DOMINANCE AS FUNCTION OF WITHIN ORGANISM
ENVIRONMENT IN KERNEL-ROW NUMBER
IN MAIZE (*ZEA MAYS* L.)¹

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DOMINANCE was one of the leading observations of MENDEL and, as such, has become of first importance to genetic teaching and research. It is invoked as an explanation of hybrid vigor. It is utilized and maligned in the inheritance of all forms, particularly man, with ideas of penetrance, expressivity, etc. Most geneticists have formed a mental concept for the term, but few have tested theories covering the vital reactions by which dominance is accomplished. Worthwhile theories which have come from these attempts largely relate to one gene, one primary function reacting system. Genes affecting single chemical synthesis within the organism, *i.e.*, man, *Drosophila*, or *Neurospora*, have been shown to act on particular groups through a single chemical bond, each bond generally requiring a specific gene. If the gene mutates to an inactive allele, or is lost, the reaction will not take place. This specificity has led to a "do" concept for the dominant allele and a "do not do" for the recessive allele. In theory the effects of this specificity carry through the whole organism. This concept breaks down somewhat in considering an allelic series where the successive members of the series show graded reactions and seemingly require graded gene products.

But dominance has other possibilities. It may play a prominent part in the enigma of embryonic differentiation wherein the organism is molded into the form characteristic of its species and strain, from an apparently undifferentiated zygote. The significance of this theory becomes clear in investigations of the genetics of kernel-row number in maize. The discussion to follow deals with this problem.

Investigations in the nature of inheritance of kernel-row number in maize have generally indicated that kernel-row number is a polygenic characteristic (EMERSON and EAST 1913; LINDSTROM 1931). (The term polygenic as used here is synonymous with the lengthier term multiple-gene-determined.) This information was based on genetic analysis of lines with eight or more kernel-rows.

TAVCAR (1935) reported a true breeding four-rowed corn variety out of a red flint type. In crosses of four- by eight-rowed types he obtained, for the

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most part, hybrids which had eight rows on the base of the ear and four rows at the tip. Pictures show that in his material the shift from eight to four rows is clear-cut with two bilaterally opposed rows of alicoles dropping out to leave a four-rowed tip. His segregating material led him to postulate a two-gene hypothesis for row number inheritance between four and eight rows.

A different four-rowed line from the one used by TAVCAR (1935) was isolated from Golden Bantam and inbred by the late DR. E. W. LINDSTROM. This line was so different in appearance and origin from TAVCAR's line that a study of its genetic make-up with respect to row number was undertaken. Crosses of this four-rowed line with eight-, twelve-, and fourteen-rowed types are reported together with linkage tests between row number genes and several marker genes.

To improve the observations further, a greenhouse experiment was conducted in which the attempt was made to induce all the differentiated ear meristems of the plant to develop so that the row numbers of the ears at the various nodes could be determined. This material is pertinent to the problem of dominance and ontogeny.

MATERIALS AND METHODS

These studies may be divided into two phases. The first was conducted in the field in 1946 and the second in the greenhouse in 1947.

Field: The inbred lines of corn used with their gene designations were:

White Flint	WF 8- <i>y-p-Su</i>
Yellow Dent	Idt 14- <i>Y-Pr-Su</i>
Yellow Dent	Osf 12- <i>Y-Pr-Su</i>
Four-row Sweet	4- <i>Y-p-su</i>

Arabic numbers indicate the modal number of kernel-rows characteristic of the line. *Y* is the sixth chromosome gene for yellow (*Y*) or white (*y*) endosperm color. *Pr* is a member of the multiple allelic series of cob and pericarp color-pattern genes on the first chromosome, *Pr* being red cob, and *p*, white cob. *Su* is the fourth chromosome gene for endosperm texture; starchy (*Su*) versus sugary (*su*).

These lines are material of the GENETICS SECTION, IOWA AGRICULTURAL EXPERIMENT STATION, which were inbred and maintained by the late DR. E. W. LINDSTROM and his staff. WF is a long-time inbred out of White Flint. Idt is a field dent line out of the variety, Iodent. Osf came from Osterland's Reid. The 4-*Y-p-su* line is a four-rowed variant isolated from Golden Bantam and inbred.

The eight-, twelve-, and fourteen-rowed lines were crossed with 4-*Y-p-su* and the F_1 's either selfed or backcrossed to the four-rowed parent. All references to backcrosses are to this type unless otherwise specified.

The F_2 and backcross generations of these three crosses along with the parents were grown in the field during the summer of 1946. The mature, open pollinated top ears were harvested in the fall and evaluation was made of kernel-row number and genotype with respect to the marker genes. It was

impossible to determine heterozygous Yy and $Susu$ plants by observing segregation in the open-pollinated ears.

Kernel-row number classification was made in classes numbered continuously from four through sixteen, the odd numbers indicating intermediates. Row number data taken in the field were analyzed by means of a t -test (SNEDECOR 1946) on the difference between the mean row number associated with each qualitative gene pair.

Greenhouse: Two different lines were used in greenhouse studies along with $4-Y-p-su$:

Hickory King	HK $8-y-p-Su$
Yellow Flint	$8-Y-Pr-Su$

HK is an inbred out of the flint variety, Hickory King. The $8-Y-Pr-Su$ line is a "synthetic" inbred, maintained in part for its unusual combination of low row number and red cob.

Five groups were planted in the greenhouse: (1) $4-Y-p-su$, (2) Hickory King, (3) $(4-Y-p-su \times HK) F_1$, (4) $(4-Y-p-su \times 8-Y-Pr-Su) F_2$, and (5) the backcross $(4-Y-p-su \times 8-Y-Pr-Su) F_1 \times 4-Y-p-su$.

The greenhouse experiment was planted on January 5, 1947, using $2\frac{1}{2}$ -inch pots, later transplanting to six-inch pots in a "randomized block" design with four replications.

A photoperiod of daily decreasing length was provided for the first twenty days and thereafter, with the seasonal increasing photoperiod.

Date of anthesis (numerical day of the year) was recorded for each plant, daily at 1700 hours, and at the same time the tassel was removed. By limiting the amount of pollination, the lower ears were induced to develop.

DOMINANCE

The F_1 generation and both parents from the cross $HK\ 8-y-p-Su \times 4-Y-p-su$ were grown in the greenhouse. The data from this material consisted, in part, of the row number of each potential ear on the plant. Most plants were induced to differentiate from four to six ears.

Figure 1 shows the mean kernel-row number for each ear position, 1 being closest to the ground level, in the parents and the F_1 (data in table 1).

General observations made under field conditions where but one or two ears developed, have led to the conclusion that the eight-rowed condition is dominant over the four. This observation is based on row number determinations of the top ear, the one which usually develops. Figure 1 shows that under conditions of the greenhouse experiment, dominance depends on ear position within the plant. The top ears of F_1 's, developing under the most favorable physiological conditions, are primarily eight-rowed. The lower ears, which initiate row number later (HERSHEY 1934) under different conditions, are usually fours.

The data of table 1 presented in figure 1 show the within plant variation in F_1 is much greater than within plant variation in either of the parents. The inbred parental line used as the low row number parent varied from

FIGURE 1.—Mean kernel row number at various positions on the plant. HK 8-y-Su $\times$ 4-Y-su, parents and F₁.

4.00–4.40 to 4.86, the 4.00 average being out of the trend shown by the whole data. The trend showed a distinct effect of ear position above ground on the ear row number, the higher the position, the larger the average row number. The variation was from possibly 0.5 to 0.9 of a row. The inbred line used as high parent had row numbers which also varied with height of ear from the ground, 6.14 at the lowest position to 7.12 at the highest. The row numbers increased with distance of the ears from the ground. Judged from the trend,

TABLE 1
Mean kernel-row number of ears at various positions on the plant.
(See fig. 1)

		Position above ground level					
		1	2	3	4	5	6
HK 8-y-p-Su	n	101	101	95	66	20	2
	$\bar{x}$	6.14	6.95	7.03	7.12	6.50	7.00
4-Y-p-su	n	119	118	113	49	3	
	$\bar{x}$	4.40	4.58	4.78	4.86	4.00	
(HK 8-y-p-Su $\times$ 4-Y-p-su)F ₁	n	116	115	113	88	44	9
	$\bar{x}$	4.43	4.68	5.45	6.10	6.64	6.89

the average difference from the lowest ear to the highest would be not more than half a row number. The F_1 row numbers showed much greater variations. The ears varied from the row number of the lowest parent to that for the highest parent. The F_1 's expressed the possible row numbers of *both parents*. The change in row number of the F_1 was essentially linear with the position of ear above ground. The variation observed was more than four times that of either inbred parent line. This effect is the expression of the heterozygosity of the row number genes which we call dominance. A greater range of potential response is open to the hybrid than to homozygous or approximately homozygous plants. The various ears in the above ground positions are differentiated at different times, in basipetal succession according to HERSHEY (1934). The various physiological balances (the environment in which genes produce their effects) change as the plant grows; the ratio of soluble and condensed carbohydrates to soluble and condensed amino acids is a case-in-point. Since parents and F_1 were grown side-by-side under presumably the same external environmental conditions, the response of the F_1 is a function of the genetic environment. The parents were essentially homozygous and the F_1 is heterozygous, at least for the genes determining four and eight kernel-rows. Heterozygotes are more variable than homozygotes on a within plant basis. If a greater response potential is a usual property of hybrids, it could account for hybrid vigor. By being physiologically more adaptable, the hybrid would flourish under conditions that would only sustain homozygotes.

This basipetal decrease in kernel-row number has been observed by the author in other, higher row number material to such an extent that it appears to be the general rule. CUTLER and CUTLER (1948) have called attention to the fact that a decrease in kernel-row number toward the base of the plant can be observed in a wide range of row number types.

The apparent dominance of the eight-rowed condition in the (8×4) F_1 is governed by the physiology of the plant in a relatively advanced stage of growth (HERSHEY 1934). This may mean that, even though row number is genetically determined by one or two major genes, progressive dominance changes throughout the plant have considerable effect. This case is particularly favorable for showing how dominance may act.

These data have importance to the developmental mechanics of the unfolding organism. The F_1 individuals show that the different parts of the plant are not alike. The chemical systems within the cells which form these different parts give precedence to the effects of one genome in one place, the other genome in another and something in between in other locations. This fact is significant to any consideration of ontogeny.

The corn row number is particularly favorable material to bring out this effect, but there is reason to think it may be quite general. The gradients do not have to be linear along the body length. ALLEN (1914) pointed out that spotting of coat color in mammals and birds shows high centers of activity irregularly distributed over the body. These centers suggest the dominance of

TABLE 2

Percent frequency of four- and eight-rowed plants in segregating generations of two hybrids.

Cross	Generation	4-row	8-row	Number of plants	χ^2 (1:3) (9:7)
WF 8-y-p-su $\times$ 4-Y-p-su (field)	BC**	68.1	31.9	229	5.76*
	F ₂	49.6	51.4	558	4.52*
8-Y-Pr-su $\times$ 4-Y-p-su (greenhouse)	BC	76.1	23.9	117	0.07
	F ₂	42.7	57.3	178	0.09

* Significant, 5% level.

** Backcrosses are all to 4-Y-p-su line.

one allele in one area, that of the other allele in another area. The reacting system gains clarity in the corn case by the ordering of the dominance effects of the two genomes, but this ordering may be accidental.

Gene basis for the row numbers

The number of genes involved in the row number inheritance come into consideration when the segregates of F₂ and backcrosses are considered. The case studied to date is the limiting one of the kernel row number of the top ear.

Number of genes

Several investigators have postulated the polygenic nature of kernel-row number inheritance (EMERSON and EAST 1913; LINDSTROM 1931). With the four-rowed material used in this investigation, however, there was a suspicion that a single major gene might determine the threshold between four and eight kernel-rows.

Table 2 shows the frequency of four- and eight-rowed plants in various segregating generations. The grouping of the intermediates between four and eight was made on the basis of the row number distributions of field-grown parent populations (fig. 5). Here it was noted that the 4-Y-p-su parent gave a relatively high percentage of intermediates (row number class 5 and 6) and the eight-rowed parent gave relatively few (table 3). The percentage of intermediates in backcross and F₂ generations is essentially the same as in the

TABLE 3

*Percent frequency of row number classes in four- and eight-rowed parents.
(See also fig. 5)*

Parent	Row number class						
	4	5	6	7	8	9	10
4-Y-p-su	64.1	26.9	9.0	0.0	0.0	0.0	0.0
WF 8-y-p-su	2.4	8.5	3.7	0.0	82.9	2.4	0.0

four-rowed parent. It seems reasonable, therefore, to group these intermediates with the fours, and the seven class, with the eights.

With this grouping (table 2), a remarkably good fit to a 9:7 F_2 (1:3 BC) ratio is observed in the greenhouse material (two genes, both dominant with complementary action). A rather poor fit to this ratio is evident in the field study. However, these two crosses involve different eight-rowed parents and the segregation populations were grown under widely different conditions (greenhouse and field). This suggests alternative explanations for the fact that the data do not agree. The possibility exists that the modifier backgrounds differ sufficiently to cause the dissimilar frequencies of the two ear types among the segregates. On the other hand, these eight-rowed parents may carry different genes for the eight-rowed condition. It is evident, at least, that the number of genes involved is small.

Linkage relations of row number genes with certain qualitative genes

The F_2 and backcross generations of three different inbred crosses to the 4- $Y-p-su$ line were grown in the field in the summer of 1946, along with the four parents involved. These crosses were:

$$\begin{aligned} &WF\ 8-y-p-Su \times 4-Y-p-su \\ &Idt\ 14-Y-P^r-Su \times 4-Y-p-su \\ &Osf\ 12-Y-P^r-Su \times 4-Y-p-su \end{aligned}$$

Interest centered about testing for linkage of row number genes with the P , Y , and Su linkage groups. LINDSTROM (1931) has reported strong indications of linkage with the P -locus when eight-, ten-, twelve-, and fourteen-rowed lines are intercrossed.

The data on linkage are presented in table 4. In no instance were the monogenic ratios out of the range of expectation. Reference has been made under "Material and Methods" to the system of estimating row number and the grouping used. Error from this source was considered less using the t-test than with a $2 \times n$ contingency table of χ^2 . However, there was quite good agreement between the probability values for χ^2 and the t-probabilities shown in table 4.

Backcross and F_2 data were obtained from three different crosses as shown in the table. The mean kernel-row number associated with each allele of the segregating genes is given and the standard error of the differences in these mean kernel-row numbers is calculated. The significance of these differences is indicated as well as the "direction" of association. A minus "direction" indicates greater non-parental association between row number and the qualitative gene and a plus "direction" reflects greater parental association. For instance, in the cross $WF\ 8-y-p-Su \times 4-Y-p-su$ high row number and Su are associated in the parents, while in the F_2 high row number is associated with su which is a non-parental combination.

In the instances where the non-parental class exceeds the parental ($WF\ 8-y-p-Su \times 4-Y-p-su$) and the difference is significant, no well founded explanation is available for the reversal of linkage, consequently, any elaboration

TABLE 4
t-test for detection of linkage between kernel-row number genes
 and *Y*, *P*, and *Su* linkage groups.

Cross	Generation and number of plants	Geno- type	Mean row number	Difference between means	P t-test	Direction ¹
WF 8- <i>y-p-Su</i> × 4- <i>Y-p-su</i>	558-F ₂	<i>Y</i>	6.66	0.42 ± .212	.05	—*
		<i>y</i>	6.24			
		<i>Su</i>	5.46	1.41 ± .202	.01	—**
		<i>su</i>	6.87			
	225-BC	<i>Y</i>	5.88	0.47 ± .226	.05	—*
		<i>y</i>	5.41			
		<i>Su</i>	5.61	.04		—
		<i>su</i>	5.65			
Idt 14- <i>Y-Pr-Su</i> × 4- <i>Y-p-su</i>	180-F ₂	<i>P</i>	10.54	0.49 ± .290	.10	+
		<i>p</i>	10.05			
		<i>Su</i>	10.64	0.43 ± .279	.15	+
		<i>su</i>	10.21			
	212-BC	<i>P</i>	7.55	0.10 ± .237	.50	—
		<i>p</i>	7.65			
		<i>Su</i>	7.61	.04		+
		<i>su</i>	7.57			
Osf 12- <i>Y-Pr-Su</i> × 4- <i>Y-p-su</i>	213-F ₂	<i>P</i>	9.11	0.32 ± .241	.20	—
		<i>p</i>	8.79			
		<i>Su</i>	9.17	0.31 ± .310	.40	+
		<i>su</i>	8.86			
	210-BC	<i>P</i>	7.19	0.57 ± .228	.02	+*
		<i>p</i>	6.62			
		<i>Su</i>	6.89	.04		—
		<i>su</i>	6.93			

¹Direction indicates the parental minus the non-parental class.

* Significant, 5% level.

** Significant, 1% level.

of this point would be purely speculative. It is interesting that this same reversal of linkage has been reported before in *SuSu* × *susu* crosses (LINDSTROM 1931).

The data show a slight indication of linkage between row number genes and the *P* locus; however, the relation is not consistent and no conclusions may be drawn. None of the other genes gives any indication of being linked with row number genes.

Row number frequency distributions of segregating generations

Figures 2, 3, and 4 show the percentage frequency distributions of row number from the backcross and F₂ generations of the three crosses discussed under linkage. These distributions and even their means are apt to be misleading from a genetic point of view, since classification of a presumably

FIGURE 2.—Row number distribution of F₂ and backcross generations. WF 8-y-p-Su × 4-Y-p-su.

polygenic characteristic has been made in discrete classes and these classes, themselves, are further prescribed by certain structural possibilities in the plant. For instance, the five-row class does not indicate complete disruption of ear morphology to lay down five kernel-rows, although odd numbers of

FIGURE 3.—Row number distribution of F₂ and backcross generations. Idt 14-Y-P^r-Su × 4-Y-p-su.

PLATE I

Young corn ears showing the typical eight- (left), six- (center), and four-rowed (right) conditions. Notice the characteristic false spiral of the six-rowed ear.

FIGURE 4.—Row number distribution of F_2 and backcross generations. $Os\delta$ 12- Y - P' - Su $\times$ 4- Y - p - su .

rows have been observed and accounted for, structurally, in certain South American varieties (CUTLER 1946). The odd numbers here indicate intermediates, usually classifiable as such. Furthermore, among the even numbers, ten-, and especially six-rowed ears show a certain amount of distortion in the form of what some investigators have called a false spiral (Plate I) to distinguish it from the true spiral caused by fasciation of the spike. The six-rowed ear has not been found in true breeding strains and neither does it show up as a large class of intermediates in crosses of 4×8 . Sixes occur just as often in the four-rowed parent as they do in the F_1 or F_2 between four and eight.

The basic pattern of four, eight, and twelve rows is clearly apparent. Classification should probably be made in these groups if it were not for the bias that would enter from the placing of the intermediates. Leaving out the intermediates is another possibility but again, if the intermediates were characteristic of one group and not the other, bias would enter. A clue to this may be seen in row number distributions of the four- and eight-rowed parents (fig. 5). Here, apparently, the intermediates occur most frequently with the four-rowed condition. This would indicate that the intermediates in F_2 should be divided between the four and the eight classes on the basis of their percentage of the parents.

DISCUSSION

The fact that embryological development may be regarded as a series of progressively changing steps, in itself suggests that the genes contained within

FIGURE 5.—Row number distribution in four- and eight-rowed parents. WF 8-*y-p-su* and 4-*Y-p-su*.

the cells making these steps are a part of a progressively changing chemical environment. Genes require substrates from which to build future products. With these substrates under progressive change, it is likely that the catalyzing of a process in one stage by one allele may be increased, while at another stage it may be limited. Changes in the developmental environment may even result in complete loss of function by one allele, thus giving the other allele the control of the master reaction. Under these circumstances, allele action within the framework of development may be expected to vary. This variation would allow certain genes to be the masters of one embryological stage and the servants of another. By this functional arrangement, the flexibility necessary for form and function control may be introduced into the system. The organism may be a mosaic of such systems. When this is the case it becomes difficult to even visualize the system. On the other hand, the system may be ordered in some linear manner, thus making the successive gene expressions clear. The kernel-row number development in corn herein described is such an ordered case.

The ordering of the system becomes evident in either of the pure homozygous inbred lines, but the range of the effects is so much reduced that it

could be overlooked. It is only in the heterozygote that the full range of effect becomes evident. In the F_1 both parental haploid sets come into prominence at different developmental stages. Dominance is expressed by the low row number allele when the ear is forming in the low position on the plant. High kernel-row number is expressed when the forming ear is at the top of the plant. A gradient of internal environment is established between these limits such that the genes for the kernel ear row numbers show a progressive shift in their developmental effects. Flexibility in gene developmental control is introduced. The interactions of the genes in action, gene-controlled substrates and environment are such as to allow diversity in the development of organ systems, etc., throughout other parts of the body.

Gradients in development were postulated early, but the complexity of the systems involved have not favored further analysis. The so-called axial gradient is such a case. But it does not appear that the gradients necessarily need be linear. They could be mosaic in form and could change with advancing development. Coat color patterns in mammals and birds as mentioned earlier are illustrations of this possibility.

The hypothesis proposed here, that alleles may have slightly different functions and that the relative dominance of an allele is dependent upon the developmental stage of the organism, can be invoked as explanation for the complementary action of mutant alleles. WHITING (1951) has given data on two loci of three alleles each in *Habrobracon* and one locus of four alleles in *Mormoniella* where the mutant alleles in combination produce a wild-type phenotype. He attributes this action to complementary dominance of the two mutant alleles but has not given evidence as to the developmental stage at which each allele is expressed. If this was possible, as it has been shown in the corn kernel-row number data, then each allele probably would impinge at a different stage in the development, appearing as dominant at that particular time.

Still another explanation may be fitting for the kernel-row number data and the cases of complementary action of alleles in *Habrobracon*. GOLDSCHMIDT (1927) postulated a general theory of dominance which states that the expression of an allele in heterozygous condition depends upon the rate of a reaction in development and upon the point of cessation of that reaction in the heterozygote. If this theory were applied to the corn data where ears are both four-rowed and eight-rowed on the same heterozygous plant, we would have to say that in developing the four-rowed ear, developmental rate was slower or development ceased sooner or both factors were brought into play in one part of the plant, while in another part of the same plant another set of conditions prevailed. This explanation is not so inconceivable as it is irrelevant since it would not necessarily predict the appearance of both alleles in a heterozygote as would the hypothesis stated here.

The kernel-row numbers in the parental inbreds as contrasted with those in the F_1 's furnish an impressive demonstration of how the two genomes in a heterozygote can interact and be given expression. Elasticity in phenotypic expression is greater in the heterozygote than it is in the more homozygous inbreds. Seemingly the F_1 's should be capable of giving the best phenotype

for a variety of environments. This is certainly one of the prime considerations in hybrid vigor in corn. It seems that the increased variation shown in the hybrids must be due to either heterozygosity *per se* or to the fact that the hybrid contains more different alleles than either parent. Whichever explanation is appropriate, our conclusion must postulate that the alleles at the average heterozygous locus have different functions. We can say that the 8-row genes are dominant at the upper positions on the plant and the 4-row genes are dominant in the lower positions, but this is merely a restatement of the hypothesis of different functions. If the 8-row genes are dominant in the upper positions, then their function is different in the lower positions.

Even though we cannot determine whether the increased variation is due to within locus or between locus causes, one thing seems relatively certain from these data: the greater number of different alleles in the hybrid is the cause of the greater within plant variation in kernel row number. Greater within plant variation presumably opens a broader developmental field to the hybrid and thereby the basis for greater vigor.

The kernel-row number data have a bearing on recessive-dominance concepts. The data show that the within plant environments may give phenotypic expression to one genome at one time or to the other genome at another.

Row number genes for corn strains with customarily eight or more rows on the top ear under field conditions, appear to be fairly numerous according to the works of EMERSON and LINDSTROM. To test for these genes, and, if possible, to locate them within the chromosomes, LINDSTROM (1931) tested the first, fourth, sixth; and tenth chromosomes in maize. Using the qualitative genes *p*, *su*, *y*, and *r* in a large number of crosses involving row number differences (eight rows being the lowest), a correlation between the *P* locus and row number was found which was interpreted to indicate that one of the major row number genes was located near *p* on the first chromosome. Negative or inconsistent results were obtained with the other chromosomes.

In the crosses of the 4×8 kernel-row ear types presented here two loci appear to be needed to differentiate the four and eight rowed types. Back-cross and F_2 data fail to show linkage of row number with loci for *P*, *Y*, and *Su*. These observations agree with TAVCAR's (1935) data on the *P* and *Y* loci.

SUMMARY

The data on kernel-row number, as determined under conditions favorable to the development of four to seven ears on a plant, show the relatively homozygous inbreds of four and of eight rows are stable with 0.5 of a row number. The F_1 's, on the other hand, show dominance of the eight-rowed at the top of the plant, and of the four-rowed type at the lowest position. Between these extremes, row number increases linearly with the successive nodes up the plant. A comparable trend, but of much reduced range, is noted for the inbred parents.

These facts show that dominance within the plant follows a within plant gradient. Gene action at successive stages of development is dependent on the condition of the substrate on which it works. The inbred's flexibility in meet-

ing these environmental changes is much less than that of the heterozygotes. F_1 adaptability should allow for vigorous activity over a much larger range of conditions. The heterozygous genomes of the F_1 each express their potentialities at different phases of growth.

In crosses of an eight-rowed line by a four-rowed inbred, kernel-row number gave some indications of being under the control of two complementary genes segregating in a 9:7 ratio in F_2 and 1:3 in the backcross.

Inconclusive data resulted in the linkage study between row number genes and the *P*, *Y*, and *Su* linkage groups. A significantly higher proportion of non-parental types was obtained from some crosses.

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