Growth Studies.

II. An Interpretation of some Growth-curves.

BY

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With four Figures in the Text.

INTRODUCTION.

THE first paper of this series contained the results of a quantitative study of the growth of roots from *Tradescantia* and tomato cuttings. Graphically expressed, these results give a series of S-shaped curves, the initiation of each curve coinciding with the development of a new crop of roots of a subordinate order of branching.

Curves of this type are very familiar in quantitative investigations on growth, when the results are expressed simply as the record of mass, volume, area, or length after different periods of time. This type of curve may therefore be taken as characteristic of many growth reactions. It is proposed to consider a possible explanation of the S curve as exemplified in the growth of yeast and of roots.

No attempt will be made to summarize the extensive literature dealing with the problems of growth. A full discussion of much of the earlier work is given by D'Arcy Thompson (19), and in this paper reference will be made only to facts of interest from the particular point of view here developed. It suffices to point out that the earlier attempts at the explanation of the growth-curve fall into two categories. They are either attempts to find a mathematical formula for the graphical results obtained (Robertson (11, 12, 13), Gregory (7), Schuepp (15, 16)), or else they try to find analogies in curves expressing the relation between other types of reaction and time. The latter method of attack has resulted in the consideration of the analogy between growth and an autocatalytic chemical reaction.

Much profit can be derived from the consideration of the arguments advanced in these first attempts at generalization in a complex field, and as these aspects of the case have been too summarily dismissed by West, Briggs, and Kidd (20), in a recent survey of the literature, it may be useful to outline some of the more important points of interest.

Robertson (14) has contributed some of the most carefully controlled quantitative data yet available for study. He has actively followed both lines of attack outlined above, and has prosecuted both the mathematical analysis of his curves and also the establishment of the analogy between the S curve of growth and the curve for an autocatalytic chemical reaction. His later work shows, however, interesting modifications of his original position.

He begins with the assumption that the autocatalyst, in the successive S curves shown in the growth of certain animals, may be some part of the protoplasmic complex itself, nuclear in the first curve and cytoplasmic in subsequent stages (11, p. 587). Later, he evidently considers that the catalyst must be sought for amongst definite chemical substances, probably provided by the glands responsible for internal secretions known to be associated with growth. This change of position is important, because such a definite catalyst would probably be responsible for modifying the rate of a definite reaction or type of reaction, and such reactions could only form single items in the complex machinery necessary for growth.

Further, the experimental investigation of possible catalysts leads Robertson to a separate consideration of the two regions of different inflexion in the S curve, upon which the same catalyst appears to produce different effects.

A consideration of this change of position appears to us of value as leading to certain preliminary conclusions that seem to be important. Because the quantitative data of growth obtained under uniform external conditions can be represented upon a single curve, it by no means follows that throughout the whole period of growth the same internal factors alone remain operative. It is probably significant that Robertson's continued study of the problem leads him (1) to assume first a greater complexity of internal conditions and (2) to consider separately the different regions of his curves.

In attempting to obtain further insight into the significance of the S growth-curve we have carried the process of analysis somewhat farther, and have found it fruitful to consider this curve as consisting of three distinct regions in which different internal factors are operative. Under these circumstances a mathematical expression for the whole curve seems to have no especial significance.

We propose to consider as examples two cases of plant growth for which data are available—the growth of yeast in a limited supply of nutrient medium and the growth of roots from cuttings as recorded in the first paper of this series. No suggestion is made that the arguments advanced are of general application. Indeed, in the case of the similar curves obtained for the growth of individual leaves (Gregory (7)), it is clear that other factors have there contributed to produce the same result. Probably every case

of the occurrence of an S growth-curve will require individual analysis before profitable generalizations can be developed.

THE RATE OF GROWTH OF YEAST.

It is of interest to note that if all the data available for the growth of yeast are collated, from the time that a few cells are seeded into a definite quantity of suitable nutrient medium until the time that growth comes to a standstill, they give a curve of the general type shown in Fig. 1. Moreover, these data, though appearing in the work of different observers, show that this curve can be divided into three distinct regions, *a*, *b*, and *c*, as shown in Fig. 1. In the region *a* increase in mass is an exponential function of time, in region *b* the rate of growth is directly proportional to time, and in region *c* there is a rapid fall of growth-rate.

The nature of the earlier part of the curve (*a*) was established by Slator (17), who has shown that when the nutrient liquid is inoculated with very small amounts of yeast (1,360 to 90,000 cells per c.c.), a logarithmic rate of increase follows. This may be regarded as the natural rate of increase in

FIG. 1. The growth curve for yeast (diagrammatic).
For explanation see text.

yeast, when every cell is actively growing, and at equal intervals of time one cell gives rise to two, two to four, four to eight, and so on. This exponential rate of increase is even more readily recognized when growth is by fission, as in bacteria.

When the rate of growth becomes proportional to time, Horace Brown (6) supplies valuable evidence showing that the amount of oxygen available is the limiting factor, under the normal conditions of the culture medium. The concentration of oxygen above the nutrient fluid is constant, and hence in this part of the curve the number of cell-divisions in each unit of time also remains constant.

In the last part of the curve, it appears from Adrian Brown's work (5) that the growing crowding of the cells in the nutrient fluid causes the available oxygen supply for an individual cell to fall below the minimum quantity essential for cell-reproduction. This effect increases

with the increase in number of yeast cells, until finally cell-division practically ceases.

It is recognized that this brief statement must necessarily understate the complexity of the conditions prevailing, but it seems so essential that this picture of the mechanism should be clear, that it may be restated with the help of Fig. 2. In this figure successive generations of yeast are pictured as arising at equal intervals of time represented by the horizontal distances.

FIG. 2. Diagrammatic representation of the growth of yeast in a limited amount of nutrient solution.

Then in section *a* each cell gives rise to two cells at every time interval. In section *b* a constant number of cells gives rise to new cells, the remaining cells passing over into a resting stage. In region *c* the number of dividing cells decreases until all are in the resting stage and no growth ensues.

This simple statement neglects the possibility of variation in the rate of growth of individual cells and simply assumes a sharp contrast between the dividing and the resting condition of the cells. It will obviously support further analysis. The transition from the *a* to *b* regions of

the curve is shown to depend upon the limiting supply of oxygen. Growth under aerobic conditions must certainly be based on two general types of reversible reaction that are mutually interdependent:

- (1) the type characteristic of synthetic metabolism

- (2) the type providing for the release of energy

A limiting supply of oxygen will affect the progress of the second type of reaction and hence the rate at which *Y* is formed and energy released. Since we assume synthetic metabolism to depend on the presence of a source of energy, the first type of reaction will also slow down and *C* will be produced more slowly. The reactions of the first type have to be considered as proceeding in a long and complex chain (as in the synthesis of complex proteins from amino-acids), where *C*, the product of one reaction, forms a starting-point for the next reaction in the chain. It is improbable

that the energy relations of all these reactions are the same, and hence, when oxygen supply becomes limiting, all these reactions will not be influenced similarly, and the result will be accumulation of C from some such processes and the slowing down of others for lack of A and B.

The immediate consequence will be local accumulations within the cell, followed possibly by osmotic action and vacuolation or by the appearance of storage products. The general result will be a transition from the active growing condition to the resting stage.

This process of transition to the resting condition occurs most rapidly in the region *c* of the curve, and to judge from a later paper by Slator (18), we may assume that this is in part the result of the accumulation of

FIG. 3. The increase in weight of roots from cuttings (diagrammatic). Secondary roots appear at 2, tertiary roots appear at 3.

products in some such chemical reactions. These processes are to some extent reversible, for if yeast-cells from a culture that has ceased to grow are transferred to a fresh supply of nutrient medium, a 'lag' period ensues when there is no growth, this being followed by growth at the normal speed. This 'lag' period is presumably the time required for the removal of the accumulation products by diffusion or oxidation.

Undoubtedly this general interpretation of the existing data of the growth of yeast errs on the side of over-simplicity. It gives, however, a mental picture of the causal sequences involved, which forms a useful background for the attempt to interpret the curves obtained for the growth of roots. It has therefore been presented as an introduction to this attempt.

THE GROWTH OF ROOTS.

The growth of roots from cuttings, as shown in the first paper of this series, may be expressed by the curve given in Fig. 3. This curve consists essentially of two successive S curves.

The exponential region of the initial curve appears to represent the period during which a meristem is growing in amount, and in which each meristematic cell divides to give two meristematic cells in a given time interval, as in the *a* region of Fig. 2. Actually the data may show the position of the change later than it really occurs, since what we measure is not merely the mass of the growing meristem but probably to a greater extent the subsequent mass increase due to the differentiation of the cells. This would involve vacuolation (not measured in dry weight determinations), the deposition of thicker walls and membranes, and the inclusion of various accumulation products. There may also be an initial 'lag' period due to the transformation of resting cells in the shoots into meristematic cells, as in the case of yeast resting cells.

The meristem soon ceases to increase exponentially, and the mass increase becomes proportional to time. We have here to seek another factor governing the rate of the reaction. Loeb (9) has shown that the rate of regeneration of roots is directly proportional to the mass of the shoot upon which they are produced. The same influence can be traced in the results of the *Tradescantia* experiments (Priestley and Evershed; see *ante*, pp. 231-2). This suggests that the total mass of meristem produced on the root system will be determined by the supply of root-forming material from the shoot. Under such conditions a constant mass of shoot would maintain the activity of a constant mass of meristem, and the increase in mass of tissue would become proportional to time. In the *b* region of the curve it may therefore be supposed that an equilibrium has been attained between the secretion of root-forming materials by the shoot and their utilization in the root apex. The diffusion gradient of these materials will be approximately constant, and hence in this part of the curve the rate of food supply is assumed to be the factor limiting the rate of growth.

As in Fig. 2, the same number of cells remain actively meristematic in succeeding intervals of time, other cells passing into the resting stage, which in this case means that they proceed to vacuolate and extend in size behind the growing-point.

Since the shoot on which the roots are borne is gradually increasing in size, there should be a slight increase in growth-rate in the later parts of the curve. There is actually, however, a rapid retardation of growth (region *c*), which suggests a falling off in the supply of food to the apical meristem. In the cases examined, this retardation is associated with great regularity with the development of a crop of secondary roots, which

appeared at the same time on all plants in these cultures. The association of this appearance with the horizontal portion of the first S curve seems too close to be accidental, especially as the appearance of tertiary roots produces a similar effect in the second S curve. Tentatively, therefore, it may be supposed that the decreased growth-rate in region *c* of the growth-curve for roots is due to the diversion of food supply to the developing lateral roots. Support is given to this suggestion by the fact that the mass increase per unit of time is the same in the *b* regions of both the first and second S curves—indicating that the rate of food supply has not materially altered.

The objection may then be raised that the mass increment would be the same whether the root-forming material were used at the apical meristem or in the incipient lateral apices. This by no means follows, however, for if the supply of food material is absorbed by the developing lateral meristems, it may well be that initially the greater part of it would be used in oxidation processes involving loss of weight. Such a 'lag' period is noticed by Briggs, Kidd, and West (4) in Kreusler's data. It appears to be shown during the initial development of roots on cuttings, and is known to be a well-marked feature of the growth-curve when yeast in a resting stage is seeded into a nutrient solution (18). The pericycle cells from which lateral roots develop are not actually meristematic, and it seems probable that, as in yeast, a 'lag' stage may occur during their development into meristematic tissue. In addition, if meristematic activity is initiated above the main root apex, the food supply to the apex may temporarily cease and its rate of growth would then decrease, with a resultant decrease in the rate of membrane formation, &c., behind the apex. The flattening of the curve at the time of lateral root formation thus appears to be a very natural effect. While only further experiment can show to what extent the same curve is true for root development in general, we may now utilize the suggestion put forward to consider two further questions:

(1) The rate of growth of roots at high temperatures, as recorded by Leitch (8).

(2) The causal factors in the development of endogenous secondary roots.

THE RATE OF GROWTH OF ROOTS AT HIGH TEMPERATURES.

Leitch (8) has recently given curves for the growth-rate of *Pisum sativum* at temperatures of 30° and 35° C., one of which is reproduced in Fig. 4. Leitch was quite unable to explain these curves, and only recorded them as being the results of repeated experimental confirmation. In the light of the analysis given above, however, it seems possible to put forward an interpretation of these curves.

The rate of growth of roots from seeds must be assumed to depend on two processes: (1) the chemical reactions involved in the meristematic

activity of the growing-point ; (2) the hydrolysis and delivery of growth-promoting substances from the seed reserves. An increase of temperature probably affects the chemical reactions of the growing-point and the hydrolytic reactions in the cotyledons to a similar extent. There would thus be an increased growth-rate and increased rate of formation of food material, but the latter is not formed at the root tip and some time must elapse before it can diffuse to the growing-point from the cotyledons. We should expect to observe, therefore, an initial increase in the meristematic activity of the root tip, due to the temperature effect on the chemical reactions involved. But, as in the work of Blackman and Matthaei (1, 2), it may be assumed that the increase in rate differs in the different processes in

FIG. 4. The growth of pea roots at high temperature (35° C.). (After Leitch.)

the growth series, resulting in dislocation of metabolism. The initial increase in growth-rate will be rapidly followed, therefore, by a decrease. An hour or two after the start of the experiment an increased supply of food material becomes available, from the increased rate of hydrolysis in the cotyledons. A secondary temporary increase in growth-rate then appears, until the whole process is slowed down by increasing dislocation of metabolism.

The secondary maximum in growth-rate obtained by Miss Leitch thus falls in line with the point of view advanced here. This secondary maximum may be expected to show a relation to the length of the root at the time measurements are made, and it would seem possible to obtain interesting data as to the rate at which materials move in translocation by a development of this method.

CAUSAL FACTORS IN THE DEVELOPMENT OF ENDOGENOUS
SECONDARY ROOTS.

While the problem of the development of lateral roots cannot yet be fully discussed, it must be considered in the light of evidence hitherto unpublished.

The evidence available supports the view that the supply of sap and of food material for growth is restricted within the endodermal cylinder, which is closed at the apex by the meristematic tissues of the root tip. Within this endodermal cylinder all the cells are vacuolated and differentiated at a fairly early stage, with the exception of the endodermis and the pericycle, which remain relatively embryonic for a much longer time. The fact that they occupy the most favourable position in relation to the balance of supply of food from the conducting elements and of oxygen through the intercellular spaces of the cortex may possibly be the reason for this. The endodermal cylinder is thus lined along the inside with a relatively embryonic tissue, and owing to the normal action of osmosis a considerable hydrostatic sap-pressure also accumulates inside it (Priestley (10)).

Some factor then induces the development of meristematic activity on the part of some of the pericycle cells, usually those opposite the xylem. The exact position of the new activity seems to depend either on the degree of maturation of the pericycle cells or upon the slow accumulation of something diffusing downwards from the shoot, since the lateral roots never approach the root apex closely, but always develop acropetally.

It has been observed that the formation of phellogen below a wound is preceded by a blocking of the exposed surface, a factor presumably leading to increased hydrostatic pressure in the cells beneath the surface, and it has been pointed out also that cork formation is confined to places receiving a free supply of nutrient sap. In addition, the phellogen in roots normally develops inside the endodermis. Both these groups of observations support the suggestion that the supply of nutrient sap and the development of hydrostatic pressure within the endodermis are important factors in initiating the development of the latent activity of the pericycle cells, and in explaining the endogenous origin of lateral roots.

The initiation of this meristematic activity disturbs the gradient of substances diffusing to the main root apex, and as a consequence the growth of the main apex is lessened or stopped, as recorded in our experiments by a fall in the growth-rate. The new lateral meristems in their turn leave behind them vacuolated and differentiated tissues, and the previous growth-rate is thus restored, though apparently not increased, indicating that the total mass increase per unit of time is not dependent upon the amount of meristematic tissue, but upon some other limiting factor, probably in this case the supply of food material.

It is clear that the phenomena so described above would admit of an alternative explanation. If some factor could be found that would inhibit the growth of the main root, then the development of the lateral roots might be ascribed to the accumulation of root-producing substances in the root. So far, however, we have found no adequate cause for the diminution in growth of the main root, and we are therefore inclined to assume that the growth of the main root is temporarily held up by the development of the lateral meristems. The alternative assumption certainly agrees with the case of the fibrous roots of Monocotyledons, where the strong and early development of lateral roots is apparently associated with the inhibition of the meristem of the primary root.

SUMMARY.

1. Data, previously recorded for root growth, provide curves showing a series of successive inflexions of the S type so often obtained in growth experiments.

2. In a brief review of previous work, special attention is given to Robertson's comparison of this type of curve with that of an autocatalytic chemical reaction.

3. It is pointed out that analysis of the physiological conditions involved at different stages of growth is apparently a necessary preliminary in the interpretation of such growth-curves.

4. Such an analysis is attempted for the growth of roots, after previous consideration of the data available for yeast.

5. The early exponential portion of the curve is considered to represent the exponential increase in size of the apical meristem.

6. The mass increase then becomes proportional to time, probably because the supply of root-forming material is delivered at uniform rate.

7. The final decrease in growth is co-ordinated with the initiation of lateral meristems.

8. It is shown that the hypotheses involved give an adequate explanation of the growth of roots at high temperatures (Leitch's data), and permit certain assumptions as to the endogenous origin of lateral roots.

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