

## Simulation of Growth and Yield in Cotton: II. Environmental Control of Morphogenesis<sup>1</sup>

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### ABSTRACT

Time intervals between the appearance of leaves, floral buds and flowers at successive main stem and fruiting branch nodes of the cotton plant (*Gossypium hirsutum* L.) were studied in eight temperature regimes at the Southeastern Environmental Plant Laboratories. The time interval between such events on the main stem or the first node of the fruiting branch, as affected by temperature, would seem to provide (with some qualifications) a simple physiological time-base for modeling plant development. Our observations agreed fairly well with a physiological time concept attributed to Zaitzev in 1927.

**Additional index words:** Temperature, Flowering, Fruiting, Plastochron leaf growth.

IT has become apparent after attempting to develop plant growth models, that considerable detail about morphogenesis or organogenesis is necessary (2, 14). It has also become apparent that modeling techniques associated with appropriate experimentation will result in tremendous advances in this area. Models provide a logic and computers provide memory by which many diverse aspects of the morphogenesis of a plant can be classified and synthesized into a unified description of plant growth (16).

Of interest here is the plastochron or the "unit of time corresponding to the interval between two successive similar, periodically repeated events". These intervals often are dependent upon temperature and other environmental parameters and thereby provide a time base for plant growth (12). In otherwise comparable conditions, evidence is accumulating that these intervals are fairly constant over a wide range of photosynthetic supply values, such as might be produced under a range of naturally occurring light energy values (3, 7, 8).

According to Hector (5), Zaitzev (17) also considered time intervals between successive stages of growth which he divided into "isophases". Hereafter in this paper we will depend upon Hector's fairly extensive interpretation of Zaitzev's concept as Zaitzev's original paper was unavailable to us. His isophase is equivalent to the plastochron for time intervals on the main stem of the cotton plant; however, he used the plastochron as a basic time interval, as did Michilini (12), with multiples of the plasto-

chron to describe time intervals between unlike events. He believed that two isophases were needed for each of three growth intervals in cotton (*Gossypium hirsutum* L.) (a) from planting to expansion of cotyledons, (b) from cotyledon expansion to expansion of the first true leaf, and (c) between similar events within a fruiting branch.

Zaitzev studied the effects of temperature on most isophases that occur during the seasonal cycle of growth of a cotton plant. One could build a model upon his data alone; however, with the availability of phytotrons, it seemed appropriate to test his results. Hence, we initiated the studies described in this paper.

### MATERIALS AND METHODS

Cultural methods used in the Duke University unit of the Southeastern Plant Environmental Laboratories (SEPEL) are described elsewhere (1). Eight plants were grown at each of 32/29, 29/26, 26/26, 32/23, 23/20, 20/17, and 17/11 C day/night temperatures. Mean temperatures were 30, 27, 26, 26, 21, 18, and 13 C, respectively, for these treatments. The daytime thermal period lasted 8 hours and the photoperiod was 16 hours. Measurements on five of these plants were used in the leaf studies, but all eight plants per treatment were used in the fruiting studies.

Lengths and widths of the cotyledons and true leaves were recorded every two to five days until leaves were nearly expanded; this was not carried to full expansion since after the initial rapid growth all leaves expanded very slowly over a long period of time to what seemed to be the fully expanded state.

The dates of appearance of squares 3 mm on a side and dates of flowering were recorded. Positions of above-ground organs on the plant were also measured.

### RESULTS AND DISCUSSION

#### Seedling Growth

Figs. 1 and 2 show length  $\times$  width mean values for leaves of five plants from two of the eight treatments. Plots for the other treatments were similar in general form, except for the 17/11 C treatment where the plants senesced after one or two true leaves had expanded. The conversion factors for actual projected leaf area were 0.9 for cotyledons, 0.7 for the first true leaf, and 0.75 for subsequent leaves. Zaitzev used days to expanded cotyledons and expanded first leaf or successive leaves to calculate his isophases. This proved to be difficult to pinpoint as an event and, alternatively, we defined an event as a length  $\times$  width value of 10 cm<sup>2</sup>/leaf. Our time intervals are given in Fig. 3. The days/leaf values are plastochrons as qualified by our definition of an event, and the other time intervals are similar to Zaitzev's isophases. At the State College mid-summer monthly mean temperature of 26.5 C, Zaitzev's concept of one isophase between leaves on the main stem (2.5-3 days) and four isophases from planting through to expansion of the first true leaf (10 to 12 days) held fairly well for our arbitrary events. However, these relationships did not hold at lower temperatures and a redefinition of events did not help correct the discrepancy between his concept and our results.

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<sup>3</sup>Webster's New International Dictionary, Second Edition, 1957. G. & C. Merriam Co., Publishers, Springfield, Mass. Botanists often restrict this definition to events on the shoot apex such as the appearance of leaf or flower primordia; we use the general definition for lack of anything better.

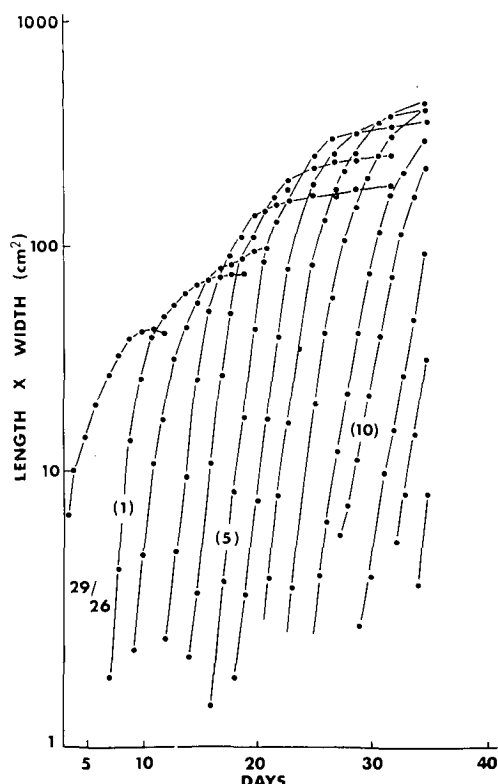


Fig. 1. Length  $\times$  width of cotyledons and several true leaves for cotton seedlings growing at 29/26 C day/night temperatures. Leaf number is shown in parenthesis on curves. Values are means for five plants.

Wadleigh and Gauch (15) in a similar analysis, found isophases of 5 days for stressed plants compared to 2.5 days for well-watered plants. Leaf extension was depressed at about 2 atmospheres and ceased at about 14 to 15 atmospheres soil water tension.

#### Phenological Data

Table 1 lists the various fruiting characteristics of these plants. Days from square to flower were similar to values observed in the Canberra phytotron (6). In the Canberra experiments, plants were grown at 21 C until the appearance of the first square, and then were transferred to the other temperatures. In the Duke experiments, plants were kept in the same temperature regime for the entire experiment. Values for the node of the first sympodium were similar to those found for other varieties in other experiments at Canberra (9, 17).

In Table 1 values are calculated for days to first square from data in Fig. 3. Days to appearance of the first true leaf were added to the product (node number of first square)  $\times$  (days per leaf). These estimates are based on measurements taken over the entire

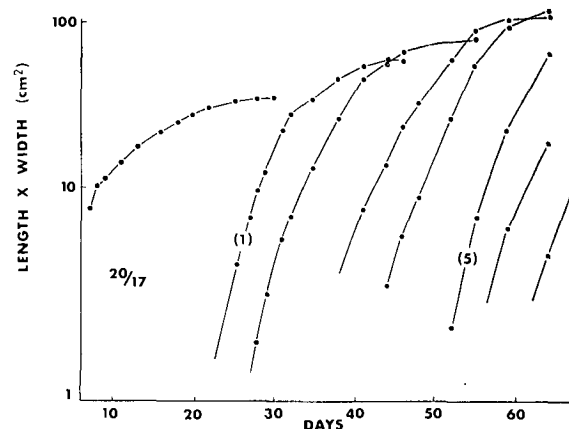


Fig. 2. Length  $\times$  width of cotyledons and several true leaves for cotton seedlings growing at 20/17 C day/night temperatures. Leaf number is shown in parenthesis on curves.

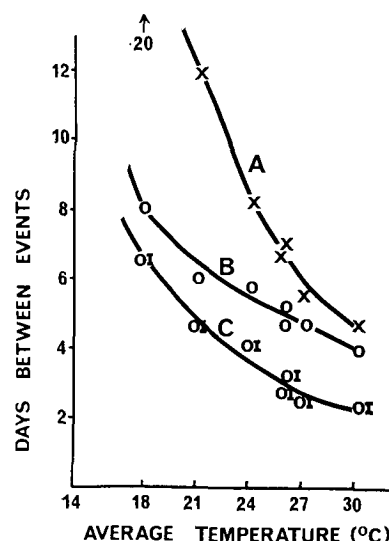


Fig. 3. (A) Days from planting to cotyledons with length  $\times$  width values of 10 cm<sup>2</sup>. (B) Days from 10 cm<sup>2</sup> cotyledons to leaves with length  $\times$  width values of 10 cm<sup>2</sup>. (C) Days per leaf where the reference point was length  $\times$  width of 10 cm<sup>2</sup>. See Figs. 1 and 2 for examples of data from which these values were estimated.

period in most cases. Therefore, the close association between calculated and actual days to first square was not unexpected.

Time between squares or flowers on successive sympodia (fruiting branches) up the main stem, as well as time intervals between squares or flowers within each sympodium, are given for various nodes on the plant in Figs. 4 and 5. The value of the highest node given represents a mean for at least four squares or flowers among the eight plants. Plants in most of the treatments often aborted squares on the second

Table 1. Phenotypic data for cotton plants at different temperatures, Duke experiments.

	Average temperature							SE	Number of observations
	18	21	24	26†	26†	27	30		
Node no., of position of first sympodium (fruiting branch)	6, 5	5, 5	6, 5	8, 5	7, 0	7, 5	10, 8	0, 24	8
Days from planting to first square	75	45, 5	39	37, 5	33, 6	30	34	0, 58	8
Isophase prediction of above*	71	44	41	39	30	29	34	na†	
1/R <sub>A</sub> , days from 1 $\times$ w of 10 to 100 cm <sup>2</sup> divided by 2, 3	4, 6§	3, 1	2, 3	2, 2	2, 0	1, 6	1, 5	0, 09	6, 5
Days from first square to first flower	73, 5	41	31	28	27	26	22, 5	0, 49	8
Node no., of position to first large monopodium (vegetative branch)	2, 2	3, 1			4, 6	4, 6	4, 6	0, 18	8
Weight per flower, g	0, 46	0, 5	0, 46		0, 54	0, 45	0, 35	na	
Weight per boll, day 1	0, 30	0, 27	0, 33		0, 27	0, 24	0, 22	na	

\* Using data from Fig. 3: days to reference point on first true leaf plus days/leaf multiplied by node of the first sympodium. † 26 = 26/26, 26 = 32/23 C day/night temperature. All others, add 2\* for day temperature (8 hr); subtract 1\* for night temperature (16 hr). ‡ Not available. § n = 2.

sympodial unit of the fruiting branch, but the leaf developed to normal size.

All these observations, together with similar information from the 32/23 and 26/26 treatments are summarized in Fig. 6 as mean values for each treatment, excluding the longest two plastochrons at 27 C and 30 C which occurred at high node numbers. Zeitzov's concept appears to hold well down to at least 21 C. However, we differ as to the number of isophases required between events within a sympodium. Similar differences have been reported among genotypes (4).

There are good reasons why intervals between events within and between sympodia differ. Events on the main stem are associated with initiation of leaf primordia on the shoot apex. Events within a sympodium

involve the production of a floral bud, flower, open boll, a prophyll, a leaf, two internodes, and new axillary buds in the leaf axil and in the prophyll axil (11). The growth of this fruiting branch unit, exclusive of the flower or boll, then ceases, with the production of a new floral unit coming from the axillary bud of the leaf, or occasionally of the prophyll. As many as seven such floral units have been found within a sympodium. It should be pointed out that while events within a sympodium take more time, similar events between sympodia such as flowering at the second or third fruiting sites, depend upon the leaf plastochron and, therefore, require only one isophase.

### Time Intervals

For one estimate of plastochrons (time intervals between *like* events), we used Mauney's (10) Table 5, days to floral initiation, his assumption that initiation took place when the node of the first floral branch was in the axil of the third leaf below the apical meristem, and the node number of the first sympodium, his Table 4, or

$$\text{Plastochron} = \frac{\text{Days to floral initiation (Table 5)}}{\text{Node of floral branch (Table 4) + 2 - 1}}$$

As Mauney assumed, there were two more leaves at nodes above the newly initiated floral bud. We subtracted from the total number of leaves on the main stem the first true leaf which was already preformed in the seed before planting. This plastochron then is for leaves initiated on the mainstem apex from the time of planting, with no allowance for a time period during germination before meristematic growth begins.

For isophases (including some estimates of time intervals between *unlike* events), values were taken from

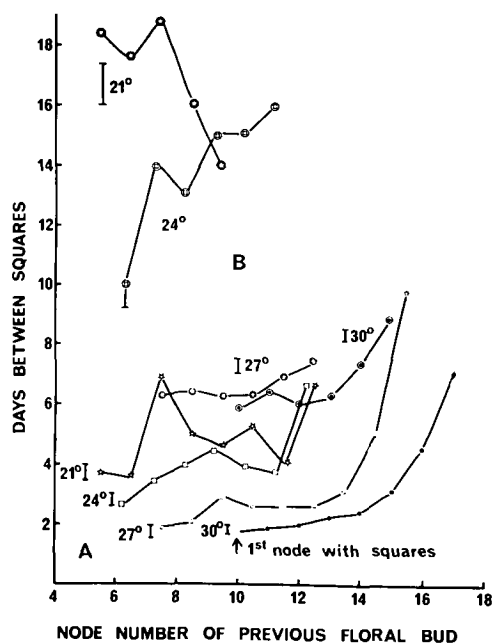


Fig. 4. Rate of production of squares or floral buds 3 mm on a side for plants growing from 21 to 30 C. (A) Days between first squares on successive fruiting branches on the main stem. (B) Days between the first two squares within the same fruiting branch or sympodium. Values given are the means for 8 plants. The abscissa gives the main stem node to which the sympodium is attached.

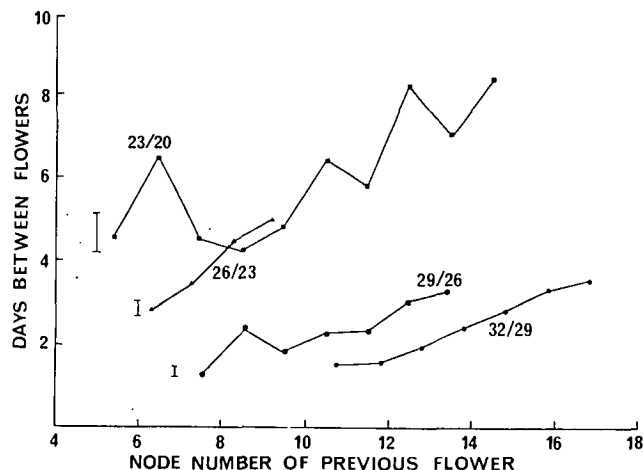


Fig. 5. Days between production of first flowers on successive fruiting branches on the main stem for plants growing from 21 to 30 C.

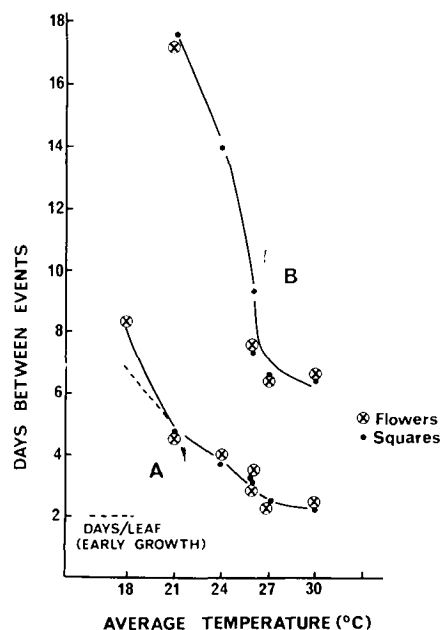


Fig. 6. Average time intervals between production of successive squares and flowers. (A) First squares or flowers on successive fruiting branches on the main stem and (B) between first two buds or flowers on the same fruiting branch. Days/leaf from Fig. 4 is put in broken line where it deviates from rate of production of squares and flowers between successive fruiting branches on the main stem.

Mauney's Fig. 1, days to five expanded leaves, and following Zaitzev we assumed four isophases to the first true leaf and four more to the expansion of the fifth leaf. Similar estimates were made from Canberra data (unpublished). All these estimates are presented in Table 2 along with Zaitzev's values. The ratio between time intervals at 30 C compared to those at 20 C was often a little more than two. Although the various estimates agreed reasonably well, some discrepancies were apparent, possibly because of difficulties in pinpointing exact dates of events at low temperatures. We might note also that the effects of changing temperature have not been studied and they need further attention (13).

Included in Fig. 7 are leaf plastochrons as well as the time required to expand a leaf from 1 × w of 10

Table 2. Comparison of time intervals between appearances of two successive organs as determined from our measurements and estimates from the literature.

Temp. °C	Duke plastochron	Days between events			
		Zaitzev isophase values	Plastochron		Isophases, Zaitzev definition
			Mauney*	Hesketh†	
15		7.3			
18	8.3	5.4			
20		4.4			
21	4.6		3.8	4.8	
22			3.5	4.7	5.7
24	3.6	3.0	3.0	3.1	4.2
25			2.5		3.7
26	3.0				3.5
27	2.4	2.6			3.3
28			2.2		3.1
30	2.3	2.4	2.1	2.2	2.9
32		2.4	2.0		2.7
Ratio 20/30	2.2	1.8	2.0	2.2	2.2

\* Using Mauney's Tables 4 and 5 and his assumptions about time of floral initiation.  
† Canberra data (unpublished, for variety 'M-8'). ‡ Using the hatched line in Mauney's Fig. 1.

to 100 cm<sup>2</sup> divided by 2.303. Such values are the reciprocals of the relative rate of leaf expansion, or 1/R<sub>A</sub><sup>4</sup> in days, by definition. The relative leaf growth rates and our arbitrary events are affected relatively the same by temperature.

From the date of the first square, days from squaring to flowering, and the boll period (days from flowering to boll opening), one can generate a fruiting map of the plant with squares every isophase on successive sympodia up the main stem and every 2.7 isophases within a sympodium, with dates for flowering, and boll opening for surviving floral buds and bolls. Given fruiting sites per sympodium, one can generate a maximum theoretical squaring rate which will approach the reciprocal of the plastochron on the main stem multiplied by the number of fruiting sites per sympodium. These maps and squaring rates are encountered often in the literature (5); now we offer better temperature corrections.

$$^4 R_A = (\ln A_2 - \ln A_1) / (t_2 - t_1); \text{ as } t_2 \rightarrow t_1, R_A \rightarrow (1/A) (dA/dt).$$

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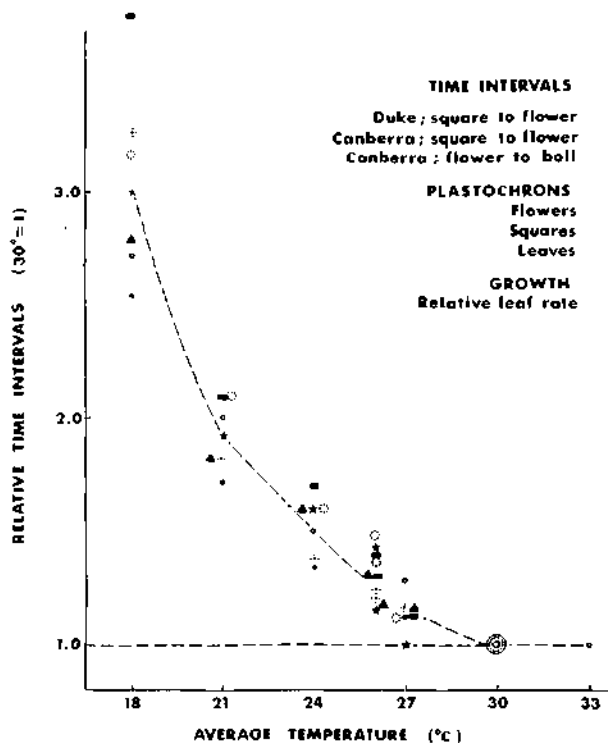


Fig. 7. Relative change in isophase or plastochron with decreasing temperature with the time interval at 30 C for each process plotted being set to 1.0. The reciprocals of these values are developmental rates, the mean of which are a linear function of temperature.