THE NATURE OF THE GROWTH RATE.*

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(Received for publication, March 5, 1920.)

Recent studies (Robertson (1908) and Reed and Holland) have shown that the rate of growth of certain organisms corresponds to the rate of an autocatalytic reaction. At the present time it seems profitable to extend the inquiry to several different types of plants and to learn something of their growth rates.

The Growth Rate of Pear Shoots.

During the season of 1919, weekly measurements were made of the growth of shoots of young Bartlett pear trees. The young shoots of the pear (Pyrus communis L.) are good material for such inquiry because of their vigorous growth and generally unbranched condition during the 1st year. The trees on which the shoots were selected and marked had been planted 3 years previously. They made good growth during the season in which the measurements were being made, but, on account of their age, produced no fruit. On April 24, 1919, fifty shoots on twenty-six trees in different parts of the orchard were selected. One shoot was subsequently broken and had to be eliminated. The remaining forty-nine shoots were measured each week until September 3, at which time elongation had ceased. The length of each new shoot was determined weekly by measuring the distance from its base to the apical bud. Though a few shoots did not cease elongation until the 133rd day (September 3) the average length of the growing season of all shoots was 97 ± 1.7 days.

* Contribution No. 65 from the University of California Graduate School of Tropical Agriculture and Citrus Experiment Station.
Robertson has called attention to the correspondence between growth of organisms and autocatalysis. He has shown that the rate of growth may also be expressed by the differential equation

\[ \frac{dx}{dt} = kx (a - x) \]

in which \( x \) is the size of the organism at time \( t \); \( a \) is the final size of the organism; and \( k \) is a constant. When integrated, the above equation becomes

\[ \log \frac{x}{a - x} = K(t - t_i) \]

where \( K = ak \), \( t_i \) is the time at which the organism has reached half its final size; i.e., the time when \( x = \frac{a}{2} \). With the assistance of tables which Robertson (1910–15) has prepared, the constants and the theoretical values of \( x \) are easily obtained from observational data. The value of \( a \) was taken as 114 cm. and \( t_i \) as 47.4 days. Table I shows the computations made and the several values of \( K \). With the average value of \( K \) the values of \( x \) were calculated by the formula and are given in the fourth column of Table I. The agreement between the two is good except for the first three measurements. Fig. 1 shows the curve obtained from the calculated values together with the observed values of mean length at weekly intervals during the growing season.

This growth rate is of considerable physiological interest if we compare it with the growth rates of organisms mentioned elsewhere in the literature. Attention may be called to the fact that we are here dealing with the mean growth of a number of separate shoots on a small population of trees.

A word concerning the heterogeneity of the population may be useful. On the final day of measurements the shoots ranged in length from 69 to 171 cm. with an average of 113 cm. The standard deviation of the measurements was 21.14 cm. This indicates that we are dealing with a random selection of material and not one which was so closely selected that it was not representative of the shoots of such trees.
## TABLE I.

Growth Rate of Bartlett Pear Shoots for the Season of 1919.

<table>
<thead>
<tr>
<th>$t$</th>
<th>$x$ (observed).</th>
<th>$K$</th>
<th>$x$ (calculated).</th>
</tr>
</thead>
<tbody>
<tr>
<td>days</td>
<td>cm.</td>
<td></td>
<td>cm.</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0.0331</td>
<td>8.1</td>
</tr>
<tr>
<td>7</td>
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<td>0.0292</td>
<td>10.7</td>
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<tr>
<td>14</td>
<td>11</td>
<td>0.0264</td>
<td>15.4</td>
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<tr>
<td>21</td>
<td>19</td>
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<tr>
<td>35</td>
<td>40</td>
<td>0.0256</td>
<td>38.1</td>
</tr>
<tr>
<td>42</td>
<td>48</td>
<td>0.0194</td>
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</tr>
<tr>
<td>49</td>
<td>59</td>
<td>0.0194</td>
<td>54.4</td>
</tr>
<tr>
<td>55</td>
<td>69</td>
<td>0.0243</td>
<td>69.0</td>
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<tr>
<td>63</td>
<td>76</td>
<td>0.0194</td>
<td>80.4</td>
</tr>
<tr>
<td>70</td>
<td>86</td>
<td>0.0215</td>
<td>88.8</td>
</tr>
<tr>
<td>77</td>
<td>94</td>
<td>0.0228</td>
<td>95.6</td>
</tr>
<tr>
<td>84</td>
<td>100</td>
<td>0.0233</td>
<td>100.9</td>
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<td>102</td>
<td>0.0241</td>
<td>104.8</td>
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<tr>
<td>98</td>
<td>108</td>
<td>0.0247</td>
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</tr>
<tr>
<td>105</td>
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</tr>
<tr>
<td>112</td>
<td>111</td>
<td>0.0244</td>
<td>110.9</td>
</tr>
<tr>
<td>119</td>
<td>112</td>
<td>0.0243</td>
<td>111.9</td>
</tr>
<tr>
<td>126</td>
<td>113</td>
<td>0.0260</td>
<td>112.6</td>
</tr>
</tbody>
</table>

Average ........................................ 0.0242

---

**Fig. 1.** Growth rate of shoots of the pear tree. The curve represents the value obtained from the equation $\frac{x}{114 - x} = K(t - 47.4)$; points within the circles represent observed lengths at intervals of 7 days.
The data suggest that each shoot has a more or less independent supply of the catalytic agent which exercises such an important influence upon the rate at which growth proceeds.

The Growth Rate of Young Walnut Trees.

The data upon which this study is based were obtained from material growing in the grounds of the Citrus Experiment Station at Riverside.

In the spring of 1916 seeds of *Juglans nigra* L. (black walnut) had been planted in rows for nursery propagation work. The young trees which grew from these seeds were used for study in the summer of 1917; i.e., during their second season of growth. A part of the trees were grafted in the spring of 1917 with scions of *Juglans regia* (Persian walnut). A few weeks after growth from the scions started, all new shoots were removed, except one which furnished the data for the observations on this species. The balance of the *Juglans nigra* trees grew on during the second summer.

The *Juglans nigra* seedlings were selected on April 17 and marked by a line of India ink on the stem from which the distance to the terminal bud could be measured when desired. From a portion of the trees all laterals on the wood of the previous year were removed before measurements were begun, and the observations on these pruned trees were separately recorded. The growth from the *Juglans regia* scions was soon sufficient to afford measurements, and they were marked on May 29.

Measurements were made at each day of observation to determine the height of the tree stem from the ink mark to the terminal bud of the main axis. This could be ascertained with comparatively little error. It was planned to make measurements at intervals of 7 days, but other circumstances made it necessary to vary this interval at times. The exact length of the intervals is stated in Table II.

The population thus gave an opportunity for studying the following points: (a) the growth of seedling trees in the 2nd year of their life; (b) the growth of similar trees from which all laterals had been removed at the beginning of the 2nd year; and (c) the growth from scions of a distinct species growing on the same roots as (a) and (b).
Group (a) contained nineteen trees, Group (b) fifteen trees, and Group (c) twenty-five trees.

The mean height of the selected trees on the several days of measurement is represented graphically in Fig. 2. The data show that *Juglans nigra* grew quite uniformly from the commencement of the measurement on April 17 until about June 19 (the 62nd day). Between June 19 and August 6 (between the 62nd and 110th days) growth was considerably more rapid, but after August 6 growth gradually diminished until it ceased about September 3.

The mean growing period of this group of trees was 124 days after April 17. The coefficient of variability of the population at each
time of measurement had an approximate value of 25. There are fluctuations from this value, but the trees showed little tendency to increase in variability until near the end of the growing period.

The *Juglans nigra* trees from which all laterals were removed in the spring before growth began made the same type of growth as their unpruned neighbors, but in every case their mean height was less. The commonly accepted belief is to the effect that removing the lateral branches from a plant increases the growth of the main axis, but the results of this work directly contradict the above mentioned belief.

The mean growing period of the pruned seedlings was 122 days, or practically the same as that of the unpruned seedlings. Comparison of the figures shows that the pruned seedlings increasingly lagged behind their unpruned neighbors as the season advanced.
The *Juglans regia* trees were measured from June 5 to October 22. The data afforded by these measurements are shown in Table II. The average length of their growing season was 116 days from June 5, which means that the average tree ceased to grow on September 28, though it was October 22 before all trees ceased to increase in height.

We may proceed to examine the growth rate of these trees by a method which has elucidated many problems in the domain of physical chemistry.

![Graph](https://example.com/graph.png)

**Fig. 3.** Growth rate of *Juglans nigra* trees showing two cycles. Curves show computed values; points within circles show observed mean height at various intervals. AOB are axes for the upper curve.

Reference to the graph representing the mean height of the trees at successive intervals shows that the curve consists of two rather distinct parts, indicating that the growth period comprised in these records consisted of two cycles. The curve rises rather regularly from the 1st to the 62nd day, then rises more steeply to near the 110th day, when it takes a nearly horizontal position. A few simple calculations will show that the growth curve does not follow the path of a single autocatalytic reaction.
The period was therefore divided into two cycles, the first of which
ended at the 62nd day, and the second of which began at approximately the time the first cycle ended. Reference to Table III will
show the computations made. Since we are interested in rate it will
be proper to move our base line up to a point near that at which the
first cycle actually started. Actually 50 cm. were subtracted from
each mean in order to give a curve which would start near the inter-
section of the abscissa with the ordinate. For the first cycle the value
of \( a \) was taken as 32, and \( t_1 \) as 23.5. Accordingly

\[
\log \frac{x}{32 - x} = K (t - t_1)
\]

From this, the several values of \( K \) were computed and found to be fairly uniform. The average value of \( K \) was taken as 0.0325, and from it the values of \( x \) were computed by the above formula. The
root-mean-square deviation \( \sqrt{\frac{\sum dx^2}{n}} \) from the observed values was only 0.78 cm. It will thus be seen that the agreement between observed and calculated values is good.

### Table III.

Height of *Juglans nigra* Trees. Comparison of Observed Values with Those Computed from the Formula \( \log \frac{x}{a - x} = K (t - t_1) \).  

<table>
<thead>
<tr>
<th></th>
<th>( x - 50 ) (observed)</th>
<th>( x - 50 ) (calculated)</th>
<th>( x - 50 ) (observed)</th>
<th>( x - 50 ) (calculated)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( t ) days</td>
<td>cm.</td>
<td>cm.</td>
<td>cm.</td>
<td>cm.</td>
</tr>
<tr>
<td>7</td>
<td>6.2</td>
<td>0.0375</td>
<td>7.2</td>
<td>62</td>
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<tr>
<td>14</td>
<td>11.2</td>
<td>0.0283</td>
<td>10.5</td>
<td>69</td>
</tr>
<tr>
<td>21</td>
<td>14.4</td>
<td>0.0348</td>
<td>14.5</td>
<td>84</td>
</tr>
<tr>
<td>28</td>
<td>19.1</td>
<td>0.0380</td>
<td>18.7</td>
<td>87</td>
</tr>
<tr>
<td>34</td>
<td>21.5</td>
<td>0.0296</td>
<td>22.0</td>
<td>96</td>
</tr>
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<td>41</td>
<td>23.5</td>
<td>0.0252</td>
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<td>110</td>
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<td>55</td>
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<td>0.0317</td>
<td>29.2</td>
<td>117</td>
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<tr>
<td>62</td>
<td>30.9</td>
<td>0.0374</td>
<td>30.3</td>
<td>131</td>
</tr>
</tbody>
</table>

Average .................. 0.0325 .................. 0.0423
The data for the second cycle were similarly treated. The values were all diminished by 79 cm. The value of \( a \) was taken as 56 and that of \( t_1 \) as 85. The mean value of \( K \) was determined to be 0.0423 and from this the values of \( x - 79 \) were calculated by the same general formula as for the other cycle. The agreement between the calculated and observed values is quite good. A graphical representation of the values is shown in Fig. 3.

It thus appears that between April 17 and September 4 the growth of this population of *Juglans nigra* trees fell into two distinct cycles and that the rate of growth for each cycle followed closely the course of an autocatalytic reaction.

A similar type of growth rate was also found for the *Juglans nigra* trees from which the laterals had been removed at the beginning of the season. It has been shown (Reed and Holland) that the smaller members of a population have a type of growth rate similar to that of the larger individuals. That is, both groups were found to correspond to the equation which states that the growth in unit time is proportional to the product of the height at that time and the amount yet to grow, multiplied by a constant.

The growth rate of the *Juglans regia* trees was likewise studied. Here again it is advisable to deduct a constant amount from each height measurement in order to bring the base line near the point of origin of the part of the growth curve studied. In this case \( x_1 = x - 50 \). The value of \( a \) was found by approximations to be 153.2 cm. and \( t_1 = 96 \). We therefore have

\[
\log \frac{x}{153.2 - x_1} = K(t - 96)
\]

Table IV shows the observed values of \( x_1 \), the various values of \( K \), and the calculated values of \( x_1 \) with the mean value of \( K \). The root-mean-square deviation is 3.5 cm. The smallness of this divergence becomes apparent when we note that the probable errors of the mean values of \( x \) (Table III) are greater than 3.5 except in the first six cases. A graphic representation is given in Fig. 4.

It will be noted that the data for the growth rate of *Juglans regia* extend from June 5 to October 15. There appears to be but one growth cycle between these dates. This period begins close to the
time at which \textit{Juglans nigra} began its second growth cycle. We do not know whether \textit{Juglans regia} had two growth cycles, but the presumption is in favor of such an hypothesis.

Data such as these afford a new insight into certain phases of growth in the organic world. They show that the growth rate of these or-

\begin{table}
\centering
\begin{tabular}{|l|c|c|c|}
\hline
$t$ & $x_1$ (observed) & $K$ & $x$ (calculated) \\
\hline
days & cm. & & cm. \\
55 & 13.2 & 0.0250 & 15.9 \\
62 & 17.8 & 0.0261 & 22.1 \\
69 & 24.9 & 0.0264 & 29.9 \\
84 & 52.6 & 0.0233 & 53.2 \\
87 & 60.2 & 0.0210 & 58.8 \\
96 & 76.6 & & 76.6 \\
103 & 90.6 & 0.0229 & 90.5 \\
110 & 102.0 & 0.0213 & 103.6 \\
117 & 112.4 & 0.0210 & 115.1 \\
131 & 126.0 & 0.0190 & 134.7 \\
138 & 134.0 & 0.0201 & 138.0 \\
144 & 138.8 & 0.0205 & 141.9 \\
151 & 145.2 & 0.0229 & 145.1 \\
158 & 148.4 & 0.0244 & 147.5 \\
165 & 149.2 & 0.0228 & 149.2 \\
172 & 150.0 & 0.0222 & 150.4 \\
179 & 150.8 & 0.0216 & 151.2 \\
\hline
Average & 0.0228 & & \\
\hline
\end{tabular}
\caption{Height of \textit{Juglans regia} Trees. Comparison of Observed Values with Those Calculated from the Formula \( \frac{x}{a-x} = K (t-t_0) \).}
\end{table}

organisms follows a course as definite and as predictable as that of a chemical reaction. On the basis of pure chance we should not expect often to find a group of individuals which should follow a definite rate of development more closely than the laws of random sampling would require.

The onset of dormancy in the two species of \textit{Juglans} is worthy of notice. It should be remembered that the two lots of trees grew in adjoining rows in the nursery and received similar care as to irrigation,
Nevertheless the *Juglans regia* trees grew 42 days later than the *Juglans nigra* trees. It is well known that there is a great difference between these species in respect to distribution and resistance to cold weather. *Juglans regia* is reported to be a native of Persia, the Himalayas, and China, while *Juglans nigra* is a native of the eastern United States. The remarkable fact, as far as these notes are concerned, is that *Juglans nigra* trees went into a condition of dormancy early in September, while *Juglans regia* trees, growing in adjoining rows and with similar care, grew until the middle of October.

This observation sustains the conclusion drawn from the foregoing studies on the rate of growth, and indicates that the extent of the growth cycle as well as the amount of growth is controlled by internal genetic factors.

![Graph of Growth Rate](image)

**Fig. 4.** Growth rate of *Juglans regia* trees. The curve represents the values obtained from the equation \( \log \frac{x}{153.2-x_1} = K (t-96) \); points within circles represent the observed mean height at various intervals.
The Reliability of Various Criteria for Determination of the Growth Rate.

It will be well to discuss certain questions which will arise in the mind of the reader. He desires to know, for example, whether the growth rate will conform to a differential equation when we use some other criterion, e.g. weight, as a measure of growth. An examination of all possible measures of growth should be made, especially in view of the statement sometimes heard that growth is a process so complex that no single equation can successfully represent it.

It should be noted at the outset that every measure which is a mean of separate determinations of mass or volume is accompanied by an inevitable error. This error is made up of two separate errors. The first is due to the fact that the individuals measured were not truly representative of the population, i.e. they did not constitute a good "random sample"; the second is due to the errors which arise in the use of the measuring device (meter stick or balances). If the errors are of a purely random nature they will largely offset one another in a large series, but in a small series they may materially affect the mean. We need not expect, therefore, to find agreement between observed and calculated values as close as the physical chemist obtains with his material. A difference of not more than 10 per cent of the calculated value may be regarded as sufficiently accurate to inspire confidence in the results.

Kreusler has recorded the growth of several varieties of maize at 7 day intervals. Height of plant, green weight (entire plant), and dry weight (entire plant) were determined on fairly large samples of plants. I have found that the growth rate of the different varieties determined by Kreusler follows the equation previously used

$$\frac{dx}{dt} = kx(a-x)$$

The determinations made upon one variety (Hühner-maís) will be given as an illustration. Those who are interested may profitably compute the growth rates of the other varieties which Kreusler followed. Reference to Table V shows undoubted errors in the weight of the samples at various dates. These can only be due to the use of too small a number of plants to give a true representation of the
population at that date. Table V shows a comparison of the growth rates of maize (Hühner-mais), with the height, green weight, and dry weight of the plants, recorded at intervals of 7 days. I have determined the value of $K$, the growth constant, for each measurement and, from the average value of all determinations, have calculated the value of $x$ for corresponding values of $t$, using the tables prepared by Robertson (1910–15). The average divergence of the three sets of values is not large, particularly in view of the errors above mentioned. The results show a sufficiently good correspondence to inspire confidence in their reliability.

It will be seen that the growth rate of the maize plants follows the course of an autocatalytic reaction no matter whether we use as a criterion mean height, green weight, or dry weight. Their growth is similar to a chemical reaction in which one of the products of the reaction acts as a catalyst.

Attention may next be directed to some data recently published (Eckles and Swett) on the growth of heifers. The measurements

<table>
<thead>
<tr>
<th>$t$</th>
<th>Mean height</th>
<th>Mean green weight</th>
<th>Mean dry weight</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$x$ (observed)</td>
<td>$K$</td>
<td>$x$ (calculated)</td>
</tr>
<tr>
<td>days</td>
<td>cm.</td>
<td>cm.</td>
<td>gm.</td>
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<tr>
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<tr>
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<td>0.0632</td>
</tr>
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</table>
appear to have been carefully made and at regular intervals. They therefore afford good material for study. Eckles and Swett used various criteria for measuring the heifers. They concluded that height at the withers is the most reliable measure, though for comparative studies weight is also useful.

In computing the growth rate of these animals I have used a slightly different equation; viz., \( \frac{dx}{dt} = k(a - x) \) which upon integration becomes \( x = a(1 - e^{-kt}) \).

![Graph](../images/graph.png)

**Fig. 5.** Growth rate of Jersey heifers represented by mean weight. The curve shows the values obtained from the equation \( x = 850(1 - e^{-0.065t}) \); points within circles represent observed weights at intervals of 2 months.

The rate as thus expressed is directly proportional to the amount of growth yet to be made. It is therefore more rapid at the outset and slower near maturity than the formula used for computing the growth rate of maize in Table V. In the case of the heifers, \( a \), the weight at 3 years of age, was found by a series of approximations to be 850 pounds, and \( k \), the growth constant, was 0.065. The equation used for determining the calculated values of \( x \) was therefore \( x = 850(1 - e^{-0.065t}) \) (Fig. 5).
It will be seen that the observed and calculated values of $x$ agree very well, especially when one bears in mind the extent of variability in biological material. In the latter part of the period the observed values are consistently higher than the calculated. These weight differences are plainly due to the increase in weight during pregnancy. The first parturition occurred at 30 months. As it is, however, the root-mean-square deviation between observed and calculated weights is only 20 pounds.

Inquiry may next be directed to the rate at which these animals increased in size and to the value of different kinds of measurements. Eckles and Swett found that the most reliable size measurement was the height of the animal at the withers. The mean height at birth was 66.1 cm.; at 4 years it was 125.6 cm. It thus appears that at birth the calf is a little more than half as tall as the mature cow. When we come to study the growth rate it is evident that we cannot use the postnatal life period as the complete growth cycle, because the animal has attained over half its height before birth. Let us assume that height growth begins near the beginning of the gestation period, then

\[ x = 128 \left( 1 - e^{-0.08(t+9)} \right) \]

FIG. 6. Growth rate of Jersey heifers represented by height at withers. The curve shows the values obtained from the equation $x = 128 \left( 1 - e^{-0.08(t+9)} \right)$; points within circles represent observed heights at various intervals.
we shall use $t+9$ as the time instead of $t$, the observed time from birth. By a series of approximations, 128 was taken as the value of $a$, and 0.08 as the value of $k$. The formula used was then $x = 128 \left(1 - e^{-0.08(t+9)}\right)$ (Fig. 6). The agreement for the most part is strikingly close. The close correspondence between the observed heights and those calculated by the formula bears out the observation of Eckles and Swett that the growth of the skeleton of the cow is less influenced by conditions of gestation and lactation than the other criteria of growth.

Summing up the data on the growth rate of Jersey heifers as given above, it appears that they grow by a definite rate which can be represented as a reaction in which the increase in any given interval is proportional to the amount of growth yet to be accomplished. It does not greatly matter whether one uses height at withers or weight, though the former is slightly more accurate.

In the case of maize and of heifers it appears that growth proceeds by a definite quantitative rate, no matter whether height or weight is used as a criterion.

SUMMARY.

1. The growth rate of organisms may be considered as a chemical reaction which gives the mature organism as its end-product. The organism grows at a definite rate which is, at any moment, proportional to the amount of growth yet to be made.

2. Shoots of young pear trees measured at weekly intervals during the growing season showed a rate similar to that of an autocatalytic reaction.

3. Young walnut trees showed distinct cycles of growth in a single season, but the growth in each cycle proceeded at a rate corresponding to an autocatalytic reaction.

4. The growth rate follows a definite, quantitative course though judged by different criteria. Data are presented for maize in which green weight, dry weight, and height of the plant are used. Data for cattle show that either weight or height of the animal may be used as a criterion.
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