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Genotype-Environment Interaction for Awn Development in Isogenic Lines of Barley

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Summary. Awn length of four isogenic lines of barley differing by two genes for awn development (A and B) and their short linkage blocks was evaluated at a wide range of plant densities (0.002 to 3.345 m²/plant) for two years. Awn development was reduced at high plant density. The quarter-awned genotype ($aaBB$) became phenotypically awnless ($aabb$) at high plant density. Similar results were obtained each year and the genotype x plant density effect was the major portion of the genotype-environment interaction variance. Additive (α_A, α_B) and additive x additive (α_{AB}) gene effects were computed for each plant density for lateral and central floret awn length. For lateral awns α_{AB} was not affected, but α_A and α_B increased with decreased plant density. In contrast, for central awns α_A and α_{AB} decreased and α_B increased with decreased plant density.

Central floret awns measured at each spike node showed that high plant density reduced awn development most in the lower half of the spike. This is the zone of most rapid awn differentiation and since culm elongation and spike growth rates were greatly increased by high plant density, it was suggested that rapid growth invoked a stress on awn development and differentially altered the expression of A and B.

Introduction

Differential genotype response to environmental changes is an important characteristic of plant, and to a lesser extent, animal populations. Progress from selection on either population or individual performance is influenced by the presence of genotype-environment interactions. Considerable attention has been given to the analysis of genotype-environment interactions in plants (ALLARD and BRADSHAW 1964; MATZINGER 1963; GARDNER 1963); however, in most instances the characters studied were governed by many genes with small effects. Such characters were evaluated because of economic importance or ease of measurement. Simply inherited characters have not been used a great deal because changes in character expression are not usually subject to modification by environmental influences and a measurement scale is not conveniently available. Clearly, the use of characters governed by genes with large, but quantitative, phenotypic effects is advantageous because environmental effects can be readily defined and measured; furthermore, the environment can be modified experimentally by chemical and physical means to induce the interaction effects. However, a uniform genetic background is necessary to avoid complications from variation in other characters. With plants, such uniformity is obtained with isogenic lines derived by mutation or through enforced heterozygosity by backcrossing or self-fertilization.

The awn of barley (*Hordeum vulgare* L.) is a linear extension of the lemma of the floret and its development is conditioned by several genes (reviewed by SMITH 1951; NILAN 1964). At least two dominant genes are required for long awn development. Several physiological functions of the awn are known; the most notable is photosynthesis which contributes carbohydrates to the developing seed (GRUNDBACHER 1963). The awn phenotype is suitable for experimental study of environmental modifications because (1) several phenotypic expressions are produced with various combinations of known genes, (2) the development of the awn is less complicated than for many characters (BONNETT 1966; STEBBINS and YAGIL 1966), (3) the character is repetitive on each spike and many spikes may be produced on each plant, and (4) the length of the awn can be accurately measured during development and, after growth is completed, its developmental history can be charted by noting its position on the spike.

Variation in awn length due to temperature, soil moisture, and nutritional effects has been noted (ENGLEDOW 1924; HUBER 1931; SCHULTE 1955). WOODWARD and RASMUSSON (1957) found that awn development was influenced by genes for dwarfness and spike density. In the present study isogenic lines differing by two genes (Lk and Lk_1, referred to as A and B here) for awn development were utilized. The isogenic lines were derived by backcrossing and selection so that the expected length of the linkage blocks associated with each locus is 5.6 crossover units. The isogenic lines were subjected to a wide range of environmental conditions in a two-year plant density study. Variation in plant density resulted in large differences in tiller number, plant height, seed size, and other characters (QUALSET, SCHALLER, and WILLIAMS 1965). It was the purpose of this study to investigate environmental effects on the quantitative action of the two genes, A and B, in isogenic materials and to illustrate the use of isogenic lines in the study of genotype-environment interactions.

Materials and Methods

The isogenic lines: The awnless variety, C. I.5631, was used to introduce awnlessness by backcrossing into 'Atlas', a fully-awned type. MYLER (1942) found that two genes conditioned awn length and that the four homozygous types were phenotypically distinguishable:

'Full-awned' ($AABB$), long awns on lateral and central florets

'Half-awned' ($AAbb$), short awns on lateral and central florets

'Quarter-awned' (*aaBB*), awnless or very short awns on lateral and short awns on central florets
'Awnless' (*aabb*), awnless lateral florets and very short awns on central florets.

Seven backross and 16 selfing generations were used to develop the four isogenic lines. Selection for awnlessness and Atlas plant type was done for four or five generations after each backcross cycle. The derived awnless type was crossed with Atlas to initiate a new cycle. The four awn-type genotypes were extracted in the F_3 generation after the last backcross. Further details of the breeding history of these lines and illustrations of the phenotypes were given previously (QUALSET *et al.* 1965).

Experimental design: The four isogenic lines were grown in a split-plot field experiment for two years at Davis, California. Main plots were plant densities of 0.002, 0.023, 0.093, 1.486, and 3.345 m^2/plant and subplots were the four isogenic lines. These plant densities are equivalent to 0.1, 0.5, 1.0, 4.0, and 6.0 ft^2/plant. Three replications of 4-row plots 4.9 m long were used in the first year and four replications of 4-row plots 9.8 m long were used in the second year. The distance between rows was 30.5 cm for the first three and 61.0 cm for the last two plant densities listed above.

Measurement of awn length: Ten spikes were taken at random from each plot in the first year and five in the second year. All unbroken awns on one row each of lateral and central florets were measured. The measurements were made in sequence from the base to the apex of the spike so that awn length could be related to its nodal position on the spike. Since the number of nodes per spike was variable, the center of the spike was taken as point of reference (labeled node 1). This labeling system also relates to the developmental sequence because floret differentiation begins in the center of the spike primordium (BONNETT 1966). A detailed analysis of awn length by nodes was done in the first year only and was based on a maximum of 30 spikes for each node. A second measure of awn length, called mean awn length, is the mean length of awns of either lateral or central florets for all nodes on the spike. This was computed in both years.

Statistical analyses: Genotype-environmental interaction components of variance were computed from expectations of mean squares from a standard split plot analysis of variance. The analyses were performed on plot means. Orthogonal coefficients for the regression of awn length on plant density were calculated by the method of CARMER and SEIF (1963) for unequally spaced treatments. Additive (α_A, α_B) and additive × additive (α_{AB}) interaction effects were estimated from orthogonal comparisons among the four isogenic lines. These comparisons were given previously by QUALSET *et al.* (1965) but are presented here for reference:

$$\alpha_A = (AABB + AAbb - aaBB - aabb)/4$$
$$\alpha_B = (AABB + aaBB - AAbb - aabb)/4$$
$$\alpha_{AB} = (AABB + aabb - AAbb - aaBB)/4$$

The genotypic symbols refer to means for all replications, either for a node or for the whole spike. The α_i effects are regression coefficients and the mean square used for tests of significance is $4\alpha_i^2$.

Results

Modification of awn length: As the space available per plant was decreased, awn development was reduced for both lateral and central florets in all genotypes (Figure 1). The decrease in awn length, as related to increased plant density, was curvilinear (Table 1) and became essentially linear on the logarithmic scale as in Figure 1. Differential response of the genotypes to changes in plant density was evident in Figure 1 and by the significance of the genotype × plant density interaction in Table 1. This was most obvious for Quarter-awned in which the slope for the reduction of awn length was much greater than for the other genotypes. In fact, Quarter-awned became phenotypically awnless at high plant densities (Figure 2) and could not be distinguished from Awnless.

The analysis of awn length by nodes for central florets showed that the greatest awn development was in the lower one-half of the spike (Figures 3 and 4) and that the effect of plant density on awn development was not the same throughout the length of the spike. This is borne out in the analyses of variance in Table 2 where the nodes × plant density inter-

Table 1. *Mean squares and estimated variance components for lateral and central floret awn length of isogenic lines in a two-year plant density study*

Source of variation	Degrees of freedom	Mean square		Variance component		
		Lateral	Central	Lateral		Central
Years (Y)	1	4.23**	27.16**			
Reps in Y	5	0.17	0.08			
Plant densities (D)	4	4.87**	19.79**			
Linear	1	16.16**	63.38**			
Quadratic	1	2.13**	11.54**			
Remainder	2	0.59	2.11*			
$D \times Y$	4	0.51	0.91			
Linear × Y	1	1.15*	2.52*			
Quadratic × Y	1	0.53	0.67			
Remainder × Y	2	0.17	0.23			
Error a	20	0.22	0.46			
Genotypes (G)	3	854.01**	957.59**	σ^2_g	24.88	27.83
$G \times Y$	3	0.73**	2.90**	σ^2_{gy}	0.03	0.16
$G \times D$	12	1.28**	1.60**	σ^2_{gd}	0.17	0.21
$G \times D \times Y$	12	0.11	0.13	σ^2_{gdy}	−0.01	−0.02
Error b	75	0.15	0.20	σ^2	0.15	0.20

* $.01 < P < .05$. — ** $P < .01$.

Table 2. *Mean squares for central awn length by nodes for four isogenic lines at five plant densities*

Source of variation	Degrees of freedom	Full-awned	Half-awned	Quarter-awned	Awnless
Replications	2	3.18	1.38	2.70	1.98
Densities	4	25.57*	16.36+	54.27**	4.42*
Error a	8	4.75	5.32	2.48	0.99
Nodes	10	71.15**	22.98**	8.55**	0.98**
Nodes × densities	40	1.03**	0.38**	0.55**	0.12**
Error b	100	0.55	0.15	0.12	0.04

+ $.05 < P < .10$, * $.01 < P < .05$, ** $P < .01$.

action was significant for all genotypes. The plant density effect for Half-awned (Figure 3) was not as large as for the other genotypes; this can also be seen for mean awn length in Figure 1.

For Full-awned and Half-awned the greatest reduction in awn development occurred at nodes on the lower one-third of the spike (Figure 3) and was minimal near the apex of the spike. The lower one-third of the spike was also most strongly affected for Quarter-awned and Awnless but the awn length of upper one-third was reduced relatively more for these two genotypes than for Full- and Half-awned. The difference in awn length for the two extreme plant densities for Quarter-awned (4.0 cm) was similar to the reduction observed for Full-awned even though its potential awn development was only one-sixth as much. The awn length analysis by nodes indicated that Quarter-awned had the greatest sensitivity to variation in plant density.

Components of phenotypic variance: The specificity of genotype response to variation in plant density was indicated by the relative size of the components of the phenotypic variance (Table 1). As expected, the variance among genotypes (σ_g^2) was the major component of variance for awn length. The genotype × plant density and genotype × year variance components were significant, but the second order

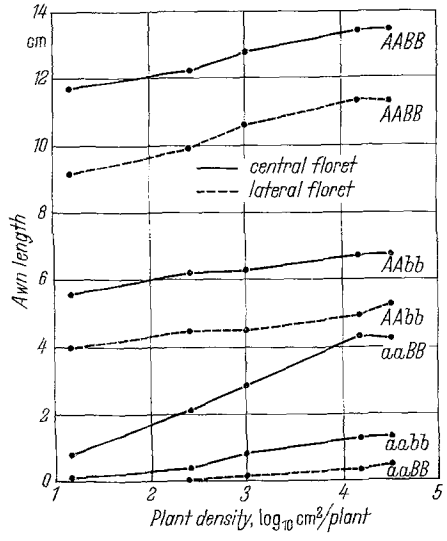

Fig. 1. Mean lateral and central awn length of four isogenic lines of barley as affected by plant density

Fig. 2. Awn development of Quarter-awned (*aaBB*) at five plant densities. From left: 3.345, 1.486, 0.093, 0.023, and 0.002 m² per plant

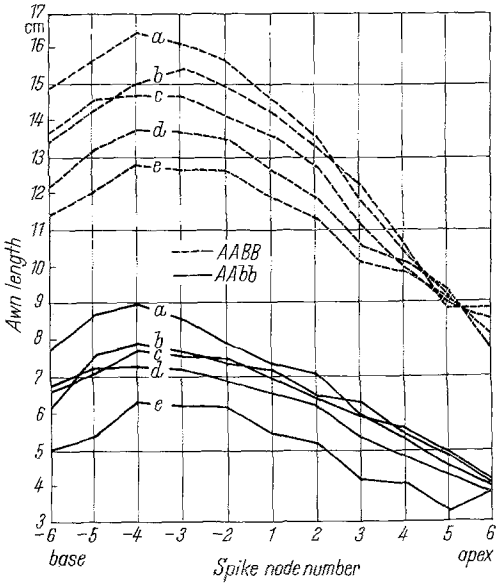

Fig. 3. Length of central awns of Full-awned (*AABB*) and Half-awned (*AAbb*) for each node at five plant densities. $a = 3.345$, $b = 1.486$, $c = 0.093$, $d = 0.023$, $e = 0.002$ m² per plant

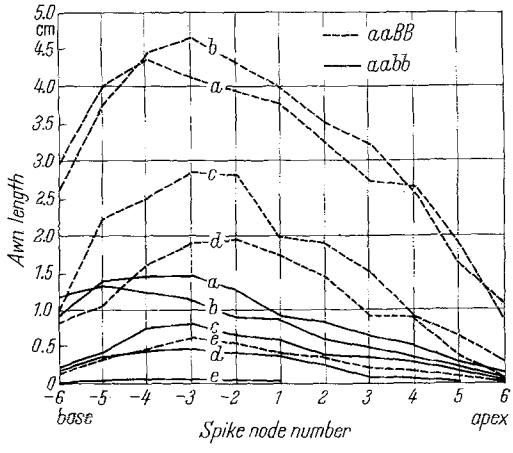

Fig. 4. Length of central awns of Quarter-awned (*aaBB*) and Awnless (*aabb*) for each node at five plant densities (see Figure 3 for plant density code)

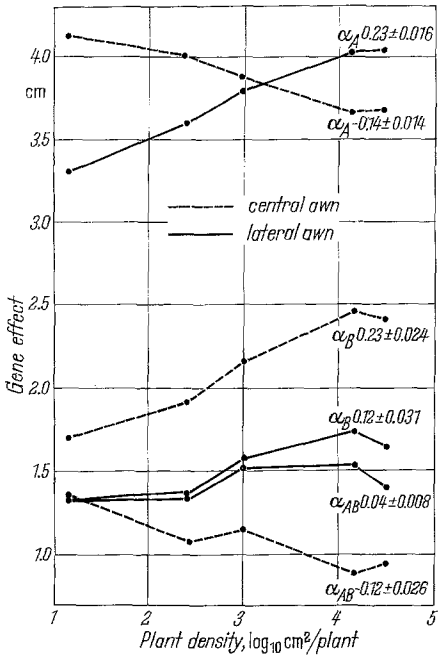

Fig. 5. Additive (α_A, α_B) and additive $\times$ additive (α_{AB}) gene effects for mean lateral and central awn length with linear regression coefficient on log plant density

Table 3. *Mean squares for partition of genotypic and genotype $\times$ plant density variance for lateral and central floret awn length. Tests of significance based on error terms in Table 1*

Source of variation	Degrees of freedom	Mean square	
		Lateral	Central
Partition of genotypic variance			
Additive A (α_A)	1	1955.65**	2080.31**
Additive B (α_B)	1	325.43**	629.26**
Add. A $\times$ add. B (α_{AB})	1	280.96**	163.19**
Partition of genotype $\times$ plant density variance			
α_A $\times$ densities (D)	4	2.78**	1.02**
α_A $\times$ D linear	1	8.02**	3.37**
α_A $\times$ D quadratic	1	1.40**	0.78
α_A $\times$ D remainder	2	0.88**	0.07
α_B $\times$ D	4	0.98**	2.86**
α_B $\times$ D linear	1	2.39**	8.52**
α_B $\times$ D quadratic	1	1.04**	2.12**
α_B $\times$ D remainder	2	0.24	0.40
α_{AB} $\times$ D	4	0.28	0.80**
α_{AB} $\times$ D linear	1	0.14	2.33**
α_{AB} $\times$ D quadratic	1	0.64*	0.62
α_{AB} $\times$ D remainder	2	0.18	0.12

* $.01 < P < .05$. — ** $P < .01$.

interaction σ^2_{gdy} was not; however, for several other characters σ^2_{gdy} was sizable (QUALSET *et al.* 1965). σ^2_{gd} was 85 and 57 percent of the genotype-environment variance for lateral and central awns, respectively, and thus made the primary contribution to the genotype-environment interaction.

Environmental influence on gene effects: For mean awn length and for each node, comparisons among the four genotypes indicated that the A locus had the greatest additive effect (α_A) on development of both lateral and central awns (Figures 5 and 6). The additive effect of the B locus (α_B) was more important

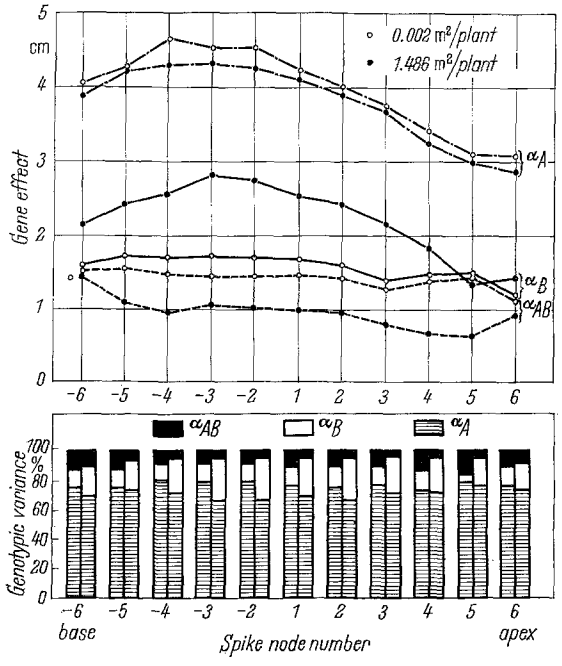

Fig. 6. Upper: α_A, α_B, and α_{AB} gene effects for central awns at each node at two plant densities. Lower: Proportion of genotypic variance attributed to α_A, α_B, and α_{AB} for each node; 0.002 and 1.486 m² per plant for left and right bars, respectively

than the additive A $\times$ additive B interaction (α_{AB}) for central awns and was about equal to α_{AB} for lateral awns.

The σ^2_{gd} variance component was further partitioned as given in Table 3. This subdivision indicated that α_A and α_B interacted with plant density for both lateral and central awns and that α_{AB} $\times$ density was significant only for central awns. The nature of these interactions can be seen from the second subdivision where the α_i effects were related to plant density on the original measurement scale (m²/plant). The linear and quadratic interactions accounted for nearly all of the gene effect $\times$ density interaction. Transformation to plant density on the logarithmic scale resulted in a linear relationship of the gene effects to plant density and in Figure 5 the interaction of gene effects with plant density can be seen clearly. The analysis at the highest density (0.002 m²/plant) indicated that α_B and α_{AB} was 13.4 and 8.3 percent of the total variance for central awns, whereas at the lowest density (3.345 m²/plant) these effects were 28.5 and 4.4 percent, respectively. α_A and α_{AB} decreased and α_B increased as the space per plant was increased for central awns. Similar relationships for lateral awns can be seen in Figure 5 and the variation in the sign of the regression coefficients shows that plant density affected the action of the A and B loci in quite different ways.

The analysis of gene effects for central awns at each node showed the same curvilinear relationship to plant density as found for the average awn length, but the data are presented only for the two extreme plant densities (Figure 6). The α_A effect was slightly smaller at the low plant density which resulted in maximum awn development. In contrast, α_B was greatly affected by plant density and its maximum occurred at low plant density. The shape of the curve for α_B was different at these two plant densities. The epistatic interaction effect, α_{AB}, was about the

same throughout the length of the spike, but was smaller at low plant density. The relative variances (Figure 6) indicated that α_B and α_{AB} were similar at high density, but α_B was 5.0 times larger at low plant density. The results for average awn and for each node show that the α_B effect was more greatly modified by environment than α_A and α_{AB}. The effect of plant density was greatest in the lower one-half of the spike for α_A and α_B and at both ends of the spike for α_{AB}.

Discussion

Isogenic Analysis

Isogenic lines differing mainly for genes affecting qualitative characters and their associated linkage blocks are useful in three basic types of genetic analyses: (1) for developmental or biochemical study of character expression and gene action, (2) quantitative genetic study of the character itself, and (3) for assay of quantitative genetic variability in short segments of chromosome marked by the genes governing qualitative characters. In each type of analysis genotype-environment interaction can be evaluated and is important to the interpretation of genetic parameters. This was well illustrated in the present study where relative gene effects were greatly affected by plant density.

Since isogenic lines provide a model situation for the evaluation of quantitative genetic parameters, it is useful to point out the general features of the present results. Genetic variation was present for two unlinked loci, each with two alleles, which had large phenotypic effects on awn development. Since most quantitative characters are governed by many genes with small effects, this represents an oversimplification of usual genetic populations. However, the fact that the *A* and *B* loci had unequal effects and were modifiable by environment to the extent that *aaBB* became phenotypically *aabb* qualifies these loci as suitable for quantitative genetic study. Background genetic variation for the character studied was minimal which was important for the study of modification of phenotypic expression, but not a particularly desirable feature in attempting to relate these results to selection response for fitness characters where genetic variability is commonly present. Small, but significant, amounts of genetic variation for other characters is generally found associated with linkage blocks marked by the major genes (FASOULAS and ALLARD 1962; QUALSET *et al.* 1965; QUALSET and SCHALLER 1966).

Since only homozygotes for the two loci were studied, dominance and dominance epistatic interaction effects could not be evaluated. Some results (e. g. MATZINGER 1963) have indicated that epistatic effects are more subject to genotype-environment interaction than additive or dominance effects. In the present study α_{AB} was not greatly affected by plant density or the position of the awn on the spike. This result is perhaps a function of the awn character which is basically more stable than many quantitative characters. The use of heterozygotes is a necessary and simple refinement for the study of quantitative gene action with isogenic lines. An analysis of gene effects for awn length using heterozygotes, but not accounting for genotype-environment interaction, will be presented elsewhere. Equal gene and genotype frequencies and viabilities were attained because the four genotypes were identifiable. This is a major advantage of isogenic materials and by the use of mixtures of various genotypes frequency dependency and fitness values can be estimated for each locus.

Plant densities introduced systematic variation in the environmental effects while years introduced a random, but relatively unimportant, element. Appropriate systematic variation of environmental variables can induce differential genotype response that is only rarely identified and analyzed in random experiments such as stratification with years or sites. Genotype performance can then be studied as a response surface which might be less subject to sampling error than the variance component approach. Additionally, causal relationships can be inferred and factors responsible for the interaction can be identified.

Awn Development

During spike development the awn grows very rapidly, up to 2 cm per day was observed by WIJEWANTHA and STEBBINS (1964). In the analysis of awn length by nodes presented here it was found that the longest awns were produced in the middle or lower one-third of the spike. This is also known to be the zone of most rapid differentiation (BONNETT 1966; NICHOLLS and MAY 1963; WIJEWANTHA and STEBBINS 1964). Furthermore, awn development was reduced more in this portion of the spike than other parts at high plant density. Plants grown at high densities differentiate spikes having approximately the same length as plants grown at low densities, but culm elongation occurs much more rapidly than at low density and fewer floret primordia complete differentiation. At high plant density rapid growth during culm elongation may result in intraplant competition for nutrients and thus reduce awn development.

It is apparent that conditions which promote rapid differentiation cause a reduction in awn development. In studies of moisture stress on plant development ASPINALL, NICHOLLS, and MAY (1964) and WILLIAMS and SHAPTER (1955) found that the organ growing most rapidly during a period of stress is most greatly modified. This was observed here where plant density influenced growth rate and invoked a stress during awn development. The reduction in awn development observed by other workers (ENGLEDOW 1924; HUBER 1931; SCHULTE 1955) occurred as a response to soil moisture stress and other conditions which affected growth rate. Their observations are compatible with the suggestion that conditions conducive to rapid growth cause a reduction in awn development.

Zusammenfassung

An 4 isogenen Gerstenlinien, die sich durch zwei Gene für Grannenbildung (*A* und *B*) und entsprechende kurze Kopplungsblocks unterscheiden, wurde zwei Jahre lang die Länge der Grannen bei verschiedener Standdichte (0,002 bis 3,345 m² je Pflanze) untersucht. Bei dichtem Bestand ergab sich eine Beeinträchtigung der Grannenbildung, der viertel-

begrannte Genotyp (*aaBB*) wurde phänotypisch grannenlos (*aabb*). Die Ergebnisse stimmten in beiden Jahren überein, der Effekt Genotyp × Standdichte hatte den Hauptanteil an der Interaktionsvarianz Genotyp:Umwelt. Additive (α_A, α_B) und additive × additive (α_{AB}) Genwirkungen wurden bei jeder Standdichte für die Grannenlänge der Seiten- und Mittelährchen errechnet. Bei den seitlichen Grannen wurde α_{AB} nicht beeinflußt, aber α_A und α_B erhöhten sich mit abnehmender Standdichte. Im Gegensatz dazu gingen bei den mittleren Grannen α_A und α_{AB} zurück, während für α_B bei abnehmender Standdichte ein Ansteigen festzustellen war.

Messungen der mittleren Grannen jeder Ähre zeigten, daß hohe Standdichte der Pflanzen die Grannenbildung am meisten in der unteren Hälfte der Ähre reduzierte. Das ist die Zone, in der sich die Grannen am schnellsten differenzieren, und da die Halm- und Ährenwachstumsraten durch hohe Standdichte stark gesteigert wurden, scheint das schnelle Wachstum auf die Grannenentwicklung hemmend einzuwirken und die Manifestierung von *A* und *B* unterschiedlich abzuändern.

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