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Clifford H. Farr

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The evolution of scientific terminology constitutes an exceedingly interesting subject for study, and may be looked upon as one of the most prevalent "growing pains" of almost any branch of science. The rapidly developing field of plant physiology is by no means an exception to this; in fact, it furnishes some of the most flagrant examples. A special term is given to a specific quantity, structure, or process, which it is made to fit apparently with great precision. And then as our knowledge extends, we find the name and the scientific entity no longer correspond. The term becomes a misfit, and is used in numerous senses by different authors. Quibbles arise; serious controversies develop largely because one scientist does not have the same concept when he writes one term that the other has when he reads it.

Anabolism and katabolism were at one time thought to be highly useful terms in classifying the chemical reaction in living things. But who will now say whether the transformation of tannin into anthocyan is a building up or a tearing down process? Respiration was at first used to refer to the taking in of oxygen and the giving off of carbon dioxide. Then it was extended to include the chemical reactions coincident upon this exchange of gases. The next step was to apply the term breathing to the gaseous exchange, and to reserve the term respiration for the intracellular chemical reactions which release energy. But it is found that some of the digestive processes within the cell, if not all of them, also release energy, so that respiration became restricted to the oxidation processes within the cell. However oxygen is also found to be involved in the formation of nucleic acid from the purine and pyrimidine bases. This process is evidently one of assimilation and not of respiration; so that the exact definition of respiration becomes increasingly difficult. Assimilation has likewise passed through a series of meanings. By some authors it is used to refer to photosynthesis, by others to absorption, as in carbon dioxide assimilation, and by still others to the endothermic reactions in organisms other than the primary synthetic processes, that is, the reactions carried on by internal energy, as opposed to the synthetic processes using external energy.

One of the most conspicuous cases of such diversity of usage is in connection with the term *growth.* As used in a broad sense it often connotates the whole phusiological activity of the organism, as when we say, "Our plants are not growing well." On the other hand it has been used in much of the agricultural literature as synonymous with yield. For instance, a recent bulletin[1] is entitled "The Influence of Calcium and Magnesium Compounds upon Plant Growth," in which the investigator measures the yield in pounds of wheat, alfalfa, and soybeans. It is obvious that growth is not used consistently even in this paper, for in the case of alfalfa, vegetative development is measured in the yield, whereas in wheat and soybeans it is reproduction. Furthermore, in the latter instances not only is dry weight increase measured, but also the water absorption and translocation, the fertility and sterility of the pollen and ovules, and the conditions of pollination, for all of these affect the total yield of seed or fruit.

A third use of the term *growth* is that of making it equivalent to dry weight increase. Some of the botanists who have been developing growth formulae have used this connotation. Dry weight increase is augmented by photosynthesis, salt absorption, and assimilation. It is diminished by respiration, digestion, and secretion. If we measure the dry weight increase of only a part of a plant, then translocation is also a modifying factor. Growth then becomes a balance between other processes, and its integrity is lost.

In the fourth place there is a tendency to regard increase in size as growth. However it is necessary to exclude such things as temporary swelling or contraction of the tissue due to temperature, osmotic changes, or colloidal hydration. Furthermore growth is to be looked upon, not merely as an enlargement of the cells, but as a multiplication of cells as well. It also involves the transformation of cells. Hence reduced to a cellular basis, growth seems to be coming more and more to be considered as the complex of processes involved in cell-division, cell-enlargement, and cell-differentiation.

The rate of cell-division has been sometimes used as a measure of growth. However, our literature is conspicuously lacking in studies on the relative rates of the various stages of cell-division. The periodicity of cell-division in plants, has, however, received considerable attention, beginning with the work of Sachs, who concluded that there is a division of labor in the plant, — synthesis by day, cell-division by night. The more recent work of

1 Wyatt. Jour. Agric. Res. 1916.

Ward, Kellicott, Karsten, Saalfelt, and Friesner has added much to our ideas of this periodicity.

But the physiology of cell-division extends much farther than the mere determination of its rate. Most growing cells of plants consist of a cell-wall, enclosing a protoplast which consists of plasma membrane enclosing the cytoplasm, embedded in which are the nucleus and cytosomes. No vacuoles or plastids are ordinarily present in rapidly dividing cells. It would seem then that three processes must be involved in cell-division: the division of the cytosomes; the division of the nucleus; and the formation of a partition consisting of a cell-wall, lined on either side with plasma membranes continuous with the membranes of the original cell.

In regard to each of these three phases of cell-division, questions arise. It has been supposed and some evidence has been accumulated which indicates that the chondriosomes divide and thereby increase in number. But recently Kozlowski[2] has come to the conclusion that they do not divide at all, but are formed *de novo* from the cytoplasmic solution.

Karyokinesis, that is nuclear division, may be either amitotic or mitotic. Aside from the time relations of the respective phases of mitosis, its chief physiological problems lie in the dynamics of spindle formation and chromosome behavior, and in the conditions involved in the initiation of nuclear division. The dynamics of mitosis has been the subject of much experimentation and discussion since the time of Giard in 1876. This literature is reviewed elsewhere.[3]

The problem of the initiation of nuclear division is one which seems at present to have a very important bearing on the physiology of development. If cell-division is the first of the three processes of growth, and nuclear division is the first of the processes of cell-division, then the initiation of nuclear division bears an important relation to the rate of the entire growth process. Little positive evidence as to the initiation of nuclear division has as yet accumulated. It may be the number of chondriosomes in the cytoplasm. Perhaps it is some external factors as light, temperature, humidity, gases, etc. Perhaps it is certain intracellular conditions as osmotic pressure, H-ion concentration, salt or ion composition, or colloidal state of nucleus or cytoplasm. It may

2 Kozlowski, Critique de l'hypothese des chondriosomes. Rev. Gen. Bot., vol. 34, pp. 641-658, pl. II. 1922.

3 Farr, C. H. Cytokinesis in the pollen-mother-cells of certain Dicotyledons. Mem. N. Y. Bot. Garden, vol. 6, pp. 253-317. 1916.

be an inherent periodicity that is dependent upon the interval since the last mitosis. It may be an enzyme effect, or a specific growth substance as vitamines or auximones. Or it may be an inhibiting substance which must be removed or neutralized.

The most prevalent ideas as to the causative factors in the initiation of mitosis have to do with volume and surface relations. One of the older views is that the ratio of cell size to cell surface tends to remain constant. As the cell increases in volume, maintaining the same shape, — the ratio of surface to size diminishes. In order to restore this ratio prehaps to permit of sufficient oxygen absorption, the cell divides beginning with nuclear division. It may also be argued that the nucleus itself divides as a result of enlargement and hence relative decrease in surface. It is found that the nucleus enlarges very little between mitoses, but just before a mitosis the enlargement is very rapid. This may be the initiating factor, but if so what initiates this enlargement? Another theory much in vogue at present is that of the nucleo-cytoplasmic relation. Robertson[4] recently lays much stress on this ratio as a determining factor in cell division. The cell increases in size between mitoses at a rather constant rate, whereas the nucleus, as noted above, does not. When, however, the nucleo-cytoplasmic ratio is restored, according to this interpretation, mitosis takes place.

The last phase of mitosis, namely cytokinesis, or the formation of the partition, may be regarded as one of several kinds, according to the number of nuclei and the method of partition formation. The simplest case is bipartition, in which only two nuclei are involved. In conjugate division, four nuclei are involved, and two binucleate cells are formed. In quadripartition four nuclei are involved, and four uninucleate cells formed. In multipartition, many nuclei are present and many cells formed. Examples of the last-named type are free-cell formation in the endosperm of Angiosperms, and the spore formation of the Mucors. The partition may be formed either by cell-plates or by furrowing.

The nature of the processes of cell-plate formation and furrowing has been the subject of some study recently. My studies[5] of

[4] Robertson. The Chemical Basis of Growth and Senescence. Lippincott. 1923.

[5] Farr. Above cited.

Farr. Cell-division by furrowing in Magnolia. Am. Jour. Bot., vol. 5, pp. 379-395. 1918.

Farr. Quadripartion by furrowing in Sisyrinchium. Bull. Torrey Bot. Club, vol. 49, pp. 51-62. 1922.

Farr. The Meiotic cytokinesis of Nelumbo. Am. Jour. Bot., vol. 9, pp. 296-306. 1922.

a number of flowering plants have lead to the conclusion that cell-plate formation is due to the diffusion of certain substances from the nuclei, reaching their highest concentration in the equatorial zone, and there precipitating a plate or causing the formation of a plate by the coagulation of cytoplasmic colloids. This seems to occur in cells which, due to enveloping cell-walls, are not able to enlarge sufficiently by the intake of water to lower the osmotic pressure of the cell, and hence the concentration of the diffusion substance, below the precipitating or coagulating concentration. In cells which can enlarge due to absence of a cell-wall or to an exceedingly elastic wall, the water will enter due to the increased osmotic pressure, and hence dilute the substance below the critical concentration. In these cells at a relatively later time in the cell cycle, furrowing may occur.

Another important question in the physiology of growth is that of the determination of the plane of partition. This is undoubtedly one of the most important features of the problem of development. The multicellular structure of mature organs is the result very largely of the size and arrangement of cells. The latter is the direct consequence of the successive planes of partition during development. In the filamentous structures of algae and fungi, the successive planes of partition are parallel. If an occasional partition is at right angles to the rest, there results a branched filament, as in moss protenema. In similar manner by varying the successive planes of partition the various plant tissues of the colonial algae, the thalloid and leafy liverworts, and of the vascular plants are formed.

At first it was thought that the partition is always across the shortest dimension of the cell. But such work as that of Bailey [6] on cambial cells has shown that this is by no means always the case. Sachs [7] proposed the principle of rectangular intersection, that is, that the new partition is always at right angles to the one preceding. However, the many oblique walls in connection with apical cells, and sex organs of ferns and other plants, seem evidence that this is not a universal law. On account of the dependence of the resultant structure on the planes of partition during development, there has been a tendency on the part of those genetically inclined to consider that the plane of partition is determined by the factors in the chromosomes. However the

6 Bailey, I. W. The Cambium and its derivative tissues. III. Amer. Journ. Bot., vol. 7, pp. 416-434, pls. 26-29. 1920.

7 Sachs, Jules. Lectures on the Physiology of Plants.

work of Rosenvinge and Miss Hurd [8] on the eggs of Fucus, leads in another direction. They found that the partition was formed at right angles to the incident rays of light. Miss Hurd further found that if these zygotes were within 0.2 mm. of each other the partition is at right angles to the radius of the group of zygotes, — that is, the plane is determined by cellular interaction. This factor was also found to be stronger than the effect of light. It would thus seem that in the development of a tissue the relationship of a cell to the other cells in the tissue may be an important factor in determining the plane of partition.

In a similar way to cell-division, cell-enlargement may be studied as to its rate, initiating factors, processes involved, cessation, etc. It is apparent that the measurement of the rate of enlargement of a tissue is not a measure of the rate of cell-enlargement alone. Cell enlargement occurs alternately with cell-division. The rate of enlargement of a tissue then may be retarded either by reducing the rate of cell-enlargement or by increasing the length of time required for cell-division. Similarly acceleration of tissue enlargement may be due to acceleration of cell enlargement or of cell-division. Light, for instance, is found to retard the rate of elongation of both stems and roots, as shown by the general observations on aetiolation, and the critical studies of Blaauw [9] and others. And yet Jeffs [10] finds that light has no effect at all on the rate of elongation of root-hairs. If these cells are affected by light in the same way as other root cells, then it must be concluded that the effect of light in retarding tissue elongation is an effect of lengthening the time required for mitosis.

Cellular interaction also doubtless plays a part, not only in determining the plane of partition, but also in effecting the rate of enlargement of cells. While some cells are tending to elongate, others are tending to remain constant in size or even to contract. The actual rate of elongation of an organ is then the resultant of the forces of tension and pressure among its cells. The internal stresses of a single cell are either abetted by the tension of neighboring cells or opposed by the pressures of neighboring cells. The root elongates most rapidly in the region adjacent to the region of cell-division at the tip. As we proceed from this region

8 Hurd, Annie May. Some orienting effects of light of equal intensity on Fucus spores and rhizoids. Proc. Nat Acad. Sci., vol. 5, pp. 201-206. 1919.

9 Blaauw, A. H. Licht und Wachstum III. Meded van de Landbouwhoogeschool, vol. 15. 1918.

10 Jeffs, R. E. The effect of light and temperature on the rate of elongation of root-hairs. Thesis. State University of Iowa. 1923.

of elongation in the direction of the region of root-hairs above, it is found that the root is elongated less and less rapidly. Jeffs found that in corn, white mustard and radish, the lowermost root-hairs, that is, those just appearing are carried along on the root downward during the first hour or so of their development. During this period their rate of elongation is accelerating, while their lateral movement is retarding. After lateral movement ceases, no further acceleraton in root-hair elongation occurs. It would seem that this might be interpreted as the consequence of cellular interaction in the tissue. If the cells of the vascular bundle are tending to remain constant in length due to their thickened walls and the cells of the cortex are still tending to elongate, then there will be a slowing up in the rate of elongation of the entire root. The epidermal cells are however able to continue at the same rate of volume increase, due to the pushing out of these root-hairs. As they are more and more retarded in their vertical elongation, they accelerate their lateral elongation, — that is, their root-hair production. This interpretation is further supported by the observations made more recently in which the root-hairs of Tradescantia show no lateral movement and no acceleration of elongation.[11]

Cell-enlargement consists of two processes: the absorption of water, and the extension of the cell-wall. Since cell-enlargement is only one phase of growth, and absorption of water is only one phase of cell-enlargement, it is apparent how much larger the problem of the physiology of growth is, than simply a matter of the absorption of water, either by osmosis or colloidal imbibition. The old discussion of intussception *versus* apposition as to the method of cell-wall extension, seems still undecided. Noll's famous experiment with Vaucheria, by which he localized cell-wall formation in the tip of the filaments, through the use of ferric chlorid and potassium ferrocyanid, was very striking, and conclusive for that form, but can hardly be applied without further study as a universal principle in plants.

Another problem in cell-enlargement is the factors concerned in the determination of the degree of enlargement. Are there inhibitors in plants which accumulate and bring this cessation of growth about? Is it that the cell enlarges until cell-division again occurs? Such might do for an explanation in meristematic tissues, but not in differentiating organs. Is it the nucleo-cytoplasmic

11 Farr. C. H. Root-hair elongation in Knop's solution and tap water. Am Jour. Bot. Vol. 12, pp. 372-383, 1925.

relations again? In some cases it may be the death of the protoplasm, as in conductive vessels and pith cells. Cellular interaction, either chemical or mechanical, also doubtless plays a part. Hormones have been given considerable attention in this connection in animals recently, and the stresses and strains between growing cells will doubtless be given more attention in plants in the near future.

Cell differentiation includes irreversible changes in shape, enlargement of vacuoles, and their formation from chondriosomes, the formation and enlargement of plastids, and changes in the cell-wall. The last includes increase in thickness, and in composition, such as suberization, lignification, cutinization, etc. It is perhaps a question as to where the line should be drawn between storage and differentiation. The deposition of starch in leucoplasts is undoubtedly storage, since it is reversible. The deposition of cellulose, on the other hand, should probably be called differentiation. Just where the formation of chlorophyll and anthocyan should be classified is not, however, so clear. One of the striking marks of differentiation is the loss of the power of cell-division. Differentiation, it is true, continues usually for a long time, without the loss of this power. It retains the ability to dedifferentiate and start off on a new line of development, but eventually the rubicon is crossed, and the cell passes from the embryonal condition entirely into that of the adult stage.

In all phases of growth cellular interaction plays an important role. It has been noted above in cell-enlargement and in the determination of the plane of partition. The study of hormones, serums, and serological reactions, and the transplanatation of ovaries, etc., serve to emphasize the part of chemical cellular interaction. Symbiosis, parasitism, disease resistance, etc. point in the same direction. The effects of mechanical cellular interaction as a factor in organic form is shown by the work of Harper on colonial algae, and by Jeffs work on root-hairs. Dr. Himmel [12] has recently completed a study of the effects of pressure on growth rate which indicates that enormous forces are developed within a tissue.

12 Himmel, Walter J. A contribution to the biophysics of Podophyllum petioles. Thesis, State University of Iowa. 1924.