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Morphological Measures of Earliness of Crop Maturity in Cotton[1]

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ABSTRACT

Certain features of the gross morphology of the cotton plant furnish clues to earliness of crop production. Three such features — *(1)* node of first fruiting branch (NFB), *(2)* number of vegetative branches (NVB), and *(3)* percentage of bolls on vegetative branches (PBV) — were used as morphological measures of earliness in the studies reported here. All of the morphological measures were significantly correlated but, because of its higher heritability and lower variability, NFB is considered the most reliable and the most practical one of the three. NFB and NVB were signficantly correlated, phenotypically, with product-quantity measures of earliness. Mean maturity date (MMD), a product-quantity measure, and NFB, a morphological measure, are separate estimates of the same phenomenon: i.e., earliness of crop maturity. Used together, they are mutually supporting and they form a relaible basis for estimating earliness in genetic studies and breeding programs.

ALL CULTIVATED American Upland cotton varieties, as well as the primitive, noncultivated races of *Gossypium hirsutum* L., are indeterminate in growth and fruiting habit. In gross morphology, the cotton plant is characterized by a central stem that develops as a monopodium and two types of side branches: (a) spirally ascending fruiting branches, sympodia, and (b) vegetative branches which, like the main stem, are monopodial in structure and which usually arise from the lower nodes of the main stem. Sympodia may arise from vegetative branches, but initiation of sympodia here is usually later than on the main stem. Bolls (fruits) are borne only on sympodia; herefore, sympodial branches are present on all plants that produce fruit. Lateral vegetative branches, though characteristic of all cottons, are not essential to crop production nor are they always developed. Whether or not vegetative branches are formed appears to depend on the interaction between the genotype of the plant and the total environment. Under reasonably favorable environmental conditions, a period of about three days elapses between the appearance of a flower bud at a given node of a given fruiting branch and the appearance of a flower bud at a corresponding node on the next occurring fruiting branch; and 6 or 7 days elapse between successive flower buds on the same fruiting branch (7, 8, 9). Thus, a succession of fruits is formed in an upward pattern, and the eventual crop is made up of bolls set over a considerable period of time. Variability in time and duration of flowering, boll setting, and crop maturation is usually, if not always, observed among cotton varieties or stocks of diverse genetic origin or background.

Difficulties encountered in devising a simple method of measuring earliness of crop maturity in cotton — one that is adequate for all problems and reliable under all conditions — can be attributed largely to the indeterminate growth and fruiting habit of the plant, and to developmental phenomena associated with plant form and fruiting patterns. However, certain features of gross morphology provide clues to the crop in terms of earliness of maturity.

This paper reports the results of an investigation of three methods of measuring or estimating earliness of crop maturity in cotton that involve the quantification of certain morphological features of the cotton plant.

REVIEW OF LITERATURE

Certain time-event and product-quantity measures of earliness of crop maturity in cotton were investigated by Richmond and Radwan (11) who reviewed the pertinent literature on time (date) of occurrence of first squares, blooms and open bolls, and on amounts or ratios of various fractions of the crop as measures of earliness. The results of a critical study of three measures that fall in the product-quantity category of earliness measures were reported by Richmond and Ray (12). These experiments emphasize the importance of choosing the proper date or period on which to base the calculations and they point out that no single measure or estimate of earliness of crop maturity is completely acceptable in all breeding situations or under all experimental conditions. Of all of the measures tested, mean maturity date (MMD) had the highest heritability and was considered the most re-

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liable one for use in genetic studies. Whether they were young flower buds, blooms or mature bolls, fruit forms of some kind were common components in the determination or calculation of these measures.

Morphological or structural indicators of earliness which are contributors to time and amount of fruiting, rather than components, have been recognized. As early as 1910, Leake (6) pointed out that, in general, the lower the (main-stem) node at which the first sympodium is initiated, the earlier the crop matures. Leake (6) and Ware (13) observed that plants which produced several strong monopodial side branches tended to be later in crop maturity than those which produced few or none. Harland (4) suggested seven approaches to the estimation of earliness in cotton; among them were the determination of: (a) the rate of growth of the main-stem axis, and (b) the main-stem node at which the first fruiting branch occurs. According to Hutchinson (5), the early maturing, prolific, annual forms which distinguish modern agricultural varieties from their wild or primitive ancestors are attributable to: (a) the loss or elimination of the short-day photo-periodic response, and (b) the reduction in the number of main-stem nodes that occur between the cotyledonary scars and the point of initiation of the first fruiting branch.

While those who have dealt with the subject obviously have recognized that heredity as well as environment contributes to the association between structural or morphological characteristics of vegetative parts of the cotton plant and crop maturity, a critical analysis of the genetics of earliness measures by morphological determinations has not come to our attention.

MATERIALS AND METHODS

Within a category of earliness measures broadly identified as morphological, three kinds or types of measurements were investigated. They have been named and described as follows:

Node of first fruiting branch (NFB) — Number of the main-stem node at which the first fruiting branch arises, determined by designating the node immediately above the cotyledonary scars as number two, and counting the successive ascending nodes until the one that gives rise to the first fruiting branch is reached.

Number of vegetative branches (NVB) — Number of vegetative branches (monopodia) that put out from the central axis.

Percentage of bolls on vegetative branches (PBV) — Number of bolls produced on fruiting branches (sympodia) arising from vegetative side branches (monopodia), expressed as a percentage of the total number of bolls produced.

In addition, the morphological measures were related to certain "product-quantity" measures of earliness: i.e., percent of crop harvested (PCH) and mean maturity date (MMD). The PCH measure was given by the percentage of the crop open through the fourth harvest and the MMD measure was based on six sequential weekly harvests.

The parents and early-generation populations of two crosses between early and late maturing lines were used in three separate field experiments. The early maturing parent of both crosses was 'C.B. 3051' and the late maturing parents were 'Z-106' and 'Contextum.' These lines represent the approximate range of earliness of maturity and found in Upland cotton and have been described by Richmond and Ray (12).

Experiment I. Parental, F_1, F_2 and backcross generations of the two crosses were grown in a four-replicate, randomized-block experiment at College Station in 1959. These generations were grown to increase seed stocks for planting subsequent experiments in this study. However, it was apparent that data on NFB would not be biased in these populations; and therefore, measurements of this character were taken. Manipulations of the plants required for production of quantities of self-pollinated and hybrid seeds would have introduced a bias in the other measures and they were not made.

Experiment II. The cross C.B. 3051 × Z-106 was used for an analysis of the components of variance. The cross with Z-106 as the late parent was selected because this line was observed as having more economic characters in common with commercial varieties than did Contextum. Parental, F_1, F_2, F_3 and certain back-cross generations were grown in a two-replicate experiment at Lubbock in 1960. Ten to 48 plots of each 9 generations (entries) were randomly arranged in each replication. The non-segregating populations (parents and F_1's) had fewer plots than the segregating populations. Each F_3 and BC_1S_1 family occurred only once in each replication. Each plot initially contained eight plants which were transplanted from the greenhouse, but on the average only about six plants per plot survived.

Experiment III. An experimental design described by Comstock and Robinson (1) was used to estimate the average degree of dominance in the action of genes affecting earliness of crop maturity, as measured by the mean maturity date (MMD) and the node number of the first fruiting branch (NFB). The experimental material was produced from backcross matings of 21 randomly selected F_2 plants of the C.B. 3051 × Z-106 cross to each of the two inbred parental stocks (C.B. 3051 and Z-106). The progenies were divided into three sets, each set having seven pairs of progenies. The members of each pair had the same F_2 (pollen) parent but different inbred (ovule) parents. The progenies were planted in a randomized-block experiment with three replications at Lubbock in 1960. Mean squares were calculated from plot means. Comparison of the progeny variance arising from genetic differences among F_2 (pollen) parents and the progeny variance arising from the interaction of the genotype of the F_2 lines and the inbred parents provided an estimate of the average degree of dominance (1).

Statistical Analysis

Heritability estimates of the NFB in the broad sense were made in Experiment I by a method suggested by Weber and Moorthy (14), where

$$\text{Heritability} = VF_2\sqrt[3]{\overline{VP_1}\ \overline{VP_2}\ \overline{VF_1}}/VF_2$$

where VF_2 = variance of the F_2 population, etc.

Components of variance were determined from Experiment II data following statistical procedures developed by Fisher (2), Fisher, Immer and Tedin (3) and Mather (10). The symbolism used was derived mainly from Mather (10). Total variation was partitioned into three components: (a) additive genetic variance, D; (b) a genetic component, H, due to the effect of dominance; and (c) variance resulting from environmental effects. Two estimates of environmental variance were made. One was based on plants within plots (E_1) and the other on plot means (E_2). The D and H components were based on plants within plots. The components were calculated from the mean variances of the two replications and their standard errors were obtained. Listed below are the populations analyzed and their corresponding components of variance:

Population		*Components of variance*
Parents and F_1:		
	Within plots	E_1
	Plot means	E_2
F_2	(within plots)	$1/2D + 1/4H + E_1$
F_3	(within plots)	$1/4D + 1/8H + E_1$
F_2	(family means)	$1/2D + 1/16H + E_2$
BC_1	(within plots)	$1/4D + 1/4H + E_1$
BC_1S_1	(within plots)	$1/4D + 1/8H + E_1$
BC_1S_1	(family means)	$1/4D + 1/16H + E_2$

Eight equations were available for estimating, by means of the least squares analysis, the four parameters E_1, E_2, D and H. The variances were not weighted for least squares analyses. Matrix algebra was used to solve for D, H, E_1, and E_2.

Certain basic assumptions underlie the methods given by Mather (10) and by Comstock and Robinson (1) for estimating the various genetic parameters. It seems reasonable that certain of these (for example, diploid segregation and gene frequency of one-half) would have validity in the present experiments. Epistatic effects are minimized by using a scale which will make the gene effects additive. Tests for additive gene action were made by comparing the means of the back-cross and F_2 popula-

tions with the means of the non-segregating generations, the parents and F_1's, using formulas from Mather (10):
$a = \overline{2BC_1} - \overline{P}_1 - \overline{F}_1$; $b = \overline{2BC_2} - \overline{P}_2 - \overline{E}_1$; and $c = \overline{4F_2} - \overline{2F_1} - \overline{P}_1 - \overline{P}_2$.
Adequacy of the scale is signified by the extent to which the values *a*, *b*, and *c* approach zero.

RESULTS

Experiment I

At College Station in 1959, only the node of the first fruiting branch (NFB) was measured. On the average the C.B. 3051 parent fruited 2.4 nodes lower than Z-106 and 3.5 nodes lower than Contextum (Table 1). Theoretical arithmetic and geometric means for the F_1, F_2, and backcross generations were essentially the same, and in most populations they agreed closely with the observed means.

Scaling tests showed a departure from the additive gene model in the means of the blackcrosses to the late maturing parent. A fit to the additive model was found in tests using the other segregating populations. The fit was not improved with logrithmic transformation.

The heritability estimate, in the broad sense, for NFB in the C.B. 3051 × Z-106 cross was .60 and in the C.B. 3051 × Contextum cross it was .43.

Experiment II

Population means and frequency distribution. Reference to the means of earliness estimates given in Table 2 will show that the parents differed significantly ($P < 0.01$) in respect to each of the measures studied. The mean node number of the first fruiting branch (NFB) of the early parent was 5.3, while the mean position on Z-106, the late parent, was 8.0. C.B. 3051 produced an average of 2.2 vegetative branches, while Z-106 produced an average of 4.3, or nearly twice as many. A greater difference between the two parents was found in the portion of the crop produced on the vegetative branches. Z-106 produced 37% of its bolls on vegetative branches while C.B. 3051 produced less than 10% of its bolls on these branches. The parents also differed significantly in the two product-quantity measures of earliness, MMD (mean maturity date) and PCH (percentage of crop harvested). The MMD of C.B. 3051 was 3.8 weeks after the beginning of the harvest period and MMD of Z-106 was 5.5 weeks. Through the fourth harvest, 44.4% of the bolls had opened in C.B. 3051, but only 5% had opened in Z-106.

Frequency distributions of the parental, F_1, F_2, and F_3 populations were plotted for measurements of earliness. Due to similarity of the frequency curves for the various measures, only one — the node of the first fruiting branch — is shown (Figure 1). The frequency distributions for all measures were typical of those expected of quantitatively inherited characters. F_1 means took an intermediate position in respect to parental means; within each measurement, means of F_1, F_2 and F_3 populations differed but little; and backcrosses to the early parent produced lower values (were earlier) than those to the late maturing parent. As tested by the standard error, the earliness measures involving vegetative branches (NVB and PBV) showed more variation in the nonsegregating populations (P_1, P_2 and F_1) than did NFB and MMD. Variability of the PBV measure was quite high. In some cases, the range of the F_2 or F_3 generation extended beyond that of the late parent. However, this probably could be attributed to relatively high environmental variation rather than transgressive segregation.

Components of variance. The statistical model on which the components of variance analyses were based assumes additivity of gene effects. The measurements were examined for conformity to the additive scale before variance analyses were performed. Although the scales did not appear to be fully adequate, only one of the equations gave evidence of definite nonconformity.

Table 1. Observed means, with their standard errors, and theoretical means based on arithmetic and geometric gene action for the number of nodes to the first fruiting branch in Experiment I.

Generation	N	Observed means	Theoretical means	
			Arithmetic	Geometric
	(C.B. 3051 × Z-106)			
P_1 (C.B. 3051)	39	4.7 ± 0.10		
P_2 (Z-106)	35	7.1 ± 0.09		
F_1	37	5.3 ± 0.09	5.9*	5.8*
F_2	32	5.6 ± 0.16	5.6	5.5
BC_1 (× P_1)	13	5.2 ± 0.20	5.0	4.9
BC_1 (× P_2)	13	6.6 ± 0.15	6.2	6.1
	(C.B. 3051 × Contextum)			
P_1 (C.B. 3051)	39	4.7 ± 0.10		
P_2 (Contextum)	18	8.2 ± 0.15		
F_1	40	5.7 ± 0.08	6.4*	6.2*
F_2	31	6.2 ± 0.14	6.1	6.0
BC_1 (× P_1)	13	5.3 ± 0.14	5.2	5.2
BC_1 (× P_2)	15	6.6 ± 0.21	6.9	6.8

* Mid-parent estimates.

Table 2. The means and standard errors for morphological and "product-quantity" measures of earliness for the populations in Experiment II.

Population	N	Node no. of 1st fruiting branch	No. of vegetative branches	% of bolls on veg. branches*	Mean maturity date†	% of crop harvested through 4th date
P_1 (C.B. 3051)	65	5.3±.17	2.2±.24	9.5±5.2	3.8±.07	41.2±3.4
P_2 (Z-106)	63	8.0±.16	4.3±.13	37.2±7.1	5.5±.05	5.0±1.0
F_1	54	6.7±.19	3.7±.20	25.7±8.9	4.9±.08	15.4±2.0
F_2	247	6.1±.09	3.4±.10	21.0±1.3	4.6±.05	21.2±1.5
F_3	308	6.5±.08	3.8±.09	21.8±1.2	4.7±.04	20.7±1.1
BC_1 (× P_1)	65	5.6±.19	2.6±.20	17.2±2.5	4.1±.07	39.2±3.3
BC_1 (× P_2)	66	7.0±.14	4.1±.17	24.7±2.0	5.1±.09	13.2±2.1
BC_1S_1 (× P_1)	147	6.2±.14	3.6±.14	21.4±1.9	4.1±.06	37.9±2.1
BC_1S_1 (× P_2)	152	7.5±.11	4.3±.14	26.4±1.6	5.3±.06	8.0±1.1

* The statistics were calculated from transformed data but the values reported are in percentages. † The mean maturity date is expressed in weeks from September 8.

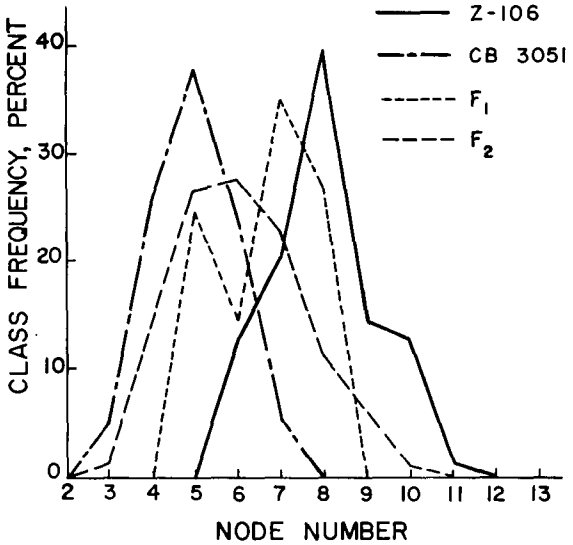

Figure 1. Frequency distributions of the node number of the first fruiting branch (NFB).

Table 3. Component of variance values calculated from data obtained from Experiment II.

Trait	Component of variance			
	D	H	E_1	E_2
Node of the 1st fruiting branch	.61± .28*	.11± .63	1.47± .08**	.25± .08**
No. of vegetative branches	.50± .49	.19± 1.10	1.85± .14**	.27± .14
% of bolls on vegetative branches	54.6 ±52.4	19.6 ±121.0	302.0 ±14.9**	36.6 ±14.4**
Mean maturity date	.24± .12	.19± .29	.27± .04**	.03± .03
% of crop harvested through 4th date	-11.4 ±58.5	358.9 ±135.8*	148.1 ±16.7**	14.3 ±16.1

* Component significantly greater than zero at the 0.05 level of probability. ** Component significantly greater than zero at the 0.01 level of probability.

Table 4. Phenotypic correlations among NFB, NVB, PVB and MMD measures.

	NVB	PBV	MMD	PCH
NFB	.45**	.22**	.40**	-.43**
NVB		.19**	.31**	-.33**
PBV			.10	-.02
MMD				-.90**

** Correlations significantly different from zero at the 0.01 level of probability.

The values for the components of variance are given in Table 3. Only one estimate of the additive genetic component (D) was significant, that being for NFB. The nonheritable, within-plot components of variance (E_1) were highly significant for all measures; and in all cases the non-heritable components of variance based on plot means (E_2) were smaller than the E_1 components. Only two estimates of the E_2 components were significant. However, Mather (10) has pointed out that an unweighted analysis would likely overestimate the E_2 components; therefore, the observed results may well have been expected.

Correlations. As shown in Table 4, significant associations were found among all of the morphological measurements, the closest relationship being between NFB and NVB. The only morphological measure of earliness that was not significantly correlated with MMD and PCH (the product-quantity measures used as the standard of comparison in these experiments) was PBV. Considering the normal growth and fruiting pattern of the cotton plant, as described in the introduction, we expected the relative amounts or percentages of fruits produced on sympodia arising from vegetative branches to have a measurable effect on mean maturity date (MMD) and percentage of the crop harvested (PCH). The nonsignificant correlations between PBV and the product-quantity measures show that this was not the case. Instead the most direct effect of the morphological characteristics on earliness or lateness in terms of time and amount of production was apparently through the NFB measure. Partial correlation coefficients tend to support the thesis just stated. The partial correlation coefficient between NVB and MMD was only .16 when NFB was held constant, while the partial correlation coefficient between NFB and MMD with NVB held constant was .31.

Linear regression coefficients, calculated from the F_2 data, indicate that a change of one node in the position of the first fruiting branch would account for slightly less than 1½ days in the MMD, and one vegetative branch would change the MMD slightly less than 1 day.

Several genotypic correlations were calculated following a method outlined by Weber and Moorthy (14). F_2 variances and covariances were used as estimates of total variation, and the geometric means of the parental and F_1 variances and covariances were used as estimates of the environmental variance. The genotypic correlation of NVB and MMD was .49 which was greater than the phenotypic correlation between these measurements. However, a high genotypic correlation (.91) was found between NFB and MMD. The genotypic correlation between NFB and NVB (.49) was approximately the same as the corresponding phenotypic correlation (.45). In attempting to determine genotypic correlations for the relationships of PBV, it was found that the mean covariances of the nonsegregating populations exceeded the covariances of the F_2; hence, no valid estimate could be made. Interpretations of genotypic correlations calculated in this manner should be undertaken with caution for the method is not a rigorous one.

Table 5. Analysis of variance, Experiment III, for the mean harvest date and node of the first fruiting branch.

Source of variance	df	Mean squares	
		Mean maturity date	Node of first fruiting branch
Sets	2		
Replication in sets	6		
Inbreds in sets	3		
F_2 parents in sets (1)*	18	.2128	2.3239
F_2 parents × inbreds in sets (2)	18	.2524	.9150
Remainder among plots (3)	78	.1146	.3431

* Expectation of mean squares: 1. = $\sigma^2 + 6\sigma^2_m$ (m = genetic differences arising from F_2 males) 2. = $\sigma^2 + 3\sigma^2_{ml}$ (ml = interaction of genotype of F_2 and inbreds) 3. = σ^2

Experiment III

The analysis of variance for Experiment III is given in Table 5. The footnote to the table gives the components of the mean squares pertinent to the analysis. Two components of variance were used to estimate the average degree of dominance. There were σm^2, the progeny variance arising from genetic differences among F_2 parents, and σml^2, the progeny variance arising from the interaction of genotypes of the F_2 and the inbred parents. Comstock and Robinson (1) showed that the variance $\sigma m^2 = 1/8D$ (additive genetic variance) and that $\sigma ml^2 = 1/4H$ (dominance variance). Thus, it was possible to estimate the average degree of dominance from these variances as $\bar{a} = \sqrt{H/D}$. The average degree of dominance, $\bar{a}$, calculated for NFB was .54, while that for MMD was 1.18. Additional estimates were calculated from the components of variance reported in Table 3; values of .42 and .89 were obtained for the $\bar{a}$'s of NFB and MMD, respectively. These results suggest that genes with incomplete or partial dominance control the NFB, but those associated with MMD have complete, or near complete, dominance.

DISCUSSION AND CONCLUSIONS

The time-event and product-quantity measures of earliness deal with time (date) of occurrence of various stages of fruit development and with amounts or ratios of various fractions of the crop. The features of the gross morphology of the cotton plant which contributed to the morphological measures investigated in the present experiments do not directly involve stage of fruit development or fractions of the mature crop. Morphological measures may well be less biased and a more direct expression of gene action than the time-event or product-quantity measures. However, practical confidence can be placed in mor-

phological measures of earliness only to the extent that they can be shown to be associated with, related to, or involved in processes that condition the amount of fruit (crop) produced at certain specified times. The mean maturity date (MMD) and percent of crop harvested (PCH) were used as standards-of-comparison in the present experiments. Two of the morphological measures, *node of first fruiting branch* (NFB) and *number of vegetative branches* (NVB), were significantly correlated, phenotypically, with both of the product-quantity measures of earliness. As previously shown, the earliness of crop maturation is probably affected more by the position of the first fruiting branch than by the number of vegetative branches. The *percentage of bolls produced on vegetative branches* (PBV) was not related to the product-quantity measures. Significant phenotypic correlations were found among all of the morphological measures investigated, but the NFB appears to be the most appropriate one for earliness investigations.

The genetic and statistical parameters that were caluculated from data on morphological measures are typical of quantitatively inherited characters, and they suggest that earliness of crop maturity is conditioned or controlled by several genes. Generally, additive gene action was indicated, but the "D" component was significant only when the NFB measure was used. Also, as evidenced by its higher heritability and lower variability (in non-segregating populations), the NFB measure is less affected by environmental factors than the other measures investigated. NFB is a sensitive measure, so sensitive in fact that significance was obtained with an average difference of less than one node. The ability of the NFB measure to discriminate among small differences in node number, as demonstrated in the present experiments, must be inherent in the method for McNamara et al. (8) reported similar results in main-stem-node-number studies of six closely related agricultural varieties.

In addition to its genetic attributes, the NFB method is so elementary and uncomplicated in nature that to use it one needs only to be able to recognize sympodia and count main-stem nodes. While the NFB measure is adaptable to any problem or program that requires the quantification of genetic earliness (earliness without close reference to total or potential yield), it will also give reliable estimates of earliness when it is impossible or impractical to collect data on the time and rate of fruiting or boll maturation.

In view of the results of the added evidence from these experiments, we believe that the MMD and NFB are the most valuable measures of earliness for use in genetic studies and breeding programs. It should be pointed out that NFB and MMD are separate measures of the same phenomenon, i.e., earliness of crop maturity. One method does not extend the numerical value or statistical reliability of the other in terms of estimating earliness; but the methods are mutually supporting in that one provides a check on the other. The selection of the measure or measures to be used will be dictated by the conditions and objectives of the program. We would not deny that other measures are more appropriate in some cases, for instance the PCH which is widely and properly used for agronomic evaluation of earliness of strains and varieties in performance trials. Other measures such as boll period and rate of fruiting may prove to have an important place in estimating earliness of crop maturity, but as yet they have not been adequately investigated.

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