Bayer L 13/59 content prepared in this laboratory were analyzed and the results always indicated over 97% recovery. The results of analysis of three commercial formulations are given in Table II.

Discussion

The polarograms for the technical materials were very similar to those for the purified Bayer L 13/59, with an observed half-wave potential of −0.68 volt against the saturated calomel electrode. The standard curves of wave height against Bayer L 13/59 in the 100 ml. of solution were found to be straight lines, which, for the capillary and experimental conditions used, had slopes of 0.124, 0.186, and 0.248 mg. of Bayer L 13/59 per mm. of wave height for sensitivities of 0.04, 0.06, and 0.08 μa. per mm., respectively.

Chloral hydrate, the major contaminant of the technical material, is reduced at a half-wave potential of −1.61 volts and consequently does not interfere. *O,O*-dimethyl 2,2-dichlorovinyl phosphate (DDVP), a decomposition product of Bayer L 13/59 (*11*), is reduced at a half-wave potential of −1.53 volts and does not interfere.

To further test the possible interference, a solution containing equal weights of chloral hydrate, DDVP, and Bayer L 13/59 was analyzed by this method. The presence of chloral hydrate and DDVP did not affect the polarographic wave for Bayer L 13/59.

This method has an accuracy of within ±2%. Four milligrams of Bayer L 13/59 in 100 ml. of solution is apparently a minimum concentration for the sensitivities specified.

Table I. Percentage of Bayer L 13/59 in Technical Products

	Sample A	Sample B	Sample C	Sample D
	94.6	97.3	96.7	97.7
	94.4	97.7	96.6	98.2
	94.8	97.2	96.8	97.8
Av.	94.6	97.4	96.7	97.9

Table II. Percentage of Bayer L 13/59 in Commercial Formulations

	Bait, %		
	1	2	10
	0.9	1.9	9.4
	1.0	1.9	9.6
	1.1	1.9	9.6
Av.	1.0	1.9	9.5

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DIETARY CARBOHYDRATES

A Review of the Effects of Different Carbohydrates on Vitamin and Amino Acid Requirements

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The literature on the effects of different carbohydrates on vitamin and amino acid requirements has been reviewed. A substantial body of evidence indicates that when a less soluble carbohydrate is substituted in the diet for a more soluble one, the requirements for most members of the vitamin B complex and for essential amino acids, reported as a percentage of the diet, decrease. The effect of complex carbohydrates in lowering vitamin B requirements has been related to changes in the intestinal microflora; however, there is no evidence to suggest that such changes influence amino acid requirements. Instead, the lower amino acid requirements appear to be a result of physiological effects on food intake, digestion, or absorption. Thus, although dietary carbohydrate serves primarily as a source of calories, indirect effects of individual carbohydrates may be of considerable nutritional significance.

Almost 60 years ago, before it was known that there were such important dietary accessories as vitamins and before the concept of indispensable amino acids had evolved, Eijkman (*12*) noticed that hens, which developed polyneuritis when fed largely on polished rice, did not do so when the rice was replaced by potato starch. Although the significance of this observation could not be appreciated at the time, it now appears to have been the first hint that vitamin requirements can be modified by the nature of the dietary carbohydrate.

Somewhat later, between 1923 and 1927, after the term vitamin had been coined, Randoin and Simonnet (*57*) published a series of papers in which they reported that the nature of the carbohydrate in the diet influenced the rapidity with which the symptoms of "vitamin B" deficiency developed in pigeons. They also noted that the relatively indigestible potato starch exerted the most pronounced protective effect. Between 1926 and 1928, Fredericia in Denmark (*15*), and Roscoe (*59*) and Kon and Watchorn in England (*38*) described the phenomenon of refection in which rats that had lost weight after being fed on a diet deficient in the vitamin B complex and containing uncooked starch, spontaneously resumed growth. Fredericia and associates (*16*) originally observed that refection occurred only occasionally in rats receiving uncooked rice starch but Kon and Watchorn (*38*) demonstrated that what was only an occasional occurrence in rats receiving diets containing rice starch became a regular occurrence when the rice starch was replaced by uncooked potato starch. These observations were received with skepticism by Mendel and Vickery (*48*), but were subsequently amply confirmed by several investigators (*35*). It was then evident that the nature of the dietary carbohydrate influenced the requirement for the B vitamins and subsequent research has been concerned with the extent to which the requirement for the various individual vitamins may be affected, the relative effects of a wide variety of carbohydrates, and the mechanism by which such effects come about. Recently the question has also arisen as to whether amino acid requirements may be affected by the type of dietary carbohydrate.

Vitamin B Content of Feces

Kon (*36*) suggested that refection occurred as a result of endogenous bacterial synthesis of the vitamin B complex. He did not, at that time, discuss how the vitamins, synthesized by intestinal bacteria, became available to the animal; but as early as 1911, Osborne and Mendel (*55*) had observed that when rats were not growing well on certain diets improvement resulted when they were given access to their feces. During the following 20 years, a considerable amount of information was obtained by a variety of workers which demonstrated that the vitamin B complex could be synthesized by microorganisms and that coprophagy, the ingestion of feces, affected to a marked degree the growth response of animals on vitamin B-deficient diets (*19*, *58*).

The reports on refection and coprophagy led Guerrant and Dutcher (*27*) to investigate the effect of the type of dietary carbohydrate on the vitamin B content of feces. They showed (*20*) that the need for thiamine and riboflavin decreased when sucrose was replaced by dextrinized cornstarch and that certain forms of fiber exerted a vitamin-sparing action. This effect they attributed to the production of more favorable conditions for the growth of microorganisms in the digestive tract. They studied the vitamin B content of rat feces by feeding groups of rats on vitamin B-deficient, purified diets containing different carbohydrates and giving parallel groups, in addition to the particular diets, their own feces or the feces of another group. Their results, published in 1934 and 1935 (*20*, *23*), showed clearly that the feces of rats receiving dextrinized cornstarch contained much more of the vitamin B complex than those of rats receiving either sucrose or glucose and that the feces of rats receiving lactose occupied an intermediate position.

The following year, 1936, Bender and associates (*5*) reported that rats receiving diets supplemented only with thiamine, survived longer if dextrin was used in place of sucrose as the dietary carbohydrate. If both thiamine and riboflavin were provided, a substantial improvement in growth resulted when sucrose was replaced by dextrin.

About this same time, Guerrant, Dutcher, and Brown (*22*) found that rats fed on a diet deficient in the vitamin B complex had to consume their feces in order to grow. When the rats were not allowed access to their feces, the weight loss of animals on the dextrin-type diet was less than that of comparable animals receiving sucrose—a hint that small amounts of vitamins might become available by a route other than by the ingestion of feces.

Morgan, Cook, and Davison (*52*) made a similar comparison of several carbohydrates and found that rats developed signs of riboflavin and pyridoxine deficiencies less rapidly when consuming lactose diets and that signs of filtrate-factor deficiency, probably pantothenic acid, developed less readily when the diet contained cornstarch. Sucrose, they said, was the carbohydrate of choice for vitamin studies because all of these deficiencies could be produced most readily in rats receiving sucrose-type diets. They suggested that lactose and cornstarch might favor the production of various vitamins by microorganisms in the intestinal tract of the rat.

Throughout this period, the role of intestinal synthesis of the B vitamins and the importance of coprophagy were widely discussed in reference to studies on refection and on the influence of digestible carbohydrates on vitamin requirements. Bliss (*7*), in a discussion of this problem, pointed out the great difficulty in completely preventing rats from consuming their own feces. The work of Guerrant and his associates (*22*) shows that the beneficial effect of dextrin on rats receiving a diet deficient in the entire vitamin B complex depended to a large extent on coprophagy.

At Wisconsin, it was found (*46*, *67*) that the requirement of the rat for riboflavin was lower if dextrin were used as the dietary carbohydrate instead of sucrose or cellulose plus sucrose. (The term dextrin is used in this paper to describe the product obtained by heating cornstarch for 2 hours in an autoclave at 15 pounds' pressure, after which it is dried at 65° to 70° C. and finely ground.) Lactose occupied an intermediate position. This beneficial effect was thought to be dependent on changes in the intestinal flora which resulted in increased intestinal synthesis of riboflavin. Thiamine synthesis was not appreciable regardless of which carbohydrate was fed. Najjar and Holt (*54*) have observed appreciable synthesis of thiamine in the intestinal tract of a man receiving Dextrimaltose as the dietary carbohydrate, but there is little evidence that thiamine synthesis is significant in laboratory animals. It thus seems probable that the major benefit of dextrin to thiamine-deficient animals is associated with coprophagy, whereas some of the more readily synthesized vitamins, particularly those required in relatively small amounts, may be absorbed directly from the intestine and that this effect may be greatest when thiamine is provided in the diet.

Requirement for Several B Vitamins

During the next few years, a number of observations were made on the effect of the type of dietary carbohydrate on the requirement for several of the B vitamins. Skeggs and Wright (*63*) found that dextrin promoted greater liver storage of pantothenic acid than did sucrose, Cerelose, or cornstarch and that the feces contained more folic acid, biotin, niacin, and pantothenic acid when dextrin replaced sucrose in the diet.

A series of related investigations was conducted by various workers at Wisconsin. Luckey and associates (*45*) showed that the growth of chicks fed on folic acid deficient diets containing dextrin was appreciably greater than that of comparable birds consuming sucrose-type diets. Sarma, Snell, and Elvehjem (*60*) while devising a biological assay for pyridoxine, observed that the growth rate was increased if dextrin was substituted for sucrose in the pyridoxine-deficient diet. The growth-promoting effect of dextrin could be decreased by adding sulfa drugs to the diet, an indication that pyridoxine synthesized by the intestinal flora in the presence of dextrin became available to the rat. Krehl and associates (*40*) reported that dextrin or glucose in the diet reduced the requirement for niacin and tryptophan below that found when the diet contained sucrose, and that the fecal excretion of niacin and folic acid by rats fed on diets deficient in these two vitamins was greatest when the diet contained dextrin, intermediate with lactose, and least with glucose or sucrose (*65*). Couch and associates (*9*) observed that dextrin was superior to sucrose in promoting egg production and hatchability in hens fed on biotin-deficient diets.

Krehl and Carvalho (*39*) showed that the growth of rats receiving pantothenic acid-deficient diets was improved when dextrin was used as the dietary carbohydrate in place of sucrose. A similar effect was observed when the diet was made deficient in biotin by the inclusion of egg white. Bacigalupo, Couch, and Pearson (*2*) compared several carbohydrates for their ability to promote vitamin synthesis in the intestinal tract of the cotton rat. They found that lactose promoted much greater synthesis of biotin, folic acid, and riboflavin than did sucrose or fructose and that galactose was intermediate.

Hundley (*33*) extended some of the earlier observations on niacin and found that the requirement for niacin was greater when the dietary carbohydrate was either fructose or sucrose than when these were replaced by glucose or cornstarch. In work with chicks, Anderson, Combs, and Briggs (*1*) evaluated the ability of D- and L-tryptophan to replace niacin. They found that D-tryptophan, which was of little value when the dietary carbohydrate was glucose, could serve as a niacin precursor when the glucose was replaced by cornstarch. There is also evidence that cornstarch affords some protection against the hemorrhagic kidneys associated with choline deficiency (*4, 18*).

The growth of vitamin B_{12} deficient rats is also affected by the type of dietary carbohydrate. At least three groups (*11, 43, 56*) have demonstrated a beneficial effect from including dextrin or cornstarch in the diet of rats receiving no direct supply of vitamin B_{12}. A further beneficial effect from the inclusion of dextrin or cornstarch in the diet was reported by Lewis and associates (*43*), who found that rats receiving a complete diet were partially protected from the growth-depressing action of a high level of iodinated casein by these two carbohydrates. Also both with chicks (*64*) and with rats (*56*), fed an apparently complete diet, a greater response to antibiotics was obtained when sucrose was the carbohydrate rather than dextrin. In both cases, the greater response was primarily because of the poorer growth of the sucrose control groups. Whatever may be the mode of action of the antibiotic, at least part of the effect can be duplicated by replacing sucrose in the diet by dextrin.

In general, the requirement for most of the members of the vitamin B complex can be reduced by including relatively insoluble carbohydrates such as dextrin or starch in the diet. In order of decreasing effectiveness, the sequence would be dextrin, cornstarch, lactose, glucose, and sucrose—although this varies somewhat with the different vitamins and with experimental conditions.

One notable exception to the general rule, reported by Leoschke, Lalor, and Elvehjem (*41*), was that mink fed on a purified diet containing dextrin as the source of carbohydrate developed a vitamin B_{12} deficiency more quickly than those receiving a similar diet containing sucrose. Also, more vitamin B_{12} was excreted in the feces of the mink receiving the sucrose basal diet. This then is one situation in which a soluble carbohydrate is more beneficial than the less soluble ones.

Amino Acid Requirements

Interest in the effect of different dietary carbohydrates on amino acid requirements arose from studies on vitamin-sparing effects. When it was found that niacin could be replaced by tryptophan it became necessary to use a low protein diet in order to produce a niacin deficiency. This procedure was used by Krehl and associates (*40*) when they compared the effects of various dietary carbohydrates on the niacin requirement of the rat. Their results showed that either niacin or tryptophan had to be added to a low protein, niacin-deficient diet containing sucrose in order to produce growth approaching that obtained with an unsupplemented diet containing dextrin. However, the sucrose-type diet, to which both niacin and tryptophan had been added, did not support as rapid a rate of growth as that obtained with a deficient diet in which dextrin was the source of carbohydrate.

About the same time Hall and Sydenstricker (*24*), who were using a low protein diet to produce a methionine deficiency, also found that their rats grew much better when they used cornstarch in place of sucrose as the source of dietary carbohydrate. They found that additional vitamins and amino acids improved the growth of the rats on the sucrose-type diet.

During some feeding experiments with chicks, Lepp, Harper, and Elvehjem (*42*) observed that the growth of chicks fed on a complete diet (before vitamin B_{12} was available) containing sucrose was less than that of chicks fed on a similar diet containing dextrin. Growth improved when the protein content of the sucrose diet was increased. Monson, Dietrich, and Elvehjem (*50*) compared several carbohydrates for their ability to support the growth of chicks on a similar basal diet and again found dextrin to be superior, with Cerelose, sucrose, and lactose following in decreasing order.

Growth of Rats on Low Protein Diets

Subsequently, Harper and Katayama (*26*) investigated the effect of the type of dietary carbohydrate on the growth of rats fed on low protein diets. They found that when sucrose was used as the dietary carbohydrate in low protein diets, from 2 to 3% more protein was required to support growth equivalent to that obtained with a similar diet in which the sucrose was replaced by cornstarch. A sparing effect on methionine specifically was also demonstrated. These effects could be shown only with diets deficient in protein and they became progressively less marked as the dietary protein was made more adequate.

Womack, Marshall, and Parks (*67*), shortly after, reported that nitrogen balance could be maintained in adult rats receiving dextrin-type diets with lower levels of essential amino acids than when sucrose was substituted for dextrin.

Liver Fat Deposition

Both Marshall and Womack (*47*) and the authors (*27, 44*) have studied the effect of the type of dietary carbohydrate on liver fat deposition. In both studies, the former with adult rats, the latter with young ones, liver fat deposition was considerably less when the diet contained dextrin than when it contained sucrose. The improved nitrogen balance (*67*) and growth (*26*) previously noted were again observed and the favorable action of dextrin in preventing an accumulation of liver fat was attributed to its effect in improving the utilization of protein. As both Singal and associates (*62*) and the group at Wisconsin (*28*) had found that the accumulation of liver fat in rats, fed on 9% casein diets containing choline, could be very largely prevented by supplementation with threonine, the prevention of excessive liver fat deposition appeared to be further evidence of a protein-sparing action of dextrin.

When a series of carbohydrates was tested for ability to stimulate the growth of young rats fed on low protein diets and to prevent excessive liver fat deposition, dextrin proved superior, glucose followed, and sucrose and fructose were well behind. The ability of dextrin to support growth beyond that obtained with sucrose was demonstrated with diets containing a variety of proteins and an amino acid mixture (*27*). The beneficial effect on liver fat content could be demonstrated with casein and an amino acid mixture resembling 9% of casein in composition but, when a low-protein diet containing egg albumin was used, dextrin was without effect. The liver fat accumulation found in rats fed on low-protein diets may be the result of a rather complex amino acid imbalance (*25*). This might, only in certain instances, be corrected by altering the dietary carbohydrate. Womack and Marshall (*66*), in further studies with adult rats receiving small quantities of essential amino acids, reported similar results regarding the relative value of various carbohydrates.

Growth of Animals Receiving Purified Diets

During this period, some further observations (*57*) were made on the effect of the type of dietary carbohydrate on the growth of chicks receiving a complete (not containing a source of unidentified growth factors), purified diet. Like the rat, the chick required more protein with sucrose as the dietary carbohydrate to maintain a growth rate equivalent to that observed when a dextrin-type diet was fed. A substantial response to antibiotics occurred when the lower level of protein was fed with sucrose but very little when dextrin was substituted for sucrose or when the protein level of the sucrose diet was increased from 18 to 25%. The primary deficiency in the diet used was tryptophan and a growth response equivalent to that obtained with dextrin or with additional protein in the sucrose diet could be obtained when the tryptophan content of the diet was increased (*6*).

In early studies, little benefit resulted from replacing sucrose with dextrin in the diet of the guinea pig; however, the provision of bulk such as cellulose or gum arabic was found to stimulate growth (*8*). In recent work, the relative merits of sucrose and dextrin have been reinvestigated with the more adequate purified diets now possible and over a range of protein levels. Again no marked improvement occurred when sucrose in the diet was replaced by dextrin (*32*). This is in marked contrast to the results of the experiments with rats and chicks. However, the purified diet for guinea pigs contains a substantial amount of bulk, which might possibly mask any benefit from dextrin, as some improvement in the growth of rats fed on low-protein diets, containing sucrose, has been obtained upon adding cellulose to such diets (*26*, *27*).

Bavetta and Ershoff (*3*) have recently shown that the growth of rats receiving a diet deficient only in tryptophan is improved if the sucrose in the diet is replaced with cornstarch. In this case, there is a decrease specifically in the requirement for a single amino acid. Similar effects have been observed in rats fed on diets deficient in either methionine (*26*) or isoleucine (*31*). Under conditions of *ad libitum* feeding the amino acid requirements of rats, reported as a percentage of the diet, may be affected by the type of dietary carbohydrate.

Mechanism by Which These Effects Come About

The mechanism by which the type of dietary carbohydrate affects the requirements for vitamins has been studied extensively, but the mechanism of the effects on amino acid requirements is only now being investigated in detail. The decrease in vitamin requirements, generally associated with the feeding of less soluble carbohydrates, is considered to be a result of increased synthesis of vitamins by intestinal microorganisms. Such increased synthesis is probably associated with a change in the type of intestinal bacteria as much as with an increase in the total number of microorganisms that may be present. Differences in the numbers of microorganisms per gram of intestinal contents have been neither striking nor consistent, and information about the change in total numbers is very difficult to obtain because it depends upon accurate measurement of differences in the amount of intestinal residue when various carbohydrates are fed. However, there is an increase in the quantity of feces excreted when sucrose is replaced by cornstarch or dextrin.

Some of the evidence for increased intestinal synthesis of vitamins (*49*), when the less soluble carbohydrates are fed, has been discussed and Elvehjem (*13*, *14*), Kon (*37*), and Johansson and Sarles (*34*) have reviewed in considerable detail the work in this field. The types of evidence available may be summarized briefly as follows:

The intestinal contents of animals receiving diets containing dextrin usually contain more B vitamins than those of comparable animals fed on diets containing sucrose. Such figures have been obtained by both biological and chemical methods on intestinal, cecal, and fecal samples.

In a number of cases, careful balance studies have demonstrated that animals fed on diets containing the less soluble carbohydrates excrete greater quantities of vitamins than they consume.

The growth-promoting effects of the less soluble carbohydrates can be decreased in some cases by including antibacterial agents, such as certain sulfa drugs, in the diet.

In some instances, microorganisms isolated from the intestinal contents of animals receiving diets containing the less soluble carbohydrates have been shown to have greater synthetic abilities than those found in the intestinal contents of comparable animals fed on sucrose-type diets.

Before discussing possible ways in which the less soluble carbohydrates may improve the utilization of dietary protein, it should be made clear that this effect is distinctly different from the classical protein-sparing action of carbohydrates, which has been studied for many years (*53*). In the latter action, the function of carbohydrate is primarily to provide energy and thereby reduce the need for protein to be broken down as an energy source with the subsequent wasting of nitrogen. That effect is most readily demonstrated when the starving animal is given access to carbohydrate. The improved utilization of low-protein diets discussed in this paper is demonstrable when the diets are of equal energy content and contain equal amounts of carbohydrate. Although protein may be spared, the effect is not due to carbohydrate, per se, but to the nature of the carbohydrate. It is considered to be a physiological effect.

Such evidence as there is for a physiological mechanism is indirect. There are two reports (*50*, *64*) with chickens as the experimental animal, in which the rate of passage of dextrin through the intestinal tract was shown to be slower than that of sucrose. Dreisbach and Nasset (*10*), using rats, found that the absorption of glucose was prolonged when the diet contained cornstarch rather than a more soluble carbohydrate. That dextrin remains undigested for a longer time in the gastrointestinal tract than does sucrose has also been observed (*29*). This is the condition which is considered to favor the intestinal synthesis of vitamins and the suggestion has been made that amino acids synthesized by intestinal microorganisms in the presence of dextrin may become available to the animal. However, when one realizes that thiamine, for example, is required only at a level of 100 γ per 100 grams of diet and that the biotin and folic acid requirements are only a fraction of this—whereas the requirement for tryptophan, the indispensable amino acid needed in least quantity, is approximately 200 mg. per 100 grams of diet—it seems improbable that intestinal synthesis of indispensable amino acids could exert a significant effect.

The suggestion has been made that the slower passage of less soluble carbohydrates through the gastrointestinal tract may permit a more efficient utilization of the dietary protein. This could be brought about, as has been suggested for the classical protein-sparing effect of carbohydrate (*17*), by having glucose and amino acids absorbed together over a longer period of time, thus reducing the extent to which amino acids are destroyed through deamination. This would be in accord with the observations of Marshall and Womack (*47*) that nitrogen retention of mature rats receiving a dextrin-type diet was greater, even under paired-feeding conditions, than that of parallel groups receiving a similar diet in which the dextrin was replaced by sucrose.

When young, rapidly growing rats receiving dextrin-type diets were pair-fed with those receiving similar diets containing sucrose, very little beneficial effect of dextrin on growth was evident but there was a decrease in the accumulation of liver fat (*27*). Although the decrease in liver fat deposition may be indicative of some improvement in protein utilization, the improved growth, regardless of the mechanism by which it is brought about, depends upon the greater food consumption of the rats receiving the dextrin-type diet. The lower food intake of the animals receiving sucrose-type diets has so far been thought of as an effect of the nutritional inadequacy of such diets rather than a cause of differences noted. This assumption may be open to question.

When the various carbohydrates are listed in order of decreasing effectiveness, with the exception of sucrose and glucose which are reversed, they follow in order of decreasing molecular weight. Thus, differences in food intake are possibly a reflection of the differences in osmotic pressure of solutions of the various carbohydrates as modified by their rates of absorption. Rats receiving a test meal containing sucrose have, for at least 5 hours afterward, a considerable quantity of fluid in their stomachs. Less fluid accumulation is found if the diet contains dextrin (*30*). Food consumption, and hence protein intake, is probably limited because of the larger fluid retention when the low-protein diet contains sucrose and the greater intake of the protein deficient diet by rats receiving dextrin not only contributes more protein per unit of body weight but also leads to improved food utilization.

The requirements for both vitamins and amino acids may be modified by changing the type of carbohydrate in the diet. The vitamin-sparing effect of the more complex carbohydrates is apparently due to their ability to promote a type of intestinal flora which synthesizes greater quantities of certain vitamins and may also destroy less. The mechanism by which amino acid requirements are decreased when the diet contains certain complex carbohydrates has received less attention, but appears to be a result of a physiological effect on food intake, digestion, or absorption, rather than an effect on the intestinal microflora.

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