

*THE GROWTH RATE OF AN ANNUAL PLANT HELIANTHUS**

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If we assume that growth is a dynamic process and that the organism is produced as its end-product, certain relations ought to exist between the size of the organism at any given time and the final size attained in time, T.

Growth begins at a slow rate, but as the reaction proceeds it goes on at an increasingly rapid rate until it reaches a maximum velocity, then the rate decreases until the reaction comes to a stop. This is precisely what happens in autocatalytic processes in which the reaction is catalyzed by one of its own products. It therefore becomes of interest to inquire whether the growth rate of an organism, or group of organisms, approximates the rate of autocatalysis. As will be shown in this article, the equation of autocatalysis expresses admirably the growth rate of plants studied.

Growth may be considered as a function of two variables. The first of these is the genetic constitution of the individual. The second is the resultant of all those factors that make up what is commonly called the environment of the organism. The factors of the first group are essentially *internal*; those of the second group, essentially *external*. In analyzing the growth process it is of interest to separate so far as possible the results of these two classes of factors. If the growth rate follows approximately the course of an autocatalytic reaction, it is safe to assume that it is controlled by some internal factor resident in the organism. If it departs from the theoretical course more widely and uniformly than might be expected upon the basis of pure chance, we may believe that some other, presumably external, factor is of sufficient weight to control or, at least, influence the growth rate.

The studies embodied in the present paper are based on measurements of a group of fifty-eight sunflowers, grown for the purpose on the grounds of the Citrus Experiment Station, Riverside, California. They were grown on a small piece of tolerably uniform soil to which water sufficient to maintain satisfactory soil-moisture conditions was applied every seven days. The plants grew from the middle of May to the middle of August during a time when heat and light were ample for plant growth. As soon as the plants had reached an average height of more than 10 centimeters, sixty of the normal, appearing plants were selected at random throughout the small plot and marked with suitable labels. (During the course of the observations, two plants had to be eliminated on account of accidents). Each plant was marked with india ink at a distance of 10 centimeters below the growing tip. This mark served as a point from which further measurements were made. The

sunflower was chosen for this work because of the fact that it grows without producing branches and it was thought that measurements of growth and weight represented the growth of the entire organism with a fair degree of accuracy. The adjacent plants were removed from the vicinity of those selected so that there was space of about 20 centimeters between any plant and its nearest neighbor. In short, environmental conditions were made as nearly uniform for the individuals in this small group as it was feasible to make them under field conditions. In the latter part of July the terminal buds began to develop into blossoms and coincidentally the plants ceased to elongate.

The plants used in these studies were evidently of mixed ancestry as shown by the presence of branched and unbranched individuals. The seed had been bought at a seedstore and nothing was known of its pedigree. The branching habit is regarded by Shull (1908) to be a Mendelian character.

TABLE 1
CONSTANTS FOR GROWTH AND VARIATION IN HEIGHT OF HELIANTHUS PLANTS

DAYS	MEAN HEIGHT	INCREASE OF MEAN HEIGHT	STANDARD DEVIATION	COEFFICIENT OF VARIABILITY
	<i>cm.</i>	<i>cm.</i>		
7.....	17.93 ± 0.14	7.93 ± 0.14	1.62 ± 1.01	9.03 ± 0.56
14.....	36.36 ± 0.43	18.43 ± 0.43	4.83 ± 0.30	13.28 ± 0.85
21.....	67.76 ± 0.78	31.40 ± 0.89	8.93 ± 0.56	13.17 ± 0.84
28.....	98.10 ± 1.38	30.34 ± 1.59	15.60 ± 0.98	15.90 ± 1.02
35.....	131.00 ± 1.73	32.90 ± 2.21	19.52 ± 1.22	14.90 ± 0.95
42.....	169.50 ± 2.21	38.50 ± 2.81	25.00 ± 1.56	14.75 ± 0.94
49.....	205.50 ± 2.92	36.00 ± 3.66	33.00 ± 2.07	16.06 ± 1.03
56.....	228.30 ± 3.41	22.80 ± 4.49	38.47 ± 2.41	16.84 ± 1.08
63.....	247.10 ± 3.80	18.80 ± 5.10	42.92 ± 2.69	17.38 ± 1.12
70.....	250.50 ± 3.76	3.40 ± 5.35	42.48 ± 2.66	16.95 ± 1.09
77.....	253.80 ± 3.99	3.30 ± 5.48	45.06 ± 2.82	17.75 ± 1.13
84.....	254.50 ± 3.89	0.70 ± 5.57	43.90 ± 2.75	17.25 ± 1.11

One important difference should be noted between the plants described by Shull and those in our series, viz: Shull's plants branched from the lower nodes of the stalk, while ours branched only from the upper nodes. Church (1915) regards the branched form as a mutant of the unbranched and believes that it is the oldest mutation on record.

The branched form usually produces a head on the apex of each branch, whereas the unbranched form produces one head from the apical bud of the stem and no other.

This mixture of branched and unbranched stems is not thought to affect the validity of the measurements upon which the present study is based, since only seventeen out of the fifty-eight plants were branched. The average heights of the two classes at maturity were close enough together to be within the range of the probable error, though the length of the average growing season of the branched plants was 4.6 days longer than that of the

unbranched plants. The number of heads produced by the branched plants ranged from three to thirteen.

Rate and Extent of Growth.—Fifty-eight plants were measured at seven-day intervals, from the time when each plant was marked 10 centimeters below the growing tip until no further elongation occurred. On the eighty-fourth day, when the last measurement was taken, the plants averaged 254.5 centimeters high to the upper side of the head, with a range from 164 centimeters to 339 centimeters. The mean growing period in days was 69.79 ± 2.17 . The mean height of the plants is shown by figures in table 1, along with the standard deviation and coefficients of variability. The mean height of plants at seven-day intervals is shown graphically in figure 1.

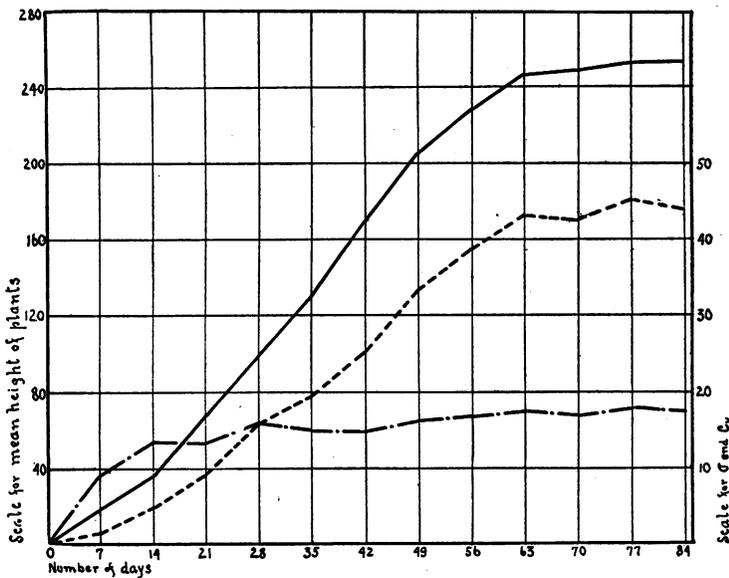


FIG. 1. GROWTH AND VARIABILITY OF HELIANTHUS

Mean height of plants —————
 Standard deviation - - - - -
 Coefficient of variability -

The data show that the plants rapidly increased in height, the maximum growth rate being exhibited between the thirty-fifth and the forty-second days, i.e., about the middle of the grand period of growth. The growth rate was smaller at the start, rapidly increasing until it reached its maximum and then declining as it approached the end of the grand period of growth.

The standard deviations of the mean values increase as the means increase, but not at a proportional rate. In this case the coefficient of variability is a better measure of the variability since its size is more nearly independent of the height of the plants. This coefficient does not increase during the latter

part of the growth period. It increased very rapidly at first, but remained fairly constant after the 28th day. The variability thus appeared to reach a constant value which changed but slightly as the plants approached maturity.

The decline in the growth rate of a plant began to appear as the flower bud on the apex of the stalk began to be differentiated. As the 'head' developed, the growth of the stalk became slower, showing agreement with the condition accompanying tassel formation which Pearl and Surface (1915) found in maize. After the flowers of the composite 'head' had been pollinated there was no fur-

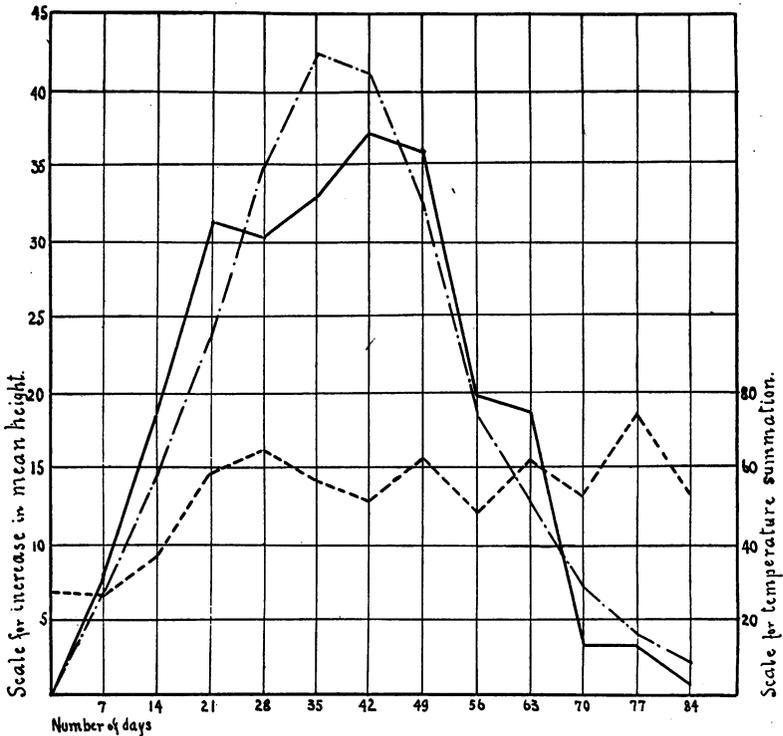


FIG. 2. INCREASES IN MEAN HEIGHT OF HELIANTHUS AT 7 DAY INTERVALS

Observed mean height —————
 Theoretical mean height - - - - -
 Temperature summations - . - . - .

ther elongation of the stalk. It is evident that from this time on the growth forces of the plant are devoted to seed-formation instead of stalk-elongation. Thus, variability in the time of blossoming may, and undoubtedly does, influence the grand period of growth and the total growth of this plant.

When the flowers have been pollinated the head which previously stood erect becomes pendant. The floral surface which is uppermost during the prepollination period, is lowermost in the post-pollination period.

An examination of the consecutive increases in mean height of the plants may help to give a clearer picture of the distribution of the growth increments of these plants. The mean growth increases observed at seven-day intervals have been plotted out in figure 2. The increases, starting from the day on which the plants were marked, show a general trend upward for the first forty-two days and a decline for the following forty-two days. Inspection of the graph shows that the line does not rise and fall smoothly, there being several abrupt changes. The mean height increased rapidly from the beginning to the twenty-first day. The rate fell off somewhat to the twenty-eighth day, then increased gradually until the maximum was reached on the forty-second day. From the forty-second to the forty-ninth day the rate fell off slightly and then declined abruptly to the fifty-sixth day. From the fifty-sixth to the sixty-third day there was only a slight decline in the rate, but from the sixty-third to the seventieth day there was a rapid decline followed by a halt until the seventy-seventh day, and then a descent to a point near the eighty-fourth day where growth ceased entirely.

The Correspondence Between Growth and Autocatalysis.—It may next be in order to inquire concerning the nature and action of some of the internal factors which influenced the growth of these plants. Studies on the growth of animals made by Robertson (1908, 1915) and of bacterial activity made by Miyake (1916) have shown the similarity of these processes to that of autocatalysis. In autocatalysis one of the products of the reaction catalyzes the reaction. Such reactions begin slowly, but as more of the catalyzing substance is produced the reaction goes on at an increasingly rapid rate. As the supply of reacting substances is used up, the reaction begins to slow down and comes eventually to a stop.

Brief mention will be made here to the formula used to express the course of an autocatalytic reaction. The reader who wishes more complete mathematical discussion should consult papers of Robertson (1915) and Miyake (1916). An autocatalytic reaction may be expressed by the differential equation

$$\frac{dx}{dt} = Kx(A - x),$$

in which A is the initial quantity of material subject to transformation, x is the amount transformed at time t , and K is a constant. The integral form of this equation is

$$\log \frac{x}{A-x} = K(t - t_1),$$

in which t_1 is the time at which the reaction has run half way to equilibrium; that is, the time at which $x = A/2$.

Translating these functions into terms of growth, we let A represent the final mass of the plant; x , the size of the plant at any time, t ; t_1 , the time at which

the mass of the plant is half the final mass, etc. Obviously it would be better to weigh the sunflower plants, but as this would require severance between the plant and the soil, it would not have been practicable to use the same plants for subsequent measurements. In the case of a straight unbranched stalk (such as most of these sunflowers were), it seems sufficiently accurate to use the height of the plant as an index of the amount of growth, at least up to the time of flowering.

In the case of these sunflowers, A is 254.5 cm., t_1 is 34.2 days, then

$$\log \frac{x}{254.5 - x} = K (t - 34.2).$$

Substitution of the various values of x and corresponding values of t gives the corresponding values of K which are shown in the third column of table 2.

TABLE 2
CONSTANTS FOR THE MEAN HEIGHT OF SUNFLOWERS AT SUCCESSIVE INTERVALS

t days	X (OBSERVED) cm.	K	X (CALCULATED) cm.	θ cm.
7.....	17.93	0.04128	17.05	-0.88
14.....	36.36	0.03851	31.43	-4.93
21.....	67.76	0.03341	55.35	-12.41
28.....	98.10	0.03274	90.09	-8.01
35.....	131.00	0.03250	132.21	+1.21
42.....	169.00	0.03794	173.06	+4.06
49.....	205.50	0.04196	205.64	+0.14
56.....	228.30	0.04312	227.01	-1.29
63.....	247.10	0.05295	239.74	-7.36
70.....	250.50	0.04997	246.87	-3.63
77.....	253.80	0.05892	250.56	-3.24
84.....	254.50		252.46	-2.04

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 0421

The average value of K determined in this way is .0421. Using this value of K we proceed to find the values of $K (t - t_1)$, and from these, with the assistance of Robertson's tables, a series of calculated values of x were obtained. These were the theoretical heights of the plants at the successive intervals provided the original equation was a correct expression of the growth rate. The divergence, θ , between the observed and the theoretical values is shown for each interval in the last column of the table. On the whole, the correspondence between the observed and the theoretical values is very satisfactory. The observed and calculated heights of the plants are shown graphically in figure 3.

More accurate comparison of these values was made by testing the goodness of fit of the theoretical to the observed curve. Employing the method given by Elderton (1902), it was found that $P = .9256$, which is taken to indicate a satisfactory fit, since in approximately ninety-two cases out of one

hundred, a random sampling would give values diverging more widely from the theoretical than those actually found.

Since the observed values agree so well with the theoretical values, it seems safe to assume that the growth rate is governed by constant internal forces rather than by external forces which would be expected to be more casual in-operation.

The theoretical values for the consecutive increases in the mean height of the plants give a smoother curve than the observed values give, as shown in figure 2. The sag in the observed curve near the twenty-eighth day does not appear in the theoretical curve. The summit of the theoretical curve is near

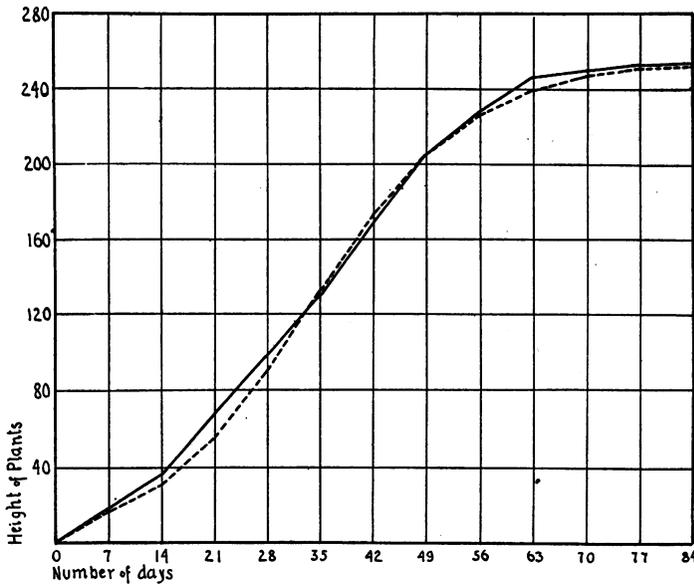


FIG. 3. COMPARISON OF OBSERVED AND CALCULATED VALUES FOR THE MEAN HEIGHT OF HELIANTHUS

Observed —————
 Calculated - - - - -

the thirty-fifth day, thus agreeing with the computed value of $t_1 = 34.2$ days, the time at which half the final height is attained and at which growth is most rapid.

The assumption having been made that the growth was more largely governed by internal than external factors, and positive evidence in favor of the assumption having been obtained, it is next in order to investigate the relationship between growth and some of the more prominent factors of the external environment.

Temperature is known to have a potent effect upon growth, especially if it departs widely from the optimum requirements of the organism. In a prob-

lem like the present, we are more concerned with the temperature summation than with the mean temperature unless the range is very large.

It is clear that we shall not arrive at a correct value if we take an arithmetical average of the maximum and minimum daily temperatures, because we do not in that way take any account of the time during which either prevailed, or of the range of temperatures. For example, the minimum temperature on a given day may be 50° and the maximum temperature 90°, an average of 70° but if the maximum temperature prevails for only two hours out of the twenty-four, while the temperature varies between 50° and 65° for most of the daily period, it is obvious that the mere arithmetical mean, 70°, is a false expression of the temperature. The values must be weighted in order to give an average which correctly represents the temperature condition.

A method of measuring temperature summations has been employed which is believed to be fairly satisfactory. It consisted in finding the product of hours multiplied by degree of temperature above 40°F. and is expressed in degree-hours. A degree-hour may be regarded as one degree of effective temperature acting for one hour. The point 40°F. was arbitrarily chosen as a basal point, at or near which plant growth will proceed. The method of obtaining the summation of effective temperature consisted in measuring with a planimeter the area between the pen tracing and the 40°F. line on thermograph records obtained from a self registering thermograph situated about 100 yards from the plantation of sunflowers. This method gives a direct index of temperatures above the 40° point, but does not take into account the efficiency of temperatures as assumed by the van't Hoff-Arrhenius principle.

The coefficient of correlation between the degree-hours and the increase in height of the sunflower plants for each seven-day interval was calculated. Its value turned out to be $r = 0.199 \pm 0.187$. There are some indications here of a positive correlation, but, since the probable error nearly equals the coefficient in magnitude, no reliance can be placed upon the existence of a correlation.

Reference to the graph showing temperature summations in figure 2, shows little correspondence with the curve representing growth increases, except in the first twenty-one days of the period.

In a somewhat similar way we have investigated the possibility of a correlation between growth rate and the coefficient of the evaporating power of the air, the latter value being obtained from the readings of a spherical porous-clay atmometer-bulb located about one hundred yards from the plants. The coefficient of correlation for these values was even less than that in the foregoing case, being 0.041 ± 0.202 . The coefficient in itself is so small as to lack significance, and when compared with its probable error it fails entirely to indicate any correlation between these two factors.

These statements are not to be construed as arguments against the effect of temperature and transpiration upon the rate of growth of plants. Our argument is merely intended to emphasize the greater importance of the inter-

nal factors in determining the growth, reproduction and senescence of the plant, factors which are so potent that they overbalance external factors so long as the latter do not too closely approach minimum or maximum values.

That the oncoming of reproductive processes induces changes in the growth rate of the organism is a fact too well known to require comment, but is well illustrated by the behavior of the sunflower.

It appears that growth, its rate, its grand period, and, to some extent, its amount are so steadily controlled by factors inherent in the genetic constitution of the sunflower that these factors are prepotent unless the external conditions depart widely or repeatedly from the optimum. Plants in this respect are more sensitive to variations in their external environment than animals, yet these studies show that even plants are not entirely dependent upon environmental (external) conditions for determining their growth rate.

It may be of interest to inquire whether the formula of autocatalysis applies, as well to the smaller plants as to the medium and large plants of this group and how the mean values of K for different groups agree.

TABLE 3
HEIGHT AND GROWTH CONSTANTS OF PLANTS ENDING IN THEIR GROWTH IN DIFFERENT QUARTILES

	QUARTILE			
	I	II	III	IV
Final height of plants. . . .	198 cm.	238 cm.	272 cm.	312 cm.
Mean value of K	0.0440±0.0011	0.0421±0.0016	0.0429±0.0017	0.0443±0.0023
Standard deviation of mean value of K	0.0052±0.0008	0.0079±0.0011	0.0079±0.0012	0.0111±0.0016

As a basis of classification we divided the plants into quartiles, based upon their heights at maturity. Quartile I, contained the smallest plants, quartile II, the next larger and so on. Since 58 is not exactly divisible by 4, the quartiles were not exactly of equal size: quartiles I and III contained 15 plants each and quartiles II and IV contained 14 each. An average of the heights of each group of plants at each time interval, t , gave a corresponding value of x , from which the several values of K were computed. (See table 3).

The mean values of K are remarkably constant for the different quartiles, in fact all are within the range of their probable errors. This may be regarded as evidence that the growth constant has the same value for all classes of plants in this population without regard to their relative heights, since the relation between the final height and the height at any given time obeys the same principle.

A brief consideration of a parallel case will make it evident that such a relation must exist in this sort of reaction. The inversion of cane sugar is a familiar case of autocatalysis in which one of the products catalyzes the reaction.

It is plain that the amounts of invert sugar finally formed in four different flasks may vary, depending upon the amount of cane sugar originally present, yet the constant of autocatalysis remains the same and the time may be the same in each case. This relation exists because the quantity dx/dt is proportional to the quantity of cane sugar remaining, which may be represented by $(a - x)$ where a is the original quantity of cane sugar at the beginning, i.e., when $t = 0$.

The senior author has discussed the distribution of these plants in the several quartiles in a paper soon to be published (Reed, 1919), showing that said distribution is due to some agency operating to cause variability in height other than purely casual agencies which might be expected upon the basis of pure chance. The data presented in table 3, indicate that no difference in the growth constants exists which can account for the larger or smaller size of a part of the population. Whether the differences in the amount of material produced, i.e., the size of the plants, is to be referred to differences in amount or activity of the catalyst, or of the substrate, cannot be discussed upon the basis of the data now in hand.

An additional point may be discussed in this connection, viz., "Are the values of the growth constants more widely dispersed from their means in one quartile than in another?" We may take the standard deviations of the means as a measure of the dispersion of the individual values. Reference to table 3 shows that the standard deviations increase from the lower to the upper quartiles, which would seem to indicate that the growth rate of the larger plants fluctuates more from the mean than is the case in the smaller plants.

Summary.—1. Measurements of sunflower plants at intervals of seven days showed that their growth rate approximated closely the course of an autocatalytic reaction.

2. The close correspondence of the actual mean height of plants to that required by the equation of autocatalysis is taken to indicate that the growth rate is governed by constant internal factors rather than by external factors which would be expected to be more casual in their influence.

3. The growth rate showed no strong correlation either with temperature-summations, or with transpiration-summations.

4. The value of the growth constant was not perceptibly different for the larger or smaller plants in this population.

*Paper 56 from the University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

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