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DIGESTION AND ABSORPTION OF CARBOHYDRATES DELIVERED DIRECTLY TO THE BOVINE OMASO-ABOMASUM

by

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INTRODUCTION

During the first few weeks of life the dietary requirements of a calf are similar to those of monogastric animals and these needs are met mainly by milk or milk substitutes. Moreover, such liquid feeds normally by-pass the rumen and reticulum of the young calf because of reflex closure of the esophageal groove. Therefore, for proper formulation of milk replacers, it is necessary to know the extent to which the calf can utilize the various possible ingredients. After the rumen has developed functionally the calf can subsist on dry feeds; and rumen microorganisms are able to convert both simple and complex carbohydrates into products which can be utilized by the animal. This reduces the need for carbohydrate digestion and absorption in the portion of the digestive tract posterior to the rumen. From a fundamental standpoint, however, it is desirable to gain more information on the digestive capacity of ruminants when the rumen and reticulum are by-passed.

Until recently, comparatively little was known regarding the calf's ability to digest carbohydrates when introduced into the digestive tract in such a way as to escape rumen fermentation. Although several recent studies have greatly contributed to a clearer understanding in this area, their scope has been confined in the young calf to the period from birth to 14 weeks of age. In general, these studies have

demonstrated that glucose and lactose are the only carbohydrates well utilized by the young calf. Some utilization of maltose was shown while starch and sucrose were poorly utilized. The inability of the calf to use starch is difficult to explain since studies have shown considerable amylase in calf pancreatic tissue.

The methods used for determining carbohydrate utilization posterior to the rumen have certain limitations. One such method is measurement of increases in blood reducing sugar after ingestion of a carbohydrate, but many factors, other than absorption of nutrients, may affect blood sugar levels. The significance of digestibility studies for determining the extent of carbohydrate utilization is limited to a degree by the microbial fermentation which occurs in the lower digestive tract. A less direct procedure has been determination of carbohydrase activity in digestive glands, but such studies fail to consider enzyme secretion rates.

The objectives of the present study were (a) to evaluate, by use of blood reducing sugar responses, the ability of the bovine (at ages ranging from approximately 2 weeks to 2 years) to utilize various carbohydrates introduced directly into the omaso-abomasal area and (b) to employ digestion studies to assess the efficacy of using blood reducing sugar values in determining carbohydrate utilization.

REVIEW OF LITERATURE

Rumen Fermentation of Carbohydrates

Rumen microorganisms will readily degrade most common carbohydrates in feeds with the concomitant release of short chain fatty acids. Evidence of such fermentation was reported in 1933 by Allcroft and Strand (1) who obtained very slight rises in blood glucose after dosing the rumen of fasted sheep with 100 g. of sucrose and 250 g. of maize starch, while the same high carbohydrate diet in the dog gave a blood sugar increment of 50%. This work was given supoort by that of Phillipson and McAnally (86) who showed glucose, fructose and sucrose were rapidly fermented in the rumen, while breakdown of starch and cellulose was at a slower rate. Schambye (101) noted little difference in blood sugar levels between the portal and arterial systems of mature sheep fed a crushed oats and hay diet. It was implied that very little grain carbohydrate escapes digestion by rumen microorganisms, therefore only small amounts of glucose are released for absorption from the alimentary tract. It was further suggested that facilities for carbohydrate digestion in the lower tract of ruminants may be limited because of the apparent lack of need for them.

Weller and Gray (116) fed a ration supplying three levels of starch to sheep fitted with abomasal fistulas.

An estimated 5% of the ingested carbohydrate passed through the abomasum when 148 g. were fed. At lower intakes, a greater percentage, but a lesser total amount escaped rumen fermentation.

In addition to the wide range of rumen bacteria possessing strong amylolytic properties, starch-digesting power has also been shown by rumen protozoa. Unlike the bacteria which secrete amylases into the extracellular fluid, digestion of starch by the protozoa occurs within the gastric sac, with the accompanying accumulation of an amylopectin-like substance in the cytoplasm of the organism (4,74).

It is not intended in the above to present an extensive review of literature pertaining to rumen fermentation of carbohydrates, but only to mention a few pertinent references for comparison with carbohydrate degradation in the alimentary tract posterior to the rumen.

Carbohydrates in Growth and Digestibility Studies

Milk replacer rations for young calves

The young calf is well equipped by nature to handle relatively large amounts of lactose from milk (6). For some time there has been considerable interest in determining the extent of utilization of other carbohydrates if substituted for lactose in a milk replacer diet. One of the earliest of such studies was that by Shaw *et al.* (103). The recovery in the feces of corn starch which had been included in the milk

at the level of 40 g. per feeding was determined on calves from 4 to 40 days of age. Starch digestion was 21, 63 and 98% at 4, 20 and 40 days of age, respectively. Norris (80), in subsequent work, reported that much larger quantities of acids and alcohols were excreted in the feces of calves fed a cereal gruel than in feces of those fed whole milk. In apparent contradiction to Shaw's results Norris proposed that any apparent utilization of starch by the calf is due to its partial breakdown in the lower tract by the microbial population. In a review of the literature, Savage and McCay (100) in 1942 stated that very little was known about utilization of starch by the young calf.

In a more recent study, Flipse et al. (41) compared the nutritive value of several carbohydrates fed as constituents of synthetic milk. Weight gains among calves receiving lactose from 2 to 33 days of age were about twice those of calves receiving glucose or corn syrup. Incidence of scours was greater in the two latter groups. Prolonged irritation of the digestive tracts of animals receiving the glucose and corn syrup was substantiated by the frequent appearance of pyloric ulcers, abomasal hemorrhages, and patchy congestion of the intestines upon post mortem examination. In a similar experiment with animals of the same age, Flipse and associates (40) demonstrated that the addition of lactose to rations containing corn syrup or starch caused much faster gains with higher feed efficiencies than when lactose was excluded from

the ration. Greatest incidence of diarrhea occurred among the starch group. It was concluded that lactose favorably influenced the utilization of the other carbohydrates. These results lend support for the common practice of including milk solids in milk replacer rations.

Noller et al. (77,78,79) fed several vegetable milk replacers to calves in which the bulk of the carbohydrate was starch. An increase in digestibility of nitrogen-free extract from about 55 to 85% was noted between 2 and 4 weeks of age. Average daily gains increased from 0.2 to 1.2 pounds between the ages of 2 to 5 weeks. It was concluded that the calf cannot effectively use milk replacers from vegetable sources prior to 4 weeks of age. These results agree quite well with those of Dollar and Porter (29,30) in which it was reported that calves did poorly up to 3 weeks on a milk replacer containing skim milk and oat flour or skim milk and flaked maize. Pre-digestion of the cereals with alpha and/or beta amylase did not seem to affect utilization. Substantial quantities of maltose, some dextrin and some glucose were revealed upon chromatographic examination of the feces. A report by Netke et al. (76) showed that the addition of 30% starch or blackstrap molasses to reconstituted skim milk caused poorer growth in young calves than the reconstituted skim milk alone. Addition of amylase seemed to have no effect upon the response of calves to starch. Raven and Robinson (91) obtained a digestibility coefficient of 53%

for corn starch added to a skim milk diet for young calves while digestibility of the milk lactose was about 97%. In a later study the same workers (92) compared the utilization of a cereal gruel to that of reconstituted skim milk. On isocaloric and isonitrogenous rations, digestible energy and nitrogen retention were less among calves on the cereal diet. Calcium and phosphorus retentions roughly paralleled those of nitrogen.

Ratcliff (90) and Ratcliff and associates (91) studied the effect of addition of distillers dried solubles to milk replacer rations. Starch digestibilities at 7 weeks of age in the group receiving solubles were 70.4% as compared to 93.6% for the control group. The calves in the solubles group grew faster, appeared healthier and had less digestive disturbances. A possible explanation given for the difference in apparent starch digestibility between the groups was the larger quantity of starch in the diet containing distillers dried solubles. These authors further suggested that the digestive upsets may have been due to starch fermentation in the lower tract and that the distillers dried solubles could have caused partial inhibition of the fermentative processes, thus accounting for the decreased starch digestibility.

In agreement with the previously mentioned results, milk replacer containing 10% of a dextrose-maltose-dextrin material was shown by Williams and Knodt (118) to produce subnormal growth in calves.

Wallace and coworkers (114) reported a high digestibility of glucose and sucrose, but somewhat lower digestibility for starch when each of these carbohydrates contributed 30% of the dry weight of a milk substitute ration. Average daily gains up to 8 weeks on the three rations were 0.8, 0.7, and 0.6 pounds, respectively. In contrast to the results of the Cornell workers are those of Huber (49) who showed low apparent digestion of the sucrose-starch portion of a test meal fed to young calves. (Sucrose and starch were added to whole milk at levels of 2.5 and 0.5%, respectively.) When 3% lactose was added to the milk, apparent digestibility was 92%. Other recent reports have also indicated relatively poor utilization of sucrose in the calf (29,30,82,110).

Reports of several experiments have shown that additional lactose can be successfully supplemented to milk or milk replacer rations, either as the pure sugar or in the form of whey (40,41,109). However, the work of Rojas and associates (98) indicates that there is a limit to the amount of lactose that a calf can utilize when added to a skim milk diet. By doubling the lactose content of skim milk, these workers noted severe diarrhea and unthriftiness among calves. Owen (84) used rations containing lactose in amounts similar to those fed by the Wisconsin workers. It was shown that the carbohydrate had a laxative effect which was ameliorated by addition of milk fat to the ration. A high apparent digestibility of the lactose was indicated by the recovery

of only minute quantities in the digestive tract contents of calves sacrificed 14 hours after feeding a test meal in which lactose constituted 30 to 60% of the dry matter.

The studies cited lend support to the view of Preston (88) that starch and sucrose are poorly utilized by young calves when these carbohydrates are fed in such a manner as to escape rumen fermentation and that glucose and lactose are apparently well utilized.

In experiments with older animals Larsen (63) and co-workers (64) evacuated the rumens of 9-month-old steers and introduced carbohydrates from four sources (glucose, maltose, starch and corn) directly into the omasum-abomasum. Digestibility and blood reducing sugar estimates indicated that glucose and maltose were well utilized while this was not true for the starch and corn. Greater amounts of pure starch and lesser amounts of starch in corn were recovered in the cecal than in the fecal contents. It was suggested that partial degradation of starch is accomplished by micro-organisms in the large intestine. However, no explanation was given for the apparent decrease in digestibility of the starch contained in corn while passing from the cecum to the rectum. It was suggested that, because of partial microbial breakdown in the colon, studies of starch digestion posterior to the rumen of young ruminants are often difficult to interpret relative to the benefit derived by the animal from starch in the feed.

Carbohydrate utilization by other species

Several recent investigations have compared utilization of different carbohydrates in young pigs. In one such experiment with semi-purified diets, Hudman et al. (52) showed gains and feed efficiencies from 1 to 5 weeks of age were best for lactose-fed pigs. Responses to diets containing yellow corn, sucrose or dextrose were somewhat lower, while diets containing corn starch, oat groats, corn flakes or pre-gelatinized starch were still more inferior. In further studies of digestion in the baby pig, the same workers noted a higher digestibility of starch in the 6-day-old pig than in the 3-day-old. No increase subsequent to 6 days was noted. The studies of Becker and associates (9,10) agree well with those of the Iowa workers (52,117) in that lactose is the carbohydrate of choice in baby pig rations. It was further shown that the pig's ability to tolerate large amounts of lactose decreases with age.

Several experiments by English workers (16,17,27,28) indicate that the newborn pig is capable of utilizing only glucose and lactose while ability to digest sucrose, maltose and dextrins develops in the first 10 days of life.

Another series of studies relating to the development of ability by the baby pig to digest carbohydrates has been made by Cunningham and Brisson (22,23) in which the intestinal loop technique was employed. In apparent contradiction

to the results of Dollar and associates, these authors present evidence that the new-born pig is able to digest maltose efficiently. However, this carbohydrate was found to impair optimum feed consumption and growth during the first few days of life. Rate of digestion of soluble starch was practically as fast as that of maltose.

Oral ingestion of carbohydrates in a subsequent study by Cunningham (21) gave results similar to those obtained from the study using the loop technique. Rate of digestion of raw starch was much slower than that of soluble starch and supplemental amylase did not alter this rate. It was suggested that the demonstrated inability of the baby pig to digest raw starch is not due to a deficiency of amylase, but rather to the difficulty encountered by the enzyme in penetrating the intact starch granule. In accordance with the above mentioned results, Lloyd and coworkers (66) suggested that the starch-digesting mechanism in the pig has completely developed by three weeks. Evidence supporting this postulate was the observed increase in digestibility of all nutrients except carbohydrates between the ages of three and seven weeks.

Investigations by a number of workers, of which only a few will be cited herein, indicate that lactose is inferior to other carbohydrates when included in rations for chickens and weaned rats (36,37,24). Morrison et al. (73) measured the nutritional efficiency with which several carbohydrates

were used by young chicks. The decreasing order in which carbohydrates were rated for chick growth was dextrin, glucose, sucrose and lactose. In an early study by Mitchell (72) with adult rats the apparent digestibilities of starch, dextrin, sucrose, maltose and lactose were 94, 90, 94, 91 and 73% respectively. Lactose promoted poorest growth while the best growth was given by corn starch. Microbial counts of the feces showed greatest flora proliferation in the lower tract of lactose-fed rats.

The Effect of Carbohydrate Administration upon Blood Reducing Sugar Levels

Cattle

As already mentioned, it is often difficult to ascertain a true measure of the utilization of a carbohydrate by digestibility studies because of fermentation processes occurring in the lower digestive tract. Another method which has frequently been used to estimate relative carbohydrate absorption is the induced rise in blood reducing sugar following a period of fasting.

Carbohydrates which are fed as normal constituents of the dry ration of ruminants are readily fermented by rumen microorganisms and fail to produce appreciable changes in blood reducing sugar (13,102,55). Barhydt and Dye (8) obtained very small post-prandial rises in blood sugar in 10- to 13-month-old calves on a hay-grain diet. From

examination of abomasal contents it was estimated that only 20 to 30 g. per day of hexose polysaccharide escaped rumen fermentation, and that this portion was not digested by the small intestine. Dougherty and coworkers (31) obtained maximum rises in blood sugar of only 30 mg.% after drenching the rumen of 2-year-old heifers with 3.7 g. of glucose per kg. body weight. Slightly greater rises were shown with adult sheep. Japanese workers (81) obtained very similar results with goats after administration of glucose via the rumen, while starch ingestion produced no blood sugar response.

There have been several studies in which carbohydrate solutions have been fed to young calves by nipple pail, thus allowing the meal to enter directly into the omasum-abomasum and escape rumen fermentation. In one such experiment, Flipse et al. (41) showed good utilization of glucose and lactose by 4-week-old calves. Blood sugar response of calves receiving corn syrup was somewhat lower and none was obtained for starch.

Dollar and Porter (29,30) reported similar results for glucose and lactose. Apparent utilization of lactose seemed to decrease between 2 and 5 weeks of age. Maltose gave no response in calves under 4 weeks and only slight responses thereafter. Addition of maltase seemed to greatly enhance maltose utilization. Dextrin, starch and sucrose all appeared not to be utilized at any of the ages tested. It

was suggested that the calf's inability to use starch may be overcome by supplementation with both amylase and maltase.

Results from the studies of Okomoto et al. (82) and Velu et al. (110) also indicate good utilization of glucose and lactose by young calves. However, the maximum increases in blood sugar shown by these groups of workers were about double those reported by Dollar and Porter. A limited response from maltose was obtained by the time the calves were about 3 weeks of age, while sucrose gave no response up to 14 weeks of age. When sucrose was inverted by invertase or citric acid, increases in blood sugar were comparable to those produced by glucose. The possibility of replacing glucose with sucrose plus invertase in milk replacer rations was suggested as economically feasible (82,110).

USDA workers (82) subjected starch from several sources to enzyme and heat treatments with the following results: Neither corn, barley, cornstarch nor dehydrated potato in the cooked or raw states caused any change in blood sugar levels. Addition of enzymes to the cooked cereals or dehydrated potato produced noticeable rises while addition of enzymes to the raw cereals did not.

Blood reducing sugar responses to ingestion of monosaccharides other than glucose were studied by the Illinois workers (110). Maximum increases in blood sugar due to galactose administration were similar to those obtained with glucose. Fructose ingestion caused much lower rises in

blood sugar than glucose or galactose.

The addition of 30% starch by Netke et al. (76) to a reconstituted skim milk diet did not cause rises in blood sugar above values obtained from the skim milk alone. Supplementing this diet with amylase did not result in a glycemic change.

That the inability of starch to cause a blood sugar response, when introduced posterior to the rumen, does not change with increasing age of the animal is indicated by the work of Larsen et al. (64) who showed that neither corn starch nor ground yellow corn resulted in any appreciable change in blood glucose following delivery of these substances into the omasum-abomasum of 9-month-old steers. A comparison of the data from this study with the previously mentioned studies in which younger calves were used suggests that the increases in blood sugar due to administration of glucose decreases with age. Barhydt and Dye (8) demonstrated a large decrease in the post-prandial blood sugar response in calves fed a constant quantity of milk via nipple pail as age increased from 2 to 5 months. This decline was accentuated when milk was removed from the regular diet. Decreased intestinal lactase activity and reduced capacity of the small intestine to absorb carbohydrates are possible factors involved in such a phenomenon.

Swine

Experiments in which blood sugar responses were used

to estimate degree of carbohydrate utilization in swine tend to strengthen conclusions drawn from the growth and digestibility studies already mentioned. Glucose and lactose are the only carbohydrates which give large increases in the newborn pig while apparent utilization of sucrose, maltose, dextrin and starch as indicated by induced blood sugar increases develops during the first 10 days. Cooked starch produced greater responses than raw. Ability to use lactose seemed to decrease after pigs were 3 weeks of age (17,21, 27,28).

Other species

In studies with humans, Kjer (57) observed that ingestion of starch caused increases in blood reducing sugar comparable to those caused by an equal quantity of glucose. Wishnofsky and Kane (119) showed that the elevations of sugar concentrations in the blood and urine of diabetics after consuming equivalent amounts of dextrose or starch were quite similar.

Blood sugar increases of the magnitude of 60 mg.% were noted in rabbits by Larner and McNickle (62) 2 hours after feeding 5 g. of starch. Quantitative identification of sugars in the blood after the starch meal showed that glucose composed 95% of the total. Maltose and two undetermined oligosaccharides were also present.

Carbohydrase Activity in the Digestive Glands

Concentrations of digestive enzymes present in the pancreas and small intestine at a specific time are not always directly proportional to the capacity of the animal for utilization of a given nutrient. Certainly there is a host of other factors which influence nutrient breakdown; however, tissue enzyme studies are thought to be important and often give a fairly accurate estimate of the animal's ability to digest its ration.

The carbohydrases first to be considered are the disaccharidases. These enzymes are almost totally secreted by the mucosa of the small intestine. However, traces of certain ones have been found in pancreatic juice (51). The site of lactase activity is thought by some authors to be within the mucosal cells while maltase and sucrase act in the lumen of the intestine (18,19,42). The possibility that intestinal microorganisms are important contributors to disaccharidase activity was investigated by Larner and Gillespie (60) in germ-free rats. It was observed that the germ-free animals possessed just as high maltase, sucrase and oligo-1, 6-glucosidase activities in both intestinal mucosa and contents as the normal ones. However, there was such large variability in the experiment that the possibility of microbial enzyme production was not disproved.

All of the enzymes necessary for the step-wise

degradation of starch were found by Larner and McNickle in the rat. These included alpha amylase, maltase and one recently identified as oligo-1, 6-glucosidase (61).

Disaccharidases

A study by Huber and associates (50) showed that lactase activity of homogenized calf intestine was highest at birth and decreased for 3 weeks thereafter. Little change was noted between 3 and 6 weeks. Lactase activity, calculated on the basis of mg. disaccharide hydrolyzed per hour by a given weight of intestinal tissue, was about fifteen times that of maltase in 1-day-old calves and decreased to a factor of seven by the time animals had reached 6 weeks of age. Maltase activity did not change appreciably from birth to 6 weeks and no sucrase was detected during this age period. Dollar and Porter (29,30) also reported a decrease with age in lactase activity and no detectable sucrase. However, maltase was shown to increase three-fold between 3 and 8 weeks. Several other reports dealing with calves and other young mammals have shown that intestinal lactase is highest at birth and tends to decrease with age (25,46,71,87). Results of an experiment by Uchino and Mori (108) indicate that lactase, maltase and sucrase are not present in the intestinal mucosa of the adult bovine.

In contrast to results obtained with calves, Walker (113) observed that the high lactase activities in intestinal tissue and contents of sheep did not change markedly between

1 and 5 weeks of age. These workers further showed that maltase activity was lowest at one week with an increase by 2 weeks and little further change by 5 weeks. Sucrase activity was not found up to 35 days of age. Likewise, no sucrase was detected by Phaneuf (85) in the digestive secretions of older sheep.

Studies with swine have shown that levels of intestinal lactase are high at birth and decrease shortly thereafter. Intestinal maltase and sucrase activities are low at birth and increase rapidly with age (7,112). Per kg. body weight, lactase activities reported in calves (29,30,49) were about one-fifth those reported in baby pigs (7).

Amylase

Although some amylase is secreted by the intestinal mucosa (112,113), the exocrine glands in the pancreas are generally accepted as the primary site of production of this enzyme. Consequently, most of the studies related to amylase activity have used either pancreatic tissue or pancreatic juice.

Despite the reported poor utilization of starch when fed to young calves in such a manner as to bypass rumen fermentation, several workers have demonstrated appreciable amylase activity in calf pancreatic tissue. This apparent physiological discrepancy will be discussed further in a later section. In a study by Huber and associates (50), amylase levels were quite low in one-day-old calves and increased

three-fold by the first week. Subsequently, little change was noted up to 6 weeks. Dollar and Porter (29,30) showed a slight increase in starch-digesting capacity of pancreatic tissue between the third and eighth week of age in calves. On a tissue weight basis, the activities observed by the English workers (29,30) are in quite close agreement with the data of Huber and associates (50).

In studies with 1- to 5-week-old lambs, a very marked increase with age in amylase activity was noted by Walker (113). Amylase levels of small intestinal tissue were about one-tenth those of the pancreas. Phaneuf (85) reported amylolytic activity in pancreatic juice of adult sheep. However, it was much less potent than that in human saliva or dog pancreatic juice.

Several researchers have reported low amylase activity in the pancreas of the new-born pig with a rapid increase up to 5 weeks of age (51,56,112). Iowa workers (51) have shown that the starch-digesting power of saliva of swine is low at birth and gradually decreases for the first seven weeks of life.

In a number of studies using human duodenal contents, it has been observed that the infant is born with quite low starch-digesting capacity. This, however, is overcome during the first few months of life (3,14,32,58). Amylase activity has also been shown to develop during early life in the dog (59).

Effect of Carbohydrates on Diarrhea

A very important consideration in carbohydrate supplementation to milk substitute rations for young mammals is the effect rendered upon feces consistency. Excessive scours, if allowed to continue, may lead to anorexia, emaciation, dehydration and death.

In a number of studies with several species, the ingestion of large quantities of lactose has been thought to be related to incidence of scours (34,37,39,53,84,97,121). One such investigation made by Blaxter and Wood (15) showed that the fluidity of the feces in young calves increased as quantity of glucose or lactose in the ration was increased from 0 to 325 g. Fischer and Sutton (37) suggested several manners in which lactose may cause diarrhea, the principal one being a hydragogue action which results in an interference with water and organic nutrient absorption. This interference is attributed to great amounts of the carbohydrate reaching the lower tract in an unhydrolyzed form.

In a review of the literature, Atkinson *et al.* (6) proposed that high levels of lactose are well tolerated by young calves and pigs but that this tolerance decreases with age. It was further proposed that a visible symptom of this decreased tolerance was the increased incidence of diarrhea if the young are maintained for too long after birth on relatively high levels of lactose. The previously mentioned

studies (29,30,49) in which there was observed a decrease in lactase content of the intestines of calves with increasing age give indirect support to this suggestion. Also the investigations (29,30) showing a decrease with age in the blood reducing sugar response of calves after ingestion of lactose support the postulate. In experiments with swine, Becker and Terrill (9) noted that rations containing up to 50% lactose could be tolerated by pigs under 9 weeks of age without causing severe diarrhea while 16-week-old animals could tolerate only 25% lactose.

As previously mentioned, Rojas et al. (98) observed severe diarrhea in calves when the lactose content of skim milk was doubled while Owen (84) observed that this laxative effect of lactose was decreased when milk fat was included in the ration. Owen's results agree with those of Huber (49) in which no scouring was noted among 1- to 6-week-old calves which were fed whole milk rations supplemented with 3% lactose.

A limited number of studies concerning the diarrheic effect of other carbohydrates have been reported. One of the main difficulties encountered when starch or starchy materials were incorporated in milk replacer rations for young calves has been the ensuing high incidence of scours (40,41,78,79, 80,89). Flipse and associates (40,41) observed that the inclusion in synthetic milk rations of starch, glucose and corn syrup, either alone or in combination, caused scouring

in calves within 2 to 4 days after animals were placed on the rations. Addition of as little as 5% lactose to one of the above mentioned rations caused feces to become firmer. Considerable scours has also been observed in calves fed rations high in glucose (76,115,98).

Even though Wallace et al. (114) reported good utilization of sucrose by young calves, more recent studies have shown that the feeding of this carbohydrate results in rather severe scouring (49,50,110). In one such study by Huber (49), addition of 2.5% sucrose and 0.5% starch to whole milk invariably caused the passage of watery feces in calves from birth up to 6 weeks of age. Such a result might be expected because of the several experiments which have demonstrated the inability of the calf to digest sucrose (29,30,49,82,110). Maltose and fructose, when fed by nipple pail at a level of 2 g. per pound body weight, have also been observed to cause scours in calves (110).

Inclusion of sucrose in a synthetic milk ration for newborn pigs caused severe diarrhea with death occurring in 40% of the pigs within about 4 days after being placed on the sucrose diet. In the pigs that lived, marked improvement in diarrheic symptoms and general health was noted by 7 days (10,11).

Carbohydrate Metabolism

To accurately interpret carbohydrate absorption studies, consideration of some of the factors other than diet which may influence concentrations of blood sugar seems necessary. It is realized that there have been a great number of studies dealing with carbohydrate metabolism in the bovine, especially pertaining to the subject of ketosis. However, only a few pertinent references which may relate to the present study are contained in this review.

Several groups of workers have reported that glucose, after being injected intravenously, is removed from the blood at a slower rate in ruminants than in non-ruminants (12,13, 43,47,54,69,96,95). Similar results have been observed for fructose and invert sugar (43,83). The effect of previous dietary on glucose disappearance rate was shown in experiments by Reid (93). After receiving an intravenous injection of 0.4 g. glucose per kg. of body weight, sheep on a high grain diet exhibited a glucose removal rate of 3.0% per minute while those on an all-roughage diet averaged 1.2% per minute.

In an experiment by McCandless and Dye (69), it was shown that as age increased, blood glucose and glucose tolerance decreased in four species of ruminants (lamb, calf, aoudad, mouflon). It was suggested that these age differences were due to metabolic changes incident to rumen

development and were related to the shift in the diet of the young animal from milk, containing a large quantity of carbohydrate suitable for hydrolysis and absorption, to a dry diet which contains little of the simple carbohydrates. Two factors mentioned by the authors which might possibly be involved are decreased ability of the tissues to take up glucose and increased gluconeogenesis by the liver. In contrast to the suggestions made by the Cornell workers (69), Ratcliff's (89) results indicate that certain changes in carbohydrate metabolism are not dependent upon rumen development. Levels of blood reducing sugar were observed to decrease with age among calves on an all-milk ration in which very little rumen development had occurred. It was suggested that some of the metabolic changes which normally accompany rumen development may actually take place in its absence.

There is evidence that uptake of blood glucose by extrahepatic tissues occurs at a slower rate in ruminants than in non-ruminants. Reid (96) observed arterio-venous differences of 2 mg.% in sheep as compared to 8 mg.% for dogs in a post-absorptive state. Values reported by Somogyi (105) for humans averaged 5 mg.% in fasting subjects and 33 mg.% after ingestion of 100 g. of glucose. Another study by Reid (94) demonstrated that the fall in blood glucose subsequent to insulin injection was considerably slower in sheep than in non-ruminants. No information was found on the effect of age on arterio-venous differences or on rate of blood sugar

decline after insulin injections.

Greater urinary losses of glucose have been shown in ruminants than in non-ruminants. After intravenous injection of 0.3 to 0.5 g. glucose per kg. body weight, it was observed by several workers that adult cattle possessed a renal threshold of about 100 mg.% and excreted about 10% of the injected glucose in the urine (12,13,43,47). Average losses in similar studies with humans have amounted to about 4% of the injected glucose.

EXPERIMENTAL PROCEDURE

Experiment 1

Blood reducing sugar study

Experimental animals and treatments Twenty-three animals from the Iowa State University dairy herd were used in this experiment. Descriptive data for these animals are given in Table 12 of the Appendix.

Five age groups and nine treatments were employed. The treatments involved feeding (into the omaso-abomasal area of the stomach) glucose, three disaccharides, four starches and a control diet. The number of animals receiving each treatment at a particular age is shown in Table 1. The order of carbohydrate treatment was randomly assigned to animals of the three older ages. Animals of groups A and B received four or five of the treatments between 2 and 4 weeks of age and the other four or five between 6 and 8 weeks. Allotment of carbohydrates within groups A and B was random. The herd numbers of animals receiving the different treatments at each age are given in Table 13 of the Appendix.

Calves of groups A and B were maintained on the normal calf-feeding program which included a limited quantity of whole milk with starter and hay fed free choice. Starter consumption seldom exceeded 4 pounds per day and usually was much less. Animals of groups C, D and E were fed alfalfa hay ad libitum and a maximum of 4 pounds of grain mixture

per day. Calves in group C received a small amount of milk during the experimental period to encourage them to retain the suckling habit. All animals received water ad libitum.

Table 1. Number of animals receiving each treatment at the various ages (Experiment 1)

Carbohydrate treatment	Group				
	A	B	C	D	E
Mean age[a] (days)	22	50	136	227	600
Control	4	4	2	4	4
Glucose	4	4	4	4	4
Lactose	4	4	4	4	4
Maltose	4	4	6	4	4
Sucrose	6	6	4	4	4
Amylose	4	4	4	4	4
Amylopectin	4	4	4	4	4
Flojel (acid-treated, solubilized corn starch)	4	4	4	4	4
Tapioca starch	4	4	4	4	4

[a]Mean ages and age ranges (in parentheses) for the various groups were: A-22 days (11-30), B-50 days (40-60), C-136 days (94-160), D-227 days (212-259), E-600 days (482-744).

Twelve hours prior to treatment all feed except water was withdrawn. Treatment consisted of delivery into the omasum-abomasum of one of the above-mentioned carbohydrates in a 5% aqueous solution for groups A, B, C, and D, and 10% aqueous solution for group E. The control consisted of an

equal amount of water. Carbohydrate solutions (and water in the case of the controls) were given by nipple pail to animals under 22 weeks, thereby taking advantage of the esophageal groove to by-pass the rumen. Animals of the two older ages were fitted with rumen fistulas. A stomach tube, used for delivery of solutions, was introduced into the rumen through the fistula, then was passed forward in the rumen and was introduced into the reticulo-omasal orifice. The anterior end of the tube was positioned in the omaso-abomasal area approximately 6 to 8 inches posterior to the reticulo-omasal orifice.

Level of administration was 2 g. per pound body weight for all carbohydrates except amylose which was administered at a 1 g. level because of its swelling properties in water. (Preliminary work had indicated that because of this adsorptive property, an amount of water too great for one feeding was needed for suspension of 2 g. amylose per pound body weight).

Collection and analysis of blood Approximately 15 ml. of blood were taken from one of the jugular veins immediately prior to the carbohydrate administration and at 0.5, 1.0, 1.5, 2.0, 3.0, 5.0 and 8.0 hours thereafter. Collections were made in 25 ml. erlenmeyer flasks to which 50 mg. of potassium oxalate and 150 mg. of sodium fluoride had been added to prevent clotting and glycolysis.

A protein-free filtrate was prepared with 1 ml. of whole blood and analyzed for total reducing sugar according to the method described by Nelson (75). Data are presented as mg. glucose per 100 ml. of whole blood.

Reporting of data Maximum increases and mean changes in blood reducing sugar were calculated. The maximum increase is defined as the highest positive change from the pre-treatment level of blood reducing sugar obtained during the 8 hours following carbohydrate administration. When the pre-treatment level was higher than all subsequent levels, the maximum increase was indicated as zero.

The mean change was calculated by subtracting the pre-treatment value from the blood sugar values taken at each half hour for 5 hours subsequent to treatment. (Levels for 2.5, 3.5, 4.0 and 4.5 hours were interpolated.) These differences were then totalled and divided by the number of observations (ten).

Observations for incidence of scours during the 8 hours subsequent to carbohydrate administration were made. Severity was rated on an arbitrary scale from zero to four. A rating of zero indicated normal, firm feces while animals passing very watery feces received a rating of four.

Heat treatment of starches

The four animals used in this phase of the experiment were 40 to 50 weeks of age. (These were the same animals

previously described in group C.) Allotment to treatment, feeding, administration of carbohydrate, bleeding and analysis of blood were all similar to those mentioned above. All starches were administered at the level of 1 g. per pound body weight.

Starches were subjected to one of the following treatments before being given to the animals: 1. Jelling--this was accomplished by placing about 10% by weight of the starch in a water suspension and heating at about 70 degrees C. for ten minutes at which temperature jelling occurred with amylopectin, Flojel and tapioca. Amylose would not jell under these conditions, thus it was excluded from this phase of the study. 2. Autoclaving dry--starch was autoclaved at a pressure of 15 pounds per square inch for 30 minutes. It then was mixed with water as described in the jelling treatment (10% starch). 3. Autoclaving in suspension--starch was suspended in hot water (55 degrees C.) and autoclaved in a manner identical to that in method 2. All of the suspensions were allowed to stand overnight before being fed.

Intravenous injection plus carbohydrate ingestion

Two fistulated steers (an Ayrshire and a Brown Swiss) from the Iowa State University dairy herd of approximately 40 weeks of age were used in this study. All methods were identical to those previously mentioned except for the following: Subsequent to pre-treatment bleeding, 0.3 g. glucose

per kg. body weight was injected intravenously (jugular vein) during a 3-minute period. A second blood sample was withdrawn from the opposite jugular vein immediately after infusion of glucose. Following this, a solution containing 2 g. carbohydrate (1 g. in the case of amylose) per pound body weight was delivered directly into the omaso-abomasal area. A third blood sample was taken 20 minutes after glucose injection. The subsequent bleeding schedule corresponded to that described in earlier work. All treatments listed in Table 1 were employed. Sequence of treatments was assigned to the steers in a random manner.

Experiment 2

Experimental animals and treatments

Four male dairy calves (2 Holsteins and 2 Brown Swiss), from the Iowa State University dairy herd, 12 to 14 weeks of age, were assigned to a series of carbohydrate treatments. A listing of the animals and the sequence of treatments are given in Table 2. Descriptive data for the animals are given in Table 12 of the Appendix.

Prior to assignment to this experiment the calves received diets composed of a limited amount of milk replacer and grain, with hay fed free choice. The experimental diet consisted of alfalfa pellets fed ad libitum, plus 3 pounds of whole milk daily per 100 pounds body weight. (Pellets were

steam-compressed and contained no fat or molasses as binding agents.) Carbohydrate was added to the milk at a level equivalent to 10% of the milk weight.

Animals received each of the treatment diets for a period of 10 days. The first 5 days were a period of adjustment to the ration during which calves remained in their respective pens which were bedded with straw. The remaining 5 days were a collection period spent in the digestion stalls. (An adjustment period of 5 days in the digestion stalls was allowed for all calves before being placed on the first treatment.)

Table 2. Sequence of carbohydrate treatment (Experiment 2)

Order of treatment	Animal number 4850	4851	4857	4858
1	Control	Flojel	Amylose	Tapioca
2	Amylopectin	Amylose	Tapioca	Control
3	Maltose	Lactose	Sucrose	Amylopectin
4	Flojel	Tapioca	Control	Maltose
5	Amylose	Sucrose	Amylopectin	Flojel
6	Lactose	Control	Maltose	Amylose
7	Tapioca	Amylopectin	Flojel	Lactose
8	Sucrose	Maltose	Lactose	Sucrose

Collection of feces and blood

All feces were collected during the 5 days that calves were in digestion stalls. At 12-hour intervals the feces were removed from the collecting pan and after thorough mixing and weighing, 10% by weight of the feces was placed in plastic bags and immediately placed in a freezer set at about -25 degrees C. Collections for each day were composited. Later, when thawed for analysis, these composites were thoroughly mixed.

On the fifth day in the digestion stalls, blood was sampled for content of total reducing sugars. The schedule of bleeding was: Immediately before the morning feeding and at 1, 2, 3, 4, 6 and 8 hours thereafter. Preparation of the protein-free filtrate and analysis for blood reducing sugar were the same as previously described.

By stimulating defecation, feces samples weighing about 25 g. were taken at 2-hour intervals during the last 24 hours of each 5-day period that each calf was in the digestion stall. These samples were immediately stored at about -25 degrees C. for subsequent analyses.

Analyses of feces

Each of the five daily composites and each of the samples taken at 2-hour intervals during the last day were analyzed separately (for each calf and for each carbohydrate, except that diurnal changes were not analyzed for controls).

Samples of feces were thawed at room temperature, thoroughly mixed and aliquots were taken for dry matter and carbohydrate contents.

Percent dry matter was determined by placing about 8 g. of feces in a pre-weighed crucible and drying the sample in an oven at a temperature of 110 degrees C. for at least 30 hours. (Preliminary work showed that after 30 hours, the dried feces reached a constant weight.)

Quantity of carbohydrate in the feces of animals on the lactose and maltose diets was determined in the following manner: 1. Five g. of feces were vigorously stirred with 20 ml. water. The mixture was centrifuged at a relative centrifugal force of 410 x g. for 20 minutes. The supernatant was decanted and retained while the residue was discarded. 2. A protein-free filtrate was prepared from the supernatant portion according to the Nelson method (75) for blood. 3. Ascending paper chromatograms were then spotted with the extract using a method adapted from Dimler et al. (26). Modifications were a) 10 microliters of solution were placed on the starting line of the paper in 5 microliter aliquots. b) The solvent system contained 1-butanol, pyridine and water (6:4:3). c) Guide strips were developed by the dip method described by Trevelyan et al. (107). d) Rather than elute the carbohydrate from the paper, small squares of paper of uniform size containing the carbohydrate spot were

cut into sixteen pieces and placed in copper reagent for determining content of reducing sugars according to the Nelson test (75). Paper squares containing no carbohydrate were treated in the same manner as those mentioned above and were used as blanks.

Guide strips from chromatograms showed only spots corresponding to glucose and galactose, indicating that hydrolysis of both the maltose and lactose was complete prior to analysis; thus disaccharide determinations were not made.

Content of soluble carbohydrate in feces of calves receiving sucrose diets was determined in the following manner: 1. A water extract was prepared by vigorously stirring 84 ml. of water and 5 g. feces. Nelson's method (75) again was used for preparation of a protein-free filtrate. 2. Two ml. aliquots of this filtrate were taken prior to hydrolysis for determination of reducing activity according to the Nelson procedure (75). 3. Hydrolysis of sucrose was accomplished by incubating the following mixture for 2.5 hours: 4 ml. of the solution mentioned in item 1, 94 ml. of dilute acetic acid (pH of 4.5) and 2 ml. of invertase solution.* Incubation temperature was 55 degrees C. and flasks were stoppered to prevent evaporation. 4. Following incubation, 2 ml. aliquots of the incubated solution were

*This was a 10% aqueous solution of invertase scales. The enzyme was obtained from Wallerstein Co., Wallerstein Square, Mariners Harbor, Staten Island 3, New York.

analyzed for total reducing sugar in accordance with Nelson's method (75).

Identical procedures were employed for analyses of carbohydrate in the feces of calves receiving the control ration as for those receiving starch. The manner of hydrolysis was similar to that described in A.O.A.C. (5) and proceeded as follows: 1. Five g. feces were washed in 25 ml. water. The mixture then was centrifuged at a relative centrifugal force of about 14,000 x g. for 20 minutes and both supernatant and residue were saved for subsequent analysis. The supernatant contained the soluble carbohydrate while the non-soluble carbohydrate was contained in the residue. 2. A protein-free filtrate of the supernatant was prepared and reducing activity of a 2 ml. aliquot was determined according to the method previously described. (Chromatographic examination of this supernatant indicated that practically all of the carbohydrate present was glucose. Traces of starch, dextrins and maltose were also identified.) 3. The residue was suspended in 20 ml. of 0.7 normal hydrochloric acid and placed in a boiling water bath for 2.5 hours. (Boiling bulbs were placed on test tubes to minimize evaporation.) 4. The hydrolyzed extract then was removed from the boiling water bath, cooled, and neutralized with 0.5 normal sodium hydroxide. Phenophthalein was used as an indicator. The pink color was removed with a few drops of 0.1 normal oxalic acid. A

protein-free filtrate was then prepared with the solution in the manner previously described.

Previously mentioned procedures were used for chromatogramming the protein-free filtrate from the hydrolyzed residues and for determining reducing activity of the carbohydrate spots on the paper. In samples from starch-fed animals, two distinct spots were shown upon development of guide strips. One corresponded to glucose and the other to a pentose (probably xylose). In daily composite samples, reducing activity of both spots was measured according to the method described by Nelson (75). However, reducing activity of only the spot corresponding to glucose was determined in the diurnal samples since the pentose undoubtedly originated in the pellets.

RESULTS

Experiment 1

Blood reducing sugar study

The methods employed in this study provided for efficient delivery of carbohydrate into the omasum-abomasum. This was substantiated by the observation that ingestion of glucose via the rumen resulted in much smaller increases in blood reducing sugar than when the rumen was by-passed with a stomach tube or through activation of the esophageal groove (Appendix, Table 14). The amount of glucose placed in the rumen was 2 g. per pound body weight (similar to that fed into the omaso-abomasal area).

Animals were kept as quiet as possible while being bled, thereby minimizing the degree of hyperglycemia due to excitement. Data from control runs (blood sampling of animals not fed carbohydrate) demonstrated that blood sugar levels underwent little diurnal variation. This indicated that if there was any change due to sampling procedure, it was constant throughout the experiment.

Blood reducing sugar values subsequent to carbohydrate ingestion for the various ages and treatments are presented in Table 14 of the Appendix. Average ages of the groups (in days) were A, 22; B, 50; C, 136; D, 227; E, 600. It will be noted that average levels of blood reducing sugar prior to carbohydrate administration decreased with age. Average

initial values for groups A, B, C, D and E were 82, 71, 54, 62, and 51 mg.%, respectively. Time of maximum increase in blood reducing sugars was 1 to 2 hours after carbohydrate ingestion. A graphic illustration of these data is given in Figures 1 to 4 for all carbohydrates except sucrose. No figure is presented for sucrose because there was little change due to treatment.

The results presented herein demonstrate that age has a very definite effect upon response of calves to the different carbohydrates. Increases in blood reducing sugar due to ingestion of glucose and lactose decreased as age increased; the rate of decline with age was greater for lactose than for glucose. Feeding maltose caused greater rises in group B than at any other age. In groups C, D and E, response due to maltose and lactose were roughly parallel.

Small and variable changes in blood reducing sugar accompanied introduction of sucrose. However, no outstanding age trends were indicated. Although an apparent small rise was noted with increased age in responses to ingestion of the sucrose and starch it was not believed to signify increased utilization of these carbohydrates because the same feature was shown with animals on the control diet.

There were marked differences in response to various carbohydrates within a particular age group. Ingestion of glucose and lactose, for example, caused increases of about 140 mg.% in 3-week-old animals, whereas maltose administration

Figure 1. Effect of ingestion of glucose into the omaso-abomasal area upon blood reducing sugar levels at various ages in the bovine, (glucose was administered at the rate of 2 g. per pound body weight).

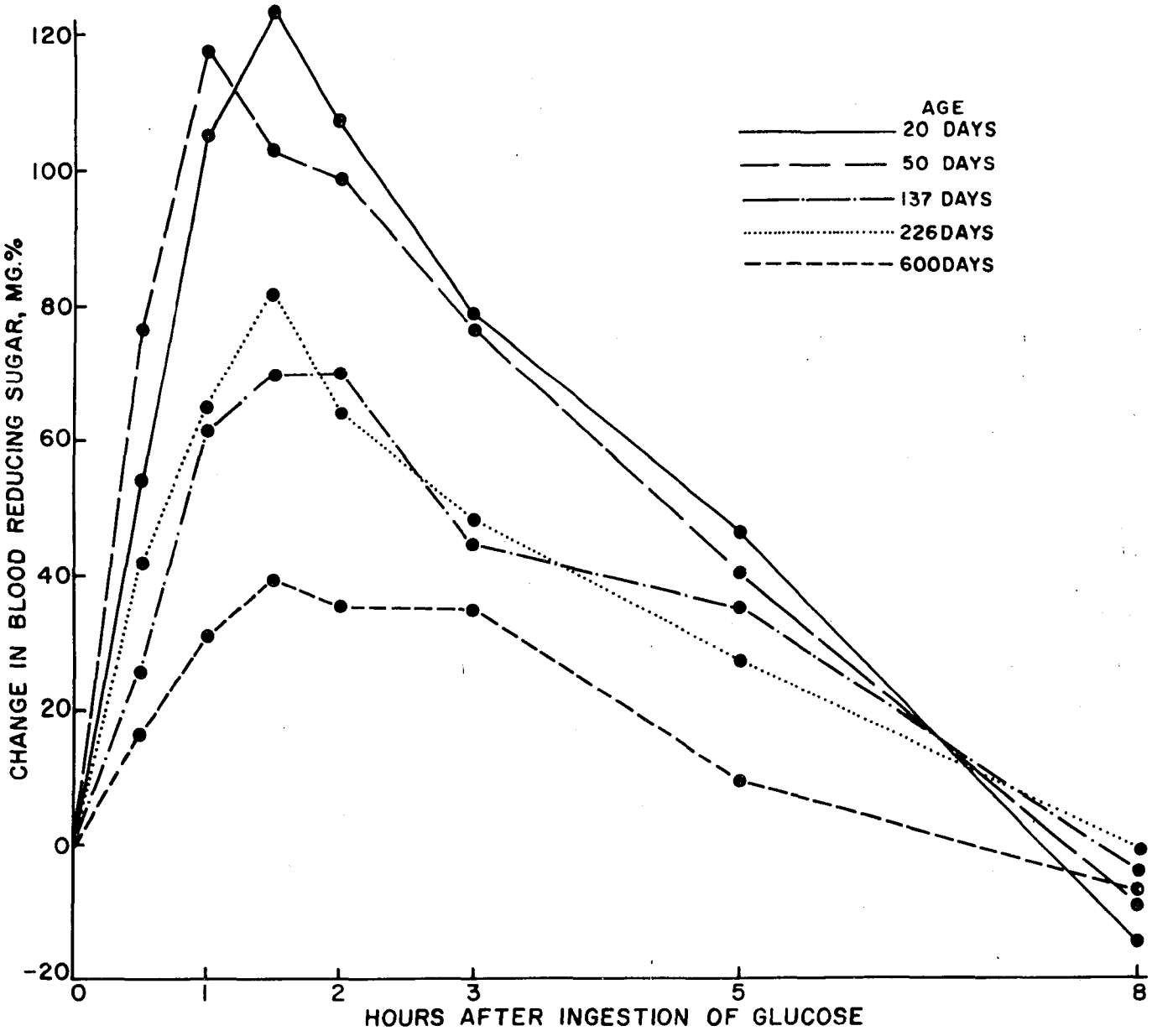

AGE
20 DAYS
50 DAYS
137 DAYS
226DAYS
600DAYS
CHANGE IN BLOOD REDUCING SUGAR, MG.%
120
100
80
60
40
20
0
-20
0
1
2
3
5
8
HOURS AFTER INGESTION OF GLUCOSE

Figure 2. Effect of ingestion of lactose into the omaso-abomasal area upon blood reducing sugar levels at various ages in the bovine, (lactose was administered at the rate of 2 g. per pound body weight).

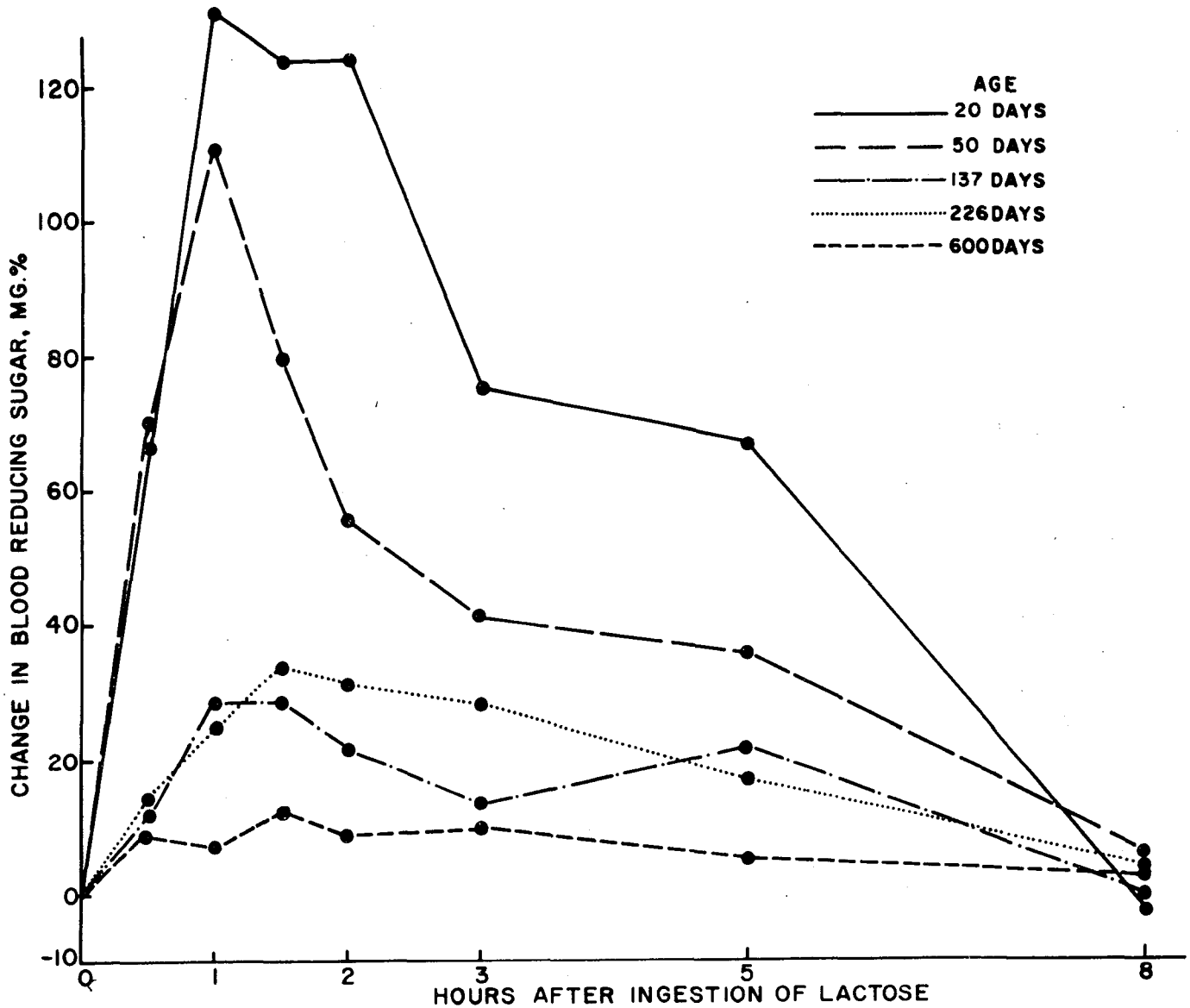

AGE
20 DAYS
50 DAYS
137 DAYS
226DAYS
600DAYS
CHANGE IN BLOOD REDUCING SUGAR, MG.%
120
100
80
60
40
20
0
-10
0
1
2
3
5
8
HOURS AFTER INGESTION OF LACTOSE

Figure 3. Effect of ingestion of maltose into the omaso-abomasal area upon blood reducing sugar levels at various ages in the bovine, (maltose was administered at the rate of 2 g. per pound body weight).

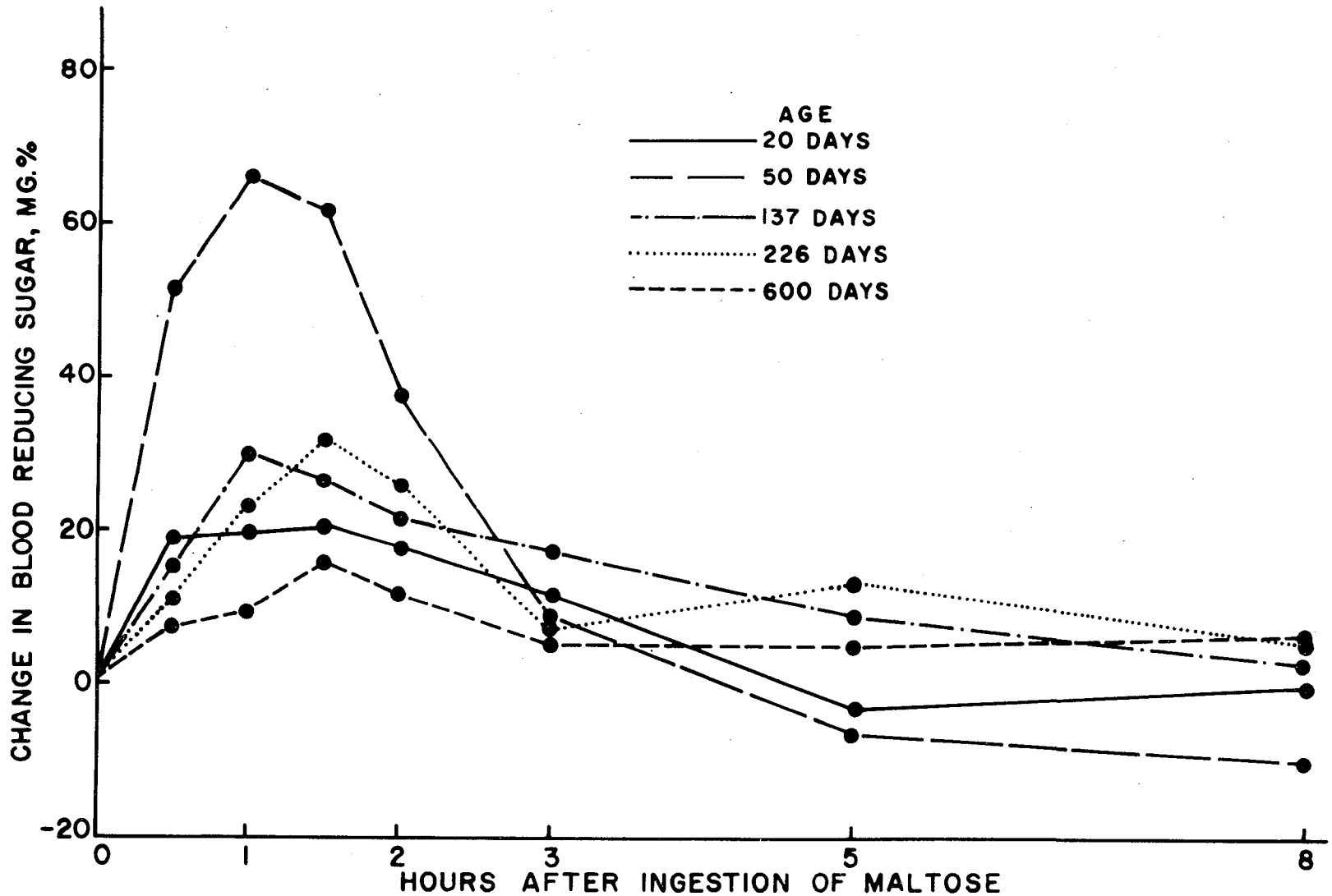
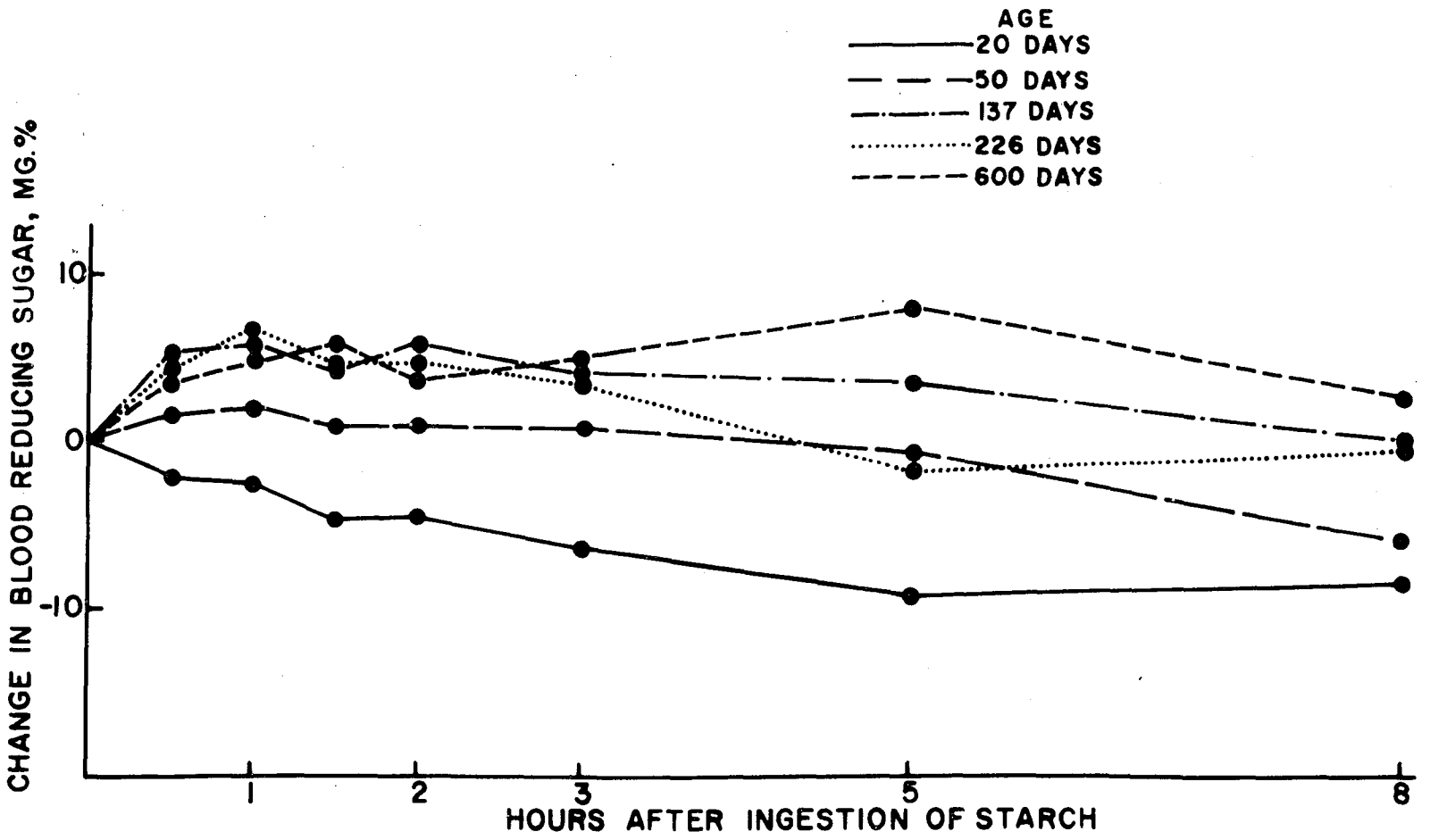

AGE
20 DAYS
50 DAYS
137 DAYS
226 DAYS
600 DAYS
CHANGE IN BLOOD REDUCING SUGAR, MG.%
80
60
40
20
0
-20
0
1
2
3
5
8
HOURS AFTER INGESTION OF MALTOSE

Figure 4. Effect of ingestion of starch into the omaso-abomasal area upon blood reducing sugar levels at various ages in the bovine, (all starches (for which data are combined) with the exception of amylose, were ingested at the level of 2 g. per pound body weight; amylose was ingested at the level of 1 g. per pound body weight).


AGE
20 DAYS
50 DAYS
137 DAYS
226 DAYS
600 DAYS
CHANGE IN BLOOD REDUCING SUGAR, MG.%
10
0
-10
1
2
3
5
8
HOURS AFTER INGESTION OF STARCH

to calves of this age resulted in a rise of only about 30 mg.%. The effects of sucrose and the starches were negligible. The response pattern for group B was similar to that just described for group A, while groups C and D differed from A and B in that the increases due to ingested lactose were much lower than those for glucose and quite similar to those for maltose. In group E the only carbohydrate which produced a marked blood reducing sugar response was glucose.

Maximum increases and mean changes in blood reducing sugar subsequent to ingestion of starch were consistently higher than those determined among animals on the control diet. However, none of these differences were statistically significant ($P < .05$). Response to the various starches was very similar. The only exception occurred with animals of the oldest age in which apparent utilization of Flojel was significantly higher than that of tapioca. Because of the small differences in blood sugar increments which were observed between the various types of starch, the starch data are combined in the above-mentioned figures.

The average maximum increases in blood reducing sugar for all ages and treatment groups are presented in Table 3 and Figure 5, while Table 4 and Figure 6 give the average mean changes. Although both types of data follow a similar pattern, some of the differences which exist between them would seem to justify presentation of both. Maximum increases and mean changes for the individual animals are

Table 3. Maximum increase in blood reducing sugar after carbohydrate ingestion (Experiment 1)

	Group					Diff. required to be significant ($P < .05$)
	A	B	C	D	E	
Mean age	22	50	136	227	600	
Treatment			mg.%			
Control	0.8	2.5	3.9[b]	1.3	9.7	4.7
Glucose	134.3	129.5	76.4	82.4	50.2	45.3
Lactose	147.7	116.8	35.8	37.4	13.8	61.2
Maltose	30.5	72.4	30.2[a]	34.3	17.0	15.4
Sucrose	8.1[a]	7.1[a]	7.6	10.7	10.9	10.7
Amylose	0.6	5.5	11.9	9.5	12.7	8.9
Amylopectin	1.7	7.8	7.3	10.0	11.2	5.3
Flojel	1.5	5.9	7.7	9.5	16.4	10.3
Tapioca	2.1	4.8	6.0	9.4	7.7	6.3
Diff. required to be significant ($P < .05$)	26.0	24.3	10.0	15.7	7.3	

[a]These values are the means of 6 animals; all other values (except those in b) are the means of 4 animals. For individual values, see Table 15 of the Appendix.

[b]Mean of 2 animals.

Table 4. Mean change in blood reducing sugar after carbohydrate ingestion (Experiment 1)

	Group					Diff. required to be significant ($P < .05$)
	A	B	C	D	E	
Mean age	22	50	136	227	600	
Treatment			mg.%			
Control	-11.8	-7.1	0.2[b]	-5.6	3.6	10.7
Glucose	77.5	78.3	45.1	49.3	27.4	49.0
Lactose	86.6	53.0	18.9	24.1	8.0	31.8
Maltose	10.5	23.9	17.4[a]	16.0	7.5	12.5
Sucrose	-2.1[a]	-1.5[a]	3.5	2.5	4.4	7.5
Amylose	-9.0	0.7	6.0	2.7	7.2	11.9
Amylopectin	-5.2	2.8	2.1	4.7	4.8	6.3
Flojel	-4.0	-1.6	4.1	1.9	8.2	9.6
Tapioca	-6.4	-2.3	2.1	1.5	1.8	7.6
Diff. required to be significant ($P < .05$)	18.4	20.8	10.1	14.1	6.4	

[a]These values are the means of 6 animals; all other values (except those in b) are the means of 4 animals. For individual values, see Table 16 of the Appendix.

[b]Mean of 2 animals.

Figure 5. Effect of age upon maximum increase in blood reducing sugar after ingestion into the omaso-abomasal area of various carbohydrates. (Each maximum increase value is an average of the greatest positive change in blood reducing sugar subsequent to carbohydrate ingestion for each treatment group within a particular age.)

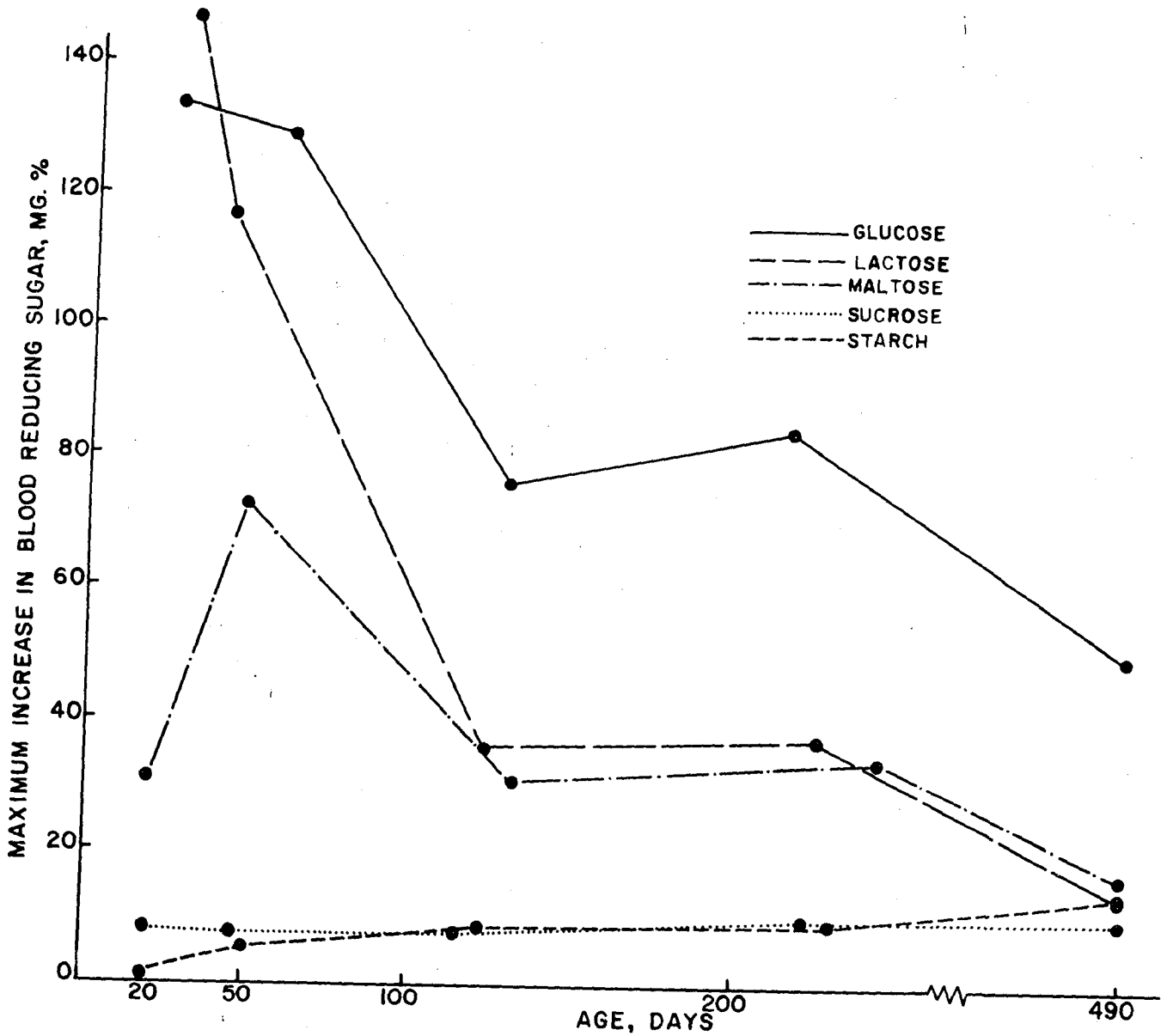
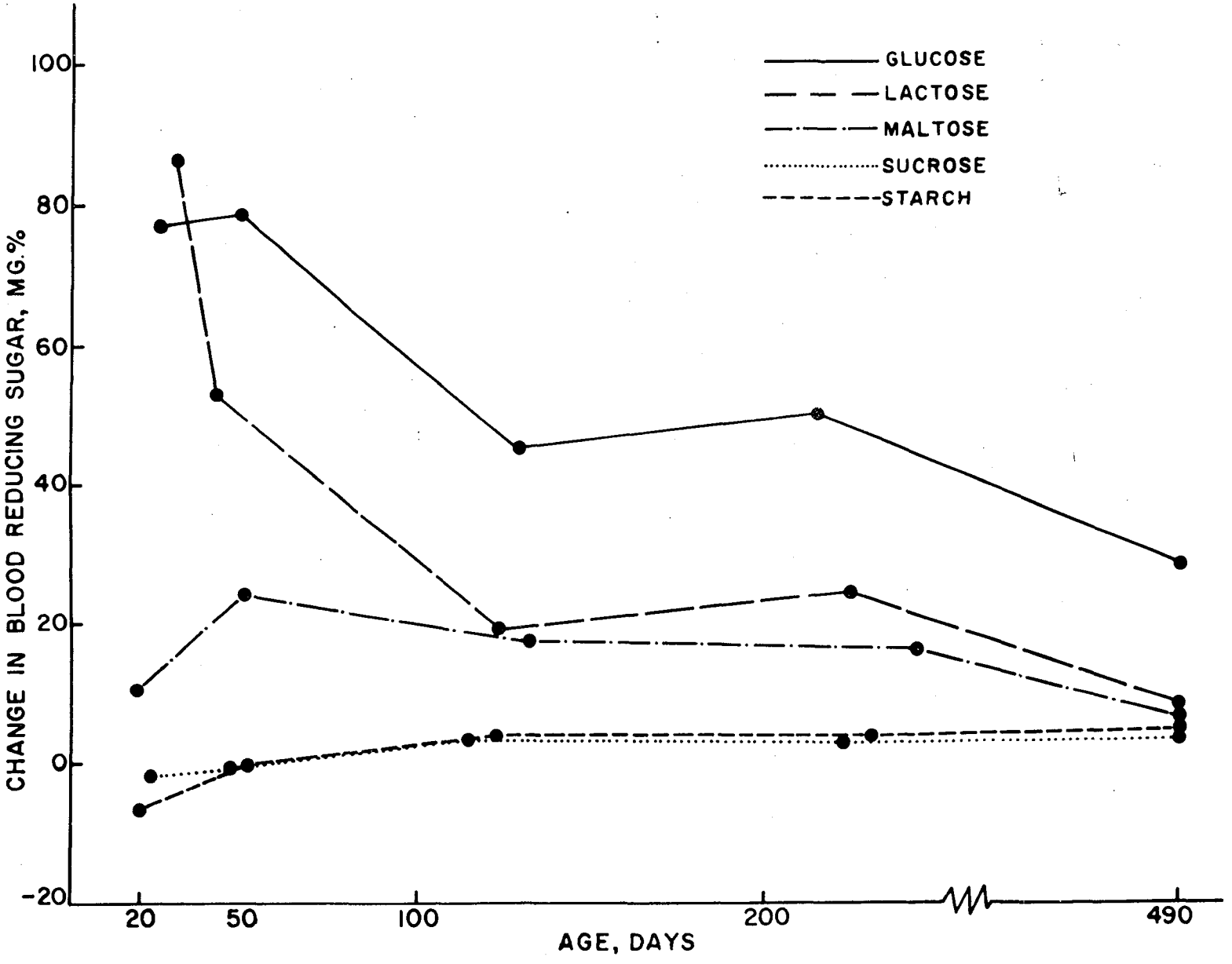

MAXIMUM INCREASE IN BLOOD REDUCING SUGAR, MG. %
140
120
100
80
60
40
20
0
20
50
100
200
490
AGE, DAYS
GLUCOSE
LACTOSE
MALTOSE
SUCROSE
STARCH

Figure 6. Effect of age upon mean change in blood reducing sugar after ingestion into the omaso-abomasal area of various carbohydrates. (Each mean change value is the average for each treatment group within a particular age. Mean changes were calculated by totalling the differences between the initial blood sugar level and those observed (or interpolated) at every one-half hour for 5 hours after carbohydrate ingestion and dividing this total by the number of observations which was 10.)


GLUCOSE
LACTOSE
MALTOSE
SUCROSE
STARCH
CHANGE IN BLOOD REDUCING SUGAR, MG.%
100
80
60
40
20
0
-20
20
50
100
200
490
AGE, DAYS

given in Tables 15 and 16 of the Appendix. Analyses of variance of maximum increases and mean changes are given in Tables 17 to 20 of the Appendix. The differences between treatment means required to be significant were calculated according to Duncan's Multiple Range Test (33) and are presented in Tables 3 and 4 along with the data to which they have reference. It will be noted that many of the above-mentioned observations bear statistical significance ($P < .05$). The high variability in blood reducing sugar measurements which has been noted by other workers (82) was also shown in this study.

A summary of the incidence and severity of diarrhea due to ingestion of the various sugars is listed in Table 5. Sucrose and maltose consistently caused watery feces at all ages. Average time for the onset of diarrhea after sucrose ingestion was somewhat less than for maltose. The interval of time between ingestion of carbohydrate and commencement of diarrhea usually increased with increasing age. The development of diarrhea subsequent to glucose intake was slight at 3 weeks of age, but became more frequent at older ages. Likewise, the incidence of diarrhea due to lactose ingestion was negligible at the two younger ages, but was high in animals older than 16 weeks. Ingestion of starch under the conditions of this experiment did not cause a single case of diarrhea.

Table 6 shows the average times for carmine to pass

Table 5. Effect of carbohydrate treatment on incidence and severity of diarrhea[a] (Experiment 1)

Group	Mean age (days)	No. observations	No. times diarrhea observed	Average score	Av. time to onset of diarrhea (hr.)
Glucose					
A	22	6	2	1.0	11.0
B	50	4	4	3.0	8.0
C	136	6	6	2.8	4.3
D	227	4	4	2.0	5.8
E	600	0	-	-	-
	Total	20	16		
	Average			2.1	6.4
Lactose					
A	22	4	0	0	-
B	50	4	2	3.5	8.0
C	136	4	4	3.0	7.25
D	227	6	6	3.5	8.0
E	600	2	2	2.0	-[b]
	Total	20	14		
	Average			2.2	7.8
Maltose					
A	22	4	4	3.5	4.3
B	50	4	4	3.3	5.5
C	136	4	4	2.8	6.0
D	227	4	4	3.5	8.0
E	600	2	2	3.0	5.0
	Total	18	18		
	Average			3.2	5.8
Sucrose					
A	22	8	8	3.4	3.3
B	50	6	6	3.7	2.3
C	136	2	2	3.0	2.0
D	227	8	7	2.6	6.3
E	600	6	6	3.0	8.0
	Total	30	29		
	Average			3.1	4.7

[a]No diarrhea was observed after animals received starch and control diets, so these data are not included in this table.

[b]Time to onset of diarrhea was not recorded.

Table 6. Effect of carbohydrate treatment on time for passage of carmine[a] through the digestive tract (Experiment 1)

Group	Mean age (days)	Av. time for pass. (hours)	No. observations	Av. time for pass. (hours)	No. observations
Glucose				Maltose	
A	22	7	1	5	2
B	50	11	2	6	4
Sucrose				Control	
A	22	4.8	4	18	2
B	50	2.9	4	18	2

[a]One-half g. carmine was dissolved in solutions containing 2 g. carbohydrate per pound body weight. The solution was then fed to calves by nipple pail.

Table 7. Effect of heat treatment of starches upon blood reducing sugar response[a] (Experiment 1)

Kind of starch	Untreated	Jelled[b]	Autoclaved[c] in dry form	Autoclaved[d] in suspension
		Maximum increase (mg.%)		
Amylose	9.5	-	28.1[e]	18.6
Amylopectin	10.0	12.9	12.1	15.9
Flojel	9.5	14.2	10.3	10.6
Tapioca	9.4	16.1	10.7	16.5
		Mean change (mg.%)		
Amylose	2.7	-	12.0	9.1
Amylopectin	4.7	5.4	6.2	8.8
Flojel	1.9	6.9	5.0	2.0
Tapioca	1.5	5.2	3.2	8.7

[a]Each value is an average of 4 animals. For individual values, see Table 17 of the Appendix.

[b]Jelling was effected by heating the 10% suspension of starch in water at 70 degrees C. for 10 minutes. Amylose would not jell under these conditions.

[c]Starch was autoclaved at 15 pounds pressure per sq. in. for 30 min. and mixed with water so as to make a 10% suspension.

[d]A 10% suspension of starch in water was prepared and then autoclaved in a manner similar to that described in c.

[e]Increases from amylose, autoclaved in the dry form, were significantly higher ($P < .05$) than those obtained from tapioca and Flojel when treated in a similar manner. None of the other means significantly differed from each other.

through the digestive tract of young animals when the marker was added to sugar solutions. It was felt that such information would indicate the time required for the particular sugar to pass through the digestive tract. As was expected, because of the rapid onset of diarrhea with sucrose, carmine appeared in the feces of sucrose-fed animals in the shortest time. Maltose passed almost as rapidly, while the passage of glucose was much slower. The appearance of carmine corresponded quite well with the beginning of diarrhea in the animals receiving maltose and sucrose, while feces of calves on lactose and control diets were always of normal consistency.

Heat treatment of starches

In Table 7 are presented the average maximum increases and mean changes in blood reducing sugar obtained from starches after being subjected to various heat treatments. (Table 22 of the Appendix lists these data by individual animals). Autoclaving amylose in the dry form or in suspension enhanced the response of animals, with the former method being superior to the latter. Other treated starches showed a consistent but non-significant advantage over the untreated.

Table 21 of the Appendix presents the actual blood reducing sugar levels at the different bleeding times, subsequent to ingestion of treated starch.

Intravenous injection plus carbohydrate ingestion

Rate of removal of glucose from the blood of the control animals receiving only the intravenous infusion (glucose was injected at a level of 0.3 g. per kg. body weight) was calculated, according to the method used by Reid (93), to be about 3% per minute. Figures 7 and 8 indicate that an exponential decrease in blood glucose occurs subsequent to the intravenous injection of glucose with levels returning to normal within 2 hours.

When calves ingested glucose, maltose or lactose in addition to the glucose injection, blood sugar decreases departed from their exponential nature and tended to plateau. The specific time of departure from the exponential may serve as an indication of the interval of time between ingestion and onset of absorption of these sugars (or their hydrolysis products). The absorption of glucose and maltose (hydrolyzed to glucose) appears to start somewhat earlier than that of lactose (hydrolyzed to glucose and galactose) and starch (hydrolyzed to glucose).

A slight plateauing from the exponential decrease in blood reducing sugar was displayed after ingestion of starch (which had been preceded by injection of glucose). These plateaus occurred at a later time and were at lower levels than those observed after ingestion of glucose, maltose and lactose. No absorption of sucrose (hydrolyzed to glucose and fructose) was indicated at any time. These data are presented in Table 8.

Figure 7. Effect of injection of glucose (0.3 g. per pound body weight) plus ingestion into the omaso-abomasal area of various sugars upon blood reducing sugar levels, (sugars were ingested at a level of 2 g. per pound body weight).

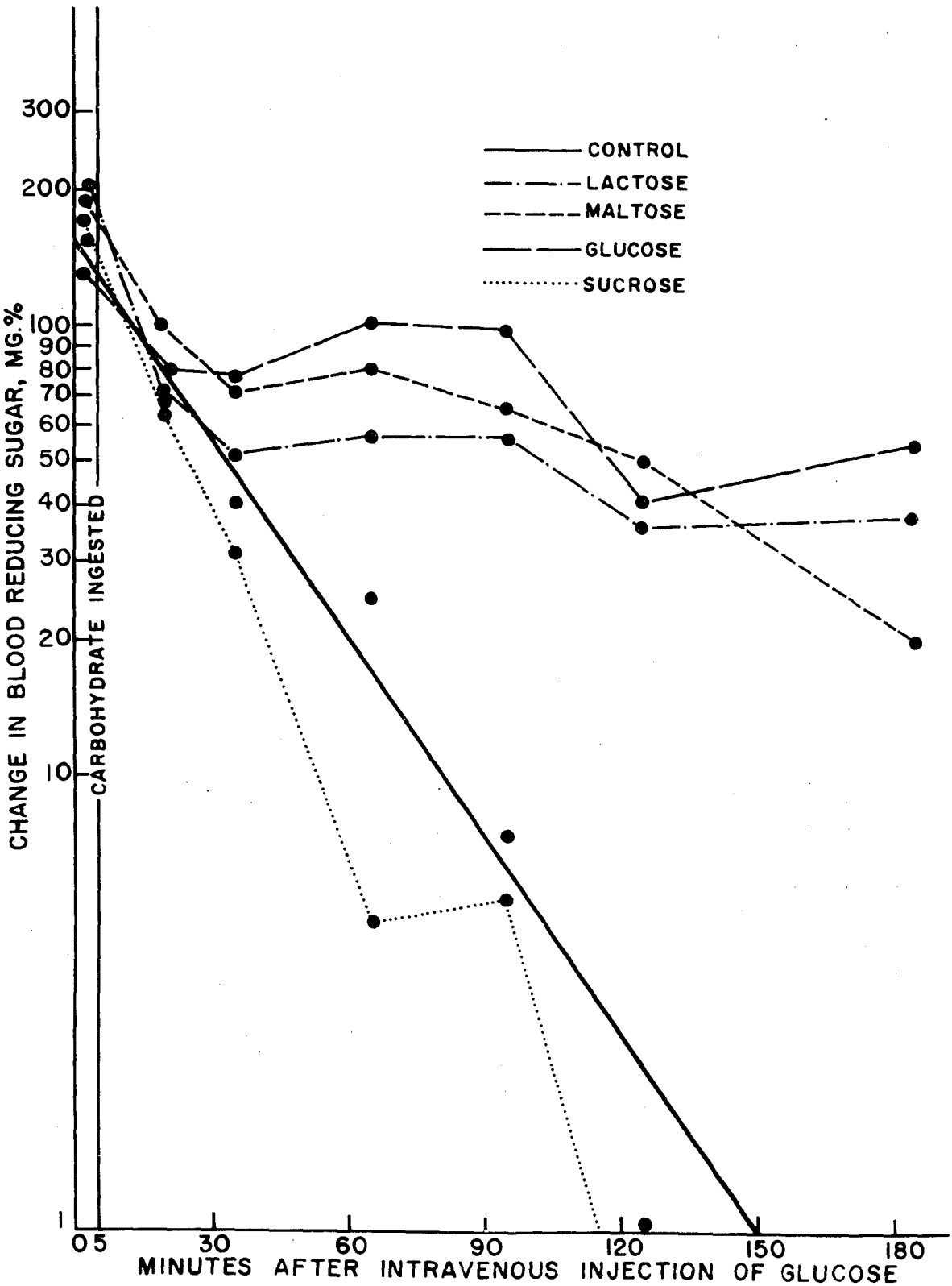

CONTROL
LACTOSE
MALTOSE
GLUCOSE
SUCROSE
CHANGE IN BLOOD REDUCING SUGAR, MG.%
CARBOHYDRATE INGESTED
300
200
100
90
80
70
60
50
40
30
20
10
1
0 5
30
60
90
120
150
180
MINUTES AFTER INTRAVENOUS INJECTION OF GLUCOSE

Figure 8. Effect of injection of glucose (0.3 g. per kg. body weight) plus ingestion of various types of starch on blood sugar levels (all starches except amylose were ingested at the level of 2 g. per pound body weight; amylose was ingested at the 1 g. level).

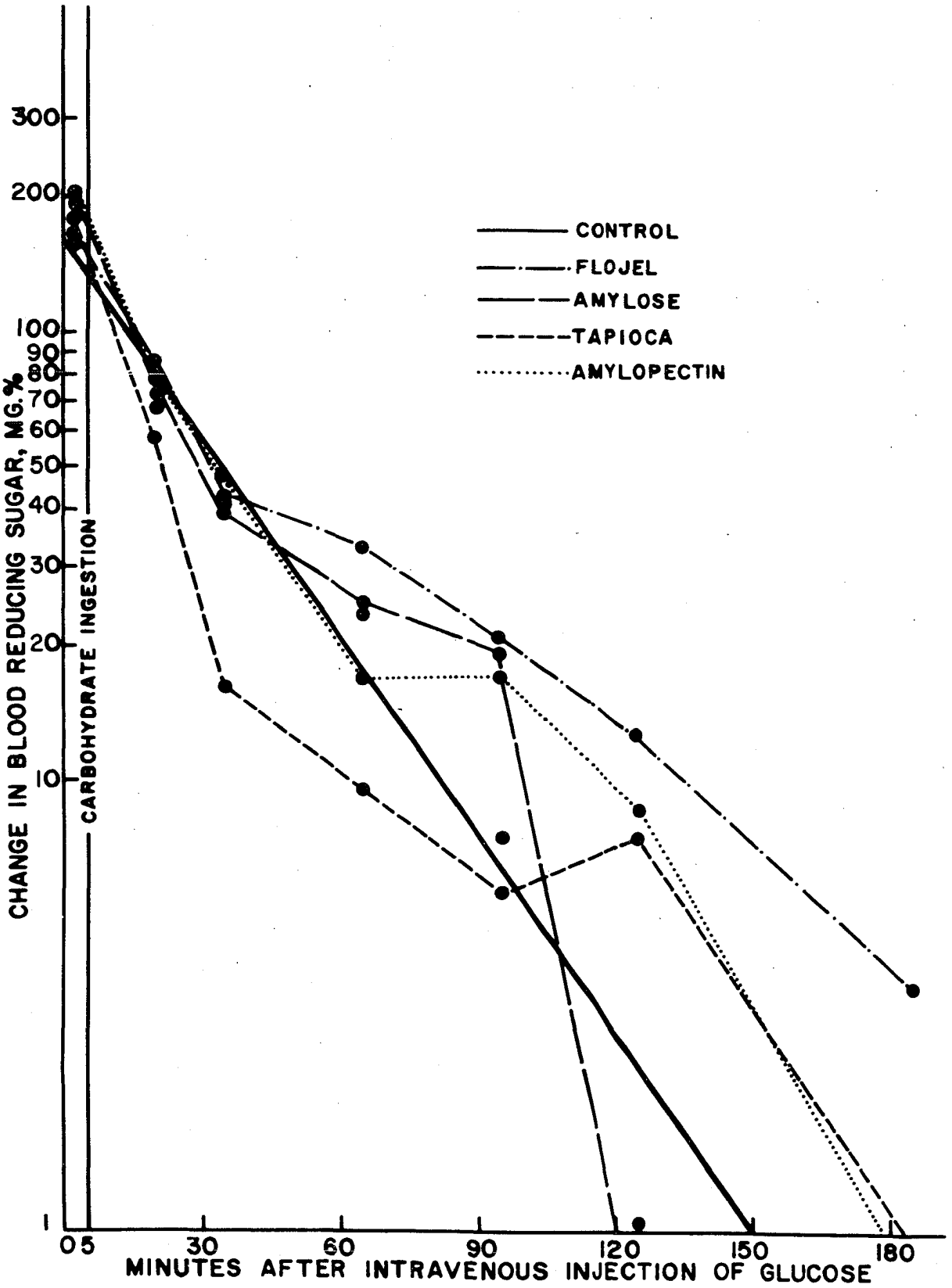

CONTROL
FLOJEL
AMYLOSE
TAPIOCA
AMYLOPECTIN
CARBOHYDRATE INGESTION
CHANGE IN BLOOD REDUCING SUGAR, MG.%
300
200
100
90
80
70
60
50
40
30
20
10
1
0 5
30
60
90
120
150
180
MINUTES AFTER INTRAVENOUS INJECTION OF GLUCOSE

Table 8. Blood reducing sugar levels after intravenous injection of glucose followed by ingestion of carbohydrate[a] (Experiment 1)

Treatment	Minutes after injection									
	0	2	20	35	65	95	125	185	305	485
	mg.%									
Control	68	231	139	108	86	76	68	61	60	65
Glucose	73	206	152	152	176	172	114	127	81	73
Lactose	73	281	155	125	130	130	109	111	103	70
Maltose	69	258	171	143	152	138	120	89	79	68
Sucrose	74	255	147	107	79	80	73	74	66	65
Amylose	74	269	146	114	99	93	73	68	62	56
Amylopectin	70	271	142	117	87	87	79	71	70	59
Flojel	61	230	145	107	95	82	74	65	57	54
Tapioca	57	237	116	73	67	63	64	57	57	52

[a]Each value is the average of 2 animals.

Experiment 2

Animals became fairly well adjusted to the digestion stalls and also to experimental diets as evidenced by the good growth during this study. The overall average daily gain per animal during the trial was 2.0 pounds. Greatest growth occurred while animals received the control ration, and poorest growth was observed during maltose feeding. However, little importance is attached to this difference because of the great variability among animals (Table 23 of the Appendix).

Animals receiving sucrose usually passed watery feces within a few hours after feeding. A similar condition resulted from feeding maltose, but to a lesser degree. Very little diarrhea developed in calves on starch and lactose rations. Both wet and dry weights of feces from calves

receiving sucrose were greater than those for calves receiving other carbohydrates (Table 24 of the Appendix). Diurnal changes in fecal dry matter are given in Table 25 of the Appendix. Moisture content in feces of sucrose-fed and maltose-fed animals was greatest from 6 to 10 hours and from 8 to 12 hours, respectively. Only small variations in fecal dry matter occurred in the other treatments.

Blood reducing sugar study

The control ration caused an appreciable rise in blood reducing sugar which can be attributed to the lactose contained in the milk. Lactose and maltose induced greater blood reducing sugar responses than did sucrose or starches, except for amylose. (Mean change differences were usually significant ($P < .05$), but maximum increases were not.) Maximum increases for sucrose were less than for controls. Greater maximum increases were noted with maltose than lactose, but this difference was not reflected in mean change values. All of the starch diets exhibited significantly higher ($P < .05$) mean changes than the control, with amylose significantly higher than other starches. Maximum increases and mean changes are presented in Table 9 while individual values for blood reducing sugar after ingestion of the test diet are listed in Table 26 of the Appendix. The analysis of variance of these data, presented in Table 27 of the

Table 9. Maximum increase and mean change in blood reducing sugar after carbohydrate ingestion via the milk[a] (Experiment 2)

Animal number	Control	Lactose	Maltose	Sucrose	Amylose	Amylo-pectin	Flojel	Tapioca	Diff. req. to be sig. ($P < .05$)
				Maximum increase					
4850	23.5	33.0	37.7	13.5	14.5	8.7	40.8	39.9	
4851	14.2	35.2	59.6	0	28.9	15.3	15.5	9.3	
4857	8.1	46.4	29.5	23.5	27.6	32.1	8.8	30.0	
4858	32.6	33.1	59.1	16.3	34.2	19.8	34.5	21.9	
Av.	19.6	36.9	46.5	13.3	26.3	19.0	24.9	25.3	14.7
Av. less control		17.3	26.9	-6.3	6.7	-0.6	5.5	5.7	
				Mean change					
4850	4.7	9.4	11.9	1.7	11.1	3.2	8.6	10.5	
4851	-0.9	8.7	12.2	-4.2	16.1	4.6	6.1	0.6	
4857	-2.7	23.5	11.9	5.7	15.1	10.9	2.7	15.2	
4858	4.9	14.3	20.8	6.6	14.2	9.6	8.8	7.9	
Av.	1.5	14.0	14.2	2.5	14.1	7.1	6.6	8.6	5.4
Av. less control		12.5	12.7	1.0	12.6	5.6	5.1	7.1	

[a]Whole milk was fed in all rations. The lactose contained therein was equivalent to approximately 0.70 g. per pound body weight of animal daily. Supplemental carbohydrate was fed at a level of 1.4 g. per pound body weight.

Appendix, shows quite high variability for maximum increases, but less for mean changes.

Digestibility studies

Content of water soluble carbohydrate in feces from animals on the control ration averaged 2.5 g. per day; thus, one may assume almost complete disappearance of the lactose in the milk. A correction for this amount (-2.5 g.) was made in calculation of fecal carbohydrate recovered from other rations. Chromatographic examination after acid hydrolysis of the water-insoluble portion of feces from the control group showed hexose was present in such small amounts that quantitative estimations were not feasible. This indicates that the hexose spot shown with feces hydrolysates of other rations resulted from the added carbohydrate and not from the pellets or milk. Substantial quantities of pentose were shown upon acid-hydrolysis of feces. This fraction was probably voided in the feces as pentosan. Because the only spot appearing on chromatograms of the hydrolysate of control-fed animals corresponded to a pentose, it may be concluded that the pentosans originated in the alfalfa pellets. Pentosan excreted per day (measured as pentose after hydrolysis) averaged about 64 g. for control and starch diets (Table 29 of the Appendix).

Apparent digestibilities of lactose and maltose were high, (94 and 97% respectively) while that of sucrose was much

lower (58%). Digestion coefficients for the different types of starch ranged from 80 to 88% with an average of 83% (Table 10). Little difference between the digestibility of the different kinds of starch was noted. The analysis of variance (Table 28 of the Appendix) shows that variability was quite high in this study. About 68% of the carbohydrate recovered from sucrose-fed animals and 25% of that recovered from starch-fed animals was in the form of monosaccharide (Table 11). (Chromatographic examination of the soluble extract of feces from animals receiving starch showed only traces of maltose and dextrins while substantial amounts of glucose were present.)

Concentration of carbohydrate in feces sampled at 2-hour intervals, during the last 24 hours that animals were in digestion stalls, was related to the time of feeding the previous meal. Over the 24-hour period each of the carbohydrates exhibited two peaks as can be seen in Figure 9. The peaks for the individual treatments occurred at approximately the same length of time subsequent to the previous feeding. Sucrose peaks were attained at about 6 hours while those for maltose and lactose were at 8 and 9 hours, respectively. The starches reached their peaks at about 11 hours. Concentrations of the various carbohydrates at their respective peaks were in approximately the same ratio as the percentage of carbohydrate recovery from the different carbohydrate diets (Table 30 of the Appendix).

Table 10. Supplemental carbohydrate voided in the feces during digestibility study[a] (Experiment 2)

Carbohydrate	Animal number 4850 g. per day In-take	4850 Out-put	4851 In-take	4851 Out-put	4857 In-take	4857 Out-put	4858 In-take	4858 Out-put	Recovery per cent	Recovery coeff. of variation	Digest. coeff. (%)
Lactose	346	4.5	336	58.7	436	0	446	25.2	6.1	21.3	93.9
Maltose	236	2.9	518	21.6	372	13.5	372	7.1	2.7	63.0	97.3
Sucrose	420	118.3	382	189.2	290	91.7	510	292.7	41.7	29.3	58.3
Amylose	304	36.8	236	42.2	272	34.5	396	97.3	16.9	29.6	83.1
Amylopectin	214	24.5	454	44.9	354	37.7	336	49.0	11.5	73.9	88.5
Flojel	264	37.9	272	49.4	400	117.2	372	52.7	19.6	49.0	80.4
Tapioca	360	68.2	372	129.8	268	24.3	268	35.2	20.3	44.3	79.7
						Av. for starches			17.1	49.2	82.9

[a]Apparent digestion of the lactose of whole milk was almost complete. Therefore recovery data for the control ration are not presented; however, these data were used in calculating recovery of supplemental carbohydrate. Each value is the mean for a 5-day period.

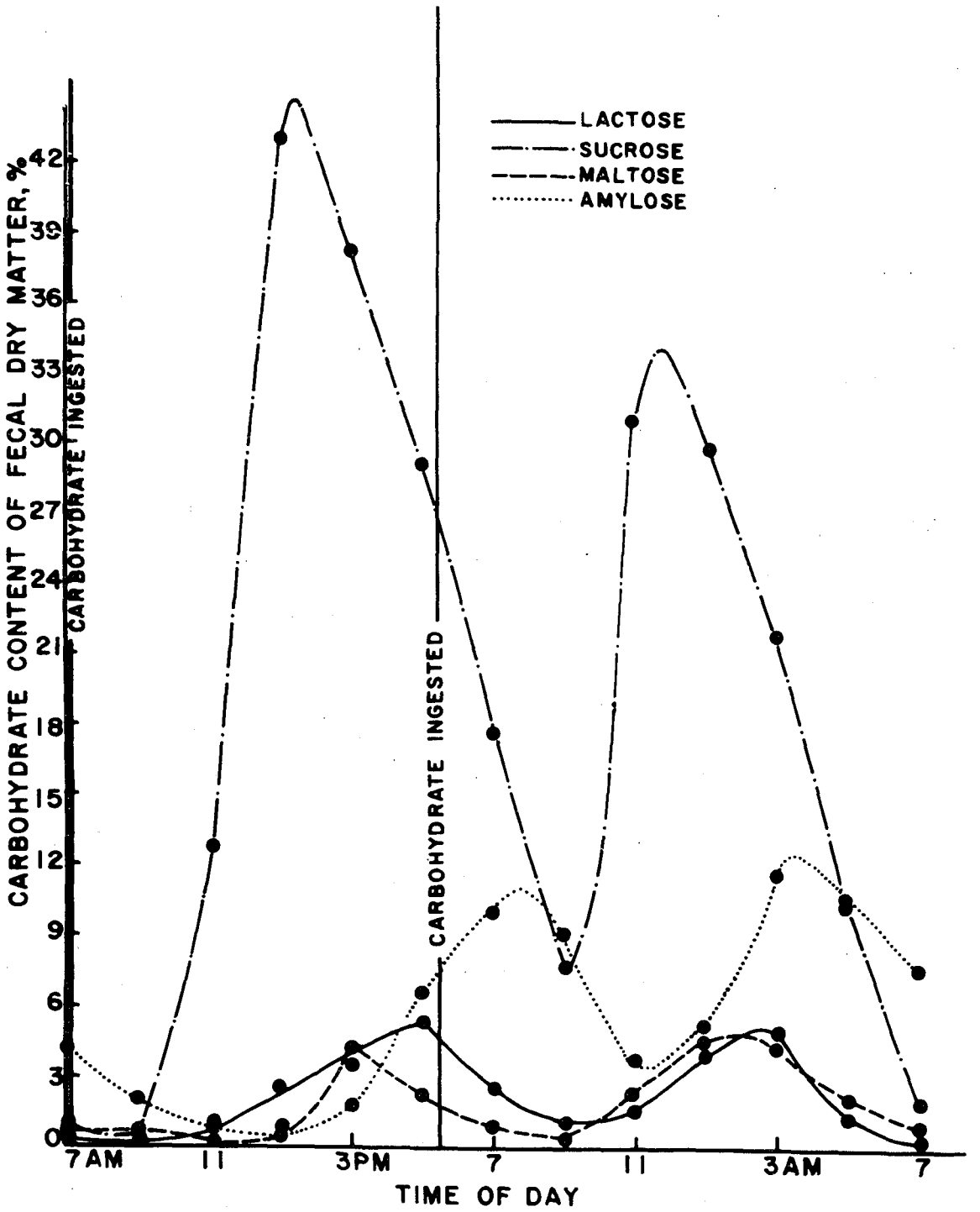
Table 11. Monosaccharide content of fecal carbohydrate[a] (Experiment 2)

Carbohydrate	Animal number 4850	4851	4857	4858	Av.
	%				
Sucrose	65.0	62.8	86.0	60.0	67.5
Amylose	25.2	11.1	16.2	18.8	18.0
Amylopectin	29.0	59.2	21.8	29.4	36.1
Flojel	30.6	15.0	11.5	52.0	23.3
Tapioca	21.0	20.3	34.2	13.4	23.2
Av. for starches	26.5	26.4	20.9	28.4	25.2

[a]All of the small amount of recovered carbohydrate in the feces of animals receiving lactose, maltose and control rations was monosaccharide. Therefore, no data are presented for these rations.

Table 31 of the Appendix presents the percent of the hexose carbohydrate in diurnal feces samples recovered as monosaccharide. It is interesting to note that this amount represents about 28% of the carbohydrate voided in starch-fed animals and 38% of that voided by sucrose-fed animals. Monosaccharide content of carbohydrate voided in the feces of starch-fed animals was similar for recovery (feces had accumulated for 12 hours prior to collection and freezing of sample) and diurnal samples (samples collected at 2-hour intervals and immediately placed in the freezer), while calculations for sucrose showed much higher percentages of monosaccharide in recovery samples than in diurnal samples. This difference for sucrose is probably due to the longer interval of time between voidance and freezing of feces for recovery samples than for diurnal samples.

Figure 9. Diurnal changes in carbohydrate (measured as hexose) of the feces following ingestion of various carbohydrates, (carbohydrate was administered at a level of 0.7 g. per pound body weight).


LACTOSE
SUCROSE
MALTOSE
AMYLOSE
CARBOHYDRATE INGESTED
CARBOHYDRATE INGESTED
CARBOHYDRATE CONTENT OF FECAL DRY MATTER, %
0
3
6
9
12
15
18
21
24
27
30
33
36
39
42
7AM
11
3PM
7
11
3AM
7
TIME OF DAY

DISCUSSION

Experiment 1

Most of the previously mentioned investigations of carbohydrate utilization posterior to the rumen have employed young calves less than 3 months old (29,30,82,110). Because of the physiological changes related to rumen development, it was thought important from a fundamental standpoint to know the capacity of older animals to digest carbohydrates when introduced posterior to the rumen. The experiments of Larsen and associates (64) provided some information in this area. However, these workers removed all material from the rumen, thus eliminating any possible influence of normal passage from the rumen upon carbohydrate digestion. Moreover, the animals were shifted abruptly from a hay-grain diet to a liquid diet.

The choice of the starches employed in this study was based partially upon their physical and chemical characteristics. Amylose is a straight chain molecule with only alpha-1, 4-glucosidic linkages while amylopectin is branched with both the alpha-1, 4- and alpha-1, 6-glucosidic linkages. If most of the amylase was specific for the straight-chained amylose, it probably would be manifested in blood reducing sugar differences between amylose and amylopectin. The results demonstrated, however, that there was little effect of the starches on blood reducing sugar. Thus, there either

was no specificity or the responses were too gradual to indicate a difference. The acid-treated, slightly solubleized Flojel was chosen for its greater solubility in water. It was thought that solubility might be a limiting factor in the poor utilization of starch by the calf. Here, again, there was no appreciable effect on blood reducing sugar levels. Tapioca was chosen because of some interest in using this starch in milk replacer rations.

The extent of functional development of the rumen and the normal ration of the animal were the main factors involved in the choice of the particular ages for experimentation. At 2 to 4 weeks the calf is dependent mainly on milk for its nutrition, and functional development of the rumen has begun. By 6 to 8 weeks dry feed provides the primary source of nutrients and rumen function has advanced greatly. The stomach compartments are approaching mature proportion and the animal is usually well adapted to a dry ration much before 16 weeks. Growth of the rumen continues until physical maturity is reached. For this reason, the study included the two older age groups.

In general, the ingestion of carbohydrate by the 136-day-old group resulted in smaller increases in blood reducing sugar than in the 227-day-old group. This was not expected because of the trend for decreasing response with age. A possible explanation may be that mechanical delivery of the test meal in the older age group was more efficient in

by-passing the rumen than the method (nipple-pail feeding) used in the 20-week-old animals. Hegland et al. (45) observed that upon feeding milk by nipple-pail, the esophageal groove functioned efficiently in by-passing the rumen of calves up to 20 weeks of age. However, the shunting mechanism was less efficient in 16- to 20-week-old animals when water instead of milk was fed.

Despite the reversal in the age trend with the two groups, it was thought that even if some carbohydrate did enter the rumen of 136-day-old animals, it was only a small quantity. This is substantiated by the fact that the observed increases in blood reducing sugars subsequent to glucose feeding at this age were far in excess of the increases obtained by placing glucose directly into the rumen.

The results reported herein support those of other studies with regard to utilization of carbohydrates by the young calf (29,30,82,110). They show glucose and lactose are well utilized by young calves, and therefore are superior to other carbohydrates for inclusion in milk replacer rations. Maltose caused substantial blood reducing sugar increases, but of a much lesser magnitude than those caused by glucose and lactose. Blood reducing sugar increases due to ingestion of sucrose and starch were negligible.

A decrease with age in response to glucose ingestion has been suggested by other workers (8,48,55), but has not been so clearly demonstrated as in this study. Possible

explanations for this phenomenon are: 1. Decreased rate of glucose absorption in the small intestine with increasing age (a decrease in the rate of absorption coupled with the intake of large quantities of glucose may have resulted in an overwhelming, by glucose, of the digestive tract), and 2. Increased rate of removal of glucose from the blood. Decreased absorption seems to be the more probable explanation for the decreased response to glucose, because removal rate in experiments where glucose has been intravenously injected tends to decline with age rather than increase (69). Such a decrease in tolerance, it seems, would cause the blood response to ingested glucose to increase rather than decrease with age. Reid's work (93) supports the theory of a decrease in the absorption rate by showing that glucose was absorbed from the small intestine of ruminants at a slower rate than from non-ruminants. An observation from the present study which also supports the theory of a decrease in absorption rate was the consistent inducement of diarrhea from the ingestion of glucose by calves at older ages but not at the younger ages. This may indicate that in this experiment substantial quantities of glucose passed through the digestive tract of older animals, unabsorbed.

It has been known for some time that a correlation exists between natural feeds of animals and the types and relative concentrations of digestive enzymes produced (111, 120). It is generally accepted that absorption of glucose

in the intestine occurs both through a passive process of diffusion and an active process in which the molecule is phosphorylated. This phosphorylation is thought to be mediated through intracellular enzymes in the mucosal cells. A possible explanation for the proposed decreased ability of the intestine to absorb glucose is that the phosphorylating enzymes, like many of the digestive enzymes, are adaptive in nature and under the normal feeding conditions of the ruminant, little glucose is released from the rumen to maintain efficient phosphorylation of glucose.

The induced response of blood reducing sugar to ingestion of lactose underwent a greater decrease with age than the response to glucose. This is probably attributable to a combination of factors. One might be the same factor responsible for the decline in the response to glucose, and another a decrease in intestinal lactase. As previously mentioned, a decrease with age in lactase activity of the intestines has been shown in calves from birth to 8 weeks of age (29,30,49,50). Similar studies with cattle of older ages might merit investigation. Increased lactase production in rats has been induced by lactose feeding (35,36). Conversely, the possibility of a decrease in intestinal lactase due to removal of lactose from the ration (as happens at the time of weaning) is suggested.

Comparison of data from both experiments of this study provides an indication of the effect of level of lactose

feeding on blood reducing sugar response. Animals in the 136-day-old group of experiment 1 were of a comparable age to animals in experiment 2. Lactose was fed at a level of 2 g. per pound body weight in experiment 1, while the amount per feeding in the second experiment was calculated to be 0.35 g. and 1.05 g. per pound body weight for the control and lactose groups, respectively. Maximum increases in blood reducing sugar were approximately the same at the two higher levels of feeding the(136-day-old animals in experiment 1 and the lactose group in experiment 2) and considerably less for the lowest level (control group of experiment 2). Values for mean change followed a similar pattern. It should be remembered that all of the lactose in the control ration and about one-third of the lactose in the lactose ration of experiment 2 came directly from the milk and seemed to be more soluble than the added lactose. The proportionately higher response from lactose observed in experiment 2 may be attributed partly to solubility. Another possible factor might have been that the lactose in experiment 2 was taken with the milk; thus, resulting in more efficient by-passing of the rumen than when carbohydrate was in an aqueous solution.

The level of maltose feeding in experiment 1 was the same as lactose (2 g. per pound body weight) while in experiment 2 it was 0.7 g. Again, there was little difference in blood reducing sugar response to the two widely varying

levels of intake. The difference in method of maltose ingestion between the experiments may have caused this apparent discrepancy.

A possible explanation for the very marked increase in response to maltose between 3 and 7 weeks is an increase in intestinal maltase. It is conceivable that under normal feeding conditions the calf may have its greatest need for maltase at this age because grain and hay are beginning to be consumed in fairly substantial quantities. Much of this material will be fermented in the rumen; however, some may pass on down the digestive tract in a semi-degraded state because of limited rumen capacity. Maltose from the starch originating in the grain would then be available for further breakdown by maltase. This need would decrease as the animal matures because the rumen increases to a size where little carbohydrate escapes fermentation. When glucose (2 g. per pound body weight) was administered directly into the rumen of 7- to 10-week old calves, two peaks (0.5 and 2.0 hours) in the post-prandial blood reducing sugar curve were noted. From this, it may be postulated that some soluble carbohydrate escaped rumen fermentation and passed to the small intestine where it was absorbed. In older animals, the peak at 2.0 hours was not evident. Such an adaptive mechanism may be supported by the results of an earlier study in which maltase activity of intestinal tissue increased only slightly from birth to 6 weeks of age when calves were

maintained on an all-liquid ration containing only a small amount of starch (50). In a similar study, in which cereal gruel was a main constituent of the ration, a three-fold increase in maltase activity was observed between 2 and 8 weeks of age (29,30).

The present study substantiates a conclusion made from earlier work that sucrose is poorly digested by the calf because of a deficiency in intestinal sucrase (49). Several other studies with young calves have shown similar results (82,110) as did the experiments by Walker (112) with sheep. The results herein, which included a much wider age range than previous studies, showed that sucrose utilization (at least as estimated by blood reducing sugar changes) is negligible at all ages in the bovine. This unique characteristic of ruminants is probably related to the fact that rumen action negates the need for intestinal sucrase.

From earlier studies of amylase activity of calf pancreatic tissue, it was calculated that the maximum rate of hydrolysis of starch to maltose in the intestine of the 1- to 6-week-old calf is about 17 g. per hour. This is based on the assumption that the total amylase activity in the pancreas just before feeding is roughly equivalent to the maximum amount which will be released into the duodenum during the time of passage of a meal. Such low amylase activity very likely is at least partially responsible for the apparent inability of the calf to digest large quantities

of starch and, consequently, for the small changes in blood reducing sugar subsequent to ingestion of starch. About 200 to 300 g. of starch were fed to the young calves in this experiment, which greatly exceeds the calculated amount that they would be able to digest.

Similar calculations for lactase and maltase activities in 3- to 6-week-old calves were about 120 g. and 15 g. per hour, respectively. It is interesting to note that the calculated potential of the calf to hydrolyze maltose was very close to that of starch (17 g. per hour); however, ingestion of maltose caused greater increases in blood reducing sugar than starch. Possible reasons for the poor response to starch will be discussed in the following paragraph.

Other factors which may be involved in the poor apparent utilization of starch by the young bovine when introduced into the omaso-abomasal area are the low solubility in water of the starch and the inability of the enzyme to penetrate the starch granule. Sumner and Myrbach (106) state that undamaged starch granules are digested very slowly and only become readily digestible upon mechanical rupturing. It is stated that this rupturing has been accomplished by treatment with heat or certain chemicals. Subjection of the various starches to the different heat treatments in the present study caused small but consistently greater increases in blood reducing sugar response than were observed with untreated starch. The advantage of treated over the untreated

starch was most evident in the case of amylose. Jelling seemed to be just as effective as the autoclaving, either in the wet or dry form, for increasing the availability of all starches except amylose (amylose was not jelled). Further investigations relating to the effect of heat and chemical treatment of starch on its utilization by calves are needed.

Preliminary in vitro work in which the four types of starch used in this study were incubated with a homogenate of calf pancreatic tissue showed greatest hydrolysis for amylopectin and tapioca, the least for amylose, and Flojel was intermediate. Prior to incubation, all starches except amylose were dissolved in water at 70 degrees C. Amylose would not dissolve at this temperature and was incubated in the undissolved state which was thought to account for the low values observed with this starch. The reason for the observed in vitro differences between the starches other than amylose is not known. It was thought that differences similar to those shown in the in vitro work might be reflected in blood reducing sugar studies; however, response to starches was low and differences either did not exist or were obscured by the weak response.

The negative response in blood reducing sugar after starch ingestion by calves at the two younger ages offers credence to previous reports that starch is very poorly utilized by young calves. Still the possibility of substantial digestion and absorption posterior to the rumen in

older animals was not negated. A very slow but rather extensive breakdown may have occurred with only a minor effect on blood reducing sugar values.

The study which combined injection of glucose with ingestion of carbohydrate was proposed to assess the theory that a slow rate of hydrolysis was responsible for the negligible response in blood reducing sugar after ingestion of starch. It was presumed that the infused glucose would keep blood reducing sugar at an elevated level so that any differences detected between calves ingesting starch and those receiving the control diet could be attributed to starch breakdown and subsequent absorption of glucose. Small differences were noted between starch-fed and control animals and may indicate some utilization of starch. However, there is some doubt that blood sugar levels were maintained at a sufficiently elevated position during the period of probable starch digestion to fully accomplish the stated objective. It is felt that similar experiments in the future should include injection of glucose 1 to 2 hours after ingestion of starch, thereby providing for sufficiently elevated blood reducing sugar levels to detect absorption of starch (hydrolyzed to glucose).

As mentioned earlier, maltose (hydrolyzed to glucose) and glucose absorption seemed to begin sooner than lactose (hydrolyzed to glucose and galactose) with respect to time of ingestion. This was shown (in the infusion studies) by

the more rapid departure from an exponential decrease exhibited by the blood reducing sugar curves plotted for glucose- and maltose-fed animals than those for animals fed lactose. The faster passage of maltose (as compared to lactose) through the digestive tract, as substantiated by the data on diarrhea, could have caused this difference in the onset of absorption of hydrolytic products of the two disaccharides. Another factor which may have influenced this difference is the greater solubility of maltose than lactose. It is apparent that the rapidity with which glucose was absorbed may be attributed to its readily absorbable state.

Incidence and severity of diarrhea subsequent to the feeding of a particular carbohydrate was inversely related to the relative utilization of certain of the carbohydrates. Supporting evidence is the response to the feeding of sucrose. This carbohydrate resulted in negligible rises in blood reducing sugar at all ages, and caused diarrhea at all ages. Apparent utilization of glucose and lactose decreased with age while diarrhea subsequent to feeding these carbohydrates was less in young animals than in older ones.

Despite its apparent indigestibility by animals at the younger ages, starch, as it was administered in this experiment, did not increase fluidity of feces. A possible explanation might be that little hydragogue action could be attributed to the starch because of its insolubility in water. It seems probable that if starch is to cause diarrhea, it must

be fed in sufficiently high levels over a long enough period of time for degradation products, resulting from bacterial fermentation of starch, to accumulate in the lower portion of the digestive tract. Adaptation of the microbial population in the cecum and colon to the starch substrate also may be necessary before the diarrheic effect of starch is evidenced.

Experiment 2

The marked increase in blood reducing sugar stimulated by the control ration can be attributed to lactose from the milk. The amount of milk fed was proportional to body weight; additionally, no trends with age in blood reducing sugar response were visably evident. Therefore, one can assume that blood reducing sugar responses due to ingested milk were essentially equal in all animals during the experimental period.

Ingestion of maltose resulted in slightly greater maximum increases in blood reducing sugar than lactose, while no difference was noted in mean change values. A marked parallel in blood reducing sugar response to lactose and maltose in animals older than 16 weeks was also shown in experiment 1. The smaller rises in blood reducing sugar resulting from ingestion of the sucrose ration as compared to the control ration may be attributed to the more rapid passage of the meal containing sucrose, thus causing some decrease in

digestibility of the milk lactose in the sucrose ration.

Mean changes in blood reducing sugar subsequent to starch ingestion were significantly higher ($P < .05$) than those following ingestion of the control ration. Though maximum increases for the starches (with the exception of amylopectin) were higher than for the control ration, the differences were not significant. These data indicate that despite the relatively small rises in blood reducing sugar resulting from ingestion of starch, such rises were more persistent than those of the control ration.

One may conclude from the difference in the persistencies of the blood reducing sugar curves that breakdown of starch to glucose occurred at a slower rate than the breakdown of the lactose contained in the control ration. It may be further concluded that for estimating apparent utilization of starch, mean change data are more meaningful than maximum increases. It is not known why response to starch in experiment 2 was greater than in experiment 1. However, a possible explanation may be that the carbohydrate in the former experiment was fed as a water suspension, while that in the latter was included in the milk.

It has been proposed that pancreatic secretions are influenced by the nature of the dietary (44). More particularly, free amino acids have been shown to cause a release of pancreozymin from the duodenal wall, which in turn is absorbed from the intestine and enhances enzyme secretion by the

pancreas (67). Such stimulation may have been operative in experiment 2 when the starch was fed in milk, but not in experiment 1 when it was fed in water. Two other factors may have influenced the greater response to starch in the present experiment. One is the longer period of starch feeding which may have resulted in increased production of amylase due to enzyme adaptation. The other factor is a greater efficiency in stimulation of the esophageal groove due to ingestion of milk (experiment 2) as opposed to water (experiment 1).

The greater blood reducing sugar response to amylose than to other starches may be associated with its strong adsorptive properties in water. It is conceivable that the water soluble enzyme would be placed in a closer proximity to its site of action because of this effect.

The higher digestibility of maltose and lactose than other carbohydrates corresponds with the blood reducing sugar data. Recovery of a very small amount of these disaccharides in the feces is in accordance with results from other experiments (49,63,84). The levels of carbohydrate fed in this study were relatively low. It is postulated that a higher intake of lactose and maltose would have resulted in lower digestion coefficients at this age (3 to 6 months). This is indicated by the diarrhea observed in animals of a comparable age when 2 g. per pound body weight of lactose or maltose were fed (experiment 1), while no diarrhea was

observed in experiment 2 at a lower level of intake. The high digestibility of maltose indicates that a deficiency of maltase was not a limiting factor in the digestion of starch in this experiment since equal levels of both carbohydrates were fed. No age differences in digestibility of carbohydrates from 3 to 6 months were visibly evident. (This was the age range of animals from the beginning to the end of the experiment.)

Even though digestion coefficients for sucrose were lower than for other carbohydrates, they were somewhat higher than was expected. Blood reducing sugar and tissue enzyme studies have invariably indicated the absence of intestinal sucrase in the bovine. Some hydrolysis of sucrose under the acidic conditions of the abomasum may have occurred, but if this were the case it should have been reflected in blood reducing sugar studies.

It is suggested that the disappearance of ingested sucrose was primarily due to hydrolysis (to glucose and fructose) and fermentation. These processes probably began in the lower digestive tract (upon contact of substrate with the saccharolytic microorganisms) and continued until feces were frozen (at which time microorganisms were inactivated) and started again when feces began to thaw. The rapid rate of sucrose passage through the digestive tract (as shown by the appearance in the feces of highest concentrations of sucrose and its hydrolytic products at 4 to 8 hours after

feeding) resulted in a relatively long period of contact between the microbial population and the sucrose prior to freezing (samples were collected and placed in the freezer 12 hours after feeding).

Disappearance of considerable sucrose (or its hydrolytic products) occurred in the interval of time between voidance and freezing during which feces remained in the collection pans. This was indicated by a much lower digestion coefficient for sucrose and its hydrolytic products (32%) calculated from diurnal samples (placed in the freezer immediately after being voided) than the 58% apparent digestibility obtained from recovery samples (collected at 12 hour intervals, thus allowing the major portion of the sucrose to remain 4 to 8 hours in the collection pans before being placed in the freezer). Total carbohydrate voided in diurnal samples was calculated by taking the carbohydrate content in fecal dry matter (averaged for the 13 collections during a day) and multiplying this value by the voided dry matter (g.).

Digestibility coefficients calculated (from diurnal samples) for lactose, maltose and starch (all starches combined) were 95, 96, and 80%, respectively; while those determined from recovery samples were 94, 97 and 83%, respectively. This indicates that little fermentation occurred with carbohydrates other than sucrose during the period that feces remained in the collection pans. Additionally, such

close agreement between the two types of calculations lend validity to the use of the diurnal data for calculating digestibility.

A possible explanation for the greater percentage of sucrose recovered as monosaccharide in recovery samples (68%) than in diurnal samples (38%) is that hydrolysis to fructose and glucose by microorganisms occurred at a faster rate than fermentation of the monosaccharides, thereby resulting in a net accumulation of monosaccharides.

Digestion coefficients for the starches ranged from 79 to 88% which are not too different from those obtained by Noller et al. (78,79) and Ratcliff (89), but which are much higher than those indicated by the data of Larsen and co-workers (64), wherein starch was found to be very poorly utilized posterior to the rumen of the bovine. An explanation for the apparent discrepancy between the present data and those of Larsen et al. (64) may partially be due to a difference in methods. Digestibility in the present study was based on total collection of feces for 5 days, while the method used by Larsen and associates (64) employed the ratio technique with chromium oxide as a marker. In the latter, samples of feces were collected at 8 and 10 hours after feeding and composited and analyzed for chromium oxide and starch. It is conceivable that the marker passed at a different rate than the starch, resulting in artificially low digestibility estimates for the starch. This may also

explain the apparent recovery of more starch than was fed in the test meal and the high variation between digestion coefficients in work by Larsen et al. (64).

An additional reason for the wide difference in starch digestibility between the two studies might have been length of time that animals were allowed to adapt to the starch-containing rations. Animals were on test diets for only 2 days in the study by Larsen et al. (64) while the present study employed a preliminary period of 5 days during which the test meal was fed to animals prior to collection of any feces. If such adaptation did occur in the present study, it was complete before the collection period began because no trends of increased digestibility of starch were noted between the first and fifth day of feces collection.

On starch rations there was very little difference between diurnal and recovery samples in the monosaccharide content of fecal carbohydrate (28 and 25 percent, respectively). These data, in addition to the very similar digestion coefficients calculated for the diurnal and recovery data of starch (80 and 83 percent, respectively) showed that hydrolysis of starch or fermentation of hydrolytic products was negligible during the interval of time between voidance and collection of feces.

Many of the earlier studies have followed the method proposed by A.O.A.C. (5) for assessing starch digestibility of rations for calves. In this method an aliquot of feces

is mixed with water. The suspension is then centrifuged and the supernatant is discarded. The present study shows that a considerable quantity of soluble carbohydrate (resulting from hydrolysis of starch) is lost by such a procedure. It is felt that improved methods for measuring the carbohydrate content of feces would be very worthwhile.

Incomplete digestion of pentosans in roughage have been reported by other workers (68). Barhydt and Dye (8) observed values similar to those shown in the present study for the amount of pentosan escaping rumen fermentation when calves of a comparable age were fed a hay-grain ration. Because pentosans and starch hydrolyze under similar conditions, any analysis of starch in feces of calves previously receiving roughage in the ration should include a method for separating products of starch hydrolysis from those of pentosan hydrolysis. This was accomplished in the present study by ascending paper chromatography.

In diurnal samples it was interesting to note that while animals were on disaccharide rations the most fluid feces occurred at the hour when carbohydrate content of the feces was highest. This was best illustrated by sucrose. Average dry matter and carbohydrate contents of the feces at the time the test meal was fed were 17.3 and 0.34 percent, respectively. Feces samples 6 hours later contained 13.5 percent dry matter and 43.1 per cent carbohydrate. Little diurnal variation was noted in dry matter content in the

feces of animals receiving starch and control rations. It appears that soluble carbohydrates which pass, undigested, through the digestive tract will increase the water content of the feces.

As previously mentioned, feeding one test meal containing starch in experiment 1 did not result in diarrhea; and it was suggested that starch must be fed for a longer period for diarrhea to develop. It would seem that the period employed in experiment 2 (10 days) was of sufficient length for inducement of diarrhea, but none was observed. In experiment 2, some starch was undoubtedly available for microbial breakdown in the lower tract, but perhaps not in sufficient quantities to cause diarrhea because of a relatively low level of feeding (0.7 g. per pound body weight) coupled with possible digestion prior to reaching this area.

Sucrose concentration in feces reached a maximum at about 6 hours after feeding with a substantial quantity of this sugar first appearing at 4 hours. This is in accordance with the data of experiment 1 in which it was observed that watery feces occurred in less than 4 hours after ingestion of sucrose.

The high degree of diurnal variability in carbohydrate content of feces indicates that if the ratio technique is to be used for estimating digestibility of a substance fed by nipple pail to the calf, it must be established that the rates of passage of both nutrient and marker are similar.

These data indicate that small differences in rate of passage of the marker and nutrient could cause calculated digestibility to be greatly in error.

It is the feeling of the author that the results of the present experiments have shown that the apparent utilization of various carbohydrates, when introduced into the omaso-abomasal area, is greatly affected by age of animal. Moreover, marked differences among carbohydrates have been observed. Many of the findings previously reported for young calves have been confirmed, and the present knowledge of carbohydrate utilization posterior to the rumen has been extended to older-aged animals.

Utilization of lactose and maltose was superior to that of starch and sucrose in both digestibility determinations and blood reducing sugar studies. However, it was shown in experiment 2 (digestibility and blood reducing sugar studies) that starch was utilized better than sucrose, while the results of experiment 1 (blood reducing sugar study) failed to detect appreciable utilization of either starch or sucrose. Microbial fermentation appeared (in digestibility studies) to account for the disappearance of considerable sucrose. Microbial breakdown of starch was also indicated. Very little difference in utilization of the different types of starch was shown in either experiment. It is indicated by comparison of data from the two experiments that a limit exists in the level of feeding for efficient use of lactose

and maltose (in 3- to 6-month-old calves). Responses in blood reducing sugar observed when about 1 g. per pound body weight of lactose or maltose was fed (experiment 1) were as great as those obtained by feeding 2 g. (experiment 2). It is suggested that available enzyme might have been the main limiting factor.

Several important areas of future investigation have been suggested by these studies. One involves the need for a more accurate method of measurement of carbohydrates (qualitatively and quantitatively) as they are voided in the feces. Closely related and greatly needed are improved methods of separating and identifying the degradation products of starch. Determination of the extent of starch hydrolysis resulting from microbial breakdown as opposed to that caused by enzymes of animal origin would seem to merit investigation. Germ-free animals might be employed in such a study. However, critical digestibility studies, utilizing animals fitted with cecal fistulas, are perhaps a more logical approach.

Further investigations to improve utilization of starches for inclusion in milk replacer rations seem important. Such studies might include heat, chemical and enzyme treatments, either alone or in combination. Enzyme levels in the digestive glands of the bovine older than 8 weeks of age have not been determined. Such knowledge would be important from a fundamental standpoint. Additionally,

improved methods for assessing quantity of enzyme secretions made available for digestion of nutrients under normal feeding conditions would be very valuable.

Several questions have been raised concerning the rate of carbohydrate absorption in the small and large intestines and the effect of rumen development upon this rate. One possible approach for studying absorptive capacity of the small intestine might be employment of the intestinal-loop technique using animals at varying ages. Animals fitted with cecal fistulas could be used for studying absorption from the large intestine.

SUMMARY

This study consisted of two experiments. Experiment 1 determined the blood reducing sugar response to ingestion into the omaso-abomasal area for each of eight carbohydrates (glucose, lactose, maltose, sucrose, amylose, amylopectin, Flojel, tapioca) in calves of five age groups (mean ages: 22, 50, 136, 227, 600 days).

Maximum increases in blood reducing sugar levels in mg.% after carbohydrate ingestion at the five successive ages, from the youngest to the oldest, were glucose: 134, 130, 76, 82, 50; lactose: 147, 117, 36, 37, 14; maltose: 31, 72, 30, 34, 17. Maximum levels occurred at 1 to 2 hours after feeding. Sucrose and starch did not cause any appreciable increase in blood reducing sugar at any age. Mean change values in blood reducing sugar were also calculated and followed a pattern similar to maximum increases.

Glucose, maltose and sucrose usually caused diarrhea in less than 8 hours after ingestion. Lactose caused diarrhea in calves 12 weeks of age and older while no diarrhea resulted from ingestion of starch.

When animals received an intravenous injection of glucose (0.3 g. per kg. body weight) prior to carbohydrate ingestion, absorption of ingested carbohydrates (or their hydrolytic products) appeared to begin at the following times (in minutes) after ingestion: glucose and maltose, 15; lactose,

30; starches, 50.

Blood reducing sugar responses in calves were moderately increased when starches were autoclaved (at 15 pounds pressure per square inch for 30 minutes) or heated in water suspension until jelling occurred.

In experiment 2, 3- to 6-month-old calves were employed to determine the digestibility of seven carbohydrates. Calves were fed milk at the rate of 3 pounds per 100 pounds body weight. The carbohydrates, added to milk and fed by nipple pail, were administered at the rate of 1.4 g. per pound body weight. Digestion coefficients (based on a 5-day total collection period) for lactose, maltose, sucrose and starches (mean value for all starches) were 94, 97, 58, and 83 percent, respectively. The data suggest that disappearance of considerable sucrose and some starch resulted from microbial fermentation.

The diurnal pattern in carbohydrate content of the feces (based on diurnal samples collected every 2 hours during a 24-hour period) exhibited two peaks which were related to time of feeding. Peaks for lactose, maltose, sucrose and starch were at about 9, 8, 6 and 11 hours after feeding, respectively.

Responses in blood reducing sugar to ingestion of the various carbohydrates as administered in experiment 2 were greatest for lactose and maltose, least for sucrose, and starch was intermediate.

LITERATURE CITED

1. Allcroft, W.M. and R. Strand. Studies on lactic acid, sugar, and inorganic phosphorus in the blood of ruminants. Biochem. J. 27:512-522. 1933.

2. Amatuzio, D.S., F.L. Stutzman, M.J. Vanderbilt, and S. Nesbitt. Interpretation of the rapid intravenous glucose tolerance test in normal individuals and in mild diabetes mellitus. J. Clin. Invest. 32:428-435. 1953.

3. Andersen, H. and C. Dueholm. Studies on duodenal juice. Acta Pediat. Suppl. 77:256-262. 1949. (Original not available for examination; abstracted from Chem. Abstr. 44:9535. 1950.)

4. Annison, E.F. and D. Lewis. Metabolism in the rumen. 1st ed. John Wiley and Sons Inc., New York. 1959.

5. Association of Official Agricultural Chemists. Official methods of analysis, 8th ed. Assn. of Off. Agri. Chem., Washington, D.C. 1955.

6. Atkinson, R.L., F.H. Kratzer, and G.F. Stewart. Lactose in animal and human feeding. A review. J. Dairy Sci. 40:1114-1132. 1957.

7. Bailey, C.W., W.D. Kitts, and A.J. Wood. The development of the digestive enzyme system of the pig during its pre-weaning phase of growth. B. Intestinal lactase, sucrase and maltase. Can. J. Agri. Sci. 36:51-58. 1956.

8. Barhydt, J.B. and J.A. Dye. Relationship between dietary carbohydrate, abomasal carbohydrate, and blood glucose in the calf. Cornell Vet. 47:76-89. 1957.

9. Becker, D.E. and S.W. Terrill. Various carbohydrates in a semipurified diet for the growing pig. Arch. Biochem. Biophys. 50:399-403. 1954.

10. _____, D.E. Ullrey, and _____. A comparison of carbohydrates in a synthetic milk for the baby pig. Arch. Biochem. Biophys. 48:178-183. 1954.

11. _____, _____, _____, and R.A. Notzold. Failure of newborn pigs to utilize dietary sucrose. Sci. 120: 345-346. 1954.

12. Bell, F.R. and E.R. Jones. Carbohydrate metabolism in bovine trypanosomiasis. Ann Trop. Med. Parasit. 40: 199-208. 1946.

13. _____ and _____. Glucose tolerance in the bovine. J. Comp. Path. and Therap. 55:117-124. 1945.

14. Berkman, E.N. Content of intestinal and pancreatic enzyme in duodenal juice of healthy children. Pediatriya. 5:31-34. 1951. (Original not available for examination; abstracted from Chem. Abstr. 46:3630. 1952.)

15. Blaxter, K.L. and W.A. Wood. Some observations on the biochemical and physiological events associated with diarrhea in young calves. Vet. Record 65:889-892. 1953.

16. Braude, R., A.M. Dollar, K.G. Mitchell, and J.W.G. Porter. Further observations on the utilization of glucose and maltose in the young pig. Proc. Nutr. Soc. 17:14. 1958.

17. _____, _____. _____, and _____. The utilization of raw and cooked starch by the young pig. Proc. Nutr. Soc. 17:15. 1958.

18. Cajori, F.A. The enzyme activity of dog's intestinal juice and its relation to intestinal digestion. Am. J. Physiol. 104:659-668. 1933.

19. _____. The lactase activity of the intestinal mucosa of the dog and some characteristics of intestinal lactase. J. Biol. Chem. 109:159-168. 1935.

20. Carnevale A., G. Cocozza, and P. DeAngelis. Enzyme activities in the duodenal secretion of infants. Pediatria. 62:344-362, 1954. (Original not available for examination; abstracted from Nutr. Abstr. and Revs. 25:694. 1955.)

21. Cunningham, H.M. Digestion of starch and some of its degradation products by newborn pigs. J. Animal Sci. 18:964-975. 1959.

22. _____ and G.J. Brisson. The effect of amylases on the digestibility of starch by baby pigs. J. Animal Sci. 16:370-376. 1957.

23. _____ and _____. Utilization of maltose by newborn pigs. J. Animal Sci. 16:574-577. 1957.

24. Degroot, A.P. and C. Engel. Detrimental effect of lactose. I. Growth experiments with rats. The Netherlands Milk and Dairy J. 2:270-289. 1957.

25. _____ and P. Hoogendoorn. The detrimental effect of lactose. II. Quantitative lactase determinations in various mammals. The Netherlands Milk and Dairy J. 2:290-303. 1957.

26. Dimler, R.J., W.C. Shaefer, C.S. Wise, and C.E. Rist. Quantitative paper chromatography of D-glucose and its oligosaccharides. Anal. Chem. 24:1411-1414. 1952.

27. Dollar, A.M., K.G. Mitchell, and J.W.G. Porter. The utilization of carbohydrates in the young pig. Proc. Nutr. Soc. 16:7. 1957.

28. _____, _____, and _____. The utilization of carbohydrates in the young pig. Proc. Nutr. Soc. 16:12-13. 1957.

29. _____ and J.W.G. Porter. Some aspects of carbohydrate utilization by young calves. Proc. 15th International Dairy Congress 1:185-189. 1959.

30. _____ and _____. Utilization of carbohydrates by the young calf. Nature 179:1299-1300. 1957.

31. Dougherty, R.W., C.S. Klavano, W.M. Dickson, and P.A. Klavano. Blood sugar levels in cattle and sheep fed various amounts of glucose. Cornell Vet. 46:397-409. 1956.

32. Douglass, F.H. Why solid foods for the new-born? Northwest Medicine, Seattle. 52:832-834. 1954.

33. Duncan, D.B. Multiple range and multiple F tests. Biometrics. 11:1-42. 1955.

34. Duncan, Dorothy L. The physiological effects of lactose. Nutr. Abstr. and Rev. 25:309-320. 1955.

35. Fischer, J.E. Effects of feeding a diet containing lactose upon B, D-galactosidase activity and organ development of the rat digestive tract. Am. J. Physiol. 188:49-52. 1957.

36. _____ and T.S. Sutton. Effects of feeding lactose on lactase production. J. Dairy Sci. 32:717. 1949.

37. _____ and _____. Effects of lactose on gastrointestinal motility: A review. J. Dairy Sci. 32: 139-162. 1949.

38. _____ and _____. Effect of previous lactose feeding on intestinal absorption of lactose in the rat. J. Dairy Sci. 36:7-10. 1953.

39. _____ and _____. Hydrolysis of sucrose, lactose and cellobiose by small intestinal mucosa in vitro. Relationship to laxation in the rat produced by these disaccharides in vivo. Ohio J. Sci. 57:75-80. 1957.

40. Flipse, R.J., C.F. Huffman, C.W. Duncan, and H.D. Webster. Carbohydrate utilization in the young calf. II. The nutritive value of starch and effect of lactose on the nutritive value of starch and corn syrup in synthetic milk. J. Dairy Sci. 33:557-564. 1950.

41. _____, _____, H.D. Webster, and C.W. Duncan. Carbohydrate utilization in the young calf. I. Nutritive value of glucose, corn syrup and lactose as carbohydrate sources in synthetic milk. J. Dairy Sci. 33:548-556. 1950.

42. Florey, H.W., R.D. Wright, and M.A. Jennings. Secretions of the intestines. Physiol. Revs. 21:31-69. 1941.

43. Goetsch, D.D., G.K.L. Underbjerg, and M.J. Swenson. Utilization of intravenously administered glucose, invert sugar and fructose in cattle. Am. J. Vet. Res. 17: 213-216. 1956.

44. Grossman, M.I., Harry Greengard, and A.C. Ivy. The effect of dietary composition on pancreatic enzymes. Am. J. Physiol. 138:676-682. 1942.

45. Hegland, R.B., M.R. Lambert, N.L. Jacobson, and L.C. Payne. Effect of dietary and managemental factors on reflex closure of the esophageal groove in the dairy calf. J. Dairy Sci. 40:1107-1113. 1957.

46. Heilskov, N.S.C. Studies on animal lactase. II. Distribution in some of the glands of the digestive tract. Acta. Physiol. Scand. 24:84-89. 1951.

47. Holmes, J.R. Carbohydrate metabolism in the bovine. I. Intravenous glucose tolerance in the healthy cow. J. Comp. Path. and Therap. 61:1-14. 1951.

48. _____. Carbohydrate metabolism in the bovine. III. The effect of the administration of glucose by mouth to normal cattle of various ages. J. Comp. Path. and Therap. 62:41-53. 1952.

49. Huber, J.T. Relationship of age and diet to digestive enzyme activity in the calf. Unpublished M.S. Thesis. Library, Iowa State University of Science and Technology. Ames, Iowa. 1958.

50. _____, P.A. Hartman, N.L. Jacobson, and R.S. Allen. Digestive enzyme activity in the young calf. J. Dairy Sci. 41:743. 1958.

51. Hudman, D.B., D.W. Friend, P.A. Hartman, G.C. Ashton, and D.V. Catron. Digestive enzymes of the baby pig. Pancreatic and salivary amylase. J. Agri. Food Chem. 5:691-693. 1957.

52. _____, V.C. Speer, G.C. Ashton, and D.V. Catron. Comparison of sources of carbohydrates for the baby pig. J. Animal Sci. 14:1209-1210. 1955.

53. Hull, T.G. and L. Rettger. The influence of milk and carbohydrate feeding on the character of the intestinal flora. IV. Diet versus bacterial implantation. J. Bact. 2:47-71. 1917.

54. Jarrett, I.G. and B.J. Potter. Carbohydrate metabolism in the young lamb. Aus. J. Exp. Biol. Med. Sci. 30: 207-212. 1952.

55. Kennedy, W.L., A.K. Anderson, S.I. Bechdel, and J.F. Shigley. Studies on the composition of bovine blood as influenced by gestation, lactation and age. J. Dairy Sci. 22:251-260. 1939.

56. Kitts, W.D., C.R. Bailey, and A.J. Wood. The development of the digestive enzyme system of the pig during its pre-weaning phase of growth. A. Pancreatic amylase and lipase. Can. J. Agri. Sci. 36:45-50. 1956.

57. Kjer, K. Investigations into the relation of blood sugar in starch in normal persons. Acta. Medica Scand. 61:159-174. 1925.

58. Klumpp, T.G. and A.V. Neale. The gastric and duodenal contents of normal infants and children. The duodenal enzyme activity and the gastric and duodenal reactions. (H-ion). Am. J. Diseases Children. 40:1215-1229. 1930.

59. Kryuchkova, A.P. Amylase and lipase as indexes of changes in the functional condition of the pancreas during the course of ontogenesis. J. Physiol. (U.S.S.R.) 27:437-444. 1939. (Original not available for examination; abstracted from Chem. Abstr. 34:5137. 1940.)

60. Larner, Joseph and R.E. Gillespie. Gastrointestinal digestion of starch. III. Intestinal carbohydrase activities in germ-free and non germ-free animals. J. Biol. Chem. 225:279-285. 1957.

61. Larner, Joseph and C.M. McNickle. Action of intestinal extracts on "branched" oligosaccharides. J. Am. Chem. Soc. 76:4747-4748. 1955.

62. _____ and _____. Products of gastrointestinal starch and digestion. Fed. Proc. 14:242. 1955.

63. Larsen, H.J. Digestion and absorption of carbohydrates in the young bovine. Unpublished Ph.D. Thesis. Library, Iowa State University of Science and Technology. Ames, Iowa. 1953.

64. Larsen, H.J., G.E. Stoddard, N.L. Jacobson, and R.S. Allen. Digestion of carbohydrates posterior to the rumino-reticular area of the young bovine. J. Animal Sci. 15:473-484. 1956.

65. Lindsay, D.B. The significance of carbohydrate in ruminant metabolism. Vet. Res. and Annot. 5:104-128. 1959.

66. Lloyd, L.E., E.W. Crampton, and V.G. Mackay. The digestibility of ration nutrients by the three-vs. seven-week old pig. J. Animal Sci. 16:383-388. 1957.

67. Magee, D.F. and E.G. Anderson. Changes in pancreatic enzymes brought about by alteration in the nature of the protein diet. Am. J. Physiol. 181:79-82. 1955.

68. Marshall, R.A. The digestion of pentosans in hay by sheep. Brit. J. Nutr. 3:1-2. 1949.

69. McCandless, E.L. and J.A. Dye. Physiological changes in intermediary metabolism of various species of ruminants incident to functional development of the rumen. Am. J. Physiol. 162:434-446. 1950.

70. McCarthy, R.D. and E.M. Kesler. Relation between age of calf, blood glucose, blood and rumen levels of volatile fatty acids and in vitro cellulose digestion. J. Dairy Sci. 39:1280-1287. 1956.

71. Mendel, L.B. The alimentary enzymes of the embryo. Am. J. Physiol. 15:13-15. 1906.

72. Mitchell, H.S. Comparative physiological value of five carbohydrates, based on growth and fecal analysis. Am. J. Physiol. 79:537-541. 1927.

73. Morrison, W.J., L.S. Dietrich, and C.A. Elvehjem. Effect of different carbohydrates on chick growth. Brit. Abstr. A-III: Col. 924. 1951.

74. Naer, H. Amylolytic activity in the rumen of sheep. J. Agri. Res. 40:308-310. 1950.

75. Nelson, N. A photometric adaptation of the Somogyi method for the determination of glucose. J. Biol. Chem. 153: 375-380. 1944.

76. Netke, S.P., K.E. Gardner, and K.A. Kendall. Physiological responses of dairy calves to certain carbohydrates when added to a milk replacer diet. J. Dairy Sci. 43:892. 1960.

77. Noller, C.H., C.F. Huffman, G.M. Ward, and C.W. Duncan. Dried whey and lactose as supplements to vegetable milk replacers. J. Dairy Sci. 39:992-997. 1956.

78. _____, G.M. Ward, and C.F. Huffman. The relationship between growth of young calves and digestibility of nutrients in milk and vegetable milk replacers. Proc. Distiller's Feed Conf. 11:16-20. 1956.

79. _____, _____, A.D. McGilliard, C.F. Huffman, and C.W. Duncan. The effect of the age of the calf and availability of nutrients in vegetable milk replacer rations. J. Dairy Sci. 39:1288-1297. 1956.

80. Norris, L.C. The production of volatile fatty acids in the intestinal tract of calves fed whole milk or cereal gruel. Cornell Agri. Expt. Sta. Memoir 90. 1925.

81. Obara, J. and H. Watase. The effects of administration of some carbohydrates and fatty acids upon the blood glucose level of goats. The National Institute of Health. (Japan) 32:372-377. 1957.

82. Okomoto, M., J.W. Thomas, and T.L. Johnson. Utilization of various carbohydrates by young calves. J. Dairy Sci. 42:920. 1959.

83. O'Toole, J.J. and J.A. Dye. Utilization of fructose in the ruminant and non-ruminant. Rept. N.Y. State Vet. Coll. Cornell Univ. 1953-54:20-21. 1955.

84. Owen F.G. Interrelationships of lactose, lipids, and minerals in nutrient utilization by the calf. Unpublished Ph.D. Thesis. Library, Iowa State University of Science and Technology. Ames, Iowa. 1956.

85. Phaneuf, Louis-Phillipe. Studies on the secretory activity of the duodenum, pancreas and cecum of the sheep. Unpublished Ph.D. Thesis. Library, Cornell University. Ithaca, New York. 1957. (Original not available for examination; abstracted from Dissertation Abstr. 18: 1079. 1958.)

86. Phillipson, A.T. and R.A. McAnally. Studies on the fate of carbohydrates in the rumen of sheep. J. Exp. Biol. 19:199-214. 1942.

87. Plimmer, R.H.A. The presence of lactose in the intestines of animals and the adaptation of the intestine to lactase. J. Physiol. (London) 35:29-31. 1906-7.

88. Preston, T.R. The nutrition of young animals. Proc. Nutr. Soc. 17:63-71. 1958.

89. Ratcliff, L.R. Factors affecting nutrient utilization by dairy calves. Unpublished Ph.D. Thesis. Library, Iowa State University of Science and Technology. Ames, Iowa. 1948.

90. _____ and N.L. Jacobson. Use of corn distillers dried solubles and of enzymes in calf feeds. Proc. Distiller's Feed Conf. 12:22-27. 1957.

91. Raven, A.M., and K.L. Robinson. Studies of the nutrition of the young calf, a comparison of starch, lactose and hydrogenated palm oil, with butterfat, in milk diets. Brit. J. Nutr. 12:469-482. 1958.

92. _____ and _____. Studies of milk substitute diets for calves. I. The nutritional value of certain meal mixtures as compared with whole milk. Res. and Exp. Record, Ministry of Agri., Northern Ireland. 8:19-22. 1959.

93. Reid, R.L. Studies on the carbohydrate metabolism of sheep. Aus. J. Agri. Res. 9:788-796. 1958.

94. _____. Studies on the carbohydrate metabolism of sheep. III. The blood glucose during insulin hypoglycemia. Aus. J. Agri. Res. 2:132-145. 1951.

95. _____. Studies on the carbohydrate metabolism of sheep. V. Effect of hyperglycemia and of insulin on the rate of extrahepatic glucose assimilation. Aus. J. Agri. Res. 3:160-167. 1952.

96. _____. Studies on the carbohydrate metabolism of sheep. The uptake by the tissues of glucose and acetic acid from the peripheral circulation. Aus. J. Agri. Res. 1:338-354. 1950.

97. Riggs, L.K. and A. Beaty. Some unique properties of lactose as a dietary carbohydrate. J. Dairy Sci. 30:739-750. 1947.

98. Rojas, Jorge, B.S. Schweigert, and I.W. Rupel. The utilization of lactose by the dairy calf fed normal and modified milk diets. J. Dairy Sci. 31:81-87. 1948.

99. Ronning, M. and H.J. Benevenga. B-vitamin requirements of calves fed a high carbohydrate diet. J. Dairy Sci. 43:892.

100. Savage, E.S. and C.M. McCay. The nutrition of calves; A review. J. Dairy Sci. 25:595-650. 1942.

101. Schambye, P. Volatile acids and glucose in portal blood of sheep. 2. Sheep fed hay and hay plus crushed oats. Nord. Vet. Med. 3:748-762. 1951.

102. _____ and A.T. Phillipson. Volatile fatty acids in portal blood of sheep. Nature 164:1094. 1949.

103. Shaw, R.H., T.E. Woodward, and R.P. Norton. Digestion of starch by the young calf. J. Agri. Res. 12:575-578. 1918.

104. Somogyi, M. Determination of blood sugar. J. Biol. Chem. 160:69-73. 1945.

105. _____. Studies of arteriovenous differences in blood sugar. I. Effect of alimentary hyperglycemia on the rate of extrahepatic glucose assimilation. J. Biol. Chem. 174:189-200. 1948.

106. Sumner, J.B. and K. Myrback. The enzymes. Vol. I. Academic Press Inc., New York. 1951.

107. Trevelyan, W.E., D.P. Procter, and J.S. Harrison. Detection of sugars on paper chromatograms. Nature 166:444-445. 1950.

108. Uchino, S. and M. Mori. Supplementary researches on the enzyme actions of cow intestinal mucosa. J. Japan. Soc. Food Nutr. 3:105-107. 1951. (Original not available for examination; abstracted from Chem. Abstr. 48:3512. 1954.)

109. Van Poucke, R.F., F.W. Hill, R.A. Quercher, and N.E. Rodgers. Studies on the value of whey products in early calf nutrition. J. Animal Sci. 6:491. 1947.

110. Velu, J.G., K.A. Kendall, and K.E. Gardner. Utilization of various sugars by the young dairy calf. J. Dairy Sci. 43:546-552. 1960.

111. Vonk, H.J. The specificity and collaboration of digestive enzymes in Metazoa. Biol. Revs. Cambridge Phil. Soc. 12:245-284. 1937.

112. Walker, D.M. The development of the digestive enzyme system of the young animal. II. Carbohydrase enzyme development in the young pig. J. Agri. Sci. 52: 357-363. 1959.

113. _____. The development of the digestive system of the young animal. III. Carbohydrase enzyme development in the young lamb. J. Agri. Sci. 53:374-380. 1959.

114. Wallace, H.D., J.K. Loosli, and K.L. Turk. Substitutes for fluid milk in feeding dairy calves. J. Dairy Sci. 34:256-264. 1951.

115. Weise, A.C., B.C. Johnson, H.H. Mitchell, and W.B. Nevens. Synthetic rations for the dairy calf. J. Dairy Sci. 30:87-94. 1947.

116. Weller, R.A. and F.V. Gray. The passage of starch through the stomach of the sheep. J. Exp. Biol. 31:40-48. 1954.

117. Wilbur, R.D., D.V. Catron, L.Y. Quinn, V.C. Speer, and V.W. Hays. Intestinal flora of the pig as influenced by diet and age. J. Nutr. 71:169-175. 1960.

118. Williams, J.B. and C.B. Knodt. The supplementation of milk replacements with enzymes and other products. J. Animal Sci. 10:975-980. 1951.

119. Wishnofsky, M. and A.P. Kane. The effect of equivalent amounts of dextrose and starch on glycemia and glycosuria in diabetics. Am. J. Med. Sci. 189:545-550. 1935.

120. Yonge, C.M. Evolution and adaptation in the digestive enzyme system of the metazoa. Biol. Revs. 11:87-115. 1937.

121. Young, F.B. Response of dairy calves to whole milk replacements containing dried whey product. J. Dairy Sci. 36:600. 1953.

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APPENDIX

Table 12. Descriptive data for animals employed in this study

Experiment number		Breed	Sex	Date of birth
1	4483	Holstein	Male	6-6-57
	4491	Holstein	Male	6-21-57
	4507	Holstein	Male	7-8-57
	4524	Holstein	Male	8-21-57
	4723	Ayrshire	Male	10-19-58
	4725	Brown Swiss	Male	10-21-58
	4728	Brown Swiss	Male	11-1-58
	4734	Holstein	Female	11-18-58
	4735	Holstein	Female	11-19-58
	4753	Holstein	Male	12-31-59
	4755	Holstein	Male	1-6-59
	4772	Holstein	Male	2-24-59
	4777	Brown Swiss	Female	3-3-59
	4810	Holstein	Male	6-8-59
	4811	Holstein	Male	6-9-59
	4818	Holstein	Female	7-9-59
	4819	Holstein	Female	7-10-59
	4864	Brown Swiss	Female	10-4-59
	4865	Brown Swiss	Female	10-4-59
	4888	Holstein	Male	11-7-59
	4889	Holstein	Male	11-8-59
	4900	Holstein	Male	12-11-59
	6033	Holstein	Male	12-11-59
2	4850	Brown Swiss	Male	8-26-59
	4851	Brown Swiss	Male	8-28-59
	4857	Holstein	Male	9-11-59
	4858	Holstein	Male	9-11-59

Table 13. Herd numbers of individual animals in blood reducing sugar study[a] (Experiment 1)

Mean age (days)	Treatment								
	Control	Glucose	Lactose	Maltose	Sucrose	Amylose	Amylo-pectin	Flojel	Tapioca
Group A 22	4818	4810	4810	4818	6033	4818	4810	4818	4818
	4819	4811	4811	4819	4900	4819	4811	4819	4819
	4900	4864	4864	4888	4818	4888	4864	4888	4888
	6033	4865	4865	4889	4819	4889	4865	4889	4889
					4888				
					4889				
Group B 50	4810	4818	4818	4810	4810	4864	4818	4810	4810
	4811	4819	4819	4811	4811	4865	4819	4811	4811
	4864	4888	4888	4864	4818	4810	4888	4864	4864
	4865	4889	4889	4865	4819	4811	4889	4865	4865
					4864				
					4865				
Group C 136	4753	4725	4725	4725	4725	4725	4725	4725	4725
	4755	4728	4728	4728	4728	4728	4728	4728	4728
		4753	4753	4734	4753	4753	4753	4753	4753
		4755	4755	4735	4755	4755	4755	4755	4755
				4755					
				4753					
Group D 227	4723	4723	4723	4723	4723	4723	4723	4723	4723
	4728	4728	4728	4728	4728	4728	4728	4728	4728
	4772	4772	4772	4772	4772	4772	4772	4772	4772
	4777	4777	4777	4777	4777	4777	4777	4777	4777
Group E 600	4507	4507	4507	4507	4507	4507	4507	4507	4507
	4483	4483	4483	4483	4483	4483	4483	4483	4483
	4491	4524	4524	4524	4524	4524	4524	4524	4524
	4524	4491	4491	4491	4491	4491	4491	4491	4491

[a]Positions of animals herein correspond to the respective blood reducing sugar values presented in Tables 15 and 16 of the Appendix.

Table 14. Blood reducing sugar levels after carbohydrate ingestion (Experiment 1)

Treatment	Mean age (days)	Hours after ingestion							
		0	0.5	1.0	1.5	2.0	3.0	5.0	8.0
		mg.%							
Control	20	91	88	84	79	81	79	73	72
	50	77	78	74	71	69	69	67	63
	136[a]	57	56	56	58	59	58	57	53
	227	68	67	64	63	63	60	61	59
	600	54	55	57	58	60	58	58	62
Glucose	20	69	123	174	194	176	147	114	52
	50	65	141	182	168	163	143	104	55
	136	60	83	119	136	129	102	85	55
	227	61	104	127	143	126	108	88	60
	600	58	74	89	97	93	92	67	49
Lactose	20	76	142	209	199	199	150	142	68
	50	75	145	186	154	130	116	112	80
	136	60	70	88	87	80	72	81	58
	227	63	76	90	95	94	91	79	67
	600	52	61	59	64	59	61	56	56
Maltose	20	88	106	106	108	105	99	84	87
	50	72	123	138	133	110	81	65	62
	136[b]	52	68	82	79	74	69	60	57
	227	56	66	79	87	80	65	69	60
	600	50	58	59	65	62	55	55	53
Sucrose	20[b]	88	79	81	89	92	87	83	77
	50[b]	67	64	64	69	68	67	64	62
	136	50	52	54	48	56	51	55	54
	227	64	65	67	67	72	72	61	63
	600	51	49	51	53	57	61	54	55
Amylose	20	90	82	82	79	83	82	80	82
	50	75	77	81	76	77	76	75	72
	136	52	57	59	61	61	56	56	51
	227	64	66	68	72	69	68	60	62
	600	46	49	52	51	52	53	56	50
Amylopectin	20	73	71	72	72	70	67	62	67
	50	67	71	70	71	74	67	70	65
	136	51	56	56	51	50	53	51	48
	227	59	64	65	63	65	64	60	58
	600	51	53	54	54	53	53	59	52

[a]These values are the means of 2 animals.

[b]These values are the means of 6 animals. All other values (except those cited in a and c) are the means of 4 animals.

Table 14 (Continued)

Treatment	Mean age (days)	Hours after ingestion							
		0	0.5	1.0	1.5	2.0	3.0	5.0	8.0
		mg.%							
Flojel	20	77	76	76	73	73	71	71	71
	50	67	68	69	67	66	65	61	56
	136	49	55	53	52	53	55	54	49
	227	69	70	74	73	71	68	68	69
	600	47	52	54	56	54	56	59	53
Tapioca	20	84	84	84	80	79	77	73	70
	50	76	77	74	73	72	74	75	68
	136	51	55	56	55	54	51	52	51
	227	59	66	66	62	60	59	56	58
	600	51	53	54	56	55	53	53	52
Glucose placed in the rumen	59	70	85	74	69	76	59	52	54
	98[c]	65	78	78	76	72	65	56	58
	560	60	75	61	55	52	53	55	51

[c]These values are the means of 5 animals.

Table 15. Maximum increase in blood reducing sugar after carbohydrate ingestion[a] (Experiment 1)

Mean age (days)	Treatment: Control	Glucose	Lactose	Maltose	Sucrose	Amylose	Amylo-pectin	Flojel	Tapioca
					mg.%				
Group A									
22	0	98.2	94.4	33.2	0	0	0	4.8	3.5
	0	172.1	107.5	21.6	6.6	0	5.1	0	0
	0	165.1	207.7	26.6	8.8	0.9	0	0	0
	3.2	101.8	181.1	40.7	13.5	1.5	1.7	1.2	4.7
					12.7				
					6.7				
Average	0.8	134.3	147.7	30.5	8.1	0.6	1.7	1.5	2.1
Group B									
50	4.1	105.2	119.3	65.0	4.2	14.6	9.1	0	5.2
	0.6	108.4	38.3	81.3	25.4	2.6	3.8	0	0
	5.2	170.3	137.1	74.9	0	9.7	10.9	17.0	4.4
	0	134.1	172.6	68.5	11.2	5.3	7.3	6.6	9.6
					2.0				
					0				
Average	2.5	129.5	116.8	72.4	7.1	8.1	7.8	5.9	4.8
Group C									
136	3.2	60.7	22.7	27.6	7.1	8.7	8.7	3.3	5.5
	4.6	84.7	45.2	28.0	7.0	10.2	7.3	14.9	0
	-	65.5	22.4	23.8	7.8	15.8	5.3	3.5	11.2
	-	91.9	53.3	41.7	8.4	12.7	8.0	9.0	7.2
				27.7					
				32.3					
Average	3.9	76.4	35.8	30.2	7.6	11.9	7.3	7.7	6.0

[a] Position of values herein correspond to the respective animals listed in Table 13 of the Appendix.

Table 15 (Continued)

Mean age (days)	Control	Glucose	Lactose	Maltose	Sucrose	Amylose	Amylo-pectin	Flojel	Tapioca
				Treatment					
				mg.%					
Group D									
227	0.5	62.5	33.1	25.0	17.0	11.7	5.0	5.3	4.7
	0	68.2	25.8	39.6	13.0	0	9.5	4.8	6.9
	0	71.4	27.8	17.1	4.1	8.9	7.7	8.9	14.2
	2.0	126.7	62.8	55.4	8.1	17.4	17.9	18.9	11.9
Average	0.8	82.4	37.4	34.3	10.7	9.5	10.0	9.5	9.4
Group E									
600	15.4	64.7	11.6	14.3	9.7	13.5	12.2	9.8	8.5
	8.0	36.3	21.6	12.0	7.4	7.5	8.0	17.5	3.5
	5.3	53.8	10.6	17.5	7.1	10.6	11.1	12.4	6.9
	10.0	45.8	11.6	24.1	19.5	19.2	13.3	25.9	11.8
Average	9.7	50.2	13.8	17.0	10.9	12.7	11.2	16.4	7.7

Table 16. Mean change in blood reducing sugar after carbohydrate ingestion[a] (Experiment 1)

Mean age (days)	Treatment: Control	Glucose	Lactose	Maltose	Sucrose	Amylose	Amylo-pectin	Flojel	Tapioca
					mg.%				
Group A									
22	-28.3	39.3	42.9	10.6	-8.7	-28.6	-5.9	-4.6	-3.2
	-5.0	116.0	92.7	9.1	0.7	-6.3	1.7	-6.2	-8.9
	-11.9	88.0	109.5	11.1	1.5	-1.0	-8.7	1.4	-8.2
	-2.1	66.5	101.1	11.3	4.1	-0.2	-7.9	-6.7	-5.3
					-11.8				
					1.4				
Average	-11.8	77.5	86.6	10.5	-2.1	-9.0	-5.2	-4.0	-6.4
Group B									
50	-12.7	37.9	55.2	27.0	-1.2	1.7	6.2	-8.4	-5.2
	-9.7	74.6	22.8	37.2	6.7	-1.6	-3.2	-7.5	-9.2
	-1.0	143.3	78.8	19.9	-6.8	3.9	3.5	5.7	-0.9
	-5.1	57.3	55.0	11.5	1.4	-1.2	4.5	3.8	6.1
					-3.2				
					-6.1				
Average	-7.1	78.3	53.0	23.9	-1.5	0.7	2.8	-1.6	-2.3
Group C									
136	0.3	19.2	9.3	14.5	2.9	3.0	-1.4	1.1	2.3
	0.1	48.8	22.7	14.8	4.4	5.6	3.0	10.9	-5.3
		43.6	9.7	15.4	2.3	7.2	1.5	0.5	5.3
		68.7	33.7	21.5	4.2	8.2	5.3	4.0	6.0
				20.1					
				17.9					
Average	0.2	45.1	18.9	17.4	3.5	6.0	2.1	4.1	2.1

[a]Position of values herein correspond to the respective animals listed in Table 13 of the Appendix.

Table 16 (Continued)

Mean age (days)	Control	Glucose	Lactose	Maltose	Sucrose	Amylose	Amylo-pectin	Flojel	Tapioca
				Treatment					
					mg.%				
Group D									
227	-7.2	37.7	14.2	14.4	5.4	7.0	2.3	-1.1	1.1
	-7.4	42.7	16.9	16.8	3.4	5.7	5.1	0.8	5.9
	-3.2	26.8	20.0	1.2	-0.7	-9.2	2.5	-5.6	2.1
	-4.5	89.8	45.2	31.7	1.6	7.1	8.9	13.3	0.9
Average	-5.6	49.3	24.1	64.1	2.4	2.7	4.7	1.9	1.5
Group E									
600	9.1	37.1	-1.9	10.1	3.3	7.7	0.2	5.4	1.5
	1.7	24.5	19.6	-2.2	2.4	4.1	2.3	7.3	0.7
	1.5	18.3	8.9	12.3	3.2	7.5	8.6	6.1	-2.7
	2.1	29.5	5.3	9.7	8.6	9.4	8.0	13.8	7.8
Average	3.6	27.4	8.0	7.5	4.4	7.2	4.8	8.2	1.8

Table 17. Analysis of variance of maximum increase in blood reducing sugar after carbohydrate ingestion at various ages (Experiment 1)

Treatment	Source of variation	d.f.	Sum of squares	Mean square	Std. error of the mean	Diff. required for significance ($P < .05$)
Glucose	Total	19	32,311			
	Age	4	21,015	5,254		
	Error	15	11,296	753	13.7	45.3
Lactose	Total	19	75,050			
	Age	4	54,463	13,616		
	Error	15	20,587	1,372	18.5	61.2
Maltose	Total	21	8,278			
	Age	4	6,782	1,696		
	Error	17	1,496	88.1	4.7	15.4
Sucrose	Total	23	846			
	Age	4	30	7.5		
	Error	19	816	42.9	3.3	10.7
Amylose	Total	19	715			
	Age	4	271	67.8		
	Treatment	15	444	29.6	2.7	8.9
Amylo-pectin	Total	19	373			
	Age	4	213	53.3		
	Treatment	15	160	10.7	1.6	5.3
Flojel	Total	19	1,056			
	Age	4	477	119		
	Error	15	579	38.6	3.1	10.3
Tapioca	Total	19	349			
	Age	4	127	31.8		
	Error	15	222	14.8	1.9	6.3
Control	Total	17	336			
	Age	4	225	56.3		
	Error	13	101	7.8	1.4	4.7

Table 18. Analysis of variance of maximum increase in blood reducing sugar after carbohydrate ingestion--comparison between treatments (Experiment 1)

Group	Mean age (days)	Source of variation	d.f.	Sum of squares	Mean square	Std. error of the mean	Diff. required for significance ($P < .05$)
A	22	Total	37	126,461			
		Treatment	8	112,178	14,022		
		Error	29	14,283	492	7.8	26.0
B	50	Total	37	96,375			
		Treatment	8	82,947	10,368		
		Error	29	12,428	429	7.3	24.3
C	136	Total	35	19,806			
		Treatment	8	17,917	2,240		
		Error	27	1,889	70	3.0	10.0
D	227	Total	35	25,796			
		Treatment	8	20,825	2,603		
		Error	27	4,971	184	4.7	15.7
E	600	Total	35	6,383			
		Treatment	8	5,353	669		
		Error	27	1,030	38	2.2	7.3

Table 19. Analysis of variance of mean change in blood reducing sugar after carbohydrate ingestion at various ages (Experiment 1)

Treatment	Source of variation	d.f.	Sum of squares	Mean square	Std. error of the mean	Diff. required for significance ($P < .05$)
Glucose	Total	19	21,005			
	Age	4	7,762	1,941		
	Error	15	13,243	883	14.8	49.0
Lactose	Total	19	21,696			
	Age	4	16,163	4,041		
	Error	15	5,533	369	9.6	31.8
Maltose	Total	21	1,623			
	Age	4	624	156		
	Error	17	999	58.8	3.8	12.5
Sucrose	Total	23	402			
	Age	4	9.0	2.3		
	Error	19	393	20.7	2.3	7.5
Amylose	Total	19	1,432			
	Age	4	660	165.0		
	Error	15	772	51.5	3.6	11.9
Amylo-pectin	Total	19	491			
	Age	4	269	67.3		
	Error	15	222	14.8	1.9	6.3
Flojel	Total	19	879			
	Age	4	364	91		
	Error	15	515	34.3	2.9	9.6
Tapioca	Total	19	535			
	Age	4	215	53.8		
	Error	15	320	21.3	2.3	7.6
Control	Total	17	1,137			
	Age	4	592	148		
	Error	13	545	41.9	3.2	10.7

Table 20. Analysis of variance of mean change in blood reducing sugar after carbohydrate ingestion--comparison between treatments (Experiment 1)

Group	Mean age (days)	Source of variation	d.f.	Sum of squares	Mean square	Std. error of the mean	Diff. required for significance ($P < .05$)
A	22	Total	37	53,235			
		Treatment	8	46,094	5,762		
		Error	29	7,140	246	5.5	18.4
B	50	Total	37	36,213			
		Treatment	8	27,388	3,424		
		Error	29	8,825	304	6.2	20.8
C	136	Total	35	8,392			
		Treatment	8	6,502	813		
		Error	27	1,890	70	3.0	10.1
D	227	Total	35	13,050			
		Treatment	8	9,165	1,146		
		Error	27	3,885	144	4.2	14.1
E	600	Total	35	2,168			
		Treatment	8	1,826	228		
		Error	27	792	29.3	1.9	6.4

Table 21. Blood reducing sugar levels after ingestion of starches subjected to various heat treatments[a] (Experiment 1)

Starch treatment	Kind of starch	Hours after administration of carbohydrate							
		0	0.5	1.0	1.5	2.0	3.0	5.0	8.0
		mg.%							
Untreated	Amylose	64	66	68	72	69	68	60	62
	Amylopectin	59	64	65	63	65	64	60	58
	Flojel	69	70	74	73	71	68	68	69
	Tapioca	59	66	66	62	60	59	56	58
Jelled	Amylopectin	56	63	67	66	64	60	52	55
	Flojel	57	61	66	69	69	64	58	58
	Tapioca	61	70	75	73	71	64	57	60
Autoclaved in dry form	Amylose	61	66	71	70	75	71	80	80
	Amylopectin	58	68	66	68	68	62	59	58
	Flojel	58	63	64	67	63	59	62	61
	Tapioca	63	69	72	71	67	65	60	59
Autoclaved in suspension	Amylose	61	69	74	77	75	70	61	64
	Amylopectin	58	66	72	71	72	69	57	56
	Flojel	65	66	72	71	73	65	62	60
	Tapioca	58	66	69	68	73	70	58	53

[a]Each value is the mean of 4 animals. See Table 7 for an explanation of the different treatments.

Table 22. Effect of heat treatment of starch upon blood reducing sugar response[a] (Experiment 1)

Animal number	Kind of starch	Untreated	Jelled	Autoclaved in dry form	Autoclaved in suspension
		mg.%			
		Maximum increase			
4723	Amylose	11.7		31.6	9.6
4728		8.9		38.5	15.9
4772		0		17.7	22.0
4777		17.4		24.4	26.8
	Average	9.5		28.1	18.6
4723	Amylopectin	5.0	17.7	7.3	10.1
4728		9.5	16.5	9.1	7.8
4772		7.7	4.4	10.1	16.0
4777		17.9	12.9	22.0	29.5
	Average	10.0	12.9	12.1	15.9
4723	Flojel	5.3	12.1	9.6	3.2
4728		4.8	14.1	9.6	1.0
4772		8.9	12.7	15.8	17.5
4777		18.9	18.0	6.2	20.7
	Average	9.5	14.2	10.3	10.6
4723	Tapioca	4.7	17.8	1.9	5.6
4728		6.9	20.5	12.1	14.4
4772		14.2	14.2	20.0	13.0
4777		11.9	11.9	8.6	33.0
	Average	9.4	16.1	10.7	16.5
		Mean change			
4723	Amylose	7.0		12.6	1.6
4728		5.7		17.3	7.8
4772		-9.2		7.9	14.3
4777		7.1		10.1	12.5
	Average	2.7		12.0	9.1
4723	Amylopectin	2.3	12.0	0.1	2.2
4728		5.1	6.2	4.7	0.6
4772		2.5	-2.5	4.0	6.8
4777		8.9	5.7	15.8	25.4
	Average	4.7	5.4	6.2	8.8
4723	Flojel	-1.1	4.0	6.7	-2.9
4728		0.8	7.0	3.9	-0.2
4772		-5.6	4.9	9.3	3.5
4777		13.3	11.8	0.8	7.4
	Average	1.9	6.9	5.0	2.0
4723	Tapioca	-2.1	5.6	-5.2	0.1
4728		0.9	8.2	7.0	4.9
4772		1.1	1.1	5.3	5.6
4777		5.9	5.9	5.7	24.0
	Average	1.5	5.2	3.2	8.7

[a]See Table 7 for an explanation of the different treatments.

Table 23. Weight changes of animals during digestibility study (Experiment 2)

Animal number	Experimental periods[a]									Av. daily gain (by animal)	Av. daily gain (by treatment)	
	1	2	3	4	5	6	7	8	9			
	lbs.											
4850	138	157	170	192	223	252	264	306		2.1	Control	2.4
											Lactose	2.3
4851	188	204	227	246	270	280	300	336	378	2.1	Maltose	1.5
											Sucrose	1.9
4857	176	178	196	216	239	257	275	293	322	1.6	Amylose	1.9
											Amylopectin	2.0
4858	190	202	220	249	270	276	296	326	372	2.0	Flojel	2.0
											Tapioca	1.9
									Average	2.0		

[a]Each experimental period was of 10 days duration. However, several times between periods animals were taken off treatment for one or two days.

Table 24. Weight of feces voided during the 5-day collection period of the digestibility study (Experiment 2)

Treatment	Animal 4850 Wet wt.	4850 Dry wt.	4851 Wet wt.	4851 Dry wt.	4857 Wet wt.	4857 Dry wt.	4858 Wet wt.	4858 Dry wt.	Average Wet wt.	Average Dry wt.	% dry matter
	kg.										
Control	11.7	2.81	31.2	6.24	18.6	4.13	19.7	3.92	20.3	4.28	21.1
Lactose	18.3	3.64	32.0	5.17	24.1[a]	4.10[a]	31.1	5.78	26.4	4.67	17.7
Maltose	19.7	4.11	38.6[a]	6.84[a]	21.1	3.71	21.2	4.13	25.2	4.70	18.2
Sucrose	51.6	9.43	45.3	7.12	28.4	5.03	38.7[a]	6.97[a]	41.0	7.14	17.3
Amylose	20.1	4.45	32.0	6.08	16.4	3.55	28.0	5.86	24.1	4.99	20.7
Amylopectin	15.9	3.20	45.4	8.72	22.5	4.50	22.1	4.81	26.5	5.31	20.0
Flojel	19.9	4.43	24.6	4.52	29.8	6.40	26.4	5.96	25.2	5.33	21.0
Tapioca	23.0	5.40	33.2	5.61	17.6	3.71	22.3	4.66	24.0	4.85	20.2
Average	22.5	4.68	35.3	6.29	22.3	4.39	26.2	5.26			

[a]Average of two periods (all other values are for one period).

Table 25. Dry matter content of diurnal feces samples collected during the digestibility study[a] (Experiment 2)

Treatment	Hour of the day												
	7a.m.[b]	9	11	1p.m.	3	5[b]	7	9	11	1a.m.	3	5	7
	% dry matter												
Control	20.2	21.4	23.0	21.4	21.8	21.4	20.3	21.0	21.1	21.1	21.4	20.9	20.9
Lactose	20.0	21.2	21.3	19.8	19.8	18.1	20.6	20.4	20.9	19.0	18.2	20.3	20.1
Maltose	18.0	17.5	16.9	18.4	15.0	16.3	18.8	17.9	17.2	15.4	15.0	16.1	18.8
Sucrose	17.3	18.5	14.3	13.5	14.2	12.5	14.4	14.3	13.1	13.1	13.7	15.1	18.1
Amylose	20.5	19.9	20.4	20.9	21.3	19.8	19.0	19.0	20.5	20.4	19.6	19.1	18.6
Amylo-pectin	19.0	18.9	20.0	20.6	21.0	21.0	20.2	20.7	21.0	20.7	20.3	19.8	20.3
Flojel	19.8	19.9	20.0	20.8	21.3	21.6	20.0	20.4	19.8	20.4	19.9	19.5	19.4
Tapioca	19.9	19.9	19.4	20.2	21.7	21.4	20.2	19.7	19.2	20.3	19.4	19.5	19.3

[a]Samples were taken at 2-hour intervals during the last 24 hours of each collection period.

[b]Time of feeding milk (containing carbohydrate) by nipple pail.

Table 26. Blood reducing sugar levels after carbohydrate ingestion via the milk[a] (Experiment 2)

Treatment	Hours after ingestion						
	0	1.0	2.0	3.0	4.0	6.0	8.0
	mg.%						
Control	67	85	71	60	62	66	71
Lactose	64	101	89	75	61	62	67
Maltose	67	114	87	75	66	65	66
Sucrose	64	76	64	62	65	65	63
Amylose	69	95	87	81	78	71	70
Amylopectin	68	87	79	75	67	70	69
Flojel	64	89	71	65	64	66	66
Tapioca	68	89	81	68	72	68	72

[a]Whole milk was fed in all rations; the lactose contained therein was equivalent to 0.35 g. per pound body wt. of animal daily. Supplemental carbohydrate was fed at a level of 0.7 g. per pound body wt. Each value is the mean of 4 animals.

Table 27. Analysis of variance of blood reducing sugar levels after carbohydrate ingestion via the milk (Experiment 2)

Source of variation	d.f.	Sum of squares	Mean square	Std. error of mean	Diff. required for significance ($P < .05$)
		Maximum increase			
Total	31	6311			
Animal	3	344	113		
Treatment	7	3159	451		
Error	21	2808	133.7	4.4	14.7
		Mean change			
Total	31	1250			
Animal	3	154	51		
Treatment	7	742	106		
Error	21	354	16.9	1.6	5.4

Table 28. Analysis of variance of percent carbohydrate recovery (Experiment 2)

Treatment	Source of variation	d.f.	Sum of squares	Mean square	Std. error of the mean
Lactose	Total	19	985		
	Animal	3	969	323	
	Error	16	26	1.6	1.3
Maltose	Total	19	70.2		
	Animal	3	24.9	8.3	
	Error	16	45.3	2.8	1.7
Sucrose	Total	19	6638		
	Animal	3	4279	1426	
	Error	16	2359	147	12.2
Amylose	Total	19	769		
	Animal	3	364	121	
	Error	16	405	25.3	5.0
Amylopectin	Total	19	1226		
	Animal	3	61	20.3	
	Error	16	1165	72.8	8.5
Flojel	Total	19	2236		
	Animal	3	760	253	
	Error	16	1476	92.3	9.6
Tapioca	Total	19	3136		
	Animal	3	1849	616	
	Error	16	1287	80.4	9.0

Table 29. Pentosan voided in the feces during digestibility study[a] (Experiment 2)

Treatment	Animal 4850	4851	4857	4858	Average
	g. per day				
Control	45.2	100.8	61.6	44.0	62.9
Amylose	58.3	39.2	30.9	85.0	53.3
Amylopectin	55.9	142.6	55.8	21.7	69.0
Flojel	80.5	72.6	100.4	59.7	78.3
Tapioca	62.7	74.1	16.9	67.1	55.2
Average	60.5	85.9	53.1	55.5	63.7

[a]Chromatographic examination of feces extract following acid hydrolysis showed a very prominent spot which corresponded best to that obtained from xylose. Each value is the mean of a 5-day period.

Table 30. Carbohydrate content of diurnal feces samples collected during the digestibility study[a] (Experiment 2)

Animal number	Hour of the day												
	7a.m.[b]	9	11	1p.m.	3	5[b]	7	9	11	1a.m.	3	5	7
	%												
Lactose													
4850	-	-	-	-	1.3	2.2	2.1	-	-	1.1	2.2	1.3	-
4851	1.3	1.2	1.6	10.7	11.3	12.3	4.6	2.7	c	13.3	13.3	3.8	2.6
4857	-	-	-	-	1.0	2.1	-	-	5.5	2.0	2.4	-	-
4858	1.1	-	-	-	-	4.1	2.4	0.6	-	-	0.9	-	0.3
Av.	0.6	0.3	0.4	2.7	3.4	5.2	2.3	0.8	1.8	4.1	4.7	1.3	0.7
Maltose													
4850	-	-	-	0.3	2.1	2.1	0.1	-	-	0.4	2.0	0.8	-
4851	-	-	-	-	3.5	2.5	-	-	2.0	4.0	3.1	-	-
4857	-	-	-	1.2	5.9	2.3	3.5	2.7	6.6	6.7	5.5	-	-
4858	2.4	1.3	-	-	4.5	2.0	-	-	-	5.8	6.6	6.8	4.0
Av.	0.6	0.3	-	0.4	4.0	2.2	0.9	0.7	2.2	4.2	4.3	1.9	1.0
Sucrose													
4850	-	-	27.2	29.0	12.7	0.6	-	9.4	29.6	22.1	-	-	-
4851	-	-	9.9	76.7	53.0	38.8	30.0	13.9	53.1	26.0	21.4	16.1	-
4857	-	-	10.5	28.2	37.3	24.3	8.7	-	-	24.0	33.7	17.2	7.9
4858	1.3	0.6	2.6	38.3	50.8	52.4	31.6	c	40.9	44.7	33.4	6.2	0.3
Av.	0.3	0.2	12.5	43.1	38.4	29.0	17.6	7.8	30.9	29.2	22.1	9.9	2.1
Amylose													
4850	2.9	3.2	-	-	5.0	4.7	7.5	6.6	1.5	-	5.1	9.3	9.2
4851	4.7	-	-	-	-	4.7	9.2	9.0	0.3	7.9	10.8	7.2	5.1
4858	4.8	2.9	-	-	-	9.7	13.4	11.4	9.1	6.5	19.3	16.0	8.9
Av.	4.1	2.0	-	-	1.7	6.4	10.0	9.0	3.7	4.8	11.7	10.8	7.7

[a]Samples were taken at 2-hour intervals during the last 24 hours of the collection period. Blanks indicate carbohydrate was too low to measure.

[b]Time of feeding milk (containing carbohydrate) by nipple pail.

[c]No sample.

Table 30 (Continued)

Animal number	7a.m.[b]	9	11	1p.m.	3	5[b]	7	9	11	1a.m.	3	5	7
	Hour of the day												
	%												
Amylopectin													
4850	c	7.8	8.4	6.1	7.9	9.9	3.6	3.1	-	-	6.6	12.8	11.6
4857	0.3	-	-	-	-	5.1	19.0	9.2	-	-	9.5	13.0	7.3
4858	5.8	-	4.3	-	-	6.5	9.5	11.1	7.0	3.6	4.9	12.4	6.4
Av.	3.1	2.6	4.2	2.0	2.6	7.2	10.7	7.8	2.3	1.2	6.8	12.6	8.4
Flojel													
4850	7.4	5.4	3.9	4.8	-	3.4	5.1	7.8	-	-	4.6	8.9	9.0
4857	-	-	-	-	-	15.8	21.1	11.4	-	-	13.1	10.3	-
4858	1.7	3.7	-	-	0.3	2.9	23.0	15.8	5.0	-	5.9	18.3	13.6
Av.	3.0	3.0	1.3	1.6	0.1	7.4	16.4	11.7	1.7	-	7.9	12.5	7.5
Tapioca													
4850	9.7	8.3	-	5.8	5.4	18.5	14.6	14.7	-	-	10.9	14.9	11.6
4851	-	-	-	-	17.4	25.0	24.1	2.2	7.2	29.5	13.3	4.6	3.6
4857	10.2	5.5	-	-	-	10.4	18.7	19.7	3.1	1.8	7.8	9.2	5.7
Av.	6.6	4.6	-	1.9	7.6	18.0	19.1	12.2	3.5	10.4	10.7	9.6	7.0
Av. of all starches													
	4.2	3.3	1.4	1.4	3.0	9.8	14.1	10.2	2.8	4.1	8.8	11.4	7.7

Table 31. Monosaccharide content of carbohydrate voided in diurnal feces samples during the digestibility study[a] (Experiment 2)

Animal number	Treatment				
	Sucrose	Amylose	Amylopectin	Flojel	Tapioca
	%				
4850	48.3	21.1	26.2	20.3	29.2
4851	49.2	4.8	No sample[b]	No sample[b]	34.3
4857	28.0	No sample[b]	44.6	25.9	28.8
4858	26.5	36.3	43.1	20.7	No sample[b]
Average	38.0	20.7	38.0	22.3	30.8

[a]Diurnal samples were immediately placed in a freezer after being voided while recovery samples were allowed to accumulate in the pan for 12 hours prior to freezing. Each value is the average monosaccharide content of carbohydrate in all diurnal samples from 4 animals.

[b]Diurnal sampling was begun after these treatments had been completed.