaka	IH	.817 ± .286	.261 ± .082	.307 ± .062	.207 ± .042
Seto-hadaka	SH	.809 ± .213	.266 ± .053	.358 ± .059	.230 ± .024
Kōgen-mugi	KG	.762 ± .267	.271 ± .068	.264 ± .059	.239 ± .032
Aizu No. 7	AZ	.723 ± .136	.345 ± .054	.207 ± .037	.285 ± .025
Sakigake	SK	.706 ± .145	.280 ± .106	.280 ± .065	.247 ± .042
Suifu	SF	.659 ± .174	.360 ± .081	.327 ± .054	.244 ± .044
Tochigi Bōzu	TC	.314 ± .176	.239 ± .037	.089 ± .023	.189 ± .013

Table 2. Total and partial correlations between density responses in different characters

		Total correlation			
		Number of culms	Number of ears	Seed yield	Plant weight
Partial correlation	Number of culms	—	0.8117**	0.3609	0.6146*
	Number of ears	0.8327**	—	0.1506	0.5212
	Seed yield	0.1673	-0.5546	—	0.8387**
	Plant weight	0.0303	0.5085	0.8828**	—

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

because a good part of dry plant weight comes from seed.

The density responses have been investigated by the coefficients of linear regression of characters on spacings. They are presented in Table 1, together with their 95% confidence intervals.

It is found from Table 1 that cultivars vary significantly in respect of the density response. The highly responsive were SZ and GS, while the lowest was TC.

Total and partial correlations between regression coefficients of plant weight, culm number, ear number and seed yield are presented in Table 2.

Total as well as partial correlations in Table 2 show that response to density in culm number is closely associated with that in ear number and the same relation also holds between plant weight and seed yield, but there seems to be very low correlation between density response in ear or culm number and that in seed yield. It means that density response in culm or ear number, or that in vegetative growth, is not the same as the density response in reproductive development: they appear to be independent from each other.

Table 3. Mean values in pure-stand and mixture with a common test variety and competitive ability in plant weight, culm number, ear number and seed yield of twelve cultivars of barley

Variety		Plant weight			Culm number			Ear number			Seed yield		
		M*	P*	C*	M*	P*	C*	M*	P*	C*	M*	P*	C*
Shizuoka Shiro 6-rowed	SZ	59.8	49.2	10.7	16.4	13.8	2.7	14.3	12.6	1.6	19.6	17.2	2.4
Golden Saitama No. 1	GS	83.2	65.1	18.1	26.8	20.6	6.2	23.8	18.5	5.3	14.9	11.6	3.3
Yane-hadaka	YH	45.3	35.0	10.3	14.2	10.8	3.4	13.2	9.8	3.4	18.1	12.9	5.2
Jōshū Shiro-hadaka	JH	34.6	37.6	-3.0	12.5	15.1	-2.6	11.7	13.5	-1.8	11.8	12.0	-0.2
Kuro-mugi	KM	36.9	29.1	7.8	12.7	11.2	1.5	11.8	9.9	1.9	16.0	12.7	3.3
Ise-hadaka	IH	33.4	35.3	-1.9	12.2	12.1	0.2	11.4	10.8	0.5	13.3	13.7	-0.4
Seto-hadaka	SH	21.8	35.3	-13.6	8.4	12.8	-4.4	7.6	11.2	-3.6	9.5	15.2	-5.7
Kōgen-mugi	KG	50.2	47.2	3.0	15.9	17.1	-1.1	14.9	16.3	-1.4	16.5	16.1	0.4
Aizu No. 7	AZ	43.8	35.6	8.3	16.6	14.6	2.0	14.5	14.5	0.0	14.7	13.8	0.9
Sakigake	SK	25.9	24.5	1.5	16.2	14.3	1.9	14.9	12.9	2.0	11.8	11.1	0.7
Suifu	SF	21.3	24.0	-2.8	18.3	17.3	0.9	15.1	15.0	0.2	8.5	11.0	-2.5
Tochigi Bōzu	TC	25.3	25.0	0.3	15.0	14.1	0.9	13.3	12.8	0.5	8.3	7.8	0.4

* P, M and C stand for mean values in pure-stand and mixture, and competitive ability, respectively.

Table 4. Total and partial correlation coefficients among competitive abilities on the basis of measurements of different characters

		Total correlation			
		Number of culms	Number of ears	Seed yield	Plant weight
Partial correlation	Number of culms	—	0.9591**	0.7762**	0.9061**
	Number of ears	0.7137*	—	0.8131**	0.8574**
	Seed yield	0.1446	0.3744	—	0.6257*
	Plant weight	0.5864	0.0172	-0.2761	—

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

Results of the spacing experiment so far described lead us to conclude that vegetative growth is more favourably influenced by wide spacing than reproductive growth.

(B) Competition experiment

Table 3 presents the results of our competition experiment with the twelve cultivars of barley. Competitive ability is estimated by the difference between the value in the mixture and that in the pure stand. Analysis of variance showed that variations among cultivars for competitive ability in plant weight, number of culms and number of ears were highly significant, while for seed yield the variation fell short of the significance level. It is found from Table 3 that GS, YH and SZ were very superior competitors while SH and JH weak.

Competitive abilities in different characters showed high plus correlations with each other with r values lying between 0.626 and 0.959, all statistically significant. Table 4 gives total and partial correlation coefficients among competitive abilities on the basis of measurements of different characters.

Total correlations in Table 4 show that competitive abilities in respect to the four

characters are highly correlated with each other, but partial correlations reveal that increase in seed yield due to competition is not highly correlated, just as it was not in Table 3, with increase in ear number, though the ear is certainly the bearer of seed. The partial correlation between competitive abilities as measured from plant weight and culm number may mean that plant weight was in this competition experiment largely influenced by vegetative growth rather than by seed weight.

(C) Relation between density response and competitive ability

Correlations were examined between density response and competitive ability for each character. Correlation coefficients between them were $r=0.144$ for seed yield, $r=0.541$ for plant weight, $r=0.407$ for number of culms and $r=0.372$ for number of ears. They all failed to reach the significance level, the coefficient for seed yield being especially low.

Discussion

It is interesting to find in the spacing experiment that vegetative growth measured by culm or ear number per plant increases in approximately linear proportion to the decrease in plant density while reproducing capacity does not increase in the same way. In other words, culm number as well as ear number increases according to the increase of interplant spacing within the range of the present experiment, but seed production does not follow suit. Seed yield reaches a plateau when the spacing surpasses a certain threshold. It is of interest to find from Table 2 that total as well as partial correlation between density response in number of culms and that in ear number was quite high, while both showed very low correlation with density response in seed yield. It means that those cultivars which show higher response in vegetative growth than others to lower density do not always promise a higher response in seed yield. Similar facts have also been found in the competition experiment.

SAKAI (1961) found in the weeding experiment with rice that in some cultivars, increase in culm or ear number due to weeding tends to bring about an increase in seed sterility effecting no increase in seed yield. The effect of weeding might involve effects of competition against weed species and those of plant density. Such an inconsistency between growth of vegetative organs and seed production seems to be of common occurrence, which might be due to an intraplant scramble between florets for the limited amount of photosynthetic products (DONALD, 1954).

There is quite often a disagreement between agronomists or plant ecologists, on the one hand, and geneticists, on the other, about the concept of competition in plants. Among agronomists and ecologists, competition is considered to include retardation of growth due to density increase in a population (HARPER, 1961). Geneticists, however, are not interested in any interaction among the individuals of the same genotype. According to the experiment on intergenotypic competition under different population densities (SAKAI, 1955), it is true that the competitive effect is apparently density-dependent, but it is understood that density merely accelerates the competitive pressure among the genotypes.

In this dispute, it is important to make clear if density response and competitive ability behave in the same way or not. Is the botanical mechanism responsible for density response the same as the botanical mechanism for intergenotypic competition?

In the present paper the results are given of a comparison between density response and competitive ability in barley. It was found from this study that the twelve cultivars were significantly variable with regard to either density response or competitive ability. Correlation coefficients between density response and competitive ability were not high enough to be regarded as significant, or apparently low especially in seed yield. Thus, we conclude from the present study that density response and competitive ability are rather different and are controlled by different genetic entities.

KIRA *et al.* (1953) derived a formula for growth of plants in a population. It is, $w = \frac{K}{D^b}$, and is called as "the competition-density effect" by them. They seem to hold a view that interplant competition and plant density are not separable from each other. What we see from the equation, however, is that it gives a relation between plant density and plant growth, that is, "the density effect", but involving no effect of competition.

Factors affecting the growth of plants in a population are considered to include: (1) genotypic effect; (2) environments, major; (3) environments, minor or due to chance; (4) developmental error or instability; (5) plant density; (6) intragenotypic competition; (7) intraspecific intergenotypic competition; (8) interspecific competition and interaction, and (9) migration.

The environments, major, are such that represent a certain conformation of soil fertility, soil moisture, micro-climatic or edaphic conditions in the area occupied by the population. The environments, minor, are those involved in causing error variation. Developmental instability which is the result of errors occurring during the development is found to be genotype-dependent. Some genotypes are very liable to show high instability in vegetative or reproductive characters while others are highly stable. The significance of developmental instability in plant evolution has been seldom discussed though it is most probably of great interest.

Intragenotypic competition is competition among plants of the same genotype. Plants growing in an isogenic population can be more or less different with regard to developmental rate due to chance or environmental variation. Differences in developmental rate might cause differences in the capacity for scramble for the common resources. Effect of this scramble, if any, however, has to be included in practice in error variation, and it may not have any consequence on the genetical destiny of the population.

It has been suggested that weakly competing genotypes can be freed from competitive pressure by emigrating from the habitat, if they are provided with higher migratory capacity (SAKAI, 1964).

Thus, it appears that factors important for genetic development of a plant population are, besides genotypic effects, plant density, intraspecific-intergenotypic competition, interspecific competition and interaction, and migration in combination

with intra- and interspecific competition. These factors are naturally genotype-dependent as exemplified by the fact that response to plant density and competitive ability are different characters controlled by different genes. Plants in a population may probably have been and still are subjected to those stresses. However, our knowledge of genetics of plant response against those stresses is too scanty at present to draw any definite conclusion.

Conclusion

From the descriptions given above, we are able to draw following conclusions:

(1) Response to density varied among the employed cultivars of barley and is accordingly considered to be under genetic control.

(2) Density response is expressed in both the vegetative and the reproductive phases. They are, however, not necessarily running parallel, i.e. they are not always correlated.

(3) Seed yield per plant generally increases in proportion to decrease in density to a certain extent, beyond which, however, it reaches a plateau.

(4) The rate of reaching a plateau in seed production is genotype dependent. Some cultivars reach the plateau even at a density at which others do not.

(5) Competitive ability measured in either vegetative or reproductive growth is again genotype-dependent as has often been evidenced. A competitive gain in vegetative growth is, however, not necessarily accompanied by that in reproductive growth as is the case in above mentioned density response.

(6) Density-response and competitive ability are considered to be different characters.

(7) Our results allow us to enumerate nine factors which we consider to affect the growth of plants in a population.

Summary

Using 12 cultivars of barley, density response was investigated at five levels of spacing, i.e. $2 \times 2 \text{ cm}^2$, $4 \times 4 \text{ cm}^2$, $8 \times 8 \text{ cm}^2$, $16 \times 16 \text{ cm}^2$ and $32 \times 32 \text{ cm}^2$ per plant. The characters examined were culm number, ear number, seed yield and plant weight. Decrease in plant density caused proportional increase in vegetative growth, that is culm number and ear number, but seed yield tended to reach a plateau when the spacing surpassed a certain spacing level though the critical density was different among genotypes. Density response in vegetative growth and that in reproductive capacity were not correlated.

Competitive ability of the same 12 cultivars was tested by a common test-variety. Comparison between competitive ability and density response showed that they were not found to be highly correlated, suggesting that they are different rather than the same traits.

Nine factors which are supposed to influence the growth of individual plants in a population are listed together with some considerations.

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動植物における競争の研究

XI. 大麦の競争力と密度反応

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大麦 12 品種を用いて栽植密度に対する反応と競争力との関係を明らかにした。栽植密度の実験は $2 \times 2 \text{ cm}^2$, $4 \times 4 \text{ cm}^2$, $8 \times 8 \text{ cm}^2$, $16 \times 16 \text{ cm}^2$, および $32 \times 32 \text{ cm}^2$ の 5 種の正方植で行い、株当り稈数、穂数、穂重および植物重を調査し、つぎのことが明かになった。栽植密度の減少とともに、稈数、穂数などの栄養的生育は増加するが、株当り穂重はある点から先は増加が止まる。この増加の止まる点はそれぞれの品種の遺伝子型によつて異なる。栄養的生育の密度反応と、繁殖能力のそれとは相関がない。競争力の実験では、検定品種「赤神力」に対し

て上記 12 品種の競争力を調べたところ、植物重、稈数、穂数に表われる競争力は品種間に有意な変異が認められた。

以上の二つの実験の結果に基づいて、競争力と密度反応を比較したところ、両者の間には相関がなかった。従来農学および生態学者の間にはしばしば競争と密度反応を混同する傾向が見られるが、この研究から両者はそれぞれ別個の植物学的特性として取扱う必要があることが示された。