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Utilization of glucose and sucrose by the weanling pig

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UTILIZATION OF GLUCOSE AND SUCROSE BY THE WEANLING PIG

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Utilization of glucose and sucrose by the weanling pig

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GENERAL INTRODUCTION

The economic return in swine production is closely related to the feed cost, which is primarily associated with the dietary protein and energy. It is desirable, in order to optimize production, to get a better understanding of the processes involved in the utilization of these dietary components.

The metabolism of an animal is the sum total of a number of integrated processes, and there is no real separation between energy and protein metabolism. Protein can be used for energy purposes, while the carbon skeletons of carbohydrates and fats may be used to synthesize nonessential amino acids. The incorporation of amino acids into body proteins requires energy, and carbohydrates can spare nitrogen by supplying energy needed for metabolism (Fuller and Crofts, 1977; Helland, 1979).

The ultimate efficiency by which a feedstuff is utilized is considered to be under the control of a network of endocrine functions, of which insulin may have a central position. The release of insulin is strongly influenced by the nature of the dietary carbohydrates. When an oral glucose tolerance test was administered to Yucatan miniature swine, Crump (1983) found the mean insulin concentration over four hours to be 3.5 ng/ml. An equimolar dose of fructose elicited only a mean response of .8 ng/ml. Oral

glucose tolerance tests with humans gave higher plasma insulin levels than when fructose or sucrose was used (Macdonald et al., 1978; Bohannon et al., 1980). Fructose stimulated insulin secretion least. Bruckdorfer and Yudkin (1975) compared dietary sucrose and corn starch in pigs fed ad libitum for 12 months. They found no differences in plasma insulin concentrations measured monthly. The lack of differences in the insulin response to dietary carbohydrates could be related to the feeding regime and infrequency of blood sampling. Sucrose and starch may not cause any differences in insulin secretion in pigs. Most of the reported information about the effect of carbohydrates on insulin secretion has come from oral tolerance tests, which may not reflect a meal-fed situation, where the insulin secretion is influenced by several other dietary components.

Sleder et al. (1980) measured plasma insulin levels in rats fed diets containing 12% lard, 22% casein, and either 66% glucose or fructose. They found significantly higher plasma insulin concentrations in rats fed the diet containing fructose. Perfusions of rat pancreas with pharmacological amounts of fructose (300 mg/ml) did not elicit any insulin response (Curry et al., 1972), while 150 mg/ml glucose did promote insulin secretion. The greatest insulin secretion was, however, obtained when 150 mg/ml glucose was perfused together with 300 mg/ml fructose.

A variety of evidence suggests that insulin is an anabolic hormone that affects the metabolism of both fat and protein. Christensen and Goel (1972) incubated slices of porcine adipose tissue and demonstrated a dose response to insulin on the conversion of glucose into fatty acids. Campion et al. (1979) studied the incorporation of L-leucine into protein in pig adipocytes and found a significant increase (16 to 36%) in protein synthesis when insulin (500 μU/ml) was present. Pozefsky et al. (1969) demonstrated a decrease in the postabsorptive release of amino acids from muscle when insulin was added in vivo. Insulin has also been shown, in vivo, to inhibit the turnover of valine in the liver (Mortimore and Mondon, 1970). No information is available, however, on the effect of insulin in vivo on protein metabolism in the fed state.

Gross energy (GE) is the heat of combustion of the diet. Losses associated with digestive processes are accounted for in the digestible energy (DE), while the metabolizable energy (ME) considers additional metabolic wastes (in urine). The net energy (NE) value of a feedstuff is energy available for metabolic functions (maintenance and growth). The heat increment is ME minus NE, and is under most circumstances regarded as waste. It is, therefore, beneficial to maximize the NE/ME ratio.

Several experiments have been conducted to evaluate the

net energy of different feedstuffs. Ewan (1978) reported a NE/ME of 63% for glucose, while Helland (1979) obtained a ratio of 85% for sucrose. This difference in NE/ME may be because of an interaction between the basal portion of the diet and the test ingredients. A corn-soy based diet was used in the sucrose trial, while the basal diet in the glucose experiment was composed of purified ingredients. In addition, uncontrolled environmental factors such as subclinical levels of disease cannot be ruled out. The difference of 22 units in the NE/ME for glucose and sucrose may also be a reflection of the different utilization of these carbohydrates by the pigs.

The first objective of this research was to determine the net energy value of glucose and sucrose. The second objective was to study effects of the dietary carbohydrate source on insulin secretion and on fat and protein metabolism.

Explanation of dissertation format

Both sections will be submitted for publication to the Journal of Animal Science. In Section I, the authors will be Ståle J. Helland, Richard C. Ewan and Allen H. Trenkle. In Section II, the authors will be Ståle J. Helland, Richard C. Ewan, Allen H. Trenkle and Steven Nissen.

SECTION I. UTILIZATION OF GLUCOSE AND SUCROSE BY THE WEANLING PIG

UTILIZATION OF GLUCOSE AND SUCROSE BY THE WEANLING PIG

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SUMMARY

Utilization of glucose and sucrose by weanling pigs was evaluated in a comparative slaughter experiment. A basal, corn-soy diet was fed alone or supplemented with isocaloric levels of glucose or sucrose. There were no differences between the carbohydrate fortified diets with respect to growth rate, feed:gain ratio or apparent digestibility of dry matter, energy or nitrogen. Nitrogen balance in grams per day, apparent biological value, or apparent net protein utilization were not different between the pigs fed the supplemented diets. There were no differences in the deposition of body energy, protein, fat or ash when the pigs were fed the sucrose or glucose diets. The gross (GE) and digestible energy (DE) of glucose was lower than for sucrose on a dry matter (DM) basis. Part of the difference in GE was removed by a higher DE/GE for glucose monohydrate. The metabolizable (ME) and net energy (NE) were similar (DM basis). The energy values, in kcal/g dry matter, for glucose and sucrose respectively were: GE, 3.68, 3.96; DE, 3.43, 3.55; ME, 3.28, 3.43; NE, 2.48, 2.62. The pigs fed sucrose had increased liver weights. This weight difference was due to a larger glycogen deposition. Exogenous insulin stimulated in vitro fatty acid production in the abdominal fat pads from pigs fed sucrose but not in fat pads of pigs fed glucose. The fat pads from the former group did utilize

glucose better than fructose for triglycerides and carbon dioxide production. The addition of insulin decreased the conversion of fructose to fatty acids and glycerol. Added insulin had no influence on respiration in the adipose tissue.

(Key words: Energy, Glucose, Sucrose, Liver, Adipose tissue, Swine).

INTRODUCTION

The main justification for the use of net energy in animal nutrition, instead of digestible or metabolizable energy, is that more of the energy losses are considered. The digestibility of energy of feedstuffs varies considerably. Tegbe and Ewan (1983) reported that the energy digestibility of dried skim milk was 99%, while that for meat and bone meal was 73%. The efficiency of utilization of digestible energy (ME/DE) of different feeds appears to be relatively constant. There are, however, differences in the efficiency by which the metabolizable energy is utilized (NE/ME). Stanley and Ewan (1982) obtained a value of 20% for the NE/ME of alfalfa meal while Helland (1979) reported a value of 85% for sucrose.

Energy comparisons between feedstuffs are complicated by differences in the quality and quantity of carbohydrates, proteins and fats. This problem is partly eliminated when refined sugars are compared, because they do not contain protein or fat. Ewan (1978) determined the NE/ME of glucose to be 63%, 22 units lower than the value reported by Helland (1979) for sucrose. This difference may be due to uncontrolled environmental factors, or to an interaction between the basal diet and the test ingredients. Ewan (1978) used a basal diet based on purified ingredients, while Helland (1979) used a corn-soy based diet. The

difference in the NE/ME could also be a reflection of the utilization of these sugars by the pig.

Sucrose is hydrolyzed to glucose and fructose in the small intestine by sucrase. Mateo and Veum (1980) found two week old pigs to perform equally well on glucose and sucrose based diets. The absorbed sugars are used as energy or stored as glycogen or triglycerides. The porcine livers have, however, a minimal capacity for fatty acid synthesis (O'Hea and Leveille, 1969). In the pig, the major site of triglyceride synthesis from sugar precursors is adipose tissue (Mersmann et al., 1981).

The objective of this study was, therefore, to compare the whole body and tissue utilization of glucose and sucrose fed to swine at isocaloric and isonitrogenous levels.

EXPERIMENTAL PROCEDURES

Sixteen crossbred pigs, averaging 5.6 kg at 28 days of age, were divided into outcome groups based upon litters. Within outcome groups pigs and treatments were randomly allotted to metabolism cages. A basal diet was formulated to supply two times the NRC (1979) recommendations for all nutrients except energy (Table 1). The basal diet was offered to all animals at 3% of body weight daily. The second and third treatments were feeding of additional glucose monohydrate (IFN 4-02-125, Table 2) at 2.34% or sucrose (IFN 4-04-701) at 2% of body weight daily. The intake of the two diets containing sugars was isonitrogenous and isocaloric (GE) per unit of body weight. The diets were offered as a water slurry in three equal portions daily. The pigs were weighed and feed intakes were adjusted at weekly intervals.

One pig from each replicate was sacrificed after a 10-d adjustment period and the ingesta free bodies were stored at -10 C, prior to grinding and drying by lyophilization. The remaining animals were used in a 38 day growth trial. Seven day urine collections were pooled in week two through five. Grab samples of fecal matter were also retained. Chromic oxide was added (3 g/kg) to the diets as a marker for digestibility. The pigs were killed by electrocution four hours after feeding. The livers were removed, frozen in dry

TABLE 1. Composition of the basal diet

Ingredient	%
Soybean meal (IFN 5-04-612)	71.00
Ground corn (IFN 4-02-935)	15.40
Soybean oil (IFN 4-07-983)	5.00
Dicalcium phosphate (IFN 6-01-080)	4.78
Ca carbonate (IFN 6-01-069)	.96
DL-methionine (IFN 5-03-086)	.80
Iodized salt (IFN 6-04-151)	.76
Antibiotic[1]	.50
L-lycine-HCl	.40
Vitamin premix[2]	.30
Trace mineral premix[3]	.10

[1]Contributed the following per kg of diet: 220 mg chlortetracycline, 220 mg sulfametazine and 110 mg penicillin.
[2]Contributed the following per kg of diet: 3,350 IU vitamin A, 404 IU vitamin D2, 100 IU vitamin E, 350 mg choline, 45.5 mg niacin, 19.8 mg pantothenic acid, 6.4 mg riboflavin, 2.0 mg pyridoxine, 1 mg menadione, 41 µg vitamin B^{12}.
[3]Contributed the following per kg of diet: 200 mg Zn, 100 mg Fe, 55 mg Mn, 11 mg Cu, 1 mg I and 1 mg Co.

TABLE 2. Chemical composition of glucose monohydrate and sucrose

Item	Unit	Glucose	Sucrose
Dry matter	%	91.00	99.94
Gross energy[1]	kcal/g	3.68	3.96

[1]Dry matter basis.

ice and acetone, and stored at -10 C. The abdominal fat pads from the sugar fed pigs were removed and placed in a 37 C Krebs-Ringer bicarbonate buffer (KRB: 121 mM NaCl, 25 mM $NaHCO_3$, 4.8 mM KCl, 2.4 mM $MgSO_4$, and 1.2 mM KH_2PO_4).

A.O.A.C. procedures (1975) were used for the determination of dry matter (DM), nitrogen (N), ether extract and ash. An adiabatic bomb calorimeter[1] was used to determine the energy content of the samples. Livers were ground in liquid nitrogen and freeze-dried. Glycogen was determined by the method of Lo et al. (1970).

The treatments used in the in vitro incubations are presented in Table 3. Immediately following slaughter, the abdominal fat pads were cut into 100 mg pieces and incubated for two hours in 3 ml of of pH 7.4 KRB-buffer, under a O_2-CO_2 atmosphere (95:5%). The incubation media contained .3 µCi/ml of (U-^{14}C) glucose or fructose. Carbon dioxide was trapped for one hour by injecting .1 ml of 30% NaOH into suspended center wells, containing filter paper. The incubations were terminated with .5 ml of 1.5 N H_2SO_4. After homogenization of the incubated segments of fat pads, the total lipids were extracted and purified by the method of Bligh and Dyer (1959). The procedure of Glass and Christophersen (1969) was used to convert the triglycerides

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[1] Parr Instrument Co., Moline, IL.

to glycerol and fatty acid methyl esters. These were separated by adding 10 ml water, mixing and centrifugation. Liberated CO_2 was assayed by the technique of Mirskey as cited by Buhler (1962).

TABLE 3. Treatments for the in vitro incubations of adipose tissue[1]

Treatments	Sugar added		Fat pad donor
	Glucose[2]	Fructose[2]	
1[3]	5 mM *	2.5 mM	sucrose fed pig
2[3]	5 mM	2.5 mM *	sucrose fed pig
3[4]	5 mM *	---	sucrose fed pig
4[4]	5 mM *	---	glucose fed pig

[1]Two pigs were used in each of four replicate incubations, and each treatment combination was repeated 3 times per replication.
[2]An asterisk indicates the location of the radioactive label.
[3]Insulin was added at .0, .1, 1.0, 2.5, 10, or 100 ng/ml of media.
[4]Insulin was added at .0, 1.0, or 10 ng/ml of media.

The energy values were calculated as outlined by Robles and Ewan (1982). The method of least squares analysis of variance (Harvey, 1960) was used for statistical analysis.

RESULTS AND DISCUSSION

Supplementation of the basal diet with carbohydrates increased ($P<.01$) the average daily gain (Table 4) and improved ($P<.05$) the feed:gain ratio. The apparent digestibility coefficient (ADC) for dry matter and energy improved ($P<.01$) as glucose or sucrose was added to the basal diet. The lower digestible (DE), metabolizable (ME, $P<.01$) and net energy (NE, $P<.05$) of the glucose diet are partly a reflection of the lower energy density of this diet. ME/DE and NE/ME were not affected by carbohydrate addition.

The ADC for nitrogen was reduced ($P<.01$) in the carbohydrate fortified diets. Nitrogen balance, however, was greater ($P<.01$) for the pigs fed sugar supplemented diets. These animals were consuming more energy than the animals fed the basal diet alone, and were able to utilize the absorbed amino acids more efficiently for protein synthesis. The improved efficiency of N utilization, when either sugar was added, is reflected by the nitrogen balance expressed either as a percentage of N ingested (apparent net protein utilization) or as a percentage of N digested (apparent biological value). Veum and Mateo (1981) evaluated utilization of glucose and sucrose in pigs from 8 to 36 days of age. The diets used were isonitrogenous but not isocaloric. They found the glucose diet to be better

TABLE 4. Effect of isocaloric addition of glucose and sucrose on performance, digestion and metabolism

Item	Unit	Basal[1]	+Glucose[2]	+Sucrose[2]	SE[3]
		Pig performance			
Daily gain	g	197[4]	481[5]	479[5]	11
Feed:gain	-	1.35[6]	1.26[6,7]	1.17[7]	.04
		Apparent digestibility coefficients			
Dry matter	%	86[4]	89[5]	90[5]	.5
Energy	%	90[4]	92[5]	92[5]	.3
Nitrogen	%	92[6]	90[7]	89[7]	.4
		Energy metabolism			
DE	kcal/g	3.80[4]	3.55[5]	3.76[4]	.01
ME	kcal/g	3.56[4,5]	3.40[5]	3.63[4]	.05
NE	kcal/g	2.31[6]	2.27[6]	2.42[7]	.05
ME	%DE	94[6]	96[6]	97[6]	1.0
NE	%ME	65[6]	67[6]	67[6]	1.1
		Nitrogen metabolism			
Balance	g/d	6[4]	14[5]	14[5]	.5
Balance[8]	%NI	42[5]	68[5]	69[5]	1.3
Balance[9]	%DN	46[4]	76[5]	78[5]	1.2

		Composition of daily gain (carcass)			
Energy	kcal	207[4]	831[5]	807[5]	37
Nitrogen	g	5[4]	12[5]	12[5]	.5
Ether extract	g	1[4]	42[5]	39[5]	3.1
Ash	g	7[4]	12[5]	12[5]	.7

[1]Basal diet was offered at 3% of body weight per day.

[2]Glucose was added at 2.34% and sucrose was added at 2% of body weight per day to make these diets isocaloric. Feeding levels were adjusted weekly.

[3]Standard error.

[4],[5]Different superscripts: significant difference between treatments ($P<.01$).

[6],[7]Different superscripts: significant difference between treatments ($P<.05$).

[8]Nitrogen balance as a percentage of nitrogen intake (apparent net protein utilization).

[9]Nitrogen balance as a percentage of nitrogen digested (apparent biological value).

than the sucrose diet with respect to apparent biological value and apparent net protein utilization. The superior utilization of the dietary protein in the glucose diet reported by Veum and Mateo (1981) cannot be explained by the ratio of dietary energy to protein, unless the protein content of the diet was a limiting nutrient. The glucose diet had 89 kcal ME per gram nitrogen while this ratio was 95 for the sucrose diet. No significant differences could be detected with respect to these parameters in the present study, in which both diets had 105 kcal ME/g N.

All of the components of the composition of daily gain were affected ($P<.01$) by the addition of glucose or sucrose to the basal diet, but there were no differences between the sugars.

The gross energy of sucrose was 3.96 kcal/g DM (Table 2). This is identical to the values reported by Fingerling et al. (1943), Just (1978) and Helland (1979), and similar to the value of 3.97 kcal/g DM (Table 5) measured by Schiemann et al. (1962). Tollett (1961), however, reported a lower value (3.53 kcal/g DM). The DE (3.55 kcal/g DM, Table 6), ME (3.43 kcal/g DM) and NE (2.53 kcal/g DM) did not differ significantly from the values of Helland (1979). The sucrose treatment in the present trial was the same as that used by Helland (1979). The DE/GE were 90% and 92%, respectively, in these two experiments. These values are

somewhat lower than the 97% reported by Fingerling et al. (1943), Schiemann et al. (1962) and Just (1978), and 96% found by Tollett (1961). The ME/DE (97%) agrees well with the other reported values. The NE/ME of 76% was close to 78% reported by Schiemann et al. (1962), and between 64% obtained by Just (1978) and 85% by Helland (1979). There was no statistical difference between the NE/ME in this experiment and the experiment reported by Helland (1979).

TABLE 5. Some energy values for sucrose and glucose

	GE	DE	ME	NE	DE/GE	ME/DE	NE/ME
	----- kcal/g DM -----				-------- % --------		
			Sucrose				
Fingerling et al. (1943)	3.96	3.86	----	2.69	97	--	--
Schiemann et al. (1962)	3.97	3.87	3.74	2.91	97	97	78
Tollett (1961)	3.53	3.39	3.36	----	96	99	--
Just (1978)	3.96	3.80	3.78	2.38	97	99	64
Helland (1979)[1]	3.96	3.65	3.53	2.99	92	97	85
			Glucose				
Diggs (1959)	3.72	3.75	3.70	----	101	99	--
Ewan (1978)[2]	3.72	3.68	3.42	2.15	99	93	63

[1]The design was identical to the sucrose portion of the present work.
[2]The dietary treatments were different from the present work.

The glucose contained 3.68 kcal/g DM (Table 2) which

corresponds well with the 3.72 kcal/g DM (Table 5) found by Diggs (1959) and Ewan (1978). The DE/GE of 93% (Table 6) is substantially lower than the 101% reported by Diggs (1959) and 99% found by Ewan (1978). The ME/DE was found to be 96%. This is between the 99% and 93% reported by Diggs (1959) and Ewan (1978), respectively. The NE/ME of 75% is 12 units higher than that obtained by Ewan (1978).

The DE and ME values for glucose, on an air-dry basis, were lower ($P<.01$) than for sucrose (Table 6). A similar trend ($P<.05$) was found for the NE. These differences are mostly due to the lower energy density (air-dry basis) of glucose, because only DE remained lower ($P<.01$) for glucose when expressed on a dry matter basis. Part the difference in GE (DM basis) of the sugars was eliminated by the higher ($P<.01$) DE/GE of glucose. There were no statistical differences between the ME and NE values (DM basis) of glucose and sucrose.

The fortification of the basal diet with sugars resulted in increased liver weights (Table 7, $P<.01$). The livers also were larger as a percentage of empty body weight ($P<.05$). The increase in liver size was greatest in the sucrose fed group. This is in agreement with the results of Fernandes et al. (1979). These authors added sucrose or glucose to the drinking water of pigs for twelve out of fourteen hours prior to killing. In the present work, the

TABLE 6. Energy availability of glucose and sucrose

Item	Unit	Glucose	Sucrose	SE[1]
		Air dry basis		
DE[2]	kcal/g	3.12	3.55	.07
ME[2]	kcal/g	2.99	3.43	.07
NE[3]	kcal/g	2.25	2.62	.12
		Dry matter basis		
DE[2]	kcal/g	3.43	3.55	.03
ME	kcal/g	3.28	3.43	.04
NE	kcal/g	2.48	2.62	.10
		Efficiency of energy utilzation		
DE/GE[2]	%	93	90	.51
ME/DE	%	96	97	.49
NE/ME	%	75	76	2.53

[1]Standard error.
[2]Difference between glucose and sucrose (P<.01).
[3]Difference between glucose and sucrose (P<.05).

dry matter percentage was not influenced by dietary treatment. The total hepatic protein, fat and ash content did, however, increase when sugar was added to the basal diet. The increase in total liver fat, protein and ash for the animals fed sugar diets, is mostly a reflection of the animal weight. This is because only small differences could be found if the liver data were expressed on a percentage basis. The addition of sugars to the basal diet resulted in an increased energy content in the livers. This was

greatest for the sucrose fed pigs ($P<.01$). The difference in energy content of the livers from the glucose and sucrose fed pigs was the result of higher ($P<.01$) glycogen deposition in the pigs fed sucrose. This is in contrast to the short-term study of Fernandes et al. (1979) where glucose and sucrose solutions were fed to pigs for 12 out of 14 hours prior to slaughter.

The basal conversion rate of glucose to fatty acids was 2538 nmoles per 100 mg abdominal fat pad per two hours of incubation (Figure 1). This is ten times the values obtained by Mersmann et al. (1981), but only a third of the levels reported by Christensen and Goel (1972).

The basal levels of fatty acid, CO_2 and glycerol production in abdominal fat pad slices were ten to fifteen times greater for glucose than for fructose ($P<.01$) when the incubation medium contained 5 mM glucose plus 2.5 mM fructose. The fatty acid production increased with insulin addition, when glucose was labelled ($P<.01$). The response was, however, only half of the one obtained with the highly insulin sensitive preparation of Christensen and Goel (1972). Addition of insulin resulted in a decline ($P<.01$) in fatty acid and glycerol production when fructose was labelled. The respiration (CO_2 production) did not respond to insulin supplementation. The detrimental effect of insulin on fructose utilization could be due to the

TABLE 7. Effect of sugar supplementation on liver composition

Item	Unit	Basal[1]	+Glucose[2]	+Sucrose[2]	SE[3]
Weight	g	341[4]	741[5]	818[6]	15.5
Weight	%Ebwt[7]	2.7[8]	3.4[9]	3.7[10]	.1
Dry matter	%	26.4[8]	25.8[8]	26.5[8]	.3
Protein	g	67[4]	136[5]	139[5]	2.6
Ether extract	g	7[8]	13[9]	14[9]	1.8
Energy	kcal	516[4]	1085[5]	1201[6]	24
Ash	g	4[4]	10[5]	10[5]	2.1
Glycogen	g	11[4]	25[4]	46[5]	6.5

[1]Basal diet was offered at 3% of body weight per day.

[2]Glucose was added at 2.34% and sucrose at 2% of body weight per day to make the intake of these diets isocaloric. Levels of feeding were adjusted weekly.

[3]Standard error.

[4],[5],[6]Different superscripts indicate treatment differences ($P<.01$).

[7]Ebwt: ingesta free body weight.

[8],[9],[10]Different superscripts indicate treatment differences ($P<.05$).

stimulatory influence on glucose metabolism.

Fat pads from pigs fed the glucose based diet did not respond to insulin (Table 8). This was in contrast to the fat pads from animals fed sucrose, in which insulin increased fatty acid production ($P<.05$). In another experiment (Helland et al., 1984), pigs fed sucrose were found to have lower plasma insulin and glucose levels. The

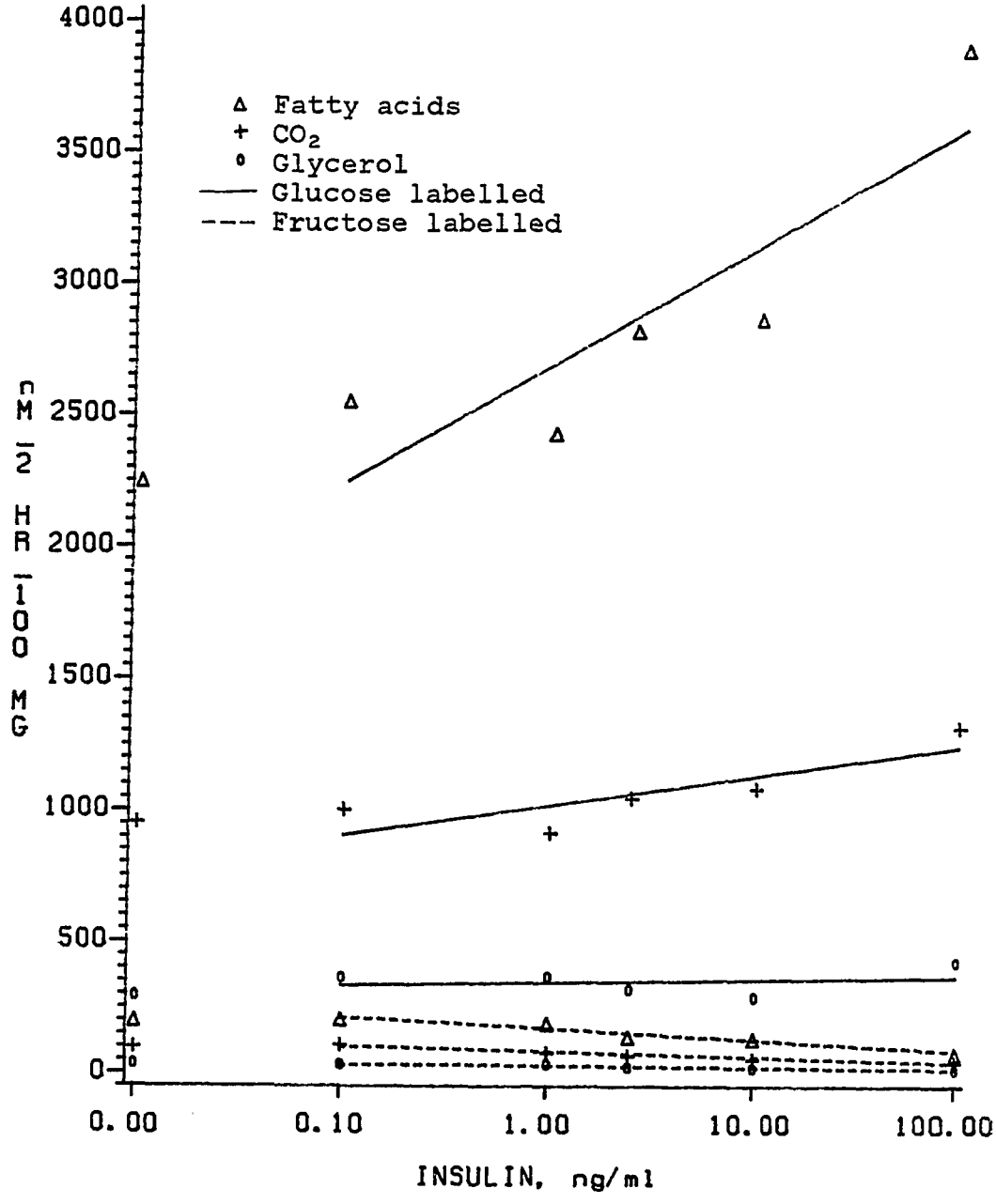

FIGURE 1. Effect of insulin addition on glucose and fructose utilization in porcine abdominal fat pads

abdominal fat pads of pigs fed sucrose are, therefore, normally exposed to less glucose and insulin, but seem to respond better to added insulin. Total lipid production from in vitro incubations is dependent on both the substrate and insulin concentrations in the medium (Christensen and Goel, 1972). The in vitro results obtained in the present trial do not necessarily reflect the in vivo situation where the glucose fed animals were exposed to both higher glucose and insulin concentrations.

TABLE 8. Effect of insulin addition and dietary treatments on glucose utilization in porcine abdominal fat pads

PRODUCT[1]	Added insulin, ng/ml 0.0	SE[2]	1.0	SE	10.0	SE
			Glucose diet			
Fatty acids	1364	413	1507	487	1472	526
CO_2	1008	236	1072	265	1126	184
Glycerol	307	98	337	128	285	115
			Sucrose diet[3]			
Fatty acids	1848[4]	384	2466[4]	167	3286[5]	654
CO_2	991	203	1039	189	989	76
Glycerol	449	150	331	13	482	42

[1]The units are mmoles of glucose converted per two hours per 100 mg tissue. The incubation medium contained 5 mM glucose.
[2]Standard error.
[3]The presence or absence of fructose in the medium did not influence the results.
[4],[5]Different superscripts indicate a significant effect of level of insulin ($P<.05$).

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SECTION II. IN VIVO LEUCINE AND α-KETOISOCAPROATE METABOLISM IN THE PIG AS INFLUENCED BY DIETARY GLUCOSE AND SUCROSE

IN VIVO LEUCINE AND α-KETOISOCAPROATE METABOLISM IN THE PIG AS INFLUENCED BY DIETARY GLUCOSE AND SUCROSE

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SUMMARY

The influence of dietary glucose (G) and sucrose (S) on protein metabolism was evaluated in growing pigs. The daily intake of the diets containing the two sugars was isocaloric and isonitrogenous. A constant infusion of L-(4,5-^{3}H) leucine and (U-^{14}C) α-ketoisocaproate (KIC) was used to measure the transfer rates of leucine and KIC. No differences were found between the animals in the fasted state. Feeding of the glucose diet was accompanied with higher mean arterial glucose (G: 168.0 and S: 139.4 mg/100 ml) and insulin concentrations (G: 4.7 and S: 3.6 ng/ml). Sucrose fed animals had a mean postprandial fructose concentration of 12.4 mg/100 ml. The dietary treatments did not influence plasma urea-nitrogen (G: 11.5 and S: 11.9 mg/100 ml) or arterial leucine levels (G: 164.4 and S: 156.6 μmoles/liter). The arterial KIC concentration was reduced after feeding, (decrease of G: 41%, from 37.6 μmoles/l and S: 39%, from 30.2 μmoles/l).

Glucose fed animals had a larger hind limb uptake of glucose (G: 16 and S: 11%) than sucrose fed pigs. Plasma fructose was removed by the hind limbs as efficiently as glucose in the sucrose fed animals. Twenty-one percent of the leucine was removed by the hind legs in glucose fed pigs while only 7% was removed in sucrose fed animals. No net hind limb metabolism of KIC could be detected from arterial-

venous differences.

Analyzing the isotope data in a whole body model indicated lower preprandial proteolysis by the sucrose fed animals (G: 4.5 and S: 4.12 $\mu moles \cdot kg^{-1} \cdot min^{-1}$). Net protein synthesis was not significantly different between the pigs fed tglucose or sucrose. The total leucine carbon flux (TCF) increased following consumption of either diet (G: +12% and S: +7%). No further changes were found in the fluxes among the sucrose fed pigs. During absorption of the diet containing glucose, however, incorporation of leucine into protein increased 18%. The percentage of TCF which was transaminated decreased only following consumption of a glucose containing meal (leucine to KIC: G: 61 to 39% and S: 66 to 63%; KIC to leucine: G: 38 to 23% and S: 40 to 41%).

(Key words: Protein utilization, Glucose, Sucrose, Whole body, Hind limbs, Swine).

INTRODUCTION

Changes in dietary carbohydrates are known to alter plasma hormone concentrations. This is particularly true for insulin (Bohannon et al., 1980). Several studies indicate that glucose and/or insulin infusions result in a decrease in whole body amino acid flux, suggesting a decrease in the rate of proteolysis (Pozefsky et al., 1969; Felig and Wahren, 1974; and Ahmed et al., 1983). These studies have all been conducted in the fasting state. It is, however, unknown if postprandial changes in insulin secretion, which occur with alterations in dietary carbohydrates, ultimately affect the metabolism of proteins.

The objective of this study was to determine if substitution of dietary glucose for sucrose results in changes in whole body and hind limb metabolism of the branched chain amino acid leucine.

EXPERIMENTAL PROCEDURES

Animals

Ten cross bred female pigs averaging 25 kg were used in a completely randomized design. The animals were surgically implanted with indwelling catheters one week prior to the study. A teflon[1] catheter (ID=.042 inch, OD=.074 inch, 20 cm long) was inserted into the femoral artery. Two silastic[2] catheters were placed in a femoral vein. The longer (ID=.041 inch, OD=.060 inch, 20 cm long) venous catheter was used for isotope infusion, while the shorter catheter (ID=.062 inch, OD=.085 inch, 16 cm long) was used for blood sampling. The location of the catheter tips was between the ileac bifurcation and the renal vessels, and was confirmed by postmortem examination. All the catheters were exteriorized on the back of the animals.

Chemicals

The specific radioactivities of L-(4,5-^{3}H) leucine and (U-^{14}C) leucine were 55 Ci/mmole and 322 mCi/mmole, respectively[3]. (U-^{14}C) leucine was converted to (U-^{14}C) α-ketoisocaproate (KIC) by the method of Nissen et al.

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[1] Penntube Plastics Co., Clifton Heights, PA.

[2] Dow Corning Co., Midland, MI.

[3] Amersham, Arlington Heights, IL.

(1981). Blood was collected into EDTA containing tubes[4]. Sodium fluoride was also added to the blood to prevent glycolysis.

Diets

The pigs were fed a corn-soy diet at 3% of body weight per day. In addition, they received either glucose monohydrate at 2.34% or sucrose at 2% of body weight per day. The daily intake per kg of body weight was 11 gm crude protein and 121 kcal of net energy for both treatments. The diets were offered as a water slurry in three equal portions daily and the diets were fed to the pigs for at least one week prior to the isotope study.

Protocol

After a 24 hour fast, the pigs were placed in standing slings. The experiments were started at approximately 7:30 am, by giving a priming dose (1.5 $\mu Ci \cdot kg^{-1}$ of ^{3}H-leucine and .44 $\mu Ci \cdot kg^{-1}$ of ^{14}C-KIC). This was followed by a two hour continuous infusion of ^{3}H-leucine and ^{14}C-KIC (.042 and .013 $\mu Ci \cdot kg^{-1} \cdot min^{-1}$, respectively) to achieve isotopic steady state. Blood was sampled at the following times: -20, -10, 0, +20, +40, +60, +90, +120, +180, +240 and +300 minutes. A meal consisting of 1/3 of the daily intake was given at zero

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[4] Sarstedt, Princeton, N.J.

time.

Chemical analysis

Whole blood concentrations of leucine and KIC were determined by the HPLC method of Nissen et al. (1981). The HPLC effluent corresponding to the leucine and KIC peaks was collected and the ^{14}C and ^{3}H radioactivity determined by dual isotope liquid scintillation counting (Beckmann 8000 scintillation counter). Plasma glucose was assayed with glucose oxidase (Flozyme glucose[5]), and plasma fructose was measured by the method of Roe (1934). The procedure of March et al. (1965) was used for plasma urea nitrogen, and plasma insulin was measured by radioimmunoassay (Trenkle, 1972).

Calculations and statistics

Whole body flux of leucine and KIC were calculated by adapting the mass transfer equations of Shipley and Clark (1972), as described by Nissen and Haymond (1981). The arterial specific radioactivities were used for whole body flux calculation. The fasted values are the average of the three blood collections before feeding. Between 60 and 240 minutes after feeding, blood specific radioactivities and concentrations of leucine and KIC were not statistically

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[5] Worthington Diagnostics, Division of Millipore Co., Freehold, New Jersey.

different. Thus, steady state was assumed. The fed values are the means of the following time points: +60, +120, +180, +240 minutes after feeding. Plasma insulin, glucose, fructose and urea-nitrogen are presented as integrated mean values, which were obtained by averaging the areas under the time-response curves. These areas were measured with a planimeter[6]. The data were analyzed by GLM procedure of the Statistical Analysis Systems (Barr et al., 1976).

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[6] Keuffel & Esser Co., West Germany.

RESULTS

The arterial concentrations and hind limb uptake of plasma glucose were not influenced by the dietary treatments after a 24 hour fast (Table 9). In the first four hours after feeding, the integrated mean glucose concentration was higher in the glucose fed than in the sucrose fed pigs (168 vs 139 mg/100 ml, $P<.05$). This increased plasma glucose concentration in the glucose fed pigs was also reflected in a larger uptake of glucose by the hind limb (27.0 vs 15.2 mg/100 ml, $P<.05$). The fasting plasma concentration of insulin (.3 ng/ml) was not affected by diet. The integrated mean arterial insulin concentration increased to 4.7 ng/ml following the consumption of the glucose diet, which was 30% higher than when sucrose was fed ($P<.05$). Fructose was only detected in the plasma after a sucrose meal. The arterial concentration of this sugar was a tenth of the plasma glucose levels (12.4 vs 139.4 mg/100 ml respectively). However, the percent uptake of glucose and fructose by the hind limb was similar (11%).

Plasma urea-nitrogen (Table 10) was not influenced by the diets or state of feeding. Whole blood KIC concentrations were the same for both groups of pigs in the fasting state. However, after feeding, the KIC concentrations decreased in animals fed both diets (37.6 to 21.9 µmoles/l for glucose, $P<.01$; 30.2 to 24.9 µmoles/l for

TABLE 9. Effect of dietary carbohydrate on plasma levels of glucose, fructose and insulin

Item	Unit	Glucose		Sucrose	
		Fast	Fed	Fast	Fed
		Arterial concentrations			
Glucose	mg/100 ml	79.4	168.0[1]	76.4	139.4
Insulin	ng/ml	.3	4.7[1]	.3	3.6
Fructose	mg/100 ml	ND[2]	ND[2]	ND[2]	12.4
		Hind limb uptake			
Glucose	mg/100 ml	2.9	27.0[1]	2.1	15.2
Fructose	mg/100 ml	0.0	0.0	0.0	1.4

[1]Significant difference between diets, in fasted or fed state ($P<.05$).
[2]Not detectable

sucrose, $P<.05$). The fall in KIC concentration was greater in the glucose fed pigs than in the sucrose fed pigs (15.7 and 5.3 μmoles/l, $P<.05$). The hind limb metabolism of leucine and KIC was not influenced by diet in the fasting state. The consumption of both meals resulted, however, in significant uptake of leucine by the hind legs. The glucose fed pigs had a greater hind limb uptake of leucine than the sucrose fed animals in the postprandial period (34.2 and 10.2 μmoles/l, $P<.05$).

In the fasting state (Table 11), the sucrose fed animals had significantly lower ($P<.05$) total leucine carbon flux (TCF) than the glucose fed animals. The TCF increased

TABLE 10. Effect of dietary carbohydrate on protein metabolism

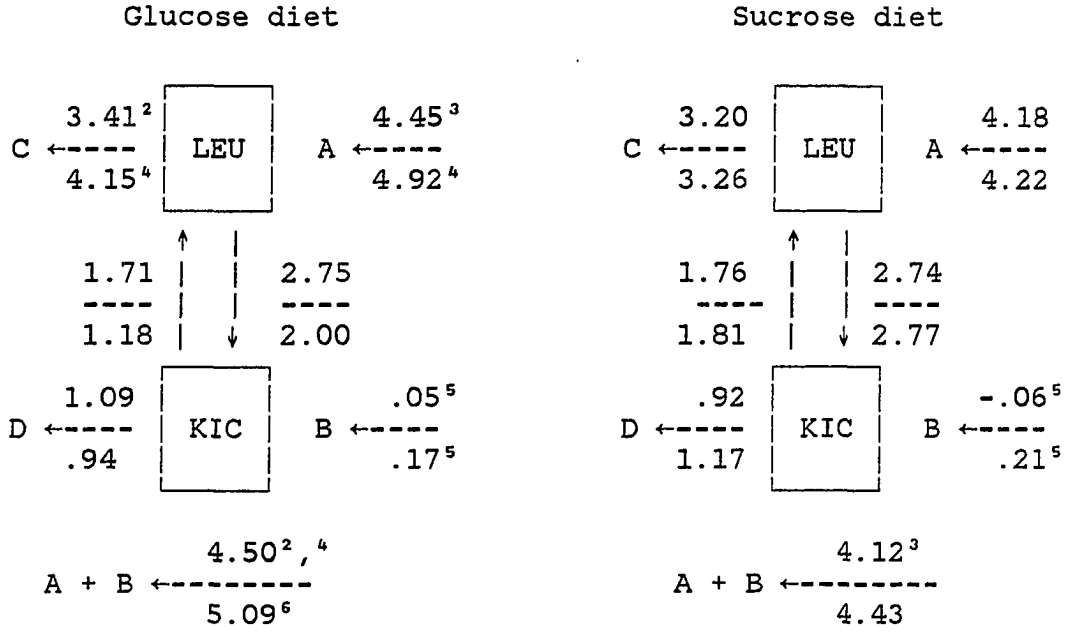
Item	Glucose		Sucrose	
	Fast	Fed	Fast	Fed
	Arterial concentrations			
Leucine[1]	160.6	164.4	153.7	156.6
KIC[1]	37.6[2]	21.9	30.2[3]	24.9
Urea-nitrogen[4]	12.3	11.5	11.1	11.9
	Hind limb uptake			
Leucine[1]	5.0[2]	34.2[5]	-2.7[2]	10.2
KIC[1]	1.2	-.3	-3.1	.6

[1]Units are in μmoles/l of whole blood.
[2]Significant difference between fed and fasted, within a diet (P<.01).
[3]Significant difference between fed and fasted, within a diet (P<.05).
[4]Units are in mg/100 ml plasma.
[5]Significant diet effect, in the fasted or fed state (P<.05).

after the consumption of either diet (4.50 to 5.09 $\mu moles \cdot kg^{-1} \cdot min^{-1}$ for glucose, P<.05; 4.12 to 4.43 $\mu moles \cdot kg^{-1} \cdot min^{-1}$ for sucrose, P<.10). The sucrose fed pigs showed no further changes in any fluxes after feeding. Feeding of the glucose diet resulted in increased protein synthesis (from 3.41 to 4.15 $\mu moles \cdot kg^{-1} \cdot min^{-1}$, P<.05). The interconversion of leucine and KIC was not influenced by feeding, when the results were expressed in absolute values ($\mu moles \cdot kg^{-1} \cdot min^{-1}$). If the interconversion of leucine and

KIC was expressed as a percentage of TCF, the percentages decreased significantly for pigs fed diets containing glucose: leucine to KIC decreased from 61% to 39% ($P<.05$), while the KIC to leucine was reduced from 38% to 23% ($P<.05$). No additional dietary effects on flux were found. The entry of KIC into the KIC pool was not found to be statistically different from zero. Net protein synthesis (protein synthesis minus proteolysis) was not different in the fasting state. In the fed state, net protein synthesis cannot be calculated due to the entry of dietary leucine along with leucine derived from endogenous proteolysis.

TABLE 11. Whole body leucine and α-ketoisocaproate flux[1]



Leu: leucine
KIC: α-ketoisocaproate
A: Proteolysis
B: Entry of KIC
A + B: Total leucine carbon flux
C: Protein synthesis
D: Oxidation

[1]The results from the fasted state are above the lines. The results from the fed state are below the lines. The units are $\mu moles \cdot kg^{-1} \cdot min^{-1}$.
[2]Significant difference between fasted and fed state within a diet ($P<.05$).
[3]Significant difference between fasted and fed state within a diet ($P<.10$).
[4]Significant difference between glucose and sucrose in the fasted or fed state ($P<.05$).
[5]Not significantly different from zero.
[6]Significant difference between glucose and sucrose in the fasted or fed state ($P<.01$).

DISCUSSION

The studies reported, here, indicate a differential peripheral tissue utilization of carbohydrate energy in pigs fed a glucose or a sucrose containing diet. The sucrose fed pigs had lower arterial glucose concentrations and correspondingly decreased hind limb uptake of sugars (glucose and fructose). Thus, the tissues of the hind limb of the sucrose fed pigs had less carbohydrate energy available for maintenance and anabolic functions during the first four hours after feeding. Other studies indicate that sucrose fed pigs have less muscle glycogen, which also suggests less energy delivered to peripheral tissues (Fernandes et al., 1979). Sucrose fed pigs have more hepatic glycogen than glucose fed animals (Helland et al., 1984).

It appears, in addition to changes in carbohydrate metabolism, that leucine metabolism in the leg tissue also responds differently to these dietary treatments. In spite of similar whole body leucine metabolism, the hind limb of glucose fed animals cleared three times as much leucine as the sucrose fed animals in the fed state. KIC, however, was not taken up or put out by the hind limb in either group. Although the blood KIC concentrations decreased after feeding, the arterial-venous difference was constant across the hind limbs. The arterial levels of leucine and KIC

reflect the metabolism of the whole body. Since there is a difference between the whole body and the hind limb metabolism of KIC and leucine, some other organs must account for the changes observed in leucine and KIC concentrations.

The change in protein metabolism in the hind limbs could be due to the higher peripheral insulin concentrations in the glucose fed pigs. Feeding of a glucose diet has also been shown to elicit a larger insulin secretion than a sucrose diet in humans (Macdonald et al., 1978). Insulin is known to increase amino acid uptake by peripheral tissues (Ahmed et al., 1983), as well as influencing KIC-leucine metabolism (Hutson et al., 1980). Other studies suggest little or no effect of insulin on protein synthesis (Nakano and Hara, 1979; Motil et al., 1981).

It cannot be determined from the studies reported here whether carbohydrate, insulin or other factors are responsible for the changes in leg metabolism of leucine. It would seem from the evidence available that glucose fed animals have more dietary energy available in the periphery, while sucrose fed animals have more energy available in the liver. If the availability of sugar energy is important for efficient protein utilization, then the glucose fed pigs will have more efficient protein metabolism in the peripheral tissues during the first four hours of the

postprandial period. Correspondingly, the sucrose fed pigs will have more efficient protein metabolism in the liver and possibly other organs. Insulin would also complement this process in the periphery.

Most parameters of whole body leucine and KIC flux in the pig are in the range of those reported in the dog (Nissen and Haymond, 1981). The overall mean value was 4.5 $\mu moles \cdot kg^{-1} \cdot min^{-1}$, which is somewhat lower than the combined mean flux of 6.5 $\mu moles \cdot kg^{-1} \cdot min^{-1}$ reported by Simon et al. (1978) and Simon et al. (1982), in which labelled leucine and lysine were infused into 30 to 40 kg pigs. The observation, in the present trial, that the entry of KIC is not significantly different from zero, is in contrast to a previous study with dogs (Nissen and Haymond, 1981), where a significant entry of unlabelled KIC into the KIC pool was measured.

In the fasting state, more proteolysis occurred in the glucose than in the sucrose fed pigs. There was no difference, however, in net protein synthesis between the groups. The entry of leucine carbon, in the postprandial period, was also greatest among the glucose fed animals. This can be accounted for by increased proteolysis and/or faster absorption of dietary leucine. The glucose fed pigs had, however, the largest postprandial insulin concentrations, and exogenous insulin is known to decrease

in vivo proteolysis in postabsorptive muscle (Pozefsky et al., 1969). It is therefore possible likely that the sucrose fed animals had a slower rate of absorption of dietary leucine. The other whole body flux parameters measured after the sucrose meal did not change from basal values. After the glucose containing meal, however, incorporation of leucine into protein increased, and both the conversion of KIC to leucine and leucine to KIC decreased. The reason for these changes is not apparent from these studies. The increase in plasma insulin, as well as the decrease in arterial KIC concentration, is consistent with the observed decrease in whole body leucine transamination. The decrease in leucine transamination with feeding was also accompanied by an increase in protein synthesis. This experiment suggests that changes in protein synthesis are mediated primarily by supply of substrate, while leucine transamination is regulated by factosr other than leucine availability. This study furthermore suggests that sucrose fed pigs are exposed to smaller fluctuations in protein and carbohydrate metabolism in the pre- and postprandial periods.

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GENERAL DISCUSSION

In Trial 1, glucose or sucrose containing diets were fed to weanling pigs for 38 days. The isocaloric and isonitrogenous dietary intake did not cause any differences in growth rate, feed/gain ratio, and apparent digestibility of dry matter energy or nitrogen.

Glucose was utilized by adipose tissue 10 to 15 times better than fructose for fatty acid, glycerol and carbon dioxide production, when the in vitro incubation media contained 5 mM glucose plus 2.5 mM fructose. The addition of insulin to the incubation media increased the production of fatty acids from glucose, and decreased the conversion of fructose to fatty acids and glycerol. The decrease in fructose utilization may be partly because glucose utilization increased when insulin was added and, suggesting a preference by adipose tissue for glucose as a substrate for fatty acid production.

The same sugar fortified diets were used in Trial 2, and the mean postprandial arterial glucose concentration was found to be ten times the mean arterial fructose concentration, in the sucrose fed pigs. The clearance by the tissues of the hind limbs was 11% for both glucose and fructose.

The whole body deposition of fat (Trial 1) was the same for both groups of animals but adipose tissue from glucose

fed pigs had lower triglyceride synthesis than the sucrose fed animals when insulin was added to the incubation medium. This discrepancy between net deposition and in vitro lipogenesis might indicate a different turnover rate of the adipose tissues from the glucose and sucrose fed pigs. It might also be an artifact related to the incubation protocol, because the glucose fed pigs were exposed to higher plasma glucose and insulin concentrations (Trial 2).

The only difference found in the livers of the sugar fed pigs, at four hours after feeding (Trial 1), was more glycogen and thus energy in the liver of sucrose fed animals. This would provide these animals with a larger store of readily available energy for the periods between meals, which subsequently could reduce the need for gluconeogenesis by these pigs.

The total energy deposition was the same for the sucrose and glucose fed animals. There were, however, differences in the energy availabilities of these sugars, when expressed as GE or DE (dry matter basis). The GE of glucose monohydrate was lower than the GE of sucrose. Part of this difference in energy concentration was removed by a higher digestibility of glucose. The ME and NE content of glucose and sucrose were the same when expressed on a dry matter basis. The energy availabilities of sucrose correspond with the values reported by Helland (1979). No

statistical comparisons were done between the energy values for glucose in the present trial and the values reported by Ewan (1978).

No differences were found in the metabolism of nitrogen (Trial 1) when expressed as grams of nitrogen retained per day, apparent biological value or apparent net protein utilization. The dynamics of nitrogen metabolism did, however, appear to be influenced by the nature of the carbohydrate fed (Trial 2). Feeding increased the hind limb clearance of leucine. This increase was largest among the glucose fed pigs. The arterial leucine concentration did, however, not differ due to the diets used or state of feeding. The arterial-venous balance across the hind limbs did not indicate any changes in KIC metabolism when the pigs were fed. This is in contrast to the decrease in arterial KIC concentrations which occurred with feeding.

The analysis of the data using a two pool model indicated lower preprandial proteolysis among sucrose fed animals. No estimates could be made for the net protein synthesis in the fed state due to the confounding effect of dietary leucine. The total leucine carbon flux was, however, largest among the pigs receiving the glucose based diet. These pigs also had the highest insulin concentrations, and were therefore not likely to have more proteolysis than the sucrose fed animals. The larger total

leucine carbon flux measured after feeding the glucose diet is probably due to faster absorption of dietary leucine. Feeding glucose reduced transamination and increased incorporation of leucine into protein. No such changes were observed when sucrose was fed.

The importance of insulin in protein metabolism could not be determined in these experiments due to multiple confounding factors (other hormones, plasma glucose and metabolites). The data in Trial 2 suggest independent control of protein synthesis and transamination.

The combined results of these two experiments suggest that there are large differences in the way glucose and sucrose influence the metabolism in the liver, adipose tissue and the hind limbs of pigs. It appears, however, that these differences do not affect the overall utilization of glucose and sucrose based diets.

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