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BIOCHEMICAL MECHANISMS OF THE BREAKDOWN OF COMPLEX MOLECULES

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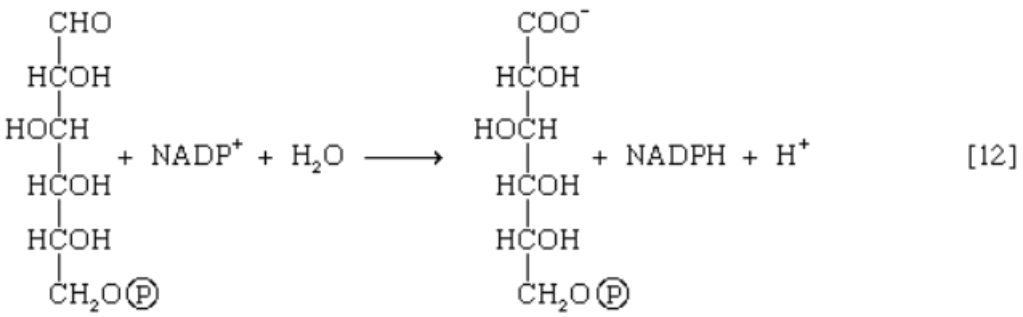
Annotation: There are two main reasons for studying a metabolic pathway: (1) to describe, in quantitative terms, the chemical changes catalyzed by the component enzymes of the route; and (2) to describe the various intracellular controls that govern the rate at which the pathway functions. Studies with whole organisms or organs can provide information that one substance is converted to another and that this process is localized in a certain tissue; for example, experiments can show that urea, the chief nitrogen-containing end product of protein metabolism in mammals, is formed exclusively in the liver. They cannot reveal, however, the details of the enzymatic steps involved. Clues to the identity of the products involved, and to the possible chemical changes effected by component enzymes, can be provided in any of four ways involving studies with either whole organisms or tissues.

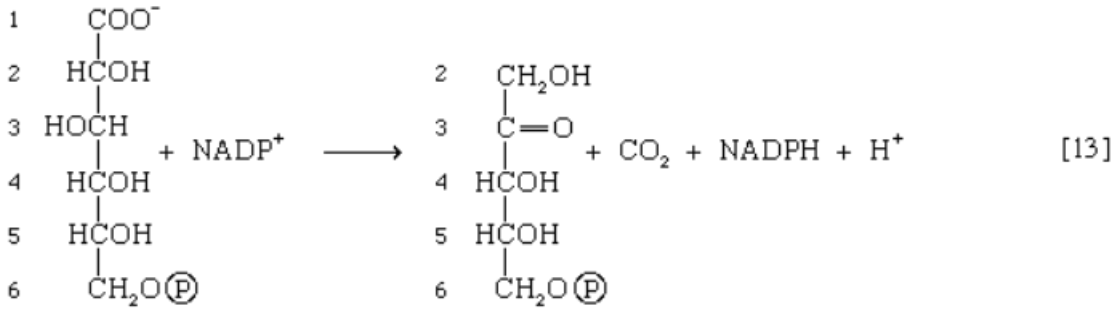
Key words: Liver, kidney, tissue, organ, urea, protein.

Many cells possess, in addition to all or part of the glycolytic pathway that comprises reactions [1, 2, 3, 4, 5, 6, 7, 8, 9, 10, and 11], other pathways of glucose catabolism that involve, as the first unique step, the oxidation of glucose 6-phosphate [12] instead of the formation of fructose 6-phosphate [2]. This is the phosphogluconate pathway, or pentose phosphate cycle. During reaction [12], hydrogen atoms or electrons are removed from the carbon atom at position 1 of glucose 6-phosphate in a reaction catalyzed by glucose 6-phosphate dehydrogenase. The product of the reaction is 6-phosphogluconate.



The reducing equivalents (hydrogen atoms or electrons) are accepted by nicotine adenine dinucleotide phosphate ($NADP^+$), a coenzyme similar to but not identical with NAD^+. A second molecule of $NADP^+$ is reduced as 6-phosphogluconate is further oxidized; the reaction is catalyzed by 6-phosphogluconate dehydrogenase [13]. The products of the reaction also include ribulose 5-phosphate and carbon dioxide. (The numbers at the carbon atoms in step [13] indicate

that carbon 1 of 6-phosphogluconate forms carbon dioxide.)



6-phosphogluconate ribulose 5-phosphate

Ribulose 5-phosphate can undergo a series of reactions in which two-carbon and three-carbon fragments are interchanged between a number of sugar phosphates. This sequence of events can lead to the formation of two molecules of fructose 6-phosphate and one of glyceraldehyde 3-phosphate from three molecules of ribulose 5-phosphate (i.e., the conversion of three molecules with five carbons to two with six and one with three). Although the cycle is the main pathway in microorganisms for fragmentation of pentose sugars, it is not of major importance as a route for the oxidation of glucose. Its primary purpose in most cells is to generate reducing power in the cytoplasm, in the form of reduced $NADP^+$. This function is especially prominent in tissues—such as the liver, the mammary gland, adipose tissue, and the cortex (outer region) of the adrenal gland—that actively carry out the biosynthesis of fatty acids and other fatty substances (e.g., steroids). A second function of reactions [12] and [13] is to generate from glucose 6-phosphate the pentoses that are used in the synthesis of nucleic acids (**see below** The biosynthesis of cell components).

In photosynthetic organisms, some of the reactions of the phosphogluconate pathway are part of the major route for the formation of sugars from carbon dioxide. In this case, the reactions occur in a direction opposite to that in which they occur in nonphotosynthetic tissues (**see** photosynthesis).

A different route for the catabolism of glucose also involves 6-phosphogluconate; it is of considerable importance in microorganisms lacking some of the enzymes necessary for glycolysis. In this route, 6-phosphogluconate (derived from glucose via steps [1] and [12]) is not oxidized to ribulose 5-phosphate via reaction [13] but, in an enzyme-catalyzed reaction [14],

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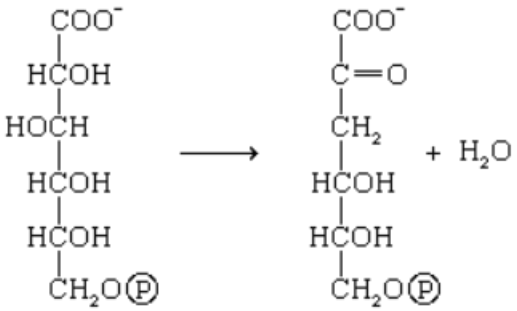
loses water, forming the compound 2-keto-3-deoxy-6-phosphogluconate

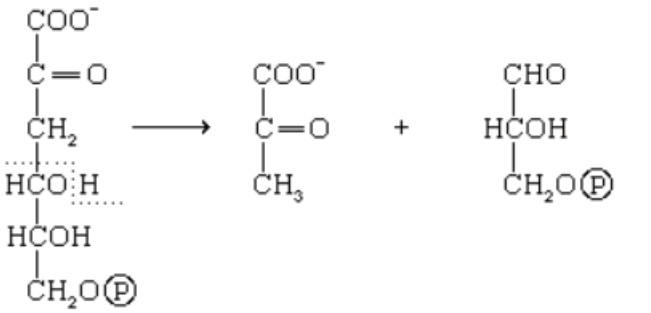


[14]

6-phosphogluconate KDPG

(KDPG).

This is then split into pyruvate and glyceraldehyde-3-phosphate [15], both of which are intermediates of the glycolytic



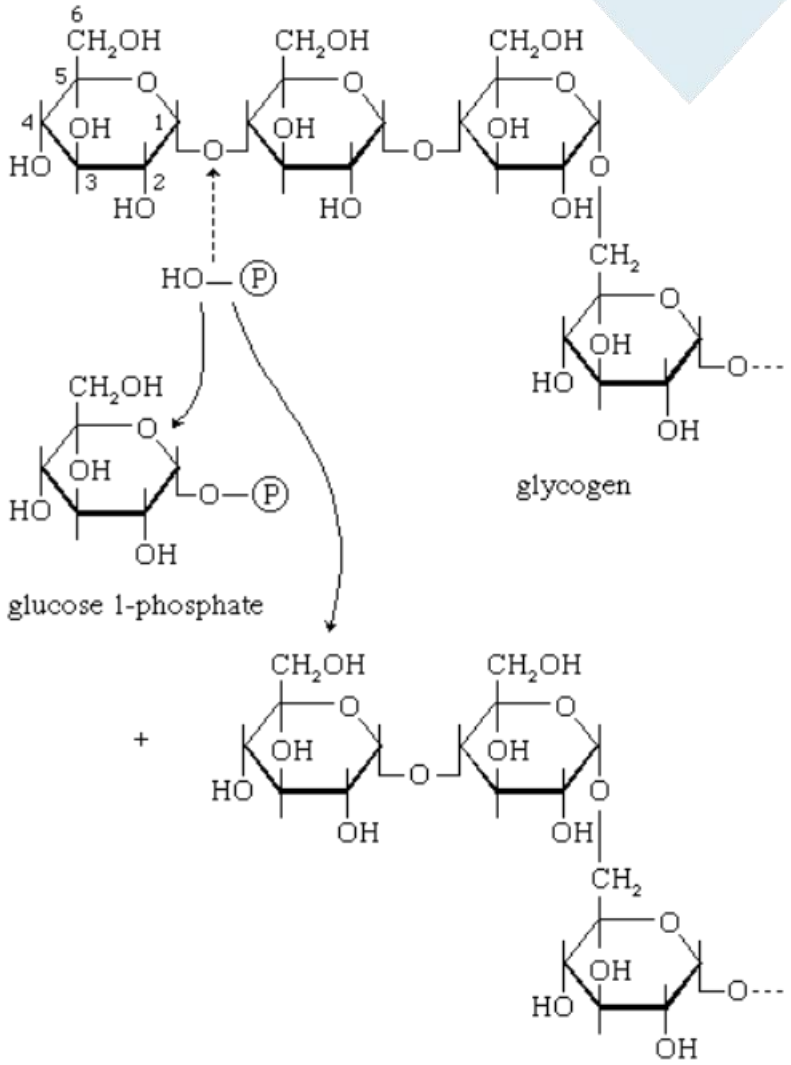
[15]

KDPG pyruvate glyceraldehyde 3-phosphate

pathway.

The main storage carbohydrate of animal cells is glycogen, in which chains of glucose molecules—linked end-to-end, the C1 position of one glucose being linked to the C4 position of the adjacent one—are joined to each other by occasional linkages between a carbon at position 1 on one glucose and a carbon at position 6 on another. Two enzymes cooperate in releasing glucose molecules from glycogen. Glycogen phosphorylase catalyzes the splitting of the 1,4-bonds by adding the elements of phosphoric acid at the point shown by the broken arrow in [16] rather than water, as in the digestive hydrolysis of polysaccharides such as glycogen and starch. The products of [16] are glucose 1-phosphate and chains of sugar molecules shortened by one unit; the chains are degraded further by repetition of step [16]. When a bridge linking two chains, at C1 and C6 carbon atoms of adjacent glucose units, is reached, it is hydrolyzed in a reaction involving the enzyme α (1 → 6) glucosidase. After the two chains are separated, reaction [16] can occur again. The glucose 1-phosphate thus formed from glycogen or, in plants, from starch is converted to glucose 6-phosphate by phosphoglucomutase [7, 8], which catalyzes a reaction very similar to that effected in step [8] of glycolysis. Glucose 6-phosphate can then undergo further catabolism via glycolysis [2, 3, 4, 5, 6, 7, 8, 9, 10] or via either of the routes involving formation

of 6-phosphogluconate



[16]

[12].

Fragmentation of other sugars

Other sugars encountered in the diet are likewise transformed into products that are intermediates of central metabolic pathways. Lactose, or milk sugar, is composed of one molecule of galactose linked to one molecule of glucose. Sucrose, the common sugar of cane or beet, is made up of glucose linked to fructose. Both sucrose and lactose are hydrolyzed to glucose and fructose or galactose, respectively. Glucose is utilized as already described, but special reactions must occur before the other sugars can enter the catabolic routes. Galactose, for example, is phosphorylated in a manner analogous to step [1] of glycolysis. The reaction, catalyzed by a galactokinase, results in the formation of galactose 1-phosphate. This product is transformed to glucose 1-phosphate by a sequence of reactions requiring as a coenzyme uridine triphosphate (UTP). Fructose may also be phosphorylated in animal cells through the action of hexokinase [1], in which case fructose 6-phosphate is the product, or in liver tissue via a fructokinase that gives rise to fructose 1-phosphate [17]. ATP supplies the phosphate group in both

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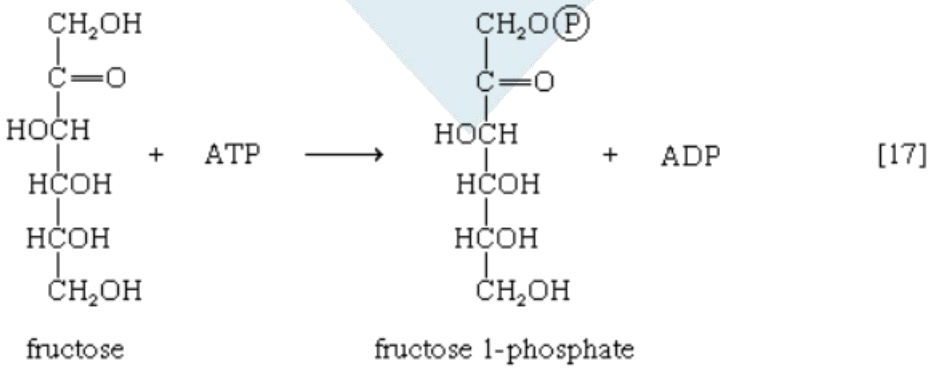
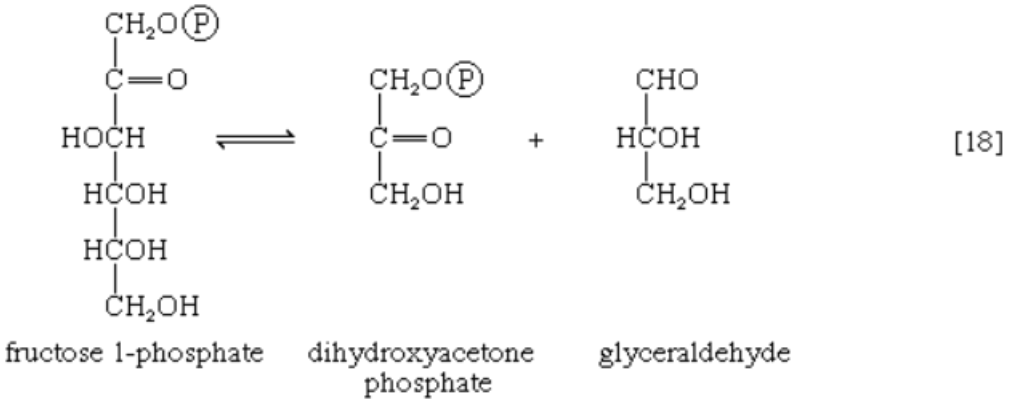


cases.

Fructose 1-phosphate is also formed when facultative anaerobic microorganisms use fructose as a carbon source for growth; in this case, however, the source of the phosphate is phosphoenolpyruvate rather than ATP. Fructose 1-phosphate can be catabolized by one of two routes. In the liver, it is split by an aldolase enzyme [18] abundant in that tissue (but lacking in muscle); the products are dihydroxyacetone phosphate and glyceraldehyde. It will be recalled that dihydroxyacetone phosphate is an intermediate compound of glycolysis. Although glyceraldehyde is not an intermediate of glycolysis, it can be converted to one (glyceraldehyde 3-phosphate) in a reaction involving the conversion of ATP to



ADP.

In many organisms other than mammals, fructose 1-phosphate does not have to undergo reaction [18] in order to enter central metabolic routes. Instead, a fructose 1-phosphate kinase, distinct from the phosphofructokinase that catalyzes step [3] of glycolysis, effects the direct conversion of fructose 1-phosphate and ATP to fructose 1,6-diphosphate and ADP.

The catabolism of lipids (fats)

Although carbohydrates are the major fuel for most organisms, fatty acids are also a very important energy source. In vertebrates at least half of the oxidative energy used by the liver, kidneys, heart muscle, and resting skeletal muscle is derived from the oxidation of fatty acids. In fasting or hibernating animals or in migrating birds, fat is virtually the sole source of energy.

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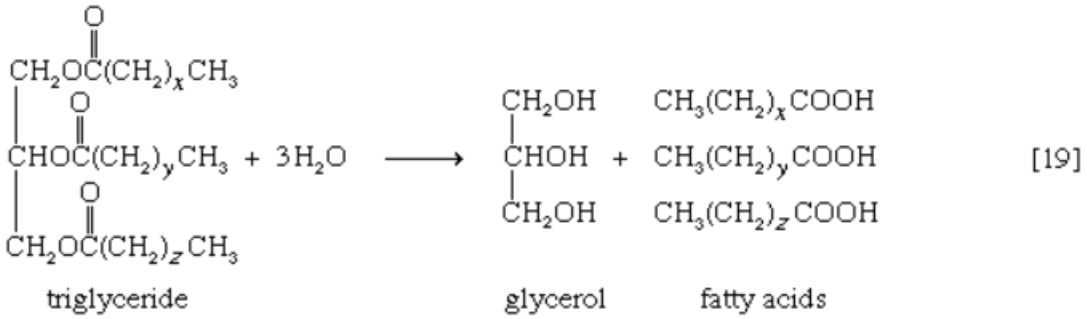

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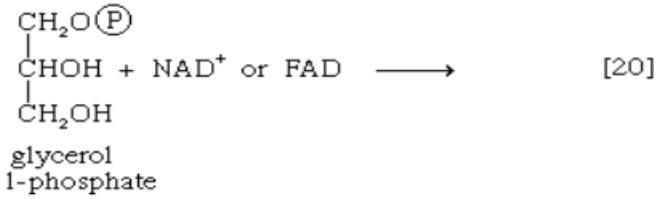
As is apparent from [19], the three molecules of fatty acid released from the triglyceride need not be identical. A fatty acid usually contains 16 or 18 carbon atoms but may also be unsaturated—that is, containing one or more double bonds (—CH=CH—). Only the fate of saturated fatty acids—of the type $CH_3(CH_2)_nCOOH$ (**n** most commonly is an even number)—is dealt with here.

Fate of glycerol

It requires but two reactions to channel glycerol into a catabolic pathway. In a reaction catalyzed by glycerolkinase, ATP is used to phosphorylate glycerol; the products are glycerol 1-phosphate and ADP. Glycerol 1-phosphate is then oxidized to dihydroxyacetone phosphate [20], an intermediate of glycolysis. The reaction is catalyzed by either a soluble (cytoplasmic) enzyme, glycerolphosphate dehydrogenase, or a similar enzyme present in the mitochondria. In addition to their different locations, the two dehydrogenase enzymes differ in that a different coenzyme accepts the electrons removed from glycerol 1-phosphate. In the case of the cytoplasmic enzyme, NAD^+ accepts the electrons (and is reduced to NADH + H^+); in the case of the mitochondrial enzyme, flavin adenine dinucleotide (FAD) accepts the electrons (and is reduced to $FADH_2$).



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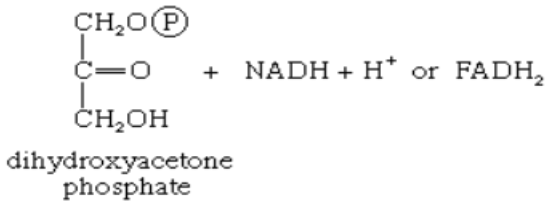

The catabolism of sugars other than glucose

Release of glucose from glycogen

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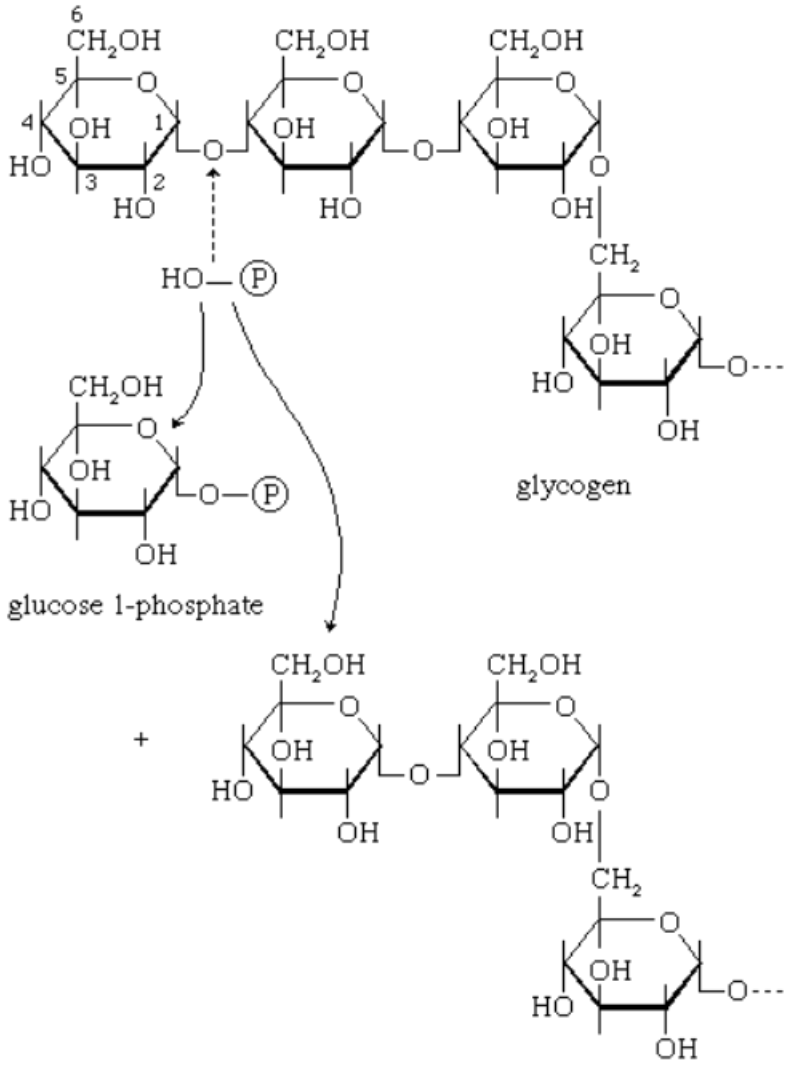

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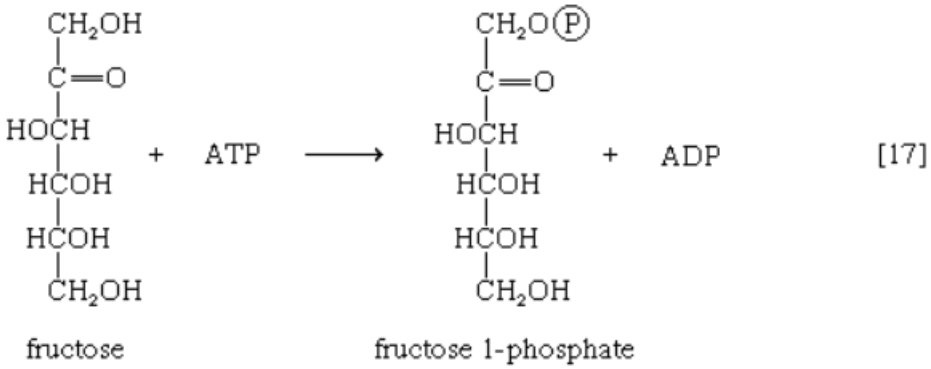

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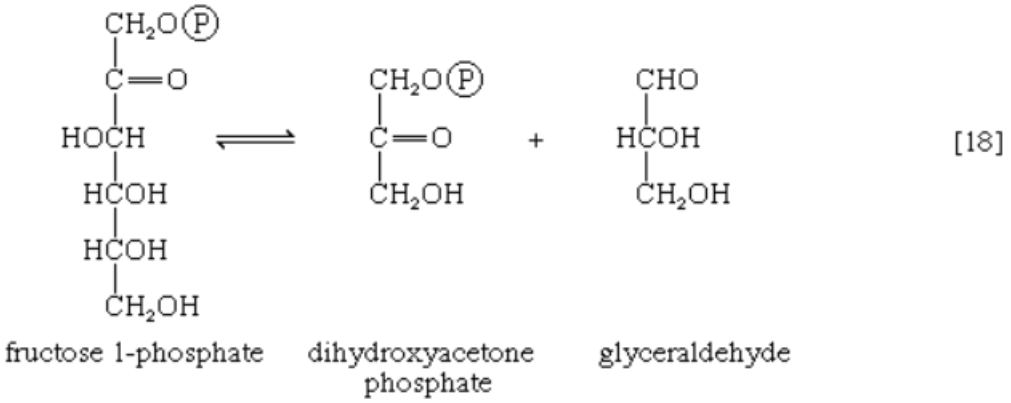

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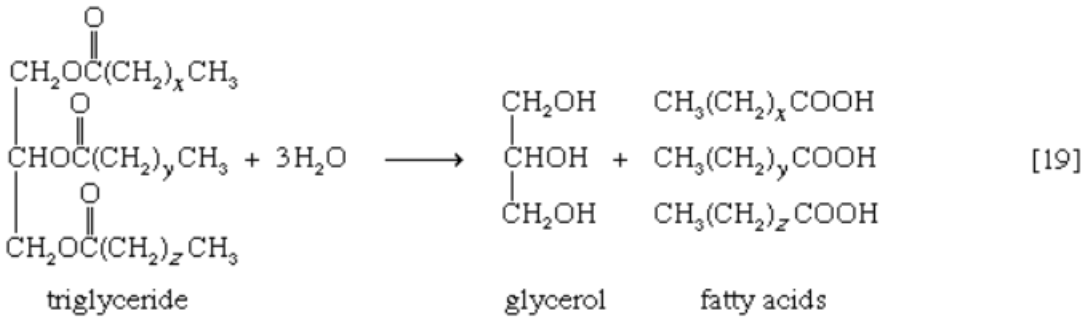

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