TIME RELATIONS OF GROWTH.

II. THE EQUIVALENCE OF AGE IN MAMMALS ESTIMATED ON THE BASIS OF THEIR GROWTH CONSTANTS.*

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I.

INTRODUCTION.

In the preceding communication of this series,1 it was explained that the smoothed curves of growth in weight of animals are usually sigmoid, yet they have the point of inflection not in the center of the curve, but where slightly over one-third of the mature body weight is reached; and that after the point of inflection the course of growth in weight may be represented by the exponential equation

\[ W = A - Be^{-kt} \]  

In this equation, \( W \) represents the weight of the animal at the age \( t \), \( A \) represents the weight of the animal at full maturity, \( e \) is the natural base of logarithms, \( B \) is a constant the significance of which was explained in detail in the preceding communication, and \( k \) represents the fractional decline in growth. It is, of course, evident from equation (1) that for the period of growth for which the equation holds true, the velocity of growth (that is the gain in weight per unit time) declines in a geometrical progression with age, and that \( k \) represents the fractional decline in the velocity of growth.

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Equation (1) is a compact description of the time relations of growth representing a period of growth during which nearly two-thirds of the mature body weight is gained. It contains no empirical constants and, as was suggested in the preceding communication, it may have a rational basis in the mechanism underlying the decline in growth. This equation may, therefore, be tentatively considered as a law of growth during the period of declining growth velocity.

\[ A = A_0 e^{-kt} \]

**Fig. 1.** The relation between the numerical values of the velocity constants of growth, \( k \), and the time required to reach 98 per cent of the mature value, \( A \), in different animals.

**II. Equivalence of Age.**

The constant \( k \) in equation (1) has a very definite meaning; it represents, as already explained, the fractional decline in the velocity of growth with age. The greater the fractional decline, \( k \), the more rapidly will the limiting or mature value \( A \) be approached. Indeed, the rapidity of approach to the mature weight, \( A \), is directly proportional to the numerical value of \( k \), as shown in Fig. 1, and the relative
The relation between the numerical value of the growth constant, \( k \), in different animals and the time required to reach 98 per cent of the mature weight (upper line) and 50 per cent of the mature weight (lower line) plotted on logarithmic coordinate paper. The linear distribution of the data on this paper indicates that the time, \( t \), required to reach a given fraction of the mature weight is inversely proportional to \( k \). That is

\[ t = \frac{c}{k} \]

\( c \) is a constant. \( c \) has a value of 4.35 when \( t \) represents the time required to reach 98 per cent \( A \); \( c \) = 1.117 when \( t \) represents the time required to reach 50 per cent \( A \).

The data on the 50 per cent line are less evenly distributed than on the 98 per cent line due to the fact that at the lower levels the period of growth preceding the point of inflection with which equation (1) is not concerned becomes a factor of relatively increasing importance.
duration of the periods of growth of two animals is, therefore, inversely proportional to the numerical values of their \( k \)'s. These facts give us a basis for computing the equivalence of growth age in different animals.

TABLE I.

<table>
<thead>
<tr>
<th>Species</th>
<th>Age equivalence</th>
<th>Weight equivalence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( \text{kg} )</td>
<td>( \text{kg} )</td>
</tr>
<tr>
<td>Jersey cow (Eckles)</td>
<td>1.000</td>
<td>4.26</td>
</tr>
<tr>
<td>Ayrshire cow (Eckles)</td>
<td>1.080</td>
<td>4.60</td>
</tr>
<tr>
<td>Holstein cow (Eckles)</td>
<td>1.174</td>
<td>5.00</td>
</tr>
<tr>
<td>Duroc-Jersey swine, females (F.B. Mumford)</td>
<td>0.870</td>
<td>3.70</td>
</tr>
<tr>
<td>Suffolk sheep, females (Murray)</td>
<td>0.292</td>
<td>1.24</td>
</tr>
<tr>
<td>Shropshire-Merino sheep, females (Murray)</td>
<td>0.287</td>
<td>1.22</td>
</tr>
<tr>
<td>Guinea pig, males (Wright)</td>
<td>0.235</td>
<td>1.00</td>
</tr>
<tr>
<td>White rat, unmated females (Donaldson, Dunn, and Watson)</td>
<td>0.084</td>
<td>0.357</td>
</tr>
<tr>
<td>White rat, males (Donaldson, Dunn, and Watson)</td>
<td>0.135</td>
<td>0.575</td>
</tr>
<tr>
<td>White rat, males (Greenman and Duhring)</td>
<td>0.154</td>
<td>0.657</td>
</tr>
<tr>
<td>Norwegian rat, males (King)</td>
<td>0.443</td>
<td>1.88</td>
</tr>
<tr>
<td>White mouse, males (Robertson)</td>
<td>0.067</td>
<td>0.280</td>
</tr>
<tr>
<td>White mouse, females (Robertson)</td>
<td>0.066</td>
<td>0.280</td>
</tr>
</tbody>
</table>

Since the preparation of this table and Figs. 13 and 14, the value of \( k \) for the Norway rat was changed from .115 to .122.

Thus, from Table I of the preceding paper, the numerical value of \( k \) of the Jersey cow is .054; of the female white rat it is .644. Therefore, 1 month in the rat is equivalent (during the phase of growth following the point of inflection) to \( 1 \times \frac{.644}{.054} \) or 11.9 months in the
cow; or 1 month in the cow is equivalent to $1 \times \frac{0.54}{0.664}$ or .08 months in the rat. Such equivalent values referred to 1 month in the Jersey cow and 1 month in the white rat are given in Table I.

<table>
<thead>
<tr>
<th>Mts.</th>
<th>Age of female rat (unmated)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>Kg.</td>
</tr>
<tr>
<td>1</td>
<td>0.20</td>
</tr>
<tr>
<td>2</td>
<td>0.18</td>
</tr>
<tr>
<td>3</td>
<td>0.15</td>
</tr>
<tr>
<td>4</td>
<td>0.14</td>
</tr>
<tr>
<td>5</td>
<td>0.10</td>
</tr>
<tr>
<td>6</td>
<td>0.08</td>
</tr>
<tr>
<td>7</td>
<td>0.06</td>
</tr>
<tr>
<td>8</td>
<td>0.04</td>
</tr>
<tr>
<td>9</td>
<td>0.02</td>
</tr>
</tbody>
</table>

**FIG. 2. Growth-equivalence of Jersey cow and unmated female white rat.** After the point of inflection, 1 month in the rat is equivalent to 11.9 months in the cow and 1 gm. of weight in the rat is equivalent to 2.068 kilos in the cow.

The period of growth preceding the point of inflection is relatively longer in the rat than in the cow.

Growth in weight-equivalence may be similarly computed by comparing the numerical values of the mature weights $A$. The value of $A$ for the Jersey cow is 420 kilos; of the female rat it is .203 kilos.
Therefore, 1 gm. in the rat corresponds to 2.07 kilos in the cow. Such equivalent values on the basis of the Jersey cow are given in Table I.

![Graph showing age-related weights of Jersey cow and unmated female white rat](image)

**Fig. 2. a.** Growth-equivalence of cow and unmated female white rat obtained on the assumption that the age when 98 per cent of the mature weight is reached is equivalent in the two animal forms. Compare with Fig. 2.

**III. Constructing Equivalence Charts with the Aid of the Numerical Values of k and A.**

Having elaborated a method for determining equivalence of growth age, we have proceeded to compare growth curves of animals in order to learn something of the distinctive peculiarities of growth curves.
of different animal forms, and incidentally to test our method of determining equivalence.

The results of these comparisons are shown in Figs. 2 to 13. In most of the graphs, the Jersey cow is taken for the standard of comparison. The observed values are represented by circles, the values computed from equation (1) are represented by smooth curves. The observed values of the animals under comparison agree satisfactorily except at the very early stages of growth with which, as pointed out, equation (1) is not concerned. The agreements between the observed values and the values computed from equation (1) are also satisfactory for the phase of growth following the points of inflection which is the only phase of growth under consideration.

The equivalence charts are self explanatory and they make more interesting reading than any comments we may offer in their behalf. It only remains to illustrate the method of preparing an equivalence chart.

We may take, for purposes of illustration, the steps involved in preparing an equivalence chart for the Jersey cow and the female white rat (Fig. 2). We have found, as already explained in the preceding section, that

\[ \frac{.054}{.644} \text{ or } .084 \text{ months in the rat} \]

Now this statement does not imply that a 1 month old rat is physiologically as old as an 11.9 months old cow; for, as pointed out, this equivalence was obtained on the basis of the numerical values of the \( k \)'s in equation (1) for the cow and rat, and equation (1) represents only the phase of growth following the point of inflection in the smoothed growth curve. The above relation, which was found to hold true for the phase of growth following the point of inflection, may or may not hold true for the phase of growth preceding the point of inflection. As a matter of fact, this relation does not hold true for the rat and the cow for the phase of growth preceding inflection (cf. Figs. 2 and 2, a). For the cow and guinea pig, on the other hand, the relation between their \( k \)'s also applies for the phase of growth preceding inflection (cf. Figs. 3 and 3, a).
All this is only equivalent to saying that conception cannot be taken as a point of reference in preparing equivalence charts which should represent equivalence of growth in weight following the point of inflection. Instead of taking conception we take for the points of

![Graph showing growth equivalence of Jersey cow and male guinea pig. 1 month in the guinea pig is equivalent to 4.26 months in the cow and 1 gm. in the guinea pig is equivalent to 509.1 gm. in the cow. Unlike the case of the rat, growth in the guinea pig appears to follow the same course as growth in the cow from conception.](image-url)
reference the ages when the curve of equation (1) cuts the age axis. We termed this age $t^*$, and its significance is illustrated in detail in Figs. 2 and 3 of the preceding communication. It is only after the age $t^*$ that 1 month in the rat is equivalent to 11.9 months in the cow.

The numerical value of $t^*$ may either be read from the graph of Figs. 2 and 3 in the preceding communication, or it may be computed...
Fig. 4. Growth-equivalence of Jersey cow and Ayrshire cow. 1 month in the Jersey cow is equivalent to 1.08 months in the Ayrshire cow; and 1 kilo in the Jersey cow is equivalent to 1.1 kilos in the Ayrshire cow.

as follows: when $t = t^*$, $W = 0$ (by hypothesis), and equation (1) becomes

\[ 0 = A - Be^{-kt^*} \]

\[ A = Be^{-kt^*} \]

\[ \log_{e} A = \log_{e} B - k t^* \]

\[ t^* = \frac{\log_{e} B - \log_{e} A}{k} \]
The work is now laid out as follows:

<table>
<thead>
<tr>
<th></th>
<th>A (Mature weight)</th>
<th>k</th>
<th>$t^*$</th>
<th>Age factor</th>
<th>Age factor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unmated female white rat</td>
<td>.203</td>
<td>.644</td>
<td>2.03</td>
<td>11.91</td>
<td></td>
</tr>
<tr>
<td>Jersey cow</td>
<td>420</td>
<td>.054</td>
<td>8.9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The values of $t^*$ in the cow and rat, namely 2.03 and 8.9 months, constitute by hypothesis one pair of corresponding points. Another pair of corresponding values may be found as follows: Let us take 8 months from conception in the rat or $8.00 - 2.03 = 5.97$ months from $t^*$ in the rat as another point of reference. 5.97 months in the rat is equivalent to $5.97 \times 11.91 = 71.1$ months in the cow from $t^*$ or $71.1 + 8.9 = 80.0$ months in the cow from conception. 8 months in the rat and 80 months in the cow (counted from conception) thus constitute the second pair of corresponding points in the ages of the cow and rat.

For weight equivalence, zero in the rat corresponds to zero in the cow and .203 kilos in the rat corresponds to 420 kilos in the cow. It only remains to uniformly graduate the axes between the points of reference, and to extrapolate the graduations if desired.

IV.

**Constructing Equivalence Charts on the Basis of Conception and the Age When 98 Per Cent of the Mature Weight Is Reached.**

We have also attempted to obtain equivalence of age values by taking conception and some convenient fraction of the mature weight $A$ as points of reference. This method is similar in principle to the method employed by Pearl and coworkers for comparing mortality curves of man, *Drosophila*, and *Proales decipiens*. This method of determining equivalence would be entirely satisfactory if the ratios between the segments of the growth preceding the point of inflection to the segments following it were the same in the animals under

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Fig. 5. Growth-equivalence of Jersey cow and Holstein cow. 1 month in the Jersey cow is equivalent to 1.174 months in the Holstein cow and 1 kilo in the Jersey cow is equivalent to 1.3 kilos in the Holstein cow.

investigation. This is the case for the Jersey cow and male guinea pig. The agreement between the curves of these two animals is as good by the use of this method (Fig. 3, a) as it is by the method of
comparing the $k$'s and $t^*$'s (Fig. 3). But the agreement between the cow and rat (Fig. 2, a) is very poor by this method throughout the whole curve while by the use of the preceding method (Fig. 2) it was good at least after the point of inflection. Both methods are useful depending on the viewpoint of the investigators; but, of course, neither method is entirely satisfactory if the several phases of growth do not occupy proportional parts of the growth curve in the animals under comparison.

**Fig. 6.** Growth-equivalence of Jersey cow and Duroc-Jersey swine. 1 month in the sow is equivalent (after the point of inflection) to 1.15 months in the cow, and 1 kilo in the sow is equivalent to 2.1 kilos in the cow. The period before the point of inflection appears to be longer in the cow than in the sow.
TABLE II

_Equivalence of Growth Age._

Ages in months counted from conception when different fractions of the mature weight, _A_, are reached. The upper rows represent ages as interpolated from growth curves in which the observed values were connected by straight lines; the lower rows represent ages as computed from formula (3).

<table>
<thead>
<tr>
<th>Percentage of mature weight</th>
<th>10</th>
<th>20</th>
<th>30</th>
<th>40</th>
<th>50</th>
<th>60</th>
<th>70</th>
<th>80</th>
<th>90</th>
<th>95</th>
<th>98</th>
<th>Mature weight (kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Holstein cow (Eckles)</td>
<td>10.5</td>
<td>13.5</td>
<td>16.0</td>
<td>19.5</td>
<td>23.8</td>
<td>28.7</td>
<td>34.0</td>
<td>43.0</td>
<td>59.0</td>
<td>65.0</td>
<td>73.4</td>
<td>83.2</td>
</tr>
<tr>
<td>Ayshire cow (Eckles)</td>
<td>10.6</td>
<td>13.1</td>
<td>16.0</td>
<td>19.4</td>
<td>23.4</td>
<td>28.2</td>
<td>34.5</td>
<td>43.3</td>
<td>58.4</td>
<td>69.0</td>
<td>79.3</td>
<td>89.2</td>
</tr>
<tr>
<td>Jersey cow (Eckles)</td>
<td>10.8</td>
<td>13.4</td>
<td>16.0</td>
<td>19.4</td>
<td>23.0</td>
<td>27.4</td>
<td>32.8</td>
<td>41.4</td>
<td>55.5</td>
<td>65.0</td>
<td>75.3</td>
<td>85.5</td>
</tr>
<tr>
<td>Duroc-Jersey sow (Mumford)</td>
<td>10.9</td>
<td>13.6</td>
<td>15.8</td>
<td>18.4</td>
<td>22.0</td>
<td>26.4</td>
<td>30.5</td>
<td>38.3</td>
<td>53.0</td>
<td>63.0</td>
<td>73.3</td>
<td>83.6</td>
</tr>
<tr>
<td>Suffolk ewe (Murray)</td>
<td>5.9</td>
<td>7.9</td>
<td>10.1</td>
<td>12.7</td>
<td>15.7</td>
<td>19.5</td>
<td>24.3</td>
<td>31.0</td>
<td>48.0</td>
<td>58.0</td>
<td>68.3</td>
<td>78.3</td>
</tr>
<tr>
<td>Guinea pig, male (Wright)</td>
<td>2.7</td>
<td>3.2</td>
<td>3.7</td>
<td>4.3</td>
<td>5.2</td>
<td>6.1</td>
<td>7.2</td>
<td>8.8</td>
<td>12.0</td>
<td>14.4</td>
<td>18.8</td>
<td>.825</td>
</tr>
<tr>
<td>White rat, unmated female</td>
<td>2.8</td>
<td>3.4</td>
<td>3.9</td>
<td>4.5</td>
<td>5.3</td>
<td>6.3</td>
<td>7.5</td>
<td>9.3</td>
<td>12.3</td>
<td>15.4</td>
<td>18.9</td>
<td>.203</td>
</tr>
<tr>
<td>White rat, male</td>
<td>1.4</td>
<td>2.0</td>
<td>2.4</td>
<td>2.8</td>
<td>3.1</td>
<td>3.4</td>
<td>3.9</td>
<td>4.5</td>
<td>5.4</td>
<td>6.8</td>
<td>8.1</td>
<td>.250</td>
</tr>
<tr>
<td>White rat, male</td>
<td>1.6</td>
<td>2.4</td>
<td>2.8</td>
<td>3.1</td>
<td>3.6</td>
<td>4.1</td>
<td>4.9</td>
<td>5.7</td>
<td>7.9</td>
<td>11.7</td>
<td>.350</td>
<td>.400</td>
</tr>
<tr>
<td>White rat, male</td>
<td>2.0</td>
<td>2.4</td>
<td>2.8</td>
<td>3.2</td>
<td>3.4</td>
<td>4.4</td>
<td>5.2</td>
<td>6.3</td>
<td>8.4</td>
<td>10.1</td>
<td>12.9</td>
<td>.400</td>
</tr>
<tr>
<td>Norway rat, male</td>
<td>1.9</td>
<td>2.8</td>
<td>3.9</td>
<td>5.7</td>
<td>7.0</td>
<td>9.1</td>
<td>11.8</td>
<td>15.7</td>
<td>20.3</td>
<td>38.0</td>
<td>34.9</td>
<td>.0235</td>
</tr>
<tr>
<td>White mouse, female</td>
<td>.85</td>
<td>1.2</td>
<td>1.4</td>
<td>1.5</td>
<td>1.9</td>
<td>2.2</td>
<td>2.6</td>
<td>3.3</td>
<td>3.9</td>
<td>5.3</td>
<td>6.7</td>
<td>.0275</td>
</tr>
<tr>
<td>White mouse, male</td>
<td>.95</td>
<td>1.1</td>
<td>1.3</td>
<td>1.5</td>
<td>1.8</td>
<td>2.0</td>
<td>2.3</td>
<td>2.7</td>
<td>3.9</td>
<td>4.8</td>
<td>5.5</td>
<td>.0275</td>
</tr>
</tbody>
</table>

_TIME RELATIONS OF GROWTH II_
V.

A Table of Equivalence of Age.

The equivalence charts are supplemented by a table of equivalent growth ages, or by a table giving the ages at which different fractions of the mature weight, $A$, are reached (Table II).

![Graph showing growth-equivalence of Jersey cow and Suffolk sheep.](image)

Fig. 7. Growth-equivalence of Jersey cow and Suffolk sheep. 1 month in the sheep is equivalent to 3.4 months in the cow. 1 kilo in the sheep is equivalent to 5.3 kilos in the cow.

The method of determining the mature weight, $A$, has been explained in the preceding communication. To calculate the age at which a given fraction of $A$ is reached, it is only necessary to solve
Fig. 8. Growth-equivalence of Jersey cow and female white mouse. 1 month in the mouse is equivalent (after the point of inflection) to 15.29 months in the cow. 1 gm. in the mouse is equivalent to 2.076 gm. in the cow.

The period of growth preceding the point of inflection is relatively longer in the mouse than in the cow.

for age, $t$, in equation (1) and substitute for the weight, $W$, the weight corresponding to the given fraction of $A$; or simply by substituting for $W$ the given fraction of $A$. Thus, from equation (1)

$$W = A - Be^{-kt}$$

$$A - W = Be^{-kt}$$

$$\log_e (A - W) = \log_e B - kt$$

$$\log_e B - \log_e (A - W) = kt$$

$$t = \frac{\log_e B - \log_e (A - W)}{k}$$
Fig. 9. Growth-equivalence of Suffolk sheep and Shropshire-Merino sheep. A unit weight in the Shropshire-Merino sheep is equivalent to 1.6 units weight in the Suffolk sheep.
Now, if it is desired to determine the age $t$ when $0.9$ of $A$ is reached, $W$ is substituted by $0.9$, and we obtain

$$t = \frac{\log_2 B - \log_2 (A - 0.9A)}{k}$$

$$= \frac{\log_2 B - \log_2 0.1A}{k}$$

Fig. 10. Growth-equivalence of unmated female white rat and female white mouse. 1 month in the mouse is equivalent (after the point of inflection) to 1.27 months in the rat. 1 gm. in the mouse is equivalent to 8.64 gm. in the rat.

The period preceding the point of inflection appears to be much longer in the rat than in the mouse; i.e., the infantile and juvenile periods appear to be relatively much longer in the rat than in the mouse.

Ages when different fractions of the mature weight are reached as computed from equation (3), and also the ages when different fractions of mature weight are reached as obtained by direct interpolation from the smoothed weight-age curves are shown in Table II. The agreement between these two sets of values is satisfactory for the
later stages of growth. The deviation between these two sets of values increases, however, with decreasing age due to the fact that the differences in the values of \( t^* \) make themselves felt in an increasing degree. These agreements and deviations are also shown graphically in Fig. 11.

**Fig. 11.** Growth-equivalence of male and female white rat of Donaldson, Dunn, and Watson. After the point of inflection, 1 month in the female is equivalent to 1.61 months in the male. 1 gm. in the female is equivalent to 1.38 gm. in the male.

The period of growth following the point of inflection is evidently much longer in the male than in the female.

in Fig. 1, a. Table II is supplemented by Fig. 15 from which different fractions of the mature weight may be easily interpolated if the numerical value of \( k \) is known. (For errors involved cf. Fig. 1, a.)

Before closing this paper, it is necessary to call attention to Donaldson's method of determining equivalence of age between man and
rat on the basis of duration of life. Donaldson assumed that the rat at 3 years is comparable in age to man at 90 years, and that approximately the same proportional relations hold for fractions of this period. One objection against this method consists, as Donaldson pointed out, in the incomplete information concerning duration of life. The objections against the assumption that the same proportional age relations hold throughout life for two unrelated animal forms have already been discussed. It may be of some interest to

\[\text{Donaldson, H. H., A comparison of the white rat with man in respect to the growth of the entire body, Boas Anniversary Volume, New York, 1906, 5.}\]
Fig. 13. Growth-equivalence of male Norway rat and male albino rat of Donaldson, Dunn, and Watson.

1 month in the albino rat is equivalent (after the point of inflection) to 3.3 months in the Norway rat. This is a remarkable fact.

The other remarkable fact is the relatively early and abrupt inflection in the curve of the Norway rat as compared to the albino rat.

The question naturally suggests itself, what would be the numerical values of $A$ and $k$ in crosses between Norway and albino rats or, more generally, how do the characters $A$ and $k$ behave in genetic operations; also what is the relation between $A$ and $k$—can these two characters be varied independently? The conception of $k$ should give the geneticist a quantitative measure in the study of inheritance of the character rate of growth, and help him in developing rapidly growing animals of large size—if such development is physiologically possible.
Fig. 14. Growth curves of the two sets of male albino rats and male Norway rat. The body weights are represented as percentages of the mature weight.

This chart is intended to indicate the effect of environment and domestication on the course of growth and on the shape of the growth curve of the rat.
know that it requires about 7 months from conception to reach 98 per cent of the mature weight in the female rat, and 216 months in man (cf. Fig. 1 of the preceding paper). 1 year in the rat corresponds to 28 years in man, which agrees within the limits of experimental error with Donaldson's estimate of equivalence.

**SUMMARY.**

The numerical values of the growth constants given in the preceding paper of this series are utilized for determining equivalence of growth age and growth weight in several animal forms. The results are presented in the form of two age-equivalence tables and fifteen age-equivalence and weight-equivalence charts.
SOURCES OF DATA.

Cattle (Eckles) and sheep (Murray): The numerical data were taken from *Univ. Missouri Agric. Exp. Station, Research Bull. 62*, 1923.

Swine: The averages were obtained from unpublished records by Professor F. B. Mumford, Dean of the College of Agriculture and Director of the Agricultural Experiment Station, University of Missouri, Columbia.

Guinea pig: The averages were kindly furnished to the writer by Dr. Sewal Wright, United States Department of Agriculture, Washington, D. C.


