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Variability in wheat: factors affecting its nutritional value

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Wheat is a common raw material used to provide energy in broiler diets. Its apparent metabolisable energy and its influence on broiler performance varies between wheat samples. Reasons for that variability can be classified as intrinsic (variety, chemical composition) and extrinsic factors (growing conditions, storage, etc.), both of which affect nutrient digestibility and availability. However, these factors are not always considered when formulating the diets for broiler chickens. Moreover, research through the years has questioned the relation between wheat AME and animal performance. This review aims to describe factors that influence the observed variability in wheat nutritive value for broiler chickens by considering origin (variety, growing conditions and post-harvest storage), chemical composition of the grain (carbohydrates and protein) and the broiler chicken.

Keywords: wheat; variety; growing conditions; storage; composition; broiler

Introduction

Wheat is an important feed ingredient for poultry diets in Europe. It contributes up to 650 g/kg diet for finishing broilers. Over 125 million tonnes of wheat per year are produced in the EU (by its 25 member status) and more than 45% of it is used in animal feed (International Grains Council, 2004). Obviously, the high rate of inclusion of wheat in poultry diets can be related to heterogeneous broiler performance, where wheat nutritive value is not well defined and quantified.

It has been reported that apparent metabolisable energy (AME) of wheat ranges from 8.49 to 15.9 MJ/kg dry matter (DM) (Mollah *et al.*, 1983; Wiseman, 2000; McCracken *et al.*, 2002). Growth performance of broilers which were fed different wheat samples differed as much as 13% (Scott *et al.*, 1998). Moreover there was no correlation

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between wheat AME and animal performance (Rose and Bedford, 1995; Scott *et al.*, 1998; Steenfeldt, 2001).

There has been a considerable amount of work designed to investigate the reasons for the variability in the nutritional value of wheat. Some studies have focused on its origin (variety, site of growth, etc.) or physical measurements (storage time, inclusion form, etc.), and their influence on AME (Preston *et al.*, 2001), nutrients digestibility (Preston *et al.*, 2001), gut structure and function (Jones and Taylor, 2001) and animal performance (Jones and Taylor, 2001; Preston *et al.*, 2001). Others have studied nutritive value of wheat as influenced by its chemical composition (crude protein, ether extract, starch, etc.) (Longstaff and McNab, 1986; Pirgozliev *et al.*, 2003). Few studies considering both physical and chemical measurements of wheat have been conducted (Carré *et al.*, 2002; McCraken *et al.*, 2002).

The present paper describes the factors that influence variability in wheat nutritive value for broiler chickens by considering variety, growing conditions, post-harvest storage, chemical composition (carbohydrates and protein) and the broiler chicken.

Wheat variety

Physical and chemical characteristics of wheat may differ according to variety. For example, wheat hardness (Oury *et al.*, 1998; Morris, 2002; Chantret *et al.*, 2005), thousand grain weight (McCracken *et al.*, 2002), viscosity (McNab and Knox, 1999; McCracken *et al.*, 2002), phytase activity (Kim *et al.*, 2002), total NSP (Carré *et al.*, 2002; McCracken *et al.*, 2002), starch content (Bhatty *et al.*, 1974; Swanston *et al.*, 2007) or gross energy content (Bhatty *et al.*, 1974) have been shown to depend on wheat cultivar. However, individual varieties do not respond in a uniform way and even in one variety, energy value is not constant (Wiseman, 2000; Angus and Wiseman, 2003). The reason why this happens is due to factors such as harvest year (Waldron *et al.*, 1994; Rose *et al.*, 2001; George and McCracken, 2003; Pirgozliev *et al.*, 2003), harvesting conditions (Zijlstra *et al.*, 1999), post-harvest storage (Kim *et al*., 2003) or growing location (McCracken *et al.*, 2002; George and McCracken, 2003) that influence physical and chemical composition within the same wheat cultivar. This makes it difficult to differentiate among them (*Table 1*). In general "soft-wheat" varieties tend to have higher starch content and higher digestible energy (DE) for pigs (Bhatty *et al.*, 1974) and higher starch digestibility and AMEn for broilers (Mollah *et al.*, 1983; Carré *et al.*, 2002; Carré *et al.*, 2003; Skiba *et al.*, 2003) than "hard-wheat" varieties. Conversely, "hard-wheat" varieties have been found to give an improved broiler growth performance compared to "soft-wheat" varieties (Scott *et al.*, 1998; Rose *et al.*, 2001).

Growing conditions

The term 'growing conditions' refers to wheat grown at different geographical locations, growing seasons, soil types, farming management and rainfall.

Precipitation level mainly influences the carbohydrate composition of wheat. A number of studies have found that drought conditions reduced, grain weight, starch and soluble NSP contents and increased CP content, total arabinoxylans, ADF, lignin and free sugar contents of wheat (Brooks *et al.*, 1982; Coles *et al.*, 1997; Ahmadi and Barker, 2001; Kim *et al.*, 2003). Grain composition (especially carbohydrates) is influenced by rainfall during the different stages of wheat growth (vegetative, growing or ripening). Kim *et al.*, (2002) found that total-P content of wheat correlated well with annual precipitation level

($r = 0.478$, $P < 0.05$) but not with precipitation during growing period. Dusel *et al.,* (1997) reported a positive correlation between annual precipitation and extract viscosity of wheat, while precipitation during the growing season was negatively correlated with extract viscosity of wheat ($r = -0.55$, $P < 0.05$). Rainy conditions just before harvest were related to low specific weight, endosperm hardness and CP content of wheat due to a high proportion of sprouted grains (Metayer *et al.*, 1993; Kruger, 1994; Rose *et al.*, 2001).

Growing season has an effect on specific weight, endosperm hardness, content of CP and starch and total, insoluble and soluble NSP content of wheat (Metayer *et al.*, 1993; Waldron *et al.*, 1994; Scott *et al.*, 1998; Choct *et al.*, 1999; Rose *et al.*, 2001; George and McCracken, 2003; Kim *et al.*, 2003; Pirgozliev *et al.*, 2003). Nevertheless, most of those effects were mainly explained by differences between environmental conditions nested within the growing season.

Growing location also affects physico-chemical parameters of wheat. In a survey of seven wheat cultivars grown in 10 different locations in France, Metayer *et al.,* (1993) found a between-region effect on specific weight, thousand grain weight (TGW) and starch content. Wheat grown in the North East of France had higher nutritional value compared to the ones grown in Brittany and the South East of France. Longstaff and McNab, (1986) found a significant difference in the starch content of two wheat varieties (Norman and Armada) when grown in the North or the South-East of the United Kingdom, with the starch content being higher in those grown in the South-East compared to the Northern areas. Variability in the CP content of wheat samples has also been correlated with nitrogen application on the growing wheat crops (Uhlen *et al.*, 2004).

If growing conditions affect chemical composition of the wheat, its nutritional value (in terms of energy and animal performance) will be also influenced. Wiseman (1997) reported a 1.1 MJ/kg DM difference (14.6 *vs.* 15.7 MJ/kg DM) in the DE content of wheat fed to pigs due to growing season. Kim *et al.,* (2004) found that variety, growing season and growing region significantly affected the DE of three different wheat varieties fed to weaner piglets. In that study they concluded that both the variety and the growing conditions, especially precipitation levels during the growing season, were the responsible of the variation observed in DE of wheat (up to 1.9 MJ/kg, on as fed-basis). Mollah *et al.,* (1983) found almost 1 MJ/kg DM difference in AME content caused solely by growing site when fed to broiler chickens. Rose *et al.,* (2001) found that chickens given different wheat batches of the same variety, grown in 1992 harvest year, had significantly lower weight gain and feed intake compared to the 1990 and 1991 harvest year batches. Pirgozliev *et al.,* (2003) reported a growing season effect on AMEn of wheats fed to broilers while animal performance was not affected.

Post-harvest storage

Post-harvest storage (period and conditions) alters the chemical composition (Ravindran *et al.*, 2001; Kim *et al.*, 2003) and hence the nutritional value of wheat (Choct and Hughes 1997, 1999; McNab and Knox, 1999; Pirgozliev *et al.*, 2006). Wheat grains harvested and stored at ambient temperature for more than 4 months show decreased total starch, soluble NSP, acid detergent fibre (ADF) and lignin and increased free sugar content (Jood *et al.*, 1993; Kim *et al.*, 2003). These changes may be the responsible for the observed increase in AME and apparent ileal energy content of stored wheat in broiler chickens diets (Choct and Hughes, 1997, 1999; Ravindran *et al.*, 2001). The activation of various in-seed enzymes and a gradual "in situ" degradation of complex

polysaccharides into smaller sugars has been proposed as the mechanism for the changes observed (Choct and Hughes, 1997; Kim *et al.*, 2003).

Storage conditions are considered important for the activation of the endogenous phytase in barley and wheat. Ockenden *et al.,* (1997) reported no decrease in phytate content of barley when kept under dry conditions, but a 10% reduction when the samples were kept at higher moisture levels (75% relative humidity). This agrees with Kim *et al.,* (2002), who did not find a reduction of phytate content in wheat samples kept for 6 months at dry conditions. Rehman and Shah (1999) found that wheat grains stored for 6 months at a temperature below 10ºC did not change their carbohydrate composition while significant biochemical changes were observed when stored at 10, 25 and 45ºC. The amylase activity of the samples decreased with storage time. Cofie-Agblor *et al.*, (1997) concluded that storage temperatures above 10ºC increased the heat production of the grain (induced by aerobic and anaerobic respiration). Gras *et al.*, (2000) studied the effect of storage temperature (23, 35, or 40ºC) and the oxygen concentration (1, 4.6 or 21%) on the quality of flour milled from stored grain. Results showed that storage temperatures at or below 23ºC ensured constant flour quality while the oxygen concentration did not affect it. This may indicate that both time and temperature influence the activity of in-seed enzymes.

Physical form of the wheat grain

Several studies have focused on how the physical form of wheat grain fed to broilers affects their performance, digestibility and AME (McIntosh *et al.*, 1962; Mollah *et al.*, 1983; Rose *et al.*, 1993; Rose *et al.*, 1995; Rose, 1996; Salah Uddin *et al.*, 1996; Preston *et al.*, 2000; Jones and Taylor, 2001; Svihus and Hetland, 2001; Bennet *et al.*, 2002; Carré *et al.*, 2002; Svihus *et al.*, 2002; Carré *et al.*, 2003; Hetland *et al.*, 2002; Carré, 2004; Carré *et al.*, 2005; Svihus *et al.*, 2004; Wu and Ravindran, 2004). The aim of the present paper is not to review the complexity of the matter but it is important to underline that any physical change of the wheat grain (i.e. steam conditioning, pelleting, grinding, etc.), implies nutrient structure modifications that may affect digestibilities and animal performance. It is known that the addition of whole wheat into broiler diets increases gizzard weight (Preston *et al.*, 2000; Jones and Taylor, 2001; Hetland *et al.*, 2002; Svihus *et al.*, 2002; Wu and Ravindran, 2004), starch digestibility (Svihus and Hetland, 2001; Hetland *et al.*, 2002) and AME (McIntosh *et al.*, 1962; Preston *et al.*, 2000). However, no consistency is reported on broiler performance (McIntosh *et al.*, 1962; Rose *et al.*, 1995; Salah Uddin *et al.*, 1996; Jones and Taylor, 2001; Bennet *et al.*, 2002; Wu and Ravindran, 2004). The reasons for the variation in performance and AME caused by wheat processing are not completely understood and no fixed relationship between processing and the ME of cereals for poultry has been established (Burt, 1976; Sibbald, 1977; Mollah *et al.*, 1983; Salah Uddin *et al.*, 1996).

Carbohydrates

Carbohydrates constitute up to 80% of the total dry matter of the wheat kernel and variation in their composition (starch *vs.* non starch polysaccharides) has a large impact on nutritional value (*Table 2*). Starch is the predominant polysaccharide (from 59 to 73%), the remaining polysaccharides (cellulose, hemicelluloses, and pentosans) are present in lesser amounts (from 8 to 15%; *Tables 2 and 3*). Soluble carbohydrates are also present in small quantities; monosaccharides (glucose, fructose and galactose);

disaccharides (sucrose and maltose), trisaccharides (glucodifructose and raffinose) and other oligosaccharides (glucofructans).

STARCH

Starch is composed by two carbohydrate components, both high molecular weight polymers of glucose; amylose and amylopectin. Amylose is an almost linear polymer containing ≈ 99% of α-(1-4) and ≈ 1% of α-(1-6) glycosidic linkages. Amylose contains more than 1000 glucose units and it has a molecular weight of around 100 kDa. Amylopectin consists of a heavily branched polymer with ≈ 95% of α-(1-4) and ≈ 5% of α-(1-6) glucose chains. Amylopectin chain ranges from ≈ 12 to 120 anhydroglucose units and its molecular weight is in the order of 10^4-10^6 kDa (Morrison, 1993; Buléon *et al.*, 1998; Tester *et al.*, 2004). In most starches amylose represents between 20 to 25% of the starch, although some waxy starches contain very little, if any, amylose (< 1%) while others, high-amylose starches, contain more than 70% amylose (Parker and Ring, 2001; Tester *et al.*, 2004). In wheat, the proportion of amylose ranges from about 18 to 35% although recently waxy wheat mutants have been developed in which amylose represents less than 3% of the starch (*Table 3*) (Nakamura *et al.*, 1995; Abdel-Aal *et al.*, 2002; Tester *et al.*, 2004).

Native starches contain between 15 and 45% crystallite material (Oates, 1997) in which amylopectin is the responsible of the crystalline structure of the starch granule (Imberty *et al.*, 1991). Three different crystalline forms are known, the A form, typical of cereal starches, consists of starch double helices packed into a monoclinic array. The B form, found in tubers and high amylose cereal starches, is a more highly hydrated and open structure consisting of double helices packed in a hexagonal array (Parker and Ring, 2001). The C form is an intermediate form between A and B (Oates, 1997). The large A granules appear 3 to 7 days after anthesis and increase in size during the grain filling period whereas the B granules are formed 12 to 14 days after anthesis and remain smaller. The C granules are initiated 21 days after anthesis (Bechtel *et al.*, 1990; Parker and Ring, 2001). Wheat A granules have a lenticular shape with diameters of 10-35 μm while B granules are spherical or orthorhombic with diameters of about 2 μm (Parker and Ring, 2001). The A granule starches contain more amylose than the B granule starches (Ando *et al.*, 2002; Ao and Jane, 2007). In wheat amylose content of the A granules can be 34% *vs.* 27% amylose content of the B granules (Ao and Jane, 2007). The proportion of small and large starch granules, by weight and by number, differed among genotypes (Li *et al.*, 2001) and affect the physicochemical properties of starch (Ao and Jane, 2007). Hard and soft wheats contain A, B and C starch granules with no obvious differences in morphology and resistance to deformation (Barlow *et al.*, 1973; Bechtel *et al.*, 1993; Turnbull and Rahman, 2002; Brites *et al.*, 2005). However, starch granules from hard and soft wheats differ in the mean surface area (Pitts *et al.*, 1989; Glenn *et al.*, 1992), size-distribution (Bechtel *et al.*, 1993) and shape (Brites *et al.*, 2005).

Starch is the largest component of the mature cereal grain, and, in wheat, can comprise as much as 73% of its DM content (Pomeranz and MacMasters, 1968; McCracken *et al.*, 2002; Carré *et al.*, 2002). Most of the AMEn of wheat depends on the utilisation of the starch fraction (content and digestibility) as it is the largest contributor to the energy supply from the grain. There is a high relationship between starch digestibility and AME values of wheat (Mollah *et al.,*1983; Rogel *et al.*, 1987b; Wiseman *et al.*, 2000; Wiseman, 2006) but not between starch content and AME (*Table 2*). Isolated wheat starch has been proved to be almost 100% digestible by chicken pancreatic α-amylase (Longstaff and McNab, 1986; Rogel *et al.*, 1987b) *in vitro* but large variation (80 to 100%) has been found *in situ* (Mollah *et al.*, 1983; Rogel *et al.*, 1987b). Chickens secrete

enough pancreatic amylase to digest dietary starch completely (Moran, 1982; Longland, 1991). This indicates that other factors within the wheat are responsible for the differences in starch digestibility observed among wheat samples. Characteristics affecting starch digestion are the amylose/amylopectin ratio, proportion of A/B-starch granules, shape and crystallinity of the starch granule, lipid content, nature of the protein matrix surrounding starch granules and the overall architecture of the starch granules. Several studies have shown that the ratio amylose/amylopectin correlates negatively with starch digestion (Åkerberg *et al.*, 1998; Abdel-Aal *et al.*, 2002; Stevnebø *et al.*, 2006) which may be partly explained by the formation of complexes between fatty acids and amylose on the surface of the starch granule (Crowe *et al.*, 2000). The proportion of A-/B- starch granules (large/small granules) is also negatively correlated to starch digestion in wheat and barley (Svihus *et al.*, 2005; Stevnebø *et al.*, 2006; Tester and Karkalas, 2006).

NON-STARCH POLYSACCHARIDES

The term 'non-starch polysaccharides' (NSP) covers a large variety of polysaccharide molecules excluding α-glucans (starch) (*Figure 1*). NSP in cereal grains are predominantly arabinoxylans (pentosans), β-glucans and cellulose. Arabinoxylans content in the wheat grain ranges from 5.68 to 8% DM from which 1.8% DM are soluble (*Table 3*). The amount of β-glucans is very low (0.8% DM as average) and the amount of insoluble cellulose is 2% DM as average (*Table 3*).

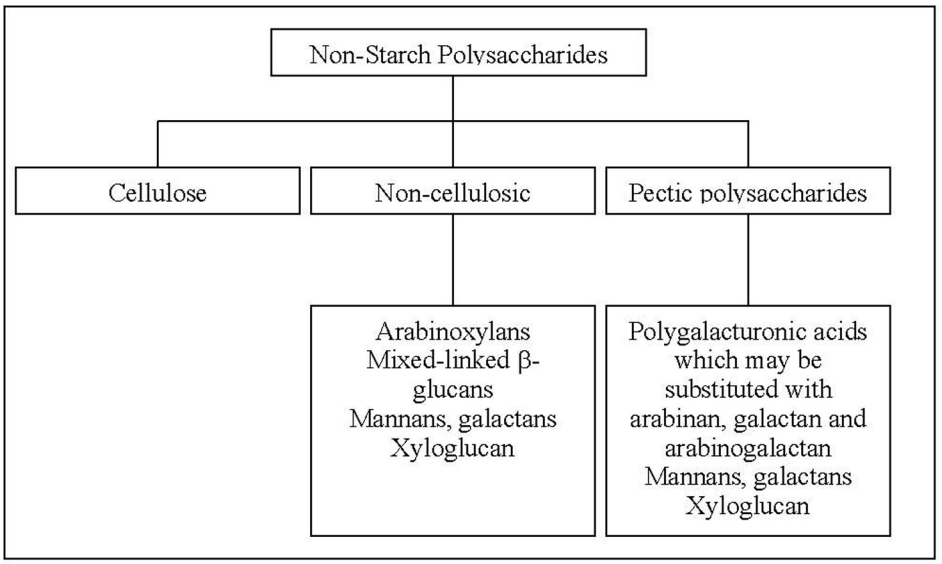

Figure 1 Non starch polysaccharides.

Arabinoxylans consist of long backbone chains of anhydro-D-xylopyranosyl residues linked together by β-(1→4) glycosidic bonds. Major substituents are single α-L-arabinofuranosyl residues. Also hexoses and hexouronic acids are present sometimes (Fincher, 1975; Amado and Neukom 1985). In addition, phenolics and proteins sometimes have been identified as side chains (Geissmann and Neukom, 1973; Neukom, 1976). Most of the arabinoxylans in cereal grains are insoluble in water but

the ones not bound to the cell walls may form viscous solutions due to their capacity to absorb water up to ten times their weight of water (Choct, 1997).

The NSP fraction of the cereal possesses antinutritive activity even when present at low levels in broiler diets (Annison, 1990; Choct and Annison, 1990, 1992). Inside the NSP, the soluble fraction has been identified as the main responsible for the negative effect as their ingestion increases viscosity of digesta (Bedford *et al.*, 1991; Bedford and Classen, 1992; Schutte *et al.*, 1995), retards the passage of food throughout the intestinal tract (Edwards *et al.*, 1992; Almirall and Esteve-García, 1994), reduces crypts depth and villi density and thickness (Viveros *et al.*, 1994; Yasar and Forbes, 2000), affects the physiology and morphology of the digestive tract (Johnson and Gee, 1981; Angkanaporn *et al.*, 1994) and interacts with the microflora of the gut (Carré *et al.*, 1995; Van der Klis and Van Voorst, 1993). As a consequence, nutrients are not well digested and absorbed and thus cannot be utilised (Choct and Annison, 1990, 1992; Van Der Klis *et al.*, 1993a,b).

The insoluble NSP fraction can absorb large amounts of water without changing the motility of the gut (Stephen and Cummings, 1979) and is not degraded by bacterial fermentation in poultry (Choct *et al.*, 1996; Langhout, 1998). Insoluble NSP have been reported to have very little or no effect on nutrient utilisation and AME of the wheat in monogastric animals (Carré, 1990; Annison, 1991; Angkanaporn *et al.*, 1994). However, a number of experiments with poultry have shown a beneficial effect of moderate levels of insoluble NSP on nutrient digestibility (Rogel *et al.*, 1987a; Hetland and Svihus, 2001; Svihus and Hetland, 2001; Hetland *et al.*, 2003). It has been postulated that an appropriate ratio between the NSP fractions soluble and insoluble may be of importance to reduce the negative effect of the soluble NSP (Choct, 1997). Although the exact mechanism by which insoluble NSP improves nutrient digestibility is not well understood, it seems to relate to its function as digesta passage rate modulator (Hetland *et al.*, 2004). This function is, at least in part, related to particle size as fine grinding has no effect on nutrient digestibility (Rogel, 1985; Hetland *et al.*, 2004).

Total and soluble NSP have been reported to negatively affect AME of wheat (*Table 2*). Numerous investigators have shown that addition of commercial xylanase enzymes to poultry diets can largely eliminate the adverse effects of NSP in the chick (Bedford *et al.*, 1991; Bedford and Classen, 1992; Veldman and Vahl, 1994; Bedford, 1995; Schutte *et al.*, 1995; Steenfeldt *et al.*, 1998a,b; Scott *et al.*, 1998; Petterson and Aman, 1989; Adeola and Bedford, 2004; Yasar and Forbes, 2000; Choct *et al.*, 2004; Wu and Ravindran, 2004) to the extent that nearly all poultry diets formulated with wheat are supplemented with an arabinoxylanase-based commercial enzyme.

Protein

Protein content of wheat ranges between 8.7-19% (*Table 2 and 3*) on a DM basis. It is distributed through all parts of the grain but mostly concentrated in the endosperm (72.5% of the total protein) and aleurone layer (15.5% of the total protein). Although the protein content depends mainly on the environment and N fertilisation (Uhlen *et al.*, 2004) the specific composition of the proteins of the endosperm is genetically determined (Wrigley *et al.* 1982; Carrillo *et al.* 1988).

Cereal proteins can be classified on the basis of morphology, biological function, solubility or chemical composition (Lásztity, 1984). In wheat it is normally used a classification based on solubility, as proposed by Osborne (1907). Hence, albumins are soluble in water; globulins are soluble in salt solutions but insoluble in water; gliadins (also called prolamins) in 70-90% ethanol and glutenins are insoluble in

neutral aqueous solutions, saline solutions or alcohol. The former two are classified as cytoplasmic or metabolically active proteins, and the latter two are largely storage proteins. The amount of total storage proteins is highly correlated with CP content of grains. Among these, the gliadin fraction correlates better with CP than glutenin (Wieser and Seilmeier, 1998; Wieser and Kieffer, 2001).

There are important differences in the amino acid composition of cytoplasmic and storage proteins. Storage proteins contain a high proportion of glutamic acid and proline and only a small proportion of lysine, arginine, threonine and tryptophan. Metabolically active proteins contain considerably less glutamic acid and proline, and have higher proportions of lysine and arginine, which give these proteins a higher nutritional value.

Wheat storage proteins (gliadins and glutenins) interact with water to form the gluten complex (rubbery mass containing about 80% of the total protein of the wheat flour). Wheat gluten proteins have been widely studied as they are the only cereal proteins to form a strong, cohesive dough that will retain gas and produce baking products. The bread-making quality of wheat flour is related to the presence and properties of the gluten proteins (Wieser and Kieffer, 2001; Don *et al.*, 2003; Wieser *et al.*, 2006).

Several studies have tried to focus on the relation between the amount of protein in the wheat kernel, and its physical and chemical characteristics, as a way to better define wheat quality. Physically, the most conclusive relationship was found between specific weight (SW) and protein content. This relationship has been reported to be negative by several researchers ($r = -0.62$, $P<0.05$, $n = 12$; McCracken *et al.*, 2002) ($r = -0.668$, $P<0.05$, $n = 18$; Kim *et al.*, 2003). Chemically, an inverse relation is thought to exist between protein and starch content (Jenner *et al.*, 1991; Simmonds, 1995; Hucl and Ravindran, 1996; Kim *et al.*, 2003).

Cereal starch granules are embedded in a protein matrix in different degrees (Lasztity, 1984; Classen, 1996). The proteins surrounding the starch granules have to be firstly degraded to expose the starch to amylases and could result in a physical barrier against starch digestion. There is evidence that the protein matrix is a major factor responsible for differences in ruminal digestion of starch (McAllister *et al.*, 1993). However, this has not been demonstrated in broilers, since low starch digestibility would be accompanied by a reduction in protein digestibility and no evidence for this link exists (Wiseman, 2006). The starch-protein interaction (hardness) can also be a factor influencing the starch digestion in broilers. The puroindoline proteins a and b (friabilin protein) are the molecular basis of wheat hardness (Morris, 2002; Hogg *et al.*, 2004). When both puroindolines are present in a wild state, grain texture is soft while it is hard when one of the puroindolines is absent or they have mutations (Morris, 2002). Negative relationships between grain hardness or particle size of wheats and starch digestibility have been reported (Carré *et al.*, 2002; Carré *et al.*, 2003). However, low starch digestibilities have been also observed even when grains have been strongly grinded (Rogel *et al.*, 1987b; Carré *et al.*, 2002).

The broiler

The problems associated with the digestion of starch and protein in wheat are considered most important during the first 10 days of age. This is because the gut of the day old chicken is sterile at birth. After hatching and eating, the animal starts to synthesise enzymes (trypsin, chymotrypsin, amylase and lipase) which reach a maximum at day 10 of age (Noy and Sklan, 1995; Nitsan *et al.*, 1991; Sklan and Noy, 2000). During the first 10 days of age there is an increase in the weights of the gastrointestinal tract and an increase in nutrient digestibility (Nitsan *et al.*, 1991) culminating in the ability to produce

sufficient and suitable endogenous enzymes to allow the bird to efficiently digest its feed. Digestion of the fibre fraction of the wheat by the birds own processes is poor, as it lacks the capacity to synthesise suitable enzymes (particularly arabinoxylanases). It relies on a resident microbial flora in its caeca to achieve fibre fermentation, and release of nutrient from that fraction of the diet.

Accessibility of the substrate by various enzymes (both endogenous and microbial) can affect total wheat digestion. The starch granules of the endosperm are embedded in a protein matrix. Processing of the wheat (milling) and/or the grinding action of the gizzard disrupt the starchy endosperm of the wheat and increase the surface area allowing better binding of the amylases. Wheat starch and wheat gluten can be almost 100% digestible and hence, their nutritive value for the animal can also be considerable. The rate of digestion of the different wheat proteins has not been reported yet. However, it seems to be very high since the starch granules are embedded in the protein matrix and starch has been reported to be rapidly digested (Waldron *et al.*, 1995; Wiseman *et al.*, 2000; Weurding, 2002). Nevertheless, the difference in the nutritive value of wheat may come from the combination of the digestion rate of the protein first and of the starch subsequently after. Waldron *et al.*, (1995) found significant differences in rate of starch hydrolysis between two wheat varieties (Dean and Beaver) with Dean samples showing 29% greater rate of starch hydrolysis than that in Beaver samples. It appears that starch digestion rate may partly explain differences in animal performance (Waldron *et al.*, 1995; Wiseman *et al.*, 2000; Weurding, 2002).

It is well documented that modern broilers are unable to adjust feed intake of diets to achieve a required nutrient intake to support growth (Forbes, 2005; Scott, 2007). Recent research suggested that limitations in feed intake of broiler chickens are the main responsible of the low growth and the high FCR observed (Scott *et al.*, 1998; Scott, 2004; 2007). The same authors postulated that what most affects voluntary feed intake is digesta passage rate, particularly in wheat-based diets, and that limitations in passage rate could be due to variability in diet hydratation time. Other factors affecting digesta passage rate are composition of the feed, i.e. polysaccharides content (Van der Klis and Van Voorst, 1993), NSP-degrading enzymes (Almirall and Esteve-García, 1994) or fat sources (Dänicke *et al.*, 1997), feed form (Hetland and Svihus, 2001) or raw material particle size (Carré, 2000; Svihus *et al.*, 2002).

Conclusions

Based on the literature presented it seems that the nutritive value of wheat grain cannot be clearly predicted from the traits measured so far. Intrinsic and extrinsic factors have been widely studied, along with certain digestibility characteristics, and it is clear that these may influence both wheat AME value and animal performance. Currently it is not possible to quantify AMEn value of the wheat from calculations involving the actual studied properties of the wheat as reported in animal studies. Moreover, the relationship between wheat AMEn value and animal performance is not constant, as two wheats with the same chemical composition may deliver different AMEn values. Equally, two wheats with the same AMEn value may give different animal performance, or vice versa. It is clear that there are other, as yet unidentified, factors within wheat that affect wheat AMEn and animal performance. Botanically, genetic variety influences the nutritive value of wheat, mainly via its chemical composition. However, wheat breeding programs continuously generate modifications to the same variety. This makes it impossible to use variety as a trait to determine nutrient composition and digestibility properties. The type of wheat and its growing conditions are more important for

predicting its nutritional feeding value than other traits. Chemically, the wheat grain can be considered one of the most intensively studied cereals. Starch, the largest component of wheat, is the major contributor to the AMEn of wheat. However, all the attempts to relate starch content or starch components with wheat AMEn have been inconsistent. Still, starch digestibility and starch digestion rate seem to be important traits related to wheat AMEn and animal performance.

NSP are considered anti-nutritional factors in non-ruminants because the animals do not synthesise the enzymes to break them down. The NSP fraction of wheat has been identified as being responsible of the high intestinal viscosity in broiler chickens and has been put forward as one of the main factors influencing negatively wheat AMEn and poultry performance. The use of commercial NSP exogenous enzymes is well documented, and is known to reduce the intestinal viscosity, having a positive effect on animal performance.

The protein fraction, mainly located in the endosperm, represents up to 16% of the wheat grain and surrounds the starch granules as a matrix. Although it dictates some of the dough properties of wheat, and is important in the bakery industry, its influence in animal nutrition has not been widely studied. Although wheat starch and gluten may be highly digestible, the difference in the nutritive value of wheat may come from the combination of the digestion rate of the protein first and of the starch subsequently. Changes in growing conditions of the wheat crop, can affect both physical and chemical parameters of the wheat grain, as well as harvest yield. Protein and starch digestion are also thought to vary between wheats grains.

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Table 1 Variation in physical and chemical parameters of some wheat varieties.

	Brigadier	Consort	Rialto	Reaper	Source
Hardness					
	79.9[1]	-	85.5[1]	-	Rose *et al.*, 2001
	56.5[2]	18.0[2]	62.5[2]	55.0[2]	Pirgozliev *et al.*, 2003
HFN[3], s					
	380	-	403	-	Rose *et al.*, 2001
	425	141	307	214	Pirgozliev *et al.*, 2003
TGW[4], g					
	39.2	39.1	-	43.7	McCracken *et al.*, 2002
	58.3	55.9	54.6	-	McNab and Knox, 1999
	46.0	52.8	52.5	57.6	Pirgozliev *et al.*, 2003
SW[5], kg/hl					
	70.5	71.4	-	72.0	McCracken *et al.*, 2002
	77.1	-	76.9	-	Rose *et al.*, 2001
	77.1	71.6	76.7	70.4	Pirgozliev *et al.*, 2003
Viscosity, cps					
	14.0	6.8	-	14.6	McCracken *et al.*, 2002
	5.6	4.0	9.6	-	McNab and Knox, 1999
	2.9	4.0	5.2	6.2	Pirgozliev *et al.*, 2003
	5.2	-	5.7	-	Rose *et al.*, 2001
Protein, g/kg DM					
	120.0	123.7	-	132.3	McCracken *et al.*, 2002
	108.0	114.4	129.2	-	McNab and Knox, 1999
	129.5	85.0	124.0	89.0	Pirgozliev *et al.*, 2003
	145.5	-	151.2	-	Rose *et al.*, 2001
	-	-	119.0	-	Steenfeldt, 2001
Oil, g/kg DM					
	15.4	17.2	-	15.2	McCracken *et al.*, 2002
	17.1	19.5	18.1	-	McNab and Knox, 1999
	15.4	18.8	16.1	16.6	Pirgozliev *et al.*, 2003
	14.9	-	16.0	-	Rose *et al.*, 2001
	-	-	24.0	-	Steenfeldt, 2001
Ash, g/kg DM					
	19.5	20.5	-	20.0	McCracken *et al.*, 2002
	15.7	14.9	15.9	-	McNab and Knox, 1999
	17.2	11.0	16.9	15.0	Pirgozliev *et al.*, 2003
Starch, g/kg DM					
	626.7	624.7	-	637	McCracken *et al.*, 2002
	680.0	668.0	663.0	724	Pirgozliev *et al.*, 2003
	754.9	-	756.0	-	Rose *et al.*, 2001
	-	-	664.0	-	Steenfeldt, 2001
Insoluble NSP[6], g/kg DM					
	106.2	95.1	-	89.5	McCracken *et al.*, 2002
	75.5	68.0	81.0	66.0	Pirgozliev *et al.*, 2003
	92.8	-	99.6	-	Rose *et al.*, 2001
	-	-	86.0	-	Steenfeldt, 2001

Table 1 Continued

	Brigadier	Consort	Rialto	Reaper	Source
Soluble NSP[6], g/kg DM					
	25.8	19.9	-	22.1	McCracken *et al.*, 2002
	32.0	24.0	35.0	26.0	Pirgozliev *et al.*, 2003
	23.0	-	20.7	-	Rose *et al.*, 2001
	-	-	29.0	-	Steenfeldt 2001

1 = measured by NIR analyzer (arbitrary units); 2 = endosperm hardness (relative units) (range 0 to 100) (soft-hard); 3 = hagberg falling number; 4 = thousand grain weight ; 5 = specific weight; 6 = non-starch polysaccharides

Table 2 Variation in physical (A) and chemical (B) characteristics of wheat and their correlation with AMEn content.

A. Physical characteristics

n[1]	Hardness	HFN[2] s	TGW[3] g	SW[4] kg/hl	Viscosity	Correlation with AMEn	Source
12	-	-	-	-	2.07-8.39[5] mPa/s	ns	Austin *et al.*, 1999
22	17-95[6]	-	-	-	1.91-6.03[7] ml/g DM	ns	Carré *et al.*, 2002[8]
15	15-88[6]	-	-	-	2.0-5.6[7] ml/g DM	r =-0.86, P< 0.01 (Viscosity)	Carré *et al.*, 2005[9]
55	-	-	33.5-46.4	59.8-62.1	1.79-5.33[5]	r =0.61, P<0.05 (TGW) r =-0.7, P< 0.05 (Viscosity)	Classen *et al.*, 1995
28	-	-	-	-	0.8-6.5[7] mPas	r=-0.43	Huyghebaert and Schöner, 1999[10]
12	-	-	33.4-47.3	63.2-77.1	5.2-17.5[5]	r =0.85, P<0.05 (SW) r =-0.74, P<0.01 (Viscosity)	McCracken *et al.*, 2002
22	10-29[11]	-	-	-	-	ns	Mollah *et al.*, 1983
25	-	-	27.4-50.0	35.6-40.3	-	ns	Scott, 2005
16	26-83[11]	-	27-45	68-81	0.7-3.2[12] ml/g DM	r=-0.87, P<0.05 (Hardness) r=-0.81, P<0.05 (Viscosity)	Skiba *et al.*, 2003
19	-	-	33-47	-	4.88-81.98[13] cps	ns	Steenfeldt, 2001
20	-	80-436	27.6-50.1	77.0-83.1	0.9-3.1[12]	r=-0.66, P<0.05 (HFN)	Svihus and Gullord, 2002
6	-	88-541	-	57.7-74.2	-	ns	Waldron *et al.*, 1994
50	-	-	34.6-59.3	69.5-80.0	-	ns	Wiseman, 2000

Table 2 Continued

B. Chemical characteristics, g/kg DM

n[1]	Starch	Protein	Soluble NSP	Total NSP	Correlation with AMEn	Source
13	-	-	-	87.6-129.2	r =-0.91, P<0.0001	Annison, 1991
12	-	-	16.8-26.1	91.7-143.5	ns	Austin *et al.*, 1999
22	688-725	96-134	-	-	ns	Carré *et al.*, 2002[8]
15	664-732	107-139	-	-	r =0.58, P< 0.05 (starch)	Carré *et al.*, 2005[9]
81	594-769	89-183	9.3-17.9	81.3-156.8	r =-0.43, P<0.01 (total NSP) r =-0.29, P<0.01 (soluble NSP)	Choct *et al.*, 1999
55	608-647	119-154	18.2-27.9	90.7-107.1	r =-0.7, P<0.05 (soluble NSP)	Classen *et al.*, 1995
28	610-721	132-183	36-101	99-145	r = 0.7, P<0.01 (starch)	Huyghebaert and Schöner, 1999[10]
12	612-656	116-147	15.6-26.3	106-144	ns	McCracken *et al.*, 2002
22	588-719	114-180	-	-	ns	Mollah *et al.*, 1983
25	-	122-199	-	-	ns	Scott, 2005
16	664-733	84-151	-	-	ns	Skiba *et al.*, 2003
16	658-722	112-127	14-39	98-117	r = -0.47, P =0.06 (total NSP)	Steenfeldt, 2001
20	614-712	109-154	-	-	r =0.49, P<0.05 (starch) r =-0.39, P<0.05 (protein)	Svihus and Gullord, 2002
6	650-721	97-129	-	-	ns	Waldron *et al.*, 1994

1 = number of wheat samples; 2 = hagberg falling number; 3 = thousand grain weight; 4 = specific weight; 5 = in vitro viscosity; 6 = measured by NIR analyzer (arbitrary units); 7 = potential applied viscosity; 8 = Calculated AMEn (Fisher and McNab, 1987); 9 = Calculated AMEn (Carré and Billouet, 1989); 10 = expressed on fresh basis; 11 = method of Symes (1961); 12 = water extract viscosity; 13 = viscosity in ileum of diets with two levels of wheat added (650 and 815 g/kg).

Table 3 Variation in the different components of starch, protein and NSP of wheat (g/kg DM). No storage influence considered.

n[1]	Starch	Amylose	Amylo-pectin	CP	Glutenin	Gliadin	Total NSP	Arabinose	Xylose	ß-Glucan	Cellulose	Reference
12	-	-	-	-	-	-	87.6-129.2 (15.2-23.5)	12.4-27.1 (3.1-5.9)	24.1-53.9 (4.0-10.3)	5.6-7.2 (1.2-2.8)	-	Austin *et al.*, 1999
20	615-689	211-335	335-454	-	-	-	-	23.5-38.0	33.5-45.7	0.9-8.1	-	Annison, 1990
5	-	-	-	-	-	-	119 (25)	29 (7)	47 (9)	8	20	Bach Knudsen, 1997
55	-	-	-	-	-	-	90.7-107.1 (18.2-27.9)	55.8-68.1[2] (12.0-20.2)		-	-	Classen *et al.*, 1995
-	-	-	-	-	-	-	114 (24)	33 (8)	48 (10)	-	20	Englyst, 1989
28	-	-	-	-	-	-	99-145 (36-101)	48-85[2] (10-25)		-	-	Huyghebaert and Schöner, 1999[3]
18	585.2-737.0	193.6-263.4	345.3-543.4	-	-	-	78.3-110.6 (7.0-14.1)	22.8-35.3 (2.3-4.7)	29.4-44.7 (2.1-5.6)	-	-	Kim *et al.*, 2003
3	-	-	-	103-123	32.2-37.2	55.9-59.4	-	-	-	-	-	Konopka *et al.*, 2007
16	-	-	-	-	-	-	98-117 (14-39)	22-28 (3-10)	36-47 (3-17)	-	14-21	Steenfeldt, 2001
14	-	-	-	87-120[4] 1073-1560[5,6]	291-488[6]	749-1094[6]	-	-	-	-	-	Wieser and Kieffer, 2001
24	-	-	-	71.3-145.1[4] 757-1791[5,6]	237-589[6]	495-1202[6]	-	-	-	-	-	Wieser and Seilmeier, 1998

Soluble fraction shown in parentheses
1 = number of wheat samples; 2 = arabinoxylans; 3 = expressed on fresh basis; 4 = protein content of the flour, Nx5.7, fresh basis; 5 = ; gluten proteins; 6 = absorbance units of HPLC corresponding to 1 mg flour.