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USE OF NON-STARCH CARBOHYDRATE ENERGY SOURCES IN PERFORMANCE HORSE FEEDS

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Introduction

Performance is determined by genetic potential, training, and nutrition. An optimal nutrient supply is needed to achieve maximal power output and stamina. The athletic horse is subjected to regular training and competes close to its physiological limits. In contrast, the exercising horse, which may also be trained for successful performance, will not reach its physiological limits during performance. However, the duration and intensity of the work performed by the equine athlete will differ markedly. Racehorses will perform intensive muscular work at high-speed, near-maximal capacity for a couple of minutes, while horses used for three-day events and endurance rides will perform less intensive muscular work at submaximal capacity for many hours. Thus, in the racehorse the causes of fatigue will mainly be related to the depletion of substrates used for energy production and the accumulation of lactate (Frape, 1988; Hiney and Potter, 1996). In contrast, in the endurance horse the causes of fatigue will be related to the heat load and fluid and electrolyte loss, in addition to the depletion of substrates used for energy production (Jansson, 1999).

During exercise the blood flow to the digestive tract decreases, while the blood flow to the locomotor and respiratory muscles increases markedly (Duren, 1998). Interestingly, the pattern of change in blood flow distribution was the same in fasted and fed horses but with significantly higher blood flows in the fed animals. In absolute terms, blood flow (ml/g tissue/min) during exercise is four to five times higher to the locomotor muscles and three to four times higher to the respiratory muscles when compared to blood flow to the digestive organs. This implies that the feeding of the performing athlete has to be made according to a long-term plan and should aim at providing the nutrients necessary for building adequate body nutrient stores. If this is done successfully, it will allow maximal performance with respect to body energy needs and will allow the animal to handle the heat load resulting from extended periods of intensive work. In addition, recovery after exercise will be faster, and this will allow the animal to perform at maximal capacity more regularly.

Digestive Processes and Nutrient Utilization

THE EQUINE DIGESTIVE SYSTEM

Anatomically, horses are classified as nonruminant herbivores or hindgut fermentors (Stevens, 1988). They use endogenous enzymes to digest carbohydrates, protein, and fat in the stomach and small intestine and utilize microflora to ferment organic matter in the hindgut. The stomach is small and composes less than 7% of the empty weight of the digestive system, while the small intestine makes up approximately 27% (Duren, 1998). The hindgut (cecum and colon) is the largest organ system in the gastrointestinal (GI) tract of the horse and accounts for approximately 64% of the empty weight of the system. The small capacity of the upper part of the digestive tract imposes limits on handling large single meals that may overwhelm the digestive capacity and allow undigested feed material to be transported to the hindgut. This may cause excessive and uncontrolled fermentation in the hindgut, with the risk of inducing various digestive problems. However, the design of the digestive tract allows large quantities of fiber-rich feeds to be continuously ingested and utilized by the horse. Due to the anatomical design of the equine GI tract, sufficient quantities of fiber in the diet are a prerequisite for normal function of the hindgut and thus for normal digestion.

HINDGUT DIGESTION

Digestion in the hindgut is extensive in the horse, and proper functioning is necessary to efficiently utilize the fiber-rich part of the diet. The hindgut harbors a vast microflora population that lives in symbiosis with the host animal and is responsible for digestion in this section of the GI tract. A substantial part of the energy in the diet is provided through microbial hindgut digestion (Glinsky et al., 1976), while there appears to be only a marginal absorption of microbial-produced amino acids from the hindgut (McMeniman et al., 1987).

Diet composition (i.e., forage to concentrate ratio, cereal source) and feed processing (i.e., grinding, hydrothermal processing) will affect the partition of digestion between the small intestine and the hindgut and will have an impact on the intensity and extent of digestion. The small intestine is the major site for protein, fat, and soluble carbohydrate digestion, and cell walls are digested in the hindgut (Hintz et al., 1971). The relative importance of hindgut digestion will increase with increased levels of forage in the diet. It has been shown that cecal pH will lower with increased starch intake (Radicke et al., 1991). The effect of starch intake was more pronounced when maize was contributing the starch as compared with oats. This could be explained by the lower small digestibility of maize starch as compared with oat starch (Kienzle, 1994). Willard et al. (1977) showed that when changing from an all-hay diet to an all-concentrate diet the cecal pH was significantly reduced and the molar proportion of acetate was reduced, but the molar proportion of propionate was increased. The dietary-induced changes in hindgut fermentation might influence the extent of hindgut digestion and could explain differences in diet digestibility and nutrient utilization.

Diet Composition

Forages should always be the foundation of an equine diet, with additional concentrate used only to increase the energy density and to supply essential nutrients not contained in the forage. Forages are composed of cell contents (protein, fat, soluble carbohydrates) and cell walls (cellulose, hemicellulose, lignin) and may vary in their relative proportions. The cell content is highly digestible (80-100%) (Fonnesbeck, 1968, 1969), and the true digestibility of the cell wall is more limited (40-50%) (Fonnesbeck, 1968, 1969). Thus, the nutritive value of forages can vary considerably and will largely be determined by the fiber content and the fiber quality. The stage of maturity will have a profound effect on the energy and nutrient content of the forage and on the horse's ability to consume offered quantities. By selecting a high-quality forage (high energy content) rather than a low-quality one, the diet proportions between forage and concentrate can be markedly affected (Table 1) and made more favorable with regards to voluntary feed intake and digestive functions (Willard et al., 1977; Radicke et al., 1991).

Table 1. Diet proportions (dry matter; DM) and total DM intake (DMI) of hay and concentrate, and of cereal grains in a hay:concentrate diet with different hay energy content calculated to cover the energy and protein requirements of a 500-kg mature equine athlete (NRC, 1989).

	Proportion of energy from hay:concentrate	
	Hay:concentrate 25:75[1]	*Hay:concentrate 50:50*[2]
Diet proportions[-3]		
Hay, kg DM	4.0	6.6
Concentrate, kg DM	7.0	5.0
Total DMI, kg	11.5	11.6
Cereal grains		
Oats	7.7	5.1
Barley	6.7	4.4
Wheat	6.4	4.2
Maize	6.4	4.2

[1] Hay 8.4 MJ DE/kg DM; 100 g crude protein/kg DM; [2] Hay 10.4 MJ DE/kg DM; 120 g crude protein/kg DM; [3] Concentrate 13.8 MJ DE/kg DM

Concentrate is included in the diets of athletic horses in order to increase the energy density of the diet, thereby making it possible to meet increased energy demands. Cereals, which are characterized by their high starch content, are the major concentrate components. However, feeding excessive amounts of starch can increase the risk of digestive and muscular problems. Total amylase secretion in the equine small intestine is considered to be a limiting factor for starch digestion (Kienzle et al., 1994) and may result in an influx of readily fermentable carbohydrates (i.e., undigested starch) to the hindgut. This could result in colic due to excessive hindgut fermentation (Potter et al., 1992a; Kienzle et al., 1994) and altered microbial activity, leading to unrestrained gas production and a reduction in hindgut pH (Beyer, 1998). Also, gastric ulcers (Beyer, 1998) and tying-up, both sporadic and recurrent exertional rhabdomyolysis (Valberg, 1998), may be related to excessive use of grains and sweet feed in equine rations. Therefore, the replacement of starch-rich cereal grains with non-starch carbohydrate feeds in the equine diet may be an alternative means of avoiding problems related to high starch intakes and undigested starch reaching the hindgut.

The dietary content of starch is markedly affected by the cereal source used in the diet (Table 1), as is the utilization of the cereal carbohydrate part of the diet (Kienzle, 1994). This will change the composition of the digesta reaching the hindgut and will alter hindgut microbial activity.

STARCH UTILIZATION

There are several factors related to the macro- and microstructure of the cereal grain that will affect starch utilization in the horse. The grain macrostructure (i.e., shape, size, husks) will largely determine the utilization of unprocessed cereal grains, but in mechanically processed grains, the macrostructure will be more or less destroyed. The grain microstructure (i.e., structure of starch granules, length and branching of the starch molecule, hydrogen bonds between molecular chains) will to a lesser extent be affected by mechanical processing, and hydrothermal processing (i.e., steam flaking, micronizing, popping, extrusion) may destroy the grain microstructure.

The ileal digestibility of cereal starch varies with grain source and with processing (Kienzle, 1994). In contrast, the total tract digestibility of cereal starches is high and often marginally affected by the grain source and processing (Meyer, 1992). The highest small intestinal starch digestibility is found in oats, and maize starch appears to be less digestible (Kienzle, 1994). The lowest small intestinal starch digestibility has been recorded for barley. A rough mechanical processing of the grain (such as rolling or crushing) does not change the ileal starch digestibility, but fine grinding (<2-mm particle size) will generally improve the ileal starch digestibility. Also, hydrothermal processing (i.e., micronizing, popping) will improve the small intestinal starch digestibility.

In a compilation of data on small intestinal starch digestibility, Kienzle (1994) found a tendency toward lower digestibility with higher starch intakes. The risk of exceeding the small intestinal starch-digesting capacity was dependent on cereal starch source but appeared to occur above an intake of 2 g starch/kg body weight (BW) per meal.

The small intestinal starch digestibility may also be affected by forage source (hay or grass meal), as well as by the proportion of forage and concentrate in the diet (Kienzle, 1994). When the forage source in the diet was grass hay, the small intestinal starch digestibility was lower (20%) than when the forage source in the diet was green meal (47%).

As pointed out by Kienzle (1994), there could be large individual differences in small intestinal starch digestibility in horses, which could partly be explained by differences in small intestinal amylase activity. In addition, individual differences in the eating behavior (i.e., pattern of hay and concentrate ingestion) may be involved in determining the small intestinal starch digestibility.

UTILIZATION OF NON-STARCH CARBOHYDRATE FEEDS

In contrast to cereals, non-starch carbohydrate feeds are characterized by having no starch and a carbohydrate fraction that is composed of sugars and/or dietary fiber. The feeds classified in this category are mainly industrial by-products. The carbohydrate fraction in molasses and syrup contains sugars, and in feeds such as beet pulp and citrus pulp, the major part is made up of dietary fiber.

Simple sugars (glucose and fructose) are effectively utilized by the horse and are absorbed in the small intestine (Meyer, 1992). This is reflected in a rapid increase in plasma glucose values, with a similar response for both glucose and fructose (Bullimore et al., 2000). As shown by Jansson et al. (2002), adult horses have no problem digesting and efficiently utilizing hydrolyzed starch (glucose:maltose:maltotriose proportion of 83:15:2) at levels of 2.5 g/kg BW per day. In contrast, there are limitations in the digestive capacity of certain disaccharides depending on age and the change in secretion of digestive enzymes (Meyer, 1992). Thus, in the foal lactose is effectively utilized due to a high activity of lactase, and sucrose is less efficiently utilized due to a limited activity of sucrase. The situation is reversed in the adult horse. According to Meyer (1992), the upper limit to dietary inclusion of lactose in the adult horse is 1 g/kg BW per day in order to avoid digestive disturbances.

Cellulose and cereal fiber sources are fermented to a limited extent by the equine hindgut microflora (Sunvold et al., 1995a,b). In contrast, fiber-rich feeds containing pectin (sugar beet pulp and citrus pulp), fructooligosaccharides, sugar alcohols, and gums could be expected to be extensively fermented in the hindgut (Sunvold et al., 1995b). However, the rate and extent of fermentation will vary considerably between fiber sources and must be considered when formulating rations for performance horses. For sugar beet pulp, inclusion levels of up to 3.0 g/kg BW per day have been used in adult horses without any negative effects on overall nutrient utilization and performance (Lindberg and Jacobsson, 1992; Lindberg and Palmgren Karlsson, 2001; Palmgren Karlsson et al., 2002).

Non-Starch Carbohydrate Feeds

NUTRITIONAL EFFECTS

Protein digestibility. Replacement of oats with sugar beet pulp (SBP) will result in reduced total tract apparent digestibility of crude protein (CP) at maintained CP content in the diet (Table 2). The reduction observed with SBP inclusion could be explained by an increase in hindgut fermentation due to an increase in the supply of easily fermentable carbohydrates (Moore-Colyer et al., 1997) and the resulting increase in fecal excretion of microbial protein (Sauer et al., 1980; Lindberg and Jacobsson, 1992). Similar effects should be expected with other easily fermentable fiber sources. In contrast, no reduction in the total tract apparent digestibility of CP could be found when barley syrup (BS) replaced oats. The digestion of BS (hydrolyzed barley starch), as well as sugars, will take place in the small intestine and should be expected to be virtually complete when the digesta reaches the hindgut. Consequently, these types of feeds will not contribute to fermentation in the hindgut.

Table 2. Nutritional effects of replacing oats with non-starch carbohydrate energy sources in horse feeds.

		Nutrient content, g/kg DM					*Digestibility, %*				
Exp.	*Diet*	*Protein*	*Fat*	*Starch*	*Sugars*	*NDF*	*Protein*	*Fat*	*NDF*	*Energy*	*Ref.*
I	OLF	109	29	179	50	460	58	22	40	52	1
	OHF	109	55	145	52	461	59	51	42	54	
	SBPLF	111	23	106	49	482	52	-5	42	51	
	SBPHF	109	49	99	50	477	53	40	42	52	
II	Oats	112	25	147	39	491	72	38	40	56	2
	SBP	116	20	86	82	485	67	8	43	54	
III	BS 0	100	26	131	19	426	59	34	42	58	3
	BS 0.5	96	24	109	62	418	54	25	37	55	
	BS 1.0	93	21	84	104	413	55	17	36	54	
	BS 1.5	90	18	61	151	405	58	13	43	60	

1. Lindberg and Palmgren Karlsson (2001). Grass hay:concentrate ratio 0.56:0.35, main concentrate ingredients; OLF (oats), OHF (oats, maize oil), SBPLF (dried unmolassed sugar beet pulp, oats), SBPHF (dried unmolassed sugar beet pulp, oats, maize oil).
2. Palmgren Karlsson et al. (2002). Grass hay:concentrate ratio 0.66:0.34, main concentrate ingredients; Oats (oats), SBP (dried molassed sugar beet pulp, oats).
3. Lindberg (unpublished data) and Jansson et al. (2002). Grass hay:concentrate ratio 0.65:0.35, main concentrate ingredients; BS 0 (oats), BS 0.5 (oats, barley syrup 0.5 kg/d), BS 1.0 (oats, barley syrup 1.0 kg/d), BS 1.5 (oats, barley syrup 1.5 kg/d).

It should be noted that a reduction in total tract digestibility of CP may not give a true reflection of the utilization of dietary CP, due to the influence of hindgut digestion. The absorption of amino acids in the small intestine may be of a similar magnitude despite differences measured in the total tract digestibility. Interestingly, the retention of digested CP and the plasma urea levels remained unchanged when oats were replaced with SBP (Palmgren Karlsson, 2001) or BS (Lindberg, unpublished data), indicating that there were no major differences in CP utilization and nitrogen metabolism between the diets.

Fat digestibility. Replacement of oats with SBP results in a reduction in the total tract apparent digestibility of crude fat (EE). This is caused by a reduction in the dietary fat content (Table 2) and by increased hindgut fermentation. With a lowered dietary fat content, the endogenous fat excretion will make a proportionally larger contribution to the fecal fat content (Meyer, 1992), and with increased hindgut fermentation, a higher endogenous excretion of fat could be expected through enhanced microbial mass (Lindberg and Jacobsson, 1992; Potter et al., 1992b). Also, replacement of oats with BS resulted in a numeric reduction in the total tract apparent digestibility of EE (Table 2) due to the reduction in dietary fat content.

As discussed for CP, a reduction in total tract digestibility of EE may not give a true reflection of the utilization of the dietary fat. It should be expected that the daily intake of fat will greatly influence the crude fat digestibility of the diet (Potter et al., 1992b). Thus, when compiling the digestibility data from diets in which oats were replaced with SBP and BS (Table 3), the crude fat digested was found to be linearly related to the daily intake of fat ($y=0.67x-111$, $r^2=0.91$). The estimated true digestibility of EE (67%) was slightly lower than other published values (Rich et al., 1981; Meyer, 1992). The estimated endogenous fecal excretion of fat in the present data was 13 g/kg DM intake or 237 mg/kg BW. This was considerably higher than values (50-100 mg fat/kg BW) suggested by Meyer (1992) but was within the range of values (9-33 g fat/kg DM intake) reported by Freeman et al. (1968). The discrepancy from the values given by Meyer (1992) may be explained by extensive microbial fermentation in the hindgut and high excretion of microbial mass.

Fiber digestibility. Despite substantial variation in the dietary carbohydrate composition when oats were replaced with SBP and BS (Table 2), the digestibility of neutral detergent fiber (NDF) remained unaffected. If the hindgut digestion was not disturbed by the change in dietary carbohydrate composition, this result should be expected when considering the large NDF contribution from hay in the diets (0.75-0.80 in Exp. I; 0.8 in Exp. II; 0.8-0.9 in Exp. III). Further, the digestibility of NDF in hay:oat diets has been shown to remain unchanged when the dietary proportions have ranged from 100:0 to 60:40 (Palmgren Karlsson et al., 2000). Thus, despite an extensive hindgut digestion of SBP (Longland et al., 1997; Moore-Colyer et al., 1997), its small contribution to the total dietary NDF content (0.14 in Exp. I; 0.06-0.13 in Exp. II) could be expected to result in minor effects on the total tract digestibility of NDF, which would fall within the normal range of variation around the mean (Palmgren Karlsson, 2001).

Energy digestibility and utilization. The digestibility of dietary energy was unaffected when oats were replaced with SBP and BS (Table 2). However, despite limited effects on the digestibility of energy, the excretion of urinary energy (in % of DE) increased (from 4.8-4.9% to 5.3-5.8%) when oats were replaced by SBP (Palmgren Karlsson, 2001). This indicates a negative influence of SBP on the utilization of dietary energy. In contrast, the replacement of oats with BS did not change the extent of urinary energy excretion (Lindberg, unpublished data).

Metabolic Effects

Postprandial glucose response. The replacement of cereal grains with non-starch carbohydrate feeds will reduce the dietary starch content and may alter the glycemic effect of the diet (Stull and Rodiek, 1988). Glucose homeostasis is under strict hormonal control, mainly by insulin, but may also be affected by diet composition. During exercise the glucose supply is primarily provided from body glycogen stores and to a minor extent from gluconeogenesis. In addition, blood glucose levels may be improved by glucose originating from the digestion of dietary starch (Hiney and Potter, 1996). In order to ensure a continuous and sufficient glucose supply for the working muscles, the body glycogen stores have to be filled by proper feeding prior to the onset of exercise. Also, feeding management during the recovery period after exercise may be of importance for the repletion of body glycogen stores (Hiney and Potter, 1996).

Diets resulting in a reduced glucose uptake will be expected to lower peak blood glucose levels and to lower the insulin response, which may have beneficial effects for the exercising horse in maintaining sufficient blood glucose levels (Frape, 1988; Hiney and Potter, 1996). However, available data are not conclusive with respect to the influence of dietary carbohydrate composition on postprandial blood glucose levels. Thus, it has been shown that diets with varying forage to grain ratios fed to ponies (Argenzio and Hintz, 1971; Hintz et al., 1971), as well as diets with varying proportions of alfalfa and corn fed to horses (Stull and Rodiek, 1988), resulted in unchanged blood glucose levels. Similarly, no marked dietary-related effect on postprandial blood glucose was observed (Figure 1) when oats were replaced with molassed SBP (Palmgren Karlsson et al., 2002) or when oats were replaced with BS (Jansson et al., 2002). However, when replacing oats with plain SBP, the postprandial increase in plasma glucose was slower and the peak concentration was lower (Lindberg and Palmgren Karlsson, 2001).

Exercise glucose response. The replacement of oats with SBP had no effect on plasma glucose levels in blood samples taken during an exercise test (ET). The horses completed a distance of 2,600 m on a 2.5% incline (Phase 3) at about 90% of VO_{2max} (~205 beats/min), following a warm-up at submaximal speed for 24 minutes (Phase 1) and a two-hour rest in a box (Phase 2) (Palmgren Karlsson et al., 2002). Also, the replacement of oats with BS had no effect on plasma glucose levels in blood samples taken during an incremental exercise (IE) test performed at a 6.25% incline at four speeds stepwise, increasing from 6 m/s to 9 m/s every second minute, or during a submaximal exercise (SE) test performed on the flat at 50-60% of VO_{2max} (5.5-7.5 m/s) for 40 minutes, which corresponded to a distance of 17 km (Jansson et al., 2002).

Postprandial insulin response. In contrast to blood glucose, a response in postprandial insulin levels is often observed when the availability of dietary carbohydrates is improved due to a change in composition (Hiney and Potter, 1996). This implies that insulin, as compared with glucose, would be a more sensitive and useful indicator of any glycemic effect of the diet.

It has been shown that the postprandial insulin levels were different when feeding the diets with SBP as compared with oats (Figure 1), with a less pronounced insulin response when oats had been replaced with SBP (Lindberg and Palmgren Karlsson, 2001; Palmgren Karlsson et al., 2002). Further, it was also noted that the oat diet resulted in higher plasma insulin values at rest than the diet where oats were replaced with SBP (Palmgren Karlsson et al., 2002). Also, when oats were replaced with BS there was a marked postprandial response in insulin (Jansson et al., 2002). However, in contrast to the studies on SBP, the replacement of oats with BS did not show any differences in insulin response that could be related to the change in dietary carbohydrate composition. These findings can be explained by the change in dietary carbohydrate availability and the resulting change in the site of digestion and absorption of digestion products. The less pronounced insulin response observed with SBP inclusion could be explained by the reduction in dietary starch content and, with a shift in carbohydrate digestion from the small intestine to the hindgut, by an increase in the supply of easily fermentable carbohydrates (Moore-Colyer et al., 1997). In contrast, when oats were replaced with BS the potential availability of the easily available part of the dietary carbohydrate fraction changed, while the composition of fermentable fraction of the diet remained unchanged. Thus, the digestion of BS (hydrolyzed barley starch), as well as of oat starch (Kienzle, 1994), will take place in the small intestine and should be expected to give a similar response in insulin, provided that the digestion of the unprocessed oat starch is virtually complete when the digesta reaches the hindgut. The insulin response suggests a significant influence of diet carbohydrate composition on nutrient utilization in horses and could possibly also have effects on the subsequent performance.

Exercise insulin response. The replacement of oats with SBP had no effect on insulin levels in blood samples taken during the ET (Palmgren Karlsson et al., 2002). Also, the replacement of oats with BS had no effect on insulin levels in blood samples taken during the IE or SE tests (Jansson et al., 2002).

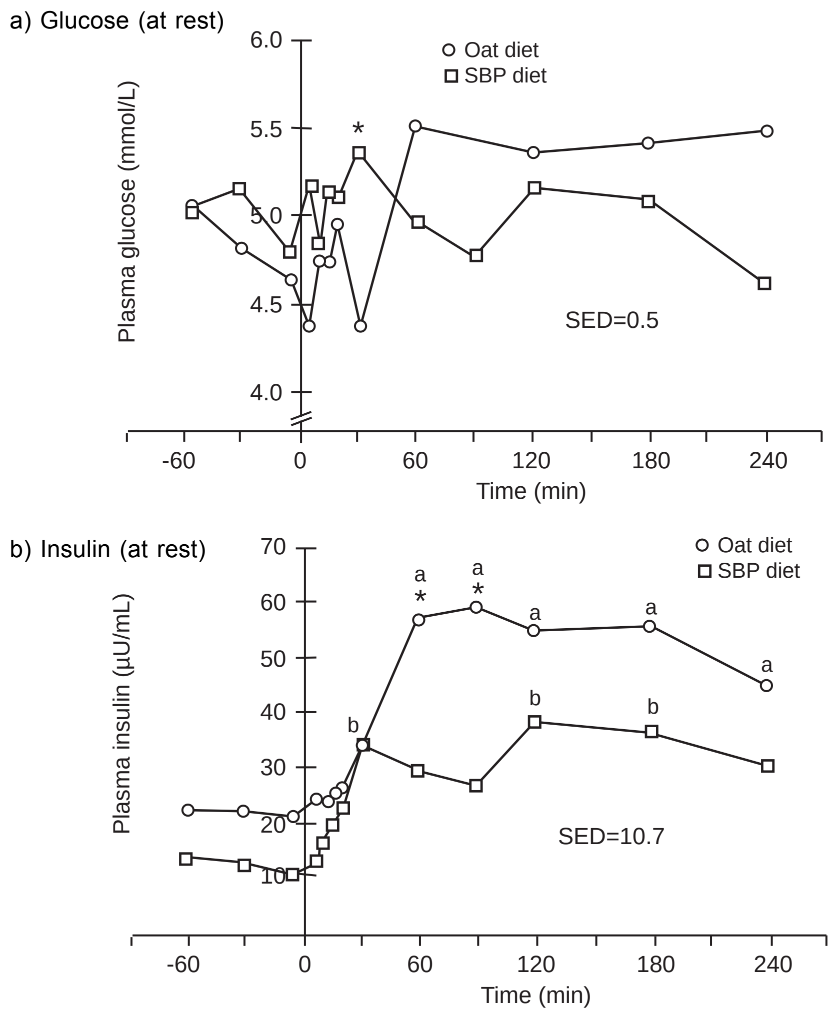

Figure 1. Concentrations of plasma glucose and insulin at rest in Standardbred horses. Oat diet and SBP diet. H = difference between diets (P<0.05). The SED (standard error of difference) refers to the comparison of diets within time. a = Oat diet: value differing significantly (P<0.05) from the preprandial mean value; b = SBP diet: value differing significantly (P<0.05) from the preprandial mean value (Palmgren Karlsson et al., 2002).

Exercise lactate response. The plasma lactate concentration increased following the intensive trots during Phases 1 and 3 of the ET (Figure 2) (Palmgren Karlsson et al., 2002). A higher peak lactate concentration was found at Phases 1 and 3, as well as five minutes after the intensive trot in Phase 1, on the oat diet than on the SBP diet. However, when oats were replaced with BS there were no dietary effects on plasma lactate concentration during the IE or SE tests (Jansson et al., 2002).

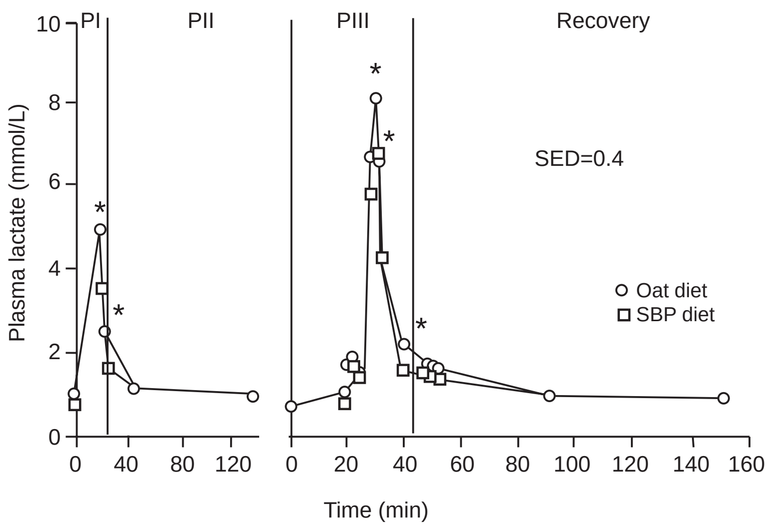

Figure 2. Concentrations of plasma lactate during the exercise test performed in Standardbred horses, where PI = Phase I (warming-up), PII = Phase II (rest) and PIII = Phase III (simulated trotting race). The SED (standard error of difference) refers to the comparison of diets within time (Palmgren Karlsson et al., 2002).

Exercise muscle glycogen and muscle lactate response. When oats were replaced with SBP, the content of muscle glycogen was similar prior to the ET, but it was higher after the ET on the SBP diet (Table 3) (Palmgren Karlsson et al., 2002). Also, the muscle lactate content increased following the ET, and the post-exercise level of muscle lactate was significantly higher on the oat diet than on the SBP diet (Table 3). When oats were replaced with BS, there was a gradual change in muscle glycogen content following the SE test, resulting in more glycogen remaining with increasing replacement of oats (Jansson et al., 2002). It was found that muscle glycogen utilization decreased (r^2=0.96) with increasing proportions of sugar in the diet (Figure 3).

Table 3. Effect of submaximal exercise on muscle glycogen and muscle lactate values (mmol/kg dry weight) in horses fed diets where oats were replaced with sugar beet pulp (SBP) (Palmgren Karlsson et al., 2002).

		Diet		
	Exercise	*Oats*	*SBP*	*Significance*
Muscle glycogen#	Before	546	597	NS
	After	394	484	P<0.05
Muscle lactate§	Before	10.8	10.4	NS
	After	38.5	22.7	P<0.05

[#] SED 39; [§] SED 3.8

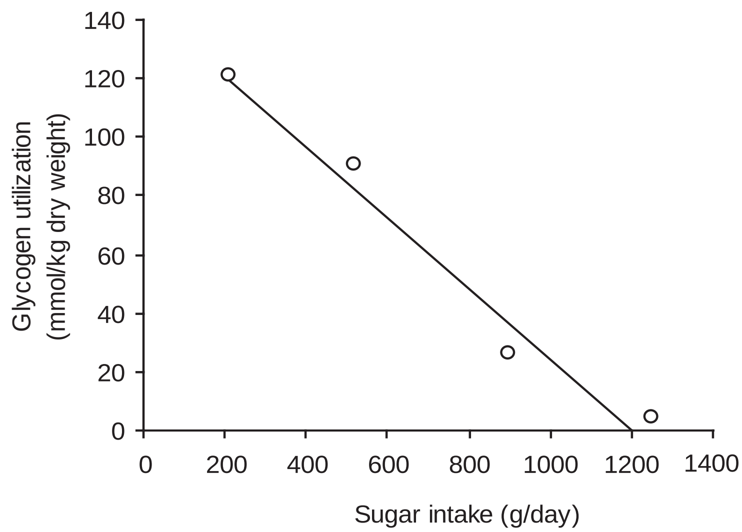

Figure 3. Muscle glycogen utilization (SEM 44) in relation to daily sugar intake (y=143.1-0.12x, R^2=0.96) (Jansson et al., 2002).

Exercise oxygen consumption (VO_2) and respiratory quotient (RQ). There was no significant dietary effect with regard to VO_2 during the performance of the SE test (Jansson et al., 2002) when oats were replaced with BS, although the VO_2 was numerically lowered with increasing replacement of oats. However, for RQ a dietary effect could be verified if the diets were pooled into HIGH (1.8-2.5 g sugar/kg BW per day) and LOW (0.3-1.0 g sugar/kg BW per day) sugar intake. Thus, RQ was consistently higher on HIGH than on LOW (0.83 vs 0.80, 0.83 vs 0.80, 0.81 vs 0.78 and 0.80 vs 0.77 (SD 0.03) at 10, 20, 30, and 40 min, respectively) during the performance of the SE test.

The data presented above show that manipulation of the dietary carbohydrate composition to modify the relative proportions of sugars, starch, and fermentable fiber in the ration could alter energy and glucose metabolism in exercising horses. In accordance with Pagan et al. (1987), a high sugar intake could be expected to augment the metabolism of carbohydrates during submaximal exercise as shown by the increased RQ. Also, as the oxygen consumption was lowered (numerically), it could be expected that a greater proportion of the energy was generated from anaerobic metabolism. However, the plasma lactate levels were not affected by diet, which could be due to the low intensity of the work and that the potential for lactate to be converted into pyruvate by the liver and muscle tissue was not limited. It could be speculated that the increased carbohydrate consumption during the submaximal exercise was due to a high availability of glucose in plasma originating from the liver because muscle glycogen utilization was reduced. This contention is supported in results presented by Pagan et al. (1987), which showed that there is a positive relationship between muscle glycogen content and RQ during low-intensity exercise.

The blood and muscle biopsy data suggest that the rate of glycogenolysis with lactate production can be modified by manipulation of the dietary carbohydrate composition. It appears likely that the dietary proportions of sugars, starch, and fermentable fiber are key elements in understanding this metabolic effect. The glycogen-saving effect of replacing oats with SBP (Palmgren Karlsson et al., 2002) could possibly be explained by a higher production of short-chain fatty acids (SCFA; i.e., acetate, propionate, and butyrate) in the hindgut as a result of the change in diet carbohydrate composition and a shift in digestion from the small intestine to the hindgut, and the subsequent increase in SCFA absorption in the portal blood. After transport into the cell the SCFA will be transformed to acetyl-CoA via specific fatty acyl-CoA ligases, thus resulting in the same key metabolite that is being produced from the beta-oxidation of fat. Therefore, the inclusion of fermentable fiber in the diet may result in a similar glucose-saving (and glycogen-saving) effect as that ascribed to the supply of fat in the equine diet (Potter et al., 1992b) by providing an alternative substrate for the aerobic energy metabolism in the muscle. Another possible, and maybe more likely, explanation to the glycogen-saving effect of replacing oats with SBP (Palmgren Karlsson et al., 2002) could be the increase in sugar intake (increase of about 350 g sugar/day when SBP replaced oats in the diet) and an increased utilization of blood-borne glucose. Acute oral administration of glucose (Geor et al., 2000) and acute ingestion of a glycemic meal (Jose-Cunilleras et al., 2002) prior to submaximal exercise have been shown to cause an augmentation of carbohydrate oxidation and utilization of blood-borne glucose during exercise. This is also supported by the data showing that muscle glycogen utilization decreased with increasing proportions of sugar in the diet (Figure 3) when oats were replaced by BS (Jansson et al., 2002). When oats replaced SBP (Palmgren Karlsson et al., 2002) the decrease in muscle glycogen content was 152 and 113 mmol/kg dry weight on the oat and SBP diets, respectively. The difference between diets (39 mmol/kg dry weight) was comparable to the glycogen-saving effect of increasing sugar intake (350 x 0.12 = 42 mmol/kg dry weight) found by Jansson et al. (2002).

Conclusion

In conclusion, the limited nutritional effects of replacing oats with non-starch carbohydrate feeds suggest that this feeding practice could be used in the horse industry to minimize the risk of digestive disturbances from excessive starch intake without impairing the overall nutrient utilization. Furthermore, a more extensive use of non-starch carbohydrate feeds to allow a manipulation of the dietary carbohydrate composition, aiming at modifying the relative proportions of sugars, starch, and fermentable fiber in the ration, may cause beneficial alterations in the energy and glucose metabolism of the exercising horse.

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