THE CARBOHYDRATE ECONOMY OF CACTI

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PREFACE.

The purpose of this work has been primarily to gather data and some necessary facts which could be brought to converge for an attack on the problems of photosynthesis. Experiments which have been in progress in the Desert Laboratory at Tucson for several years have indicated clearly that prerequisite to a rational discussion of the problems concerning the manner in which sugars are formed in the chlorophyllous leaf is a clearer understanding of the conditions governing the equilibria and mutual transformations of the various groups of carbohydrates in the leaf, as well as of the fate of these substances in the general metabolism. The complex and manifold character of the phenomenon of photosynthesis has, it would seem, not been very generally realized by workers in this field. The avenue of approach which appears most promising, at this stage at least, is that which employs chemical methods and conceptions. However, in following this line of attack, the dangers of reasoning from knowledge gained purely from *in vitro* investigations can hardly be overemphasized. Furthermore, consistent and valid results with living material can be gained only by the most careful control of conditions, such as temperature, water relations, light, and the previous history of the plant. While it is, of course, highly desirable to know the behavior of plants in the field and to develop methods for gaining such knowledge, it seems to the writer that a realization of this ideal can be hoped for only after the more fundamental principles of the phenomenon have been learned. In the study of photosynthesis it is impossible to segregate entirely the activity of sugar synthesis from that of the further metabolic transformations and from the catabolic processes which yield energy to the living organism, glycolysis. This latter phenomenon has received attention from many sides, and the application of the chemical point of view to the manner of sugar disintegration and rearrangement seems most promising as an aid to a clearer understanding of the nature and mode of the sugar break-down in the living cell.

This paper comprises the results of investigations carried out during 1916–1918. The work consisted largely of the analysis of plants which had been subjected to various experimental conditions. Of the large number of analyses made, only those are discussed here which are pertinent to the immediate subject. It is a pleasure to acknowledge here the assistance rendered in this work by Dr. J. M. McGee and Mr. R. A. Burt.

DESERT LABORATORY,
Tucson, Arizona, December 1918.

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By HERMAN AUGUSTUS SPOEHR.

I. INTRODUCTORY DISCUSSION.

The best evidence gained since the time of Sachs points to the conclusion that sugars are the first products which accumulate in the process of the photosynthesis of carbon compounds in the chlorophyllous cell. Thus, sugars may be considered the starting-point for the synthesis of the tremendous number of substances found in living things, both vegetable and animal. What the sugar or mixture of sugars is which thus commands the center of attention in the metabolism of plants and of almost all living things is still a question of much dispute and uncertainty; nor does the solution of this problem seem possible until we have gained more knowledge of the transformations which the various sugars undergo in the cell, independent of photosynthesis. It has long been known that in the leaf, under circumstances, the polysaccharides are converted into the simpler sugars and vice versa, by what appears to be the shifting of an equilibrium by means of enzyme action. It is self-evident that a knowledge of these transformations must be obtained before the problem of the first sugar synthesized can be attacked.

Not only in relation to the question of the immediate products of photosynthesis is the study of the carbohydrate equilibrium important, but also to the question of metabolism. In a very large number of plants, especially the higher ones, both the living and the lifeless matter consists in the main of material of carbohydrate nature. The lifeless matter forms the walls, vessels, supporting frame-work, and often a considerable amount of the reserve food-material. Those portions of the plant in which the manifestations of life appear, as for instance the chromatin of the nucleus and the protoplasm itself, contain a considerable quantity of carbohydrates, the lifeless being formed from the living and the living drawing upon the lifeless for support. It is, however, a question whether the difference between the living and lifeless is essentially one of chemical constitution. The idea that the living substance or protoplasm is a complex compound of more or less definite chemical constitution no longer seems tenable. Protoplasm, a mixture of so many different substances, undoubtedly varies in composition in different organisms. It is in all probability the study of the physical and chemical properties of protoplasm as a colloidal mixture (such properties as imbibition of water, electrical charges, and surface phenomena) which will yield the most illuminating results.

It seems highly improbable that the life processes consist of any one series of chemical changes or are dependent upon any particular molecule or chemical group. But rather the simpler life processes entailing energy changes may perhaps be regarded as a complex of interrelated chemical changes taking place in a certain medium or substratum. This medium, colloidal dispersion, mixture, or aggregate of various substances is the seat or substratum in which the various chemical reactions take place, the nature and course of which are determined by the complex of properties associated with water control, surface phenomena, and of course catalysts (such as inorganic salts and enzymes). These colloids do not enter into or support the chemical reactions or do so probably only in a rather indirect manner, serving primarily as a physical medium. Such a system would be of a heterogeneous nature and, of course, of the most complex type, and capable of various adsorption phenomena productive of localized action which would influence the function as well as the structure of the system. In fact, such a hypothesis would demand that the substratum be relatively stable, that the colloidal material once formed does not break down as readily as the other substances, or only after the supply of these has been exhausted. This does not mean actual or chemical stability, but rather relative to the other substances under the existing physiological conditions, as, for instance, relatively slightly dissociated by salts or other catalysts and resistant to the action of enzymes.

This colloidal material may also in part be composed of substances which do not undergo complete disintegration and thus are not excreted from the cell. The proteins in most plants, due to the high synthetic power characteristic of plants, are rarely so drastically affected that they are not again reconstituted; these substances are thus relatively stable in the sense that under normal conditions they do not disappear in the course of metabolism. The cell substratum or protoplasm should then be regarded as a complex of substances of relative stability in which the more sensitive substances break down with the liberation of energy, the formation of products of catabolism, and the synthesis of other more complex substances in varying amounts. It is, then, the combination of the intricate chemical reactions taking place in this heterogeneous colloidal system that constitutes the principle of energy change of living processes. While the chemical reactions are influenced by the nature of the medium, the latter is also a product of the chemical processes.

The conception of protoplasm as a tremendously complex "living" protein molecule arose before any considerable chemical knowledge of this group of substances had been gained. Through the extensive researches of Fischer, Kossel, Abderhalden, and many others it has become apparent that the conception of such an enormous complexity and sensitiveness of the proteins was rather unwarranted. Furthermore, the theory that proteins, carbohydrates, and fats are synthesized into elaborate complex substances before they break down and yield energy was necessitated by the prevalent idea of the relative stability of these substances in simple solution. It is now becoming more evident that under conditions such as exist in an organism (*i. e.*, in the presence of various catalysts such as inorganic salts, enzyme, acids, and alkalies), the molecules of proteins, fats, and especially carbohydrates break apart almost spontaneously. From a vast amount of physiological evidence now at hand, it appears that the energy of an organism is derived chiefly from the break-down of the material ingested as food. When the supply of nutritive material is insufficient the nature of the respiration changes and then, in all probability, the more stable substratum is drawn upon. This becomes evident in the cacti as well as in many other plants.

Kosinski[1] has shown that when *Aspergillus niger* is grown on pure water, the carbon dioxid given off falls rapidly to a value about one-quarter of that when grown on sugar. During this time the organism is probably drawing on the more stable protoplasmic substances. When sugar is made available, the carbon dioxid rises immediately, indicating the direct utilization of that substance.

The colloidal materials found in plants are in general relatively chemically stable substances, although their exact chemical nature and mode of formation as yet have not been definitely established. It now seems probable that in a sense they represent by-products or end-products of the metabolic process. The nature of this material undoubtedly varies in different plants, especially in regard to the proportion of carbohydrate and proteinaceous substances. This is indicated in the study of the behavior of the colloids of various plants. Extensive comparative investigations with different vegetable tissues, prepared "biocolloids," and especially with the cacti, have indicated that these plants behave like masses of gels composed largely of colloidal carbohydrates.[2]

In the present investigation an effort has been made to determine the nature of the carbohydrates of the cacti and to study the transformations which these undergo under various conditions. In the conception of the colloidal nature of protoplasm briefly outlined, it has been stated that this is of necessity a relatively stable system and that the colloidal material is itself a product of metabolism. One of the most striking and interesting features of these plants is the presence of large quantities of pentosans and mucilaginous material. In the cacti it has been found that water imbibition, swelling, and growth are intimately related to the presence of pentose polysaccharides. The pentosans have been found as components in varying

[1] KOSINSKI, I. Die Atmung bei Hungerzuständen und unter Einwirkung von mechanischen und chemischen Reitzmitteln bei *Aspergillus niger*. Jahrb. wiss. Bot., 37, 137–204, 1898.

[2] MACDOUGAL, D. T., and H. A. SPOEHR. The behavior of certain gels useful in the interpretation of the action of plants. Science, n. s., 45, 484–488, 1917.

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