Starch digestion capacity of poultry

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ABSTRACT Starch is quantitatively the most important nutrient in poultry diets and will to a large extent be present as intact starch granules due to very limited extent of gelatinization during pelleting. Although native starch is difficult to digest due to a semi-crystalline structure, even fast-growing broiler chickens appear to be able to digest this starch more or less completely during passage through the jejunum. However, reduced starch digestibility has been observed, particularly in pelleted diets containing large quantities of wheat. Although properties of the starch granule such as size and components on the granule surface may affect digestibility, the entrapment of starch granules in cell walls and a protein matrix may be even more important factors impeding starch digestion. In that case, this and the fact that amylase secretion is normally very high in poultry may explain the lack of convincing effects of exogenous α-amylase added to the diet. However, few well-designed experiments assessing mechanisms of starch digestion and the effect of α-amylase supplementation have been carried out, and thus more research is needed in this important area.

Key words: amylase, broiler, enzyme

INTRODUCTION

Among the nutrients in poultry diets, starch is quantitatively the most important. Diets may contain up to 50% starch on a DM basis, and starch is the most important source of energy. This is a logical consequence of cereals being the most important ingredient in poultry diets, and although Klasing (2005) has stressed that galliformes are omnivorous and not granivorous as often stated, the capacity for digesting starch is high, as will be discussed below. It is also well known that the capacity for digesting fat is limited, at least in young birds (Wiseman et al., 1998), and thus starch must be the main energy source in diets. The other potential energy sources of sugar and protein are, at least from an economic and technical point of view, not suitable as primary energy sources.

The main source of starch is seeds from plants in the grass family, where starch is stored and used as an energy source by the offspring during germination. Although this source is predominantly in the form of maize, wheat, and other cereals, starch from tubers such as cassava may also be used in poultry diets.

STARCH STRUCTURE

Starch chemical structure and digestibility in general (Svihus et al., 2005; Tester et al., 2006; Singh et al., 2010), and for broiler chickens specifically (Carré, 2004; Svihus, 2011) have been reviewed previously. Two distinct populations of starch exist. Amylopectin consists of α-1–4 glucose chains with frequent branches due to α-1–6 bonds, whereas amylose is characterized by very few branches. Indeed, no structural continuum is observed between these 2 types of α-glucans (Buléon et al., 1998). Usually, less than half the amylose will be branched and the number of branch points will be less than 20 per molecule, whereas for amylopectin the average number of branch points will be approximately once per 20 glucose units (Hizukuri et al., 1997). Whereas amylose has a molecular weight of around 100 kDa, amylopectin has a much higher molecular weight in the order of $10^4$ to $10^6$ kDa (Buléon et al., 1998). Amylose forms double helices or single helices in the native state (Buléon et al., 1998). Single helices give rise to a central cavity that can be filled with compounds such as iodine, alcohols, or fatty acids. Most starches contain between 200 to 250 g of amylose/kg, although some waxy starches contain very little, and other starches, such as amylomaize, may contain 650 to 700 g of amylose/kg (Parker and Ring, 2001). In the native state, starch is organized in very complex and large structures, where amorphous and crystalline layers alternate to form rigid, semi-crystalline granules, varying in size from 1 to 50 μm. Although the starch granule...
structure is far from completely understood (Perez and Bertoft, 2010), the semi-crystalline layer is believed to consist of alternating layers of crystalline α-glucans extending from intermittent branches of amylopectin and amorphous amylopectin branch points, respectively. It has been hypothesized that 1 growth ring is laid down per day due to variation in photosynthetic activity and thus access to glucose (Tester, 1997; Smith, 2001). As discussed by, for example, Tester et al. (2004), starch granule architecture will vary among cereal sources both in regard to size and shape of the granules and to the molecular architecture of the granule. Wheat, rye, and barley have lenticular large (10–40 μm) and spherical/polyhedral small (2–10 μm) granules in a bimodal distribution, whereas maize and sorghum have spherical/polyhedral granules (2–30 μm) with a unimodal distribution.

**STARCH DIGESTION**

It is generally accepted that the highly organized structure will pose a challenge for starch digestion, and that native starch therefore will be incompletely digested by many species. Björck et al. (2000) stated that the degree of crystallinity is inversely related to the rate of starch digestion, and Zhang et al. (2006a,b) substantiated this by concluding that the slow digestibility of native starch is related to the ordered structure of alternating crystalline and amorphous layers in the starch granule. In fact, Zhang et al. (2006a) showed that digestion of starch granules starts at surface pores and interior channels, which allows for the amylase to enter the interior and digest the granule gradually from the inside.

When native starch is exposed to high temperatures with water present, the granular structure will disintegrate in a process called gelatinization, and starch will appear as an amorphous water-soluble mass. With an excess water content (e.g., above 40%), gelatinization temperature for most cereal starches ranges between 50 and 70°C. The gelatinization process renders starch molecules more available for α-amylase, facilitating starch digestion, although consistent improvements in starch digestibility have not been observed for all species [e.g., in broilers fed starch that has been completely gelatinized in an extrusion process (Plavnik and Sklan, 1995; Zimonja and Svihus, 2009)]. Several investigations, using enzymatic or calorimetric methods, have shown that due to limited moisture content and moderate temperatures during conventional pelleting, only a small amount of starch gelatinization, varying between 5 and 30%, occurs (Skoch et al., 1981, 1983; Goelena et al., 1999; Svihus et al., 2004; Moritz et al., 2005; Zimonja et al., 2007, 2008; Zimonja and Svihus, 2009).

Even under more severe temperature and shear treatments such as expander-pelleting, starch gelatinization will not be complete. Starch gelatinization of between 22 and 36% has been reported for expanded and pelleted feeds (Goelena et al., 1999; Cramer et al., 2003; Zimonja et al., 2007). Results by Cramer et al. (2003) showed no improvements in starch digestibility with the application of expander treatment followed by pelleting. Similar observations were reported by Plavnik and Sklan (1995), where no change in apparent starch digestibility in broilers fed expanded, compared with unprocessed, feeds was observed. Zimonja and Svihus (2009) likewise failed to detect any significant improvements in starch digestibility for broiler chickens as a consequence of pelleting, although a complete gelatinization due to extrusion improved starch digestibility of wheat diets exhibiting low digestibility. Carré et al. (1991) observed an increased starch digestibility of pea-based diets after pelleting, but this may have been due to the grinding effect during the pelleting process, which released starch trapped in the protein matrix, cell walls, or both.

**DIGESTIBILITY OF STARCH IN POULTRY**

Starch in poultry diets is to a large extent present in the form of native starch granules, and keeping in mind the complex digestion process described above, a low starch digestibility, at least for fast-growing broiler chickens that consume large quantities of starch, would be expected. However, a very high starch digestibility is commonly observed even in young broiler chickens. Several studies have shown that chicks are rapidly adapting to starch digestion when fed at hatch, as indicated by high activity levels of disaccharidase (Mahagna and Nir, 1996) and α-amylase (Sklan and Noy, 2000) 2 d after hatch. Accordingly, Zelenka and Ceresnakova (2005) found that the total tract starch digestibility coefficient already exceeded 0.96 at 3 d of age for broiler chickens. The same authors also found that starch digestibility decreased ($P < 0.01$) linearly with increasing age in fast-growing broiler chickens but not in slow-growing layer chickens. Thomas et al. (2008) observed that starch digestibility in broiler chickens dropped from 5 to 7 d of age, but was restored to a normal high level at 14 d of age. Even when measured on material collected from the ileum of broiler chickens, starch digestibility has often been observed to be above 0.95 even for pelleted diets (Svihus, 2001; Hetland et al., 2002, 2003; Svihus et al., 2004; Hetland et al., 2007). This high capacity of poultry for digesting starch is truly impressive, not the least in broiler chickens, where pelleted diets and a high appetite results in material passing through the digestive tract in less than 5 h (Svihus et al., 2002, 2010). This means that in less than 5 h, the starch granules must be released from the surrounding protein and cell walls, become completely moistened followed by complete degradation by a cascade of amylases, and finally the resulting glucose must be absorbed. This is particularly impressive because in vitro studies have shown that intact normal starch granules after a pretreatment imitating the preintestinal human digestion process are incompletely digested even after 4 h under conditions resembling the small intestine (Shrestha et al., 2012). Also, in pigs an
jejunal contents. Kadhim et al. (2011) compared the 
ported a total amylase activity of around 4,000 U in 
is assumed (no chyme volume was reported), who re-
by Osman (1982) if a jejunal chyme volume of 10 mL 
latter result seems to be in line with results obtained 
ren et al. (2012), using a similar method for activity measure-
in pig jejunum to gradually increase from 73 U/mL just 
in newly weaned pigs, and Fang et al. (2012) found levels 
and Hedemann et al. (2006) reported an amylase activ-
the intestinal content. Hedemann and Jensen (2004) 
value to compare would be amylase concentration in 
per gram of protein in content). A particularly relevant 
for activity (pancreas, pancreatic juice, or intestinal 
methods used for measuring activity, target organ 
the lack of experimental data preclude firm conclusions, 
these reviews indicate that a small granule size may 
explain the high digestibility of starch from oats and 
the reports, a considerable variation among cereal species, 
among varieties within species and between individual 
hens, has been observed. This indicates that factors 
intrinsic to cereals and birds alike are affecting starch 
digestibility.

**FACTORS IMPEDING STARCH DIGESTIBILITY**

It is clear that properties of the starch ingested will 
ffect digestibility, because numerous experiments 
have reported that glucose response and digestibility of 
starch vary with starch source (Svihus et al., 2005). 
However, there is still a lack of knowledge on the exact 
causes for these variations in starch digestibility. Factors 
such as the ratio between amylose and amylopectin, 
granule size and content and properties of proteins, 
lipids, and phosphates on the surface of starch granules 
were identified as potential causes for low starch diges-
tibility (Svihus et al., 2005; Tester et al., 2006; Singh et 
al., 2010). Although the complexity of this issue and 
the lack of experimental data preclude firm conclusions, 
these reviews indicate that a small granule size may 
explain the high digestibility of starch from oats and 
the high gluten matrix may contribute to low digestibility of starch from wheat.

As pointed out before (Svihus, 2011), wheat appears 
to be predominant in papers reporting low starch di-
gestibility. Also, wheat has been shown to result in con-
sistently lower starch digestibility when used at a high 
inclusion rate and when compared with other cereals 
such as barley and oats (Svihus, 2001; Zimonja and Svi-
hus, 2009). Addition of xylanase has sometimes been
shown to improve starch digestibility of wheat diets [see Svihus (2011) for an overview of literature], indicating that fibers may affect starch digestibility. Although this is correlated with reduced viscosity (Murphy et al., 2009), the rather moderate correlation coefficient indicates that other effects of enzyme addition are also contributing. It is possible that accessibility of the starch in the wheat endosperm is an issue, and that one potential beneficial effect of enzyme addition is that enzymes degrade cell walls and thus increase access to starch and other nutrients in the endosperm cells, as discussed by Murphy et al. (2009). This hypothesis is supported by results by Amerah et al. (2009), where xylanase addition improved ME content in hard wheat, but not in soft wheat. Carré et al. (2005) found that low starch digestibility was associated with hardness of wheat, and investigated this further to elucidate causes for low starch digestibility in hard wheat varieties. On the basis of particle size analysis and microscopy of ileal contents, they found that a large part of the undigested starch was entrapped in cell wall material, particularly from areas of the endosperm close to the aleurone layer (Péron et al., 2007). The same authors did not find a large number of particles in the size class of starch granules in the ileum, which indicated that the low digestibility observed with hard wheat was not caused by structural arrangements of the starch granules.

In another experiment, it was shown that very fine grinding corrected the very low starch digestibility observed with a normal particle size distribution (Péron et al., 2005). As stated by Carré et al. (2007), this supports a conclusion that the cause for a low digestibility of starch in wheat diets is partly that starch granules are entrapped in cell walls, protein matrix, or both.

It is possible that for broilers, the short time available for digestion may be one of the causes for impaired starch digestion under some circumstances. Results have shown that digestibility of a diet with a low digestibility increases when feed intake is reduced by changing diet form from pellets to mash (Svihus and Hetland, 2001), and this indicates that feed intake may be inversely correlated with starch digestibility. Several studies have shown a significant negative correlation between feed intake for individual birds on identical diets and starch digestibility or AME value (Svihus, 2006, 2011). In data from one of these experiments, AME and total tract starch digestibility for individual birds were very strongly correlated ($r = 0.984$), and starch digestibility was inversely related to feed intake as shown in Figure 1 (Svihus, 2011). In these data, 4 out of 10 ad libitum-fed birds on a finely ground pelleted wheat diet showed signs of being feed overconsumers, characterized by a normal weight gain, a higher than average feed intake, and an AME value <2,462 kcal/kg (Svihus et al., 2010). The hypothesis that feed overconsumption leads to an overly fast feed passage that results in poor starch digestibility is consistent with observations by Hughes (2008), who showed that AME of broiler chickens increased with increasing transit time.

**EFFECT OF SUPPLEMENTAL α-AMYLASE**

Published work assessing the extent to which exogenous α-amylase may improve starch digestibility is scarce. Mahagna et al. (1995), Ritz et al. (1995), and Shapiro and Nir (1995) did not observe any improvement in starch digestibility when α-amylase was supplemented to broiler chickens during the first 14 d of age, and Moran (1982) stated that “unlike most mammals, the ability of fowl to release sufficient amylase is never a problem.” This corresponds with observations by Svihus and Hetland (2001), where digestibility was not improved by adding pancreatin to the water of broiler chickens exhibiting low starch digestibility of a wheat diet. Conversely, Gracia et al. (2003) observed a significant increase in starch digestibility when α-amylase was added to a maize-based diet, thus indicating that α-amylase secretion may be a limiting factor. Jiang et al. (2008) added increasing levels of α-amylase to broiler chicken diets and observed an increase in weight gain at the highest supplementation level. Interestingly, endogenous α-amylase production seemed to be reduced at this high level. Corroborating this, other experiments in which amylase has been included in the enzyme cocktail have shown improved nutrient utilization (Cowieson et al., 2006; Cowieson and Ravindran, 2008; Ohukosi et al., 2008), although because other enzymes were used together with amylase, these latter reports are of limited value in this context. Interestingly, Hughes et al. (1994) separated chicks from 2 breeds based on genetic variants of the pancreatic α-amylase followed by a growth trial, and concluded that one of the α-amylase genotypes from one of the breeds resulted in higher feed/gain, thus indicating that birds of certain α-amylase genotypes may cause suboptimal starch digestibility. If an impaired starch digestibility is dependent both on specific properties of the diet such as cereal type and inclusion level, and on bird-related factors such as appetite and digestive tract development, this may explain the conflicting and inconclusive results. However, the very high starch digestibility observed even under the most demanding conditions indicate that broiler chickens have the capacity to digest...
starch completely, and thus that Moran’s (1982) statement that the bird releases sufficient amylase in most cases may still be true.

The very few reports published on the addition of α-amylase to poultry diets warrant further research into this very important area of poultry nutrition. Experiments should be carried out with pure α-amylases tested with pelleted diets based on both wheat and maize, and in different bird phases, because we have seen that feed intake can play an important role. Detailed assessment of starch digestibility throughout the small intestine should be also carried out. Furthermore, experiments are warranted that address the causes of effective starch digestion in broiler chickens, including the effectiveness of intestinal chyme from broiler chickens compared with other animal species in releasing glucoamylase from starch.

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