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The overall pattern of internode lengths in both dwarf-1 and normal plants was found to be strikingly similar. The degree of expression of the gene dwarf-1 was greatest near the ear node and least at the tassel end of the plant. Apparently, the expression of the gene dwarf-1 is influenced by the location of an organ on the plant.

The mesocotyls of the dwarf-1 and normal plants elongated with increasing planting depth within certain genetic limitations. The degree of expression of the dwarf-1 gene was least at the surface planting and greatest at the deepest. Therefore, it appeared that planting depth has an effect on gene action in respect to mesocotyl length.

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## AN ANALYSIS OF GROWTH RATES IN SUBSTAGE A OF PLASTOCHRON NINE IN ZEA MAYS L.

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#### INTRODUCTION

The present study was made in an effort to determine whether heterogeneity of growth rates exists within a genetically homogeneous population during a single plastochron. Earlier studies (Abbe, Phinney, and Baer, 1951; Abbe and Stein, 1954; Stein, 1952) described growth in a sequence of plastochrons, the assumption being made that arithmetic growth occurs within each. Furthermore, these studies emphasized the average behavior of the population and thus tended to mask any variation in the rate of leaf initiation. The relatively long sampling intervals used also tended to minimize any variations of growth rate in the population sampled.

The general method of measuring rate of leaf initiation is by periodically sampling a growing population and determining the mean number of leaves initiated at the time each sample is harvested, or the average time of occurrence of plants with a given number of leaves (Stein and Weber, 1954). From such data the mean length of time between the initiation of successive leaves (termed a plastochron, Askenasy, 1880) can be calculated. By sampling a population at very short intervals, however, as was done in this experiment, it becomes possible to determine whether any variations in the rate of leaf initiation exist within a plast-

ochron. If variations in growth rate are detected, it should also be possible to determine, from these same data, whether the variations are random or follow a definite pattern.

MATERIALS AND METHODS

The seeds used for the experiment were the F<sub>1</sub> of a cross between Minnesota Station inbreds A188 and A25; 402 seeds were washed in 0.1% Hg Cl<sub>2</sub> solution, rinsed, and soaked in distilled water for twenty hours. They were then planted in washed sand in two 73x63 cm. pans.

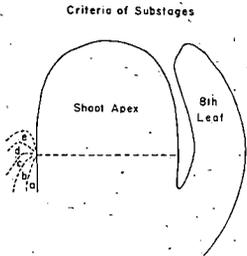


FIG. 1

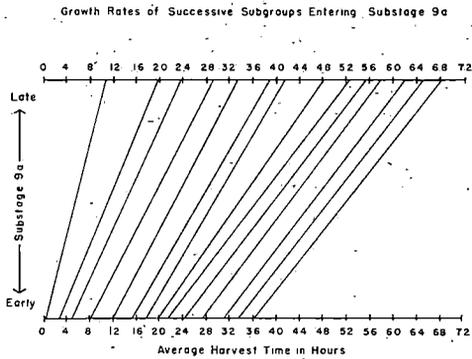


FIG. 2

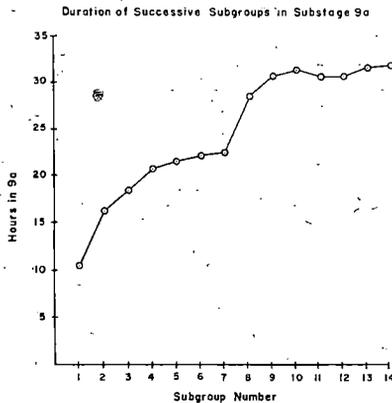


FIG. 3

The average planting distance between the rows was 4.6 cm.; between columns 4.0 cm. The pans were kept in a constant temperature chamber at 26±2°C. The plants were watered at 10:00 A.M. daily. The temperature of the water used was the same as that of the growth chamber. Il-

lumination was supplied by a bank of fluorescent lights which were turned on for 14 consecutive hours, in phase with the natural daylight period during the growing season. The Norwood light meter reading at the surface of the sand was 180 foot-candles.

After germination, small samples were taken daily to estimate the mean number of leaves initiated by the population. On the eighth day after planting, the test sample had plants which varied from late plastochron 8 to early 9, and random samples of 10 plants each were taken every 2 hours for 70 hours beginning at this time. The sampled plants were immediately killed, fixed and stored in FAA. After completion of the sampling, the shoot tips were removed, imbedded in paraffin and sectioned in the median sagittal plane. The sections were mounted on slides and stained with iron-hematoxylin. A camera-lucida drawing was made of the most median section of each apex and its youngest developing leaf. In a few cases where no truly median section was found, a careful composite was made from the adjacent sections.

In order to obtain an estimate of intraplastochronic growth, it is necessary to subdivide the plastochron. The subdivision is accomplished by a classification based upon the morphological relation between the youngest developing leaf and the shoot apex. Such a treatment has been previously used by Stein and Abbe (1949) who divide the developing shoot apex into 5 substages. These subdivisions are used in the present study and are illustrated in Fig. 1.

Although the population sampled had a range of substages from 7e through 10a, the majority of the apices were in substages 9a and 9b and detailed analysis has therefore been confined to these substages. The method of handling the data is as follows: the shoots classified in substage 9a were arranged in a series as to their time of harvest, that is from the earliest harvested apex classified in 9a to the last. They then were grouped into units of 5 apices, taking the first 5 apices, the second 5, etc. For convenience these groups of 5 apices are referred to as subgroups. Finally, the mean harvest time of each subgroup was determined. This procedure was also carried out for the apices in substage 9b.

#### OBSERVATIONS AND DISCUSSION

If we assume that the first plants entering substage 9a would also have been the first to leave it, and hence enter 9b, then the difference in the mean harvest time of the most precocious subgroup of 9a from that of 9b represents the mean duration of time the first *a* subgroup spends in substage 9a. Similarly the duration of the second 9a subgroup in substage 9a is the difference in harvest time of this subgroup from the second subgroup in the 9b series. Thus, each subgroup in 9a is considered to have an analogue in 9b when the subgroups are serially arranged as to mean harvest time. The 9b analogue of a 9a subgroup can be thought of as representing the stage of development the *a* subgroup would have reached if it had not been sacrificed.

In Table I the mean harvest time of each pair of analogous *a* and *b* subgroups is given in columns 2 and 3 respectively. In column 4. the

difference in harvest time between the successively paired subgroups, that is the duration of time each *a* subgroup remains in 9*a*, is given.

TABLE I

DURATION IN HOURS OF SUCCESSIVE SUBGROUPS IN SUBSTAGE 9 <i>a</i>			
Subgroup No.	Ave. Ttime to Substage	Duration in 9 <i>a</i> ( <i>b-a</i> )	
	<i>a</i>	<i>b</i>	
1	0.4	10.8	10.4
2	3.2	19.6	16.4
3	5.2	23.6	18.4
4	8.4	29.2	20.8
5	12.0	33.6	21.6
6	15.6	38.8	23.2
7	18.0	41.6	23.6
8	20.0	48.4	28.4
9	21.6	52.4	30.8
10	24.4	55.6	31.2
11	27.6	58.0	30.4
12	31.2	62.0	30.8
13	33.6	65.2	31.6
14	36.4	68.4	32.0
15	38.8	—	—
*		—	—
		—	—
23	68.0	—	—

\*Subgroups 15 through 23 had no analogues in substage *b*; the table has therefore been abbreviated.

It is apparent from examination of column 4 above that variations in duration in substage 9*a* do exist. In fact the first subgroup entering 9*a* spends about one-third as long in the substage as the 14th group entering the substage.

Since all the *a* subgroups must grow through the morphologically identical substage, these results can also be interpreted in terms of growth rates. This has been done in Fig. 2 where the mean harvest time of the *a* subgroups has been plotted on the lower horizontal axis and that of the *b* subgroups on the upper axis. The distance between the 2 abscissae represents the morphological unit, substage *a*. The paired subgroups have been connected by straight lines, whose slopes should be proportional to the growth rate of the *a* subgroup, in each pair, in substage 9*a*. That the slopes of these lines are not equal indicates that heterogeneity of growth rates does exist in this genetically homogeneous population.

The fact that the analagous subgroups are connected by straight lines in Fig. 2 indicates that arithmetic growth rates have been assumed. This assumption, however, has been made for small units of the population, rather than the entire population as in previous studies. Thus the error introduced by assuming arithmetic growth has been presumably minimized and a closer approximation to the true behavior of the popu-

lation has been achieved. The existence of variability of the magnitude shown in column 4 of table 1 indicates that the use of an average growth rate value for a plastochron, or a series of plastochrons, can be misleading.

Examination of column 4 of Table 1, or the slopes of the lines connecting successively paired subgroups in Fig. 2, indicates that the variations in duration or growth rates in 9a are not random. They exhibit a pattern: the earlier a subgroup enters the 9th plastochron, the shorter is its duration in substage 9a, that is the faster it is growing. This general pattern is interrupted in a few cases and this was due to extreme values for one of the 5 apices in a subgroup.

In Fig. 3, the duration in 9a has been plotted for each successive subgroup entering the substage. That a straight line will not adequately fit these points indicates that the increase in duration in 9a between successive subgroups is not uniform; or in terms of growth, the deceleration is not constant. The fact that the 9a subgroups after the 14th did not have any 9b analogues is therefore interpreted as due to their slow growth; no representatives of these subgroups had time to enter 9b before the 70 hour sampling period was completed.

It should be pointed out, however, that these results were obtained from a population utilizing its own endosperm reserves and photosynthate and either the growth rates or the overall pattern, or both may be altered in cases where mineral supplements augment these sources.

#### SUMMARY

An analysis was made of the rate of leaf formation of a genetically homogeneous population of *Zea mays* in substage a of plastochron 9. The analysis was accomplished by frequently sampling (every 2 hours) the population and averaging the harvest time for units (subgroups) of 5 successively harvested apices in the same substage.

The population was grown under uniform environmental conditions and hitherto undetected variations in the rate of leaf initiation were discovered. These variations were not random but were related to the time of entrance of a particular subgroup into the 9th plastochron. The earlier a subgroup entered the plastochron, the faster was its rate of leaf formation. The most precocious plants were found to be growing 3 times as fast as the tardiest examined.

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