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STARCH DIGESTION IN THE HORSE

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Introduction

The rate and extent of starch digestion is determined by:

1. properties of the starch granule;
2. the effect of processing;
3. associated food structures (plant cell walls);
4. transit time through the small intestine;
5. the availability and concentration of enzymes.

These factors will affect the glycemic response of the horse to feeding and the subsequent production of insulin. Resistant starch, together with undigested starch, will pass into the large intestine of the horse where it may be fermented to short chain fatty acids. Resistant starch may escape digestion in the small intestine of the horse because:

1. of physical entrapment within a food, such as in partly-milled grains and seeds (RS_1 starch);
2. starch granules have a B or C crystalline structure which is highly resistant to digestion (RS_2 starch);
3. retrogradation through food processing, mainly in the form of retro-graded amylose (RS_3 starch).

RS_3 starch is entirely resistant to digestion by pancreatic amylase in man (Englyst and Macfarlane, 1986) and this starch is commonly found in peas. RS_1 and RS_2 are quantitatively the most important forms of resistant starch found in horse feeds.

Starches and the Horse

Irrespective of starch source, total tract apparent digestibility is usually very high. For example, Arnold et al. (1981) measured digestion coefficients for corn, oats and sorghum starch as 97.0, 96.7 and 97.0% respectively. Differences are apparent between starch sources when measuring small intestinal or pre-cecal apparent digestibility of starch. Arnold et al. (1981) reported values of 78.2, 91.1 and 94.3% respectively for corn, oats and sorghum. These values were much higher than those reported by Householder (1978) but were explained on the basis of a lower dry matter intake and thus, presumably, a slower rate of passage. Several authors (e.g. Kienzle et al., 1992; Meyer et al., 1993) have confirmed that oat starch is the most digestible of the cereal starches fed to horses, followed by sorghum. Corn starch was much less digestible and, in the report by Meyer et al. (1993), barley starch was the least digestible. These differences are largely explainable on the basis of the differences between the starch granules contained in the different plant materials; oat starch granules are small and easily digested.

Processing can affect starch digestibility, although the magnitude of the effect depends on the nature of the process used. Crude physical treatments such as rolling, crushing or grinding do not significantly improve oat starch digestibility (Kienzle et al., 1992) or that of corn (Meyer et al., 1993). In contrast, fine grinding (<2mm) can improve small intestinal starch digestibility of corn (Kienzle et al., 1992; Meyer et al., 1993). Cooking, either by micronizing or popping (Householder, 1978; Meyer et al., 1993) can lead to significant improvements in pre-cecal starch digestibility, particularly with respect to corn (Meyer et al., 1993). Thus, while some starch sources are poorly degraded when raw, appropriate cooking procedures can significantly improve pre-cecal starch digestion, the best example of this being that of corn (Meyer et al., 1993).

In a review of starch digestion, Potter et al. (1992) suggested that small intestinal starch digestibility declined as starch intake increased; this relationship was confirmed by Kienzle (1994). Potter et al. (1992) further suggested that in meal-fed horses, the upper limit of starch feeding should be 3.5 to 4 g starch/kg body weight/meal. Kienzle et al. (1992) suggested that, depending on the starch source, if the intake exceeded 2 g/kg body weight/meal, there was a risk that the capacity of the small intestine to degrade starch could be exceeded. Thus, there are widely differing estimates of "safety" in terms of meal-feeding starch. A further complication is that of feed interactions; it is naïve to think that starch sources will be degraded in a constant way, irrespective of the basal diet. It has already been pointed out that transit time through the small intestine and availability of enzymes will significantly affect the process of degradation. For example, Meyer et al. (1993) demonstrated that the pre-ileal digestibility of ground corn was reduced by substituting green (*sic*) meal for hay in a mixed ration. Kleffken (1993) showed that this substitution altered the rate of passage of starch in the small intestine and this presumably accounted for the differences measured by Meyer et al. (1993). The unusual results obtained by Hinkle et al. (1983), whereby starch digestibility remained the same or increased with increasing starch intake, may be explained on the basis that roughage feeding declined and thus digesta passage rate would have declined. Animal to animal variability will mean that some horses are better able to digest starch than others are. A basic difference between horses is their effectiveness at comminuting foodstuffs and, since particle size has been shown to correlate with pre-cecal starch digestibility (Meyer et al., 1993), those animals that eat rapidly and/or have poor occlusion will have reduced small intestinal starch digestion. This has been demonstrated by Professor Meyer's group at Hannover (Landes, 1992; Wilke, 1992) in horses fed whole corn. Other differences may exist between horses in terms of enzyme production (Radicke et al., 1992). This view is supported by the fact that small intestinal degradation of ground corn was assisted (from 47.3% to 57.5%) by the addition of amylase (Meyer et al., 1993). Unquestionably, small intestinal passage rate will vary between individual horses, even when fed in the same way. Thus, the notion that there is a "safe" upper level for meal-feeding horses or ponies with starch is questionable in view of the aforementioned factors that significantly impact on the extent of starch digestion in the small intestine.

Cereal Processing- Some Recent Work

Potter et al. (1992) noted the effects of processing on cereals could be masked by differences between sources of starch. In view of this, some experiments were planned to examine the effects of processing on barley utilization by the horse, barley having been previously shown to have a low pre-cecal digestibility (Meyer et al., 1993). Barley of one variety from one field was harvested, dried and then subsequently rolled, micronized or extruded for use in a series of experiments. Animals used were mature Welsh-cross pony geldings (body weight – 280 kg) and each was fitted with a cecal cannula.

In Vivo Studies

This work has been recently reported (McLean et al., 1999a) and involved offering ponies 4 kg DM per day (in two equal meals at 09.00 and 17.00 h) of either 100% hay cubes or one of three diets (different forms of barley) consisting of a 50:50 barley: hay cube mix. The results from this incomplete Latin square changeover design experiment were in accordance with expectation in that different physical processing methods do not alter total tract apparent digestibilities *in vivo* (Potter et al., 1992). Furthermore, the apparent digestibility of the energy (DE) and crude protein of the barley were unaffected by processing; the DE contents of the rolled, micronized and extruded barley were 14.5, 14.8 and 15.0 MJ/kg DM respectively, similar to the NRC (1989) value of 15 MJ/kg DM. Apparent organic matter and starch digestibilities were respectively 841 and 967 for the rolled barley, 846 and 969 for the micronized barley and 837 and 966 g/kg for the extruded barley. *In vivo* total tract apparent digestibility studies give no indication of whether the starch was degraded by mammalian enzymes in the small intestine or by microbial enzymes in the large intestine. These ponies were fed approximately 2.4 g starch/kg body weight/meal and the apparent digestibility of the starch was uniformly high.

In Situ Studies

The three different forms of barley were incubated in the ceca of fistulated ponies to provide time-based degradation data utilizing microbial enzymes (McLean et al., 1998a). Degradation profiles were fitted to the dry matter and starch disappearance data according to Orskov and McDonald (1979). The degradation coefficient ‘a’ was greatest for the micronized barley, and significantly so ($p< 0.05$) for dry matter loss. As expected, no differences existed between the different forms of barley by 40 h of incubation, although extrusion reduced the effective degradability of dry matter to a small but significant ($p< 0.05$) extent when compared to the rolled barley. This negative effect may have been as a result of complexation during the extrusion process producing indigestible Maillard products. More importantly, at outflow rates ($k= 0.50$, 0.33 and 0.20) which reflected mean retention times (MRT) of 2, 3 or 5 h in the pre-cecal segment of the digestive tract, the DM degradability was greatest for the micronized cereal, followed by the extruded barley; the rolled barley had the lowest effective degradabilities (B.M.L. McLean-unpublished data). However, the only significant ($p<0.05$) difference was at $k=0.50$ when the effective DM degradability of micronized barley was 690.7 compared to that of 631.9 g/kg for the rolled barley. When considering starch degradation, there were no significant differences between starch degradation parameters although again, the coefficient ‘a’ for micronized barley was the highest. In contrast, comparison of the effective degradabilities of starch at $k=0.50$, 0.33 and 0.20 produced significant differences between the differently processed barleys. At $k=0.50$, micronized barley was degraded more than the other barleys and significantly so ($p< 0.05$) in respect to extruded barley. This was also the case at $k=0.33$ and at $k = 0.20$; the starch of micronized barley was significantly ($p< 0.05$) more degraded than that of the other two barleys, 929.3 compared to 857.1 for extruded and 857.8 g/kg for rolled barley. These important difference between barley sources in terms of starch degradability will have an impact on the nature of the feed residues from a meal that enter the cecum. If we assume a transit time from the esophagus to the ileo-cecal valve of 3 to 4 h, then the provision of micronized barley should result in less undigested starch entering the large intestine compared to when rolled barley is fed. If undigested starch were made available to the microflora within the large intestine of the horse, then changes in the cecal environment would be expected that would be analogous to those measured in the rumen of cows or sheep overfed cereal. There would be a reduction in pH together with a change in the molar proportions of the volatile fatty acids, increased propionate and decreased acetate.

In Vivo Studies

The effects of physical processing of barley on intra-cecal pH and volatile fatty acid parameters have recently been reported (McLean et al., 1998b). The provision of a meal supplying 2.4 g starch/kg body weight in the form of rolled, micronized or extruded barley, together with hay cubes, significantly reduced ($p< 0.05$) cecal pH and acetate and increased propionate, compared to a 100% hay cube diet, when measured 5 h post-feeding. Feeding rolled barley with the hay cubes caused lower ($p< 0.05$) acetate and higher ($p< 0.05$) propionate compared to when micronized barley was fed with the hay; these changes were apparent through most of the day following the 0900 h meal. The micronized barley increased ($p< 0.95$) acetate and lowered ($p< 0.05$) propionate compared to extruded barley at most hourly samplings throughout the day. At 5 h post-feeding, cecal pH values were 6.24, 6.33, 6.38 and 6.48 respectively for rations containing rolled, micronized and extruded barleys with hay cubes and hay cubes alone. Acetate values (mmol/mol) in the cecum were 627, 716, 685 and 764, whereas propionate levels were 302, 221, 250 and 174 respectively. As expected, the hay cubes ration resulted in the highest acetate (764) and the lowest propionate (174) values; the ration containing the micronized barley had the closest values, 716 and 221 respectively.

Mobile Nylon Bag Studies

The mobile nylon bag technique has been used to study the degradation dynamics of forages over the whole length of the digestive tract of equids (Hyslop et al., 1998) and in the pre-cecal segment (Moore-Colyer et al., 1997). Recently McLean et al. (1999b) have used the technique to investigate the degradation of purified wheat starch, chemically modified wheat starches and a purified pea starch. Bag transit times (following introduction by nasogastric tube into the stomach) to the cecum varied between 1 and 7.5 h. Pea starch was the least well degraded (probably due to the presence of resistant starch, RS_3) in the small intestine whereas wheat starch required extensive chemical modification (cross-linking) before pre-cecal degradation was significantly ($p < 0.5$) reduced. It was concluded that the mobile nylon bag technique could be used to successfully model feed degradation dynamics over time in the pre-cecal segment of the equine digestive tract. Thus, the technique was used to measure pre-cecal losses of dry matter and starch from the differently processed barleys. Initial results for the effective degradabilities of the dry matter of rolled, micronized and extruded barleys at k=0.50, 0.33 and 0.25 showed that extruded barley had significantly ($p < 0.05$) lower effective degradability at all assumed MRT; there were no differences between rolled or micronized barleys (B.M.L. McLean – unpublished data). The starch data have yet to be modelled.

Discussion

Willard et al. (1977) showed that cecal pH was affected by diet; pH was significantly ($p<0.05$) lower at 4, 5 and 6 h post-feeding 6 kg sweet feed to horses compared to when hay was fed. Furthermore, the molar proportions of acetate and propionate were altered; there was more propionate *pro-rata* when concentrate was fed and lactic acid levels were higher. An interesting observation by these authors was that horses fed the concentrate-only diet chewed wood and practiced coprophagy. The lowest mean cecal pH recorded by Willard et al. (1977) was 6.12, 6 h post-feeding concentrate.

Essentially, the results obtained by Willard et al. (1977) showed that feeding large amounts of starch-rich feed affects the cecal environment in terms of pH and in terms of the proportions of volatile fatty acids formed therein. The latter effect had already been recorded by Hintz et al. (1971) when they examined the effects of feeding different forage: concentrate ratios.

Garner et al. (1975) developed an experimental model for the induction of laminitis in horses. A gruel of 85% corn starch and 15% wood cellulose was introduced via a cecal fistula at the rate of 17.6 g/kg body weight in order to create a “grain overload.” Assuming a dry matter (values not given) for the gruel of 200 g/kg, then the starch supplied would have been about 3 g starch/kg body weight. Grain overload, together with gastrointestinal disease, are the most common predisposing factors to laminitis in horses (Slater et al., 1995). Prior to grain overload, mean cecal pH was 7.18 and this fell to 5.72, 8 h after the overload. At this pH and by this time, *Lactobacillus spp* had significantly ($p<0.05$)

increased in number (Garner et al., 1978). These authors concluded that low cecal pH causes the death of favorable organisms, releasing endotoxins, and that lactic acid accumulates and causes a generalized lactic acidosis. Radicke et al. (1991) measured the effect of feeding 1 to 2, 2 to 3, or 3 to 4 g of starch/kg body weight/meal using either oats or corn as a source of the starch. As expected, at all levels of intake, cecal pH was lower when corn was fed, and the differential between the two cereals increased in proportion to starch intake. Increasing oat starch intakes to the levels asserted as "safe" by Potter et al. (1992) did not significantly reduce cecal pH. However, feeding the same level of corn starch caused a marked reduction in cecal pH to values close to 6. Radicke et al. (1991) considered that a cecal pH of 6 represented sub-clinical acidosis, and below 6 there was considerable risk in terms of the development of clinical conditions and in terms of imbalancing cecal fermentation. This was in accord with the results obtained earlier by Garner et al. (1978). Recently, Johnson et al. (1998) fed a changing ration over a 4-week period to 400/500 kg horses. Initially, they were fed 8 kg hay, then 6 kg hay and 2 kg concentrate, then 4 kg hay and 4 kg concentrate and in the fourth week, 2 kg hay and 6 kg concentrate. The daily ration was fed in two equal parts so ultimately the horses received a meal of 3 kg concentrate and 1kg of hay. If the concentrate contained 550 g starch/kg, then the starch supplied would have been between 3.3 and 4.1 g/kg body weight, within the Potter et al. (1992) recommendations. However, the authors measured a declining fecal pH from about 6.6 to below 6 and noted abnormal behaviors similar to those recorded by Willard et al. (1977). Unfortunately, Johnson et al. (1998) failed to confirm the relevance of fecal pH to cecal pH at post mortem. A recent survey (L Paul-unpublished data) of feces from horses fed different diets confirmed that the nature of the diet can affect the fecal pH value. Horses at grass produced feces with a pH of 6.75 (n=34), racehorses fed 70% oats and 30% forage had an average fecal pH of 6.38 (n=20) and forage-fed ponies had a value of 6.49 (n=6); there was considerable between-animal and circadian variation. Johnson et al. (1998) showed that the daily feeding of 225 mg of virginiamycin prevented the extreme fall in fecal pH associated with the increased level of concentrate feeding although at the highest level, fecal pH was still significantly ($p< 0.05$) reduced compared to horses only fed hay. The starch was mostly cereal in origin, supplied by wheat and barley, so that there would be no expectation of low pre-cecal starch digestion; unfortunately, the authors did not describe the form of the concentrate. The fact that virginiamycin appeared to have some "protective" effect, possibly through suppressing lactic acid production (Rowe et al., 1994), suggests that, even with relatively low starch intakes, horses may suffer cecal dysfunction without enduring very low cecal pHs. This is in accordance with the views of Radicke et al. (1991).

Finally, another situation in which cecal function may be compromised is when horses and ponies consume grass. Fructan is a fermentable polysaccharide stored in grass which can comprise 5 to 50% of the grass DM. Fructan cannot be digested by mammalian enzymes so that if it escapes hydrolysis in the stomach, it will enter the cecum undegraded. If there is a 30% loss of non-fructan DM in the small intestine (extrapolated from data of McLean et al., 1998b) then it is possible to calculate the likely amount of fermentable fructan entering the cecum. Thus, if 25% of grass DM is fructan, then it will comprise about 32% of the DM entering the cecum. McLean et al. (1998b) measured significant ($p< 0.05$) reductions in cecal pH when only small amounts of starch entered the cecum (approximately 20% of the DM) which suggests that the ecosystem is quite sensitive to small amounts of rapidly fermentable substrate. Thus, the consumption of fructan-rich grass by horses may cause changes analogous to those measured when starch escapes small intestinal digestion; this may, perhaps, partially explain the occurrence of laminitis at grass. Unfortunately, grass fructan levels are immensely variable, unlike the level of starch in a cereal, and thus it is impossible as yet to predict likely fructan intake. However, we do know that, unlike starch, fructan cannot be degraded in the small intestine of the horse although it may be susceptible to hydrolysis in the stomach.

It is apparent that horse feeders must minimize the flow of fermentable polysaccharide to the large intestine of the horse to maintain health and to maximize substrate (glucose) availability to the performance horse. While this goal is achievable with starch by simply feeding highly degradable micronized cereals little and often, the regulation of fructan intake remains an irresolvable problem.

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