Influence of feed bulk on physicochemical properties of digesta in pigs

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By

Akhona Wate

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School of Agricultural, Earth and Environmental Science

University of KwaZulu-Natal

Pietermaritzburg

South Africa

Supervisor: Professor Michael Chimonyo

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ABSTRACT

Physicochemical properties of fibre-based diets were used to determine the influence of feed bulk on physicochemical properties of digesta within each segment of the gastrointestinal tract and digesta in pigs. In the first experiment, three pigs (14 ± 1.2 kg body weight (BW) were allocated to each of six diets containing maize cob levels at 0, 80, 160, 240, 320 and 400 g/kg DM inclusion levels for four weeks. All pigs were fed *ad libitum*. They were slaughtered, eviscerated and weights of the gut compartments were recorded, then contents of digesta from each segment were sampled for the determination of water concentration, water holding capacity (WHC) and swelling capacity (SWC). The WHC of digesta in the stomach, ileum and caecum decreased ($P < 0.05$) with maize cob inclusion level. The SWC in the stomach decreased with the inclusion level of maize cob meal. The SWC of caecal digesta increased with maize cob inclusion ($P < 0.05$). Physicochemical properties of digesta increased ($P < 0.05$) from the stomach to ileum then decreased as the digesta moved through the hindgut.

In the second experiment, four fibres namely maize cob, lucerne hay, sunflower husk and citrus pulp were used. These fibres were used in formulating diets for finishing pigs. Twenty-one complete diets were formulated by dilution of a conventional feed with increment levels of each fibre source at 0, 80, 160, 240, 320 and 400 g/kg. Each of the diets was offered *ad libitum* to four of 84 pigs weighing 80.8 ± 8.15 kg body weight, in individual pens, for 30 days. Stomach weights increased linearly with an increase in neutral detergent fibre (NDF) but increased with quadratic functions with an increase in SWC of the diet ($P <0.05$). An increase in WHC of the fibrous diets increased linearly the WHC of the proximal colon ($P <0.01$) at a faster rate compared to the WHC of the distal colon ($P <0.001$). As the SWC of the diets increased, linear increases in SWC of the digesta in the stomach ($P <0.01$) and caecum ($P <0.001$) were observed. The WHC of the digesta was negatively correlated to SWC ($P < 0.001$) in the stomach. Scaled feed intake (SFI) decreased linearly with an increase in SWC of the diet ($P < 0.001$). There was no relationship between WHC of the diet and SFI ($P > 0.05$). There was a linear decrease ($P < 0.01$) in SFI of finishing pigs as the SWC of the digesta. It can be concluded that the swelling capacity of the diets and stomach digesta in stomach are accurate predictors of scaled feed intake. Swelling capacity had great influence in the stomach weights whilst other bulking properties, such as WHC and neutral detergent fibre, affected the weight and digesta properties in the caecum, proximal and distal colon.

Keywords: Feed intake, fibre source, fibre level, gastrointestinal tract, gut size, pigs, swelling capacity, water holding capacity.

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DEDICATION

To my grandmother…

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LIST OF ABBREVIATIONS

Term / Symbol	Description	Units
ADF	Neutral detergent fibre	g/kg
ADFI	Average daily feed intake	kg/d
ADG	Average daily gain	kg/d
ADL	Acid detergent lignin	g/kg
BW	Body weight	kg
CF	Crude fibre	g/kg
CP	Crude Protein	g/kg
DF	Dietary Fibre	
DM	Dry matter	g/kg
FCR	Feed conversion ratio	
DE	Digestible energy	MJ/kg
GIT	Gastrointestinal tract	
MC	Maize cob	g/kg
NDF	Neutral detergent fibre	g/kg
LH	Lucerne hay	g/kg
NDO	Non-digestible oligosaccharides	g/kg
NSP	Non starch polysaccharides	
PU	Citrus pulp	
SAS	Statistical Analysis System	
SCFA	Short chain fatty acid	
SEM	Standard error of means	
SH	Sunflower husk	g/kg
SWC	Swelling capacity	ml/g

SFI	Scaled feed intake	
UKZN	University of KwaZulu-Natal	
WHC	Water holding capacity	g/g

CHAPTER ONE: General Introduction

1.1 Background

Although dietary fibre has traditionally been considered nutritious for ruminants, there has been a marked growing interest in introducing agro-industrial and bio-fuel by-products with high fibre content as alternative feedstuffs in pig diets. Use of dietary fibre improves animal health and welfare, and leads to a marked reduction in feed costs. Most fibre sources are readily available, cheap and can be consumed by pigs (Ndindana *et al.*, 2002; De Leeuw *et al.*, 2008).

Pig diets comprise approximately 65 % carbohydrates, of which 14 to 22 % is dietary fibre (Canibe and Bach Knudsen, 2002). Dietary fibre is the sum of plant non-starch polysaccharides (NSP) and lignin. The NSP components consist of a complex group of substances that form a matrix. It is resistant to hydrolysis by mammalian digestive secretions (Trowell, 1976; Robertson, 1988). Pigs, like humans, do not possess enzymes that hydrolyse the NSP fractions of the diet (Bach Knudsen, 2001). Pigs can, to some extent, ferment dietary fibre in the hindgut (Adesehinwa, 2008). The degree of fermentation, however, depends on the source of fibre, inclusion level, solubility, processing method, age and weight of the pig, digesta flow across the gastrointestinal tract (GIT) (Montagne *et al.*, 2003). These factors, consequently, influence voluntary feed intake and feed digestibility (Wenk, 2001; Perez Mendoza, 2010; Banino, 2012).

The functional, nutritional and physiological effects of fibrous diets are poorly predictable from monomeric composition but are more related to the physicochemical properties of feed and the digesta (Bindelle *et al.*, 2008). Properties of dietary fibre that are more important during passage of digestive tract are solubility, viscosity, physical structure, water holding capacity, swelling capacity, fermentability and binding of organic acids (Asp, 1996; Canibe and Bach Knudsen, 2002; Anguita *et al.*, 2007; Banino, 2012). Water holding capacity and swelling capacity of the digesta relate to the surrounding medium conditions (e.g. pH, ionic strength and minerals), and they can differ with the GIT segments. Changes in fibre matrices under GIT conditions and their fermentation patterns have been determined using *in vitro* methods (Hoebler *et al.*, 2000). Experiments done *in vitro* fail to describe changes that occur along the GIT (Hoebler *et al.*, 2000). Little research has been conducted to assess the effects of fibrous diets on changes in physicochemical properties and composition of the digesta. To predict voluntary feed intake, changes in physicochemical properties of the digesta along the gut segments should be considered (Canibe and Bach Knudsen, 2002; Anguita *et al.*, 2006). Ndou *et al.* (2013) argued that water holding capacity of the feed influences gut capacity. The effect of other physicochemical characteristics of the digesta, particularly in the stomach, need to be investigated. Since fermentation capacity of pigs is expected to increase with age, the role of physicochemical properties in each age group warrants investigation.

1.2 Justification

To increase sustainability of pig enterprises, increasing the efficient utilization of agro-industrial by-products and other available fibrous feedstuffs is of utmost importance. To understand the relevance and contribution of the fibrous diets to the pig, there is need to investigate how their physicochemical properties change as they pass through the gut. This assists nutritionists to determine which fibre sources add value to the pig. Physicochemical properties of the digesta determine the functional, physical, nutritional and physiological effects of fibre sources. Investigating the impact of hydration properties of the digesta on feed intake assists farmers to predict optimum inclusion levels to optimize pig performance. The need to understand the physiological implications of fibrous diets on the intestinal contents, composition and gut development assist feed compounders to formulate fibrous diets that improve the gut health and enhance welfare of growing pigs. To better understand the influence of physicochemical properties of feed in pigs, it is necessary to use a wide range of fibre sources.

1.3 Objectives

The broad objective of the study was to predict changes in the physicochemical properties of digesta in pigs fed on graded levels of fibrous feedstuffs. The specific objectives were to:

1. Determine effects of feeding incremental levels of maize cob on physicochemical properties of digesta and the size of gut segments in growing pigs;
2. Determine the relationships between the hydration properties of the feed and the digesta along the gut in finishing pigs; and
3. Predict feed intake using dietary hydration properties and the hydration properties of digesta in the stomach.

1.4 Hypotheses

The hypotheses tested were that:

1. Physicochemical properties of digesta are influenced by inclusion of maize cobs.
2. Hydration properties of the digesta affect feed intake of finishing pigs.

1.5 References

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CHAPTER TWO: Literature review

2.1 Introduction

There is a growing interest to increase fibre in pig diets. Fibre sources from crop residues and agro-industrial by-products are readily available and cheap, and have a possibility to stimulate gut health and improve pig welfare.

The major limitation for using these fibres is their physical properties that tend to make the pigs reach their gut capacity early. There is, therefore, a need to understand the effect of introducing local agro-industrial by-products and crop residues as alternative feedstuffs on physicochemical properties of the digesta in pigs. Physiological roles of dietary fibre depend on physicochemical properties, particularly hydration properties, of the digesta. A consideration of the hydration properties on feed intake enables the determination of the quantity of nutrients required for sustainable pig performance.

The current chapter discusses the physicochemical properties of fibrous diets and digesta. It also reviews the effect of fibre source, inclusion level, and physicochemical properties on feed intake and gut development in growing and finishing pigs.

2.2 Definition of dietary fibre

There are a number of definitions for dietary fibre (DeVries, 2003). In spite of the extensive research conducted on the subject, there is debate regarding the aspects that should be considered in defining dietary fibre (Cummings *et al.*, 1997; DeVries *et al.*, 1999; 2003). The difficulty in defining dietary fibre is mainly due to a large collection of chemical compositions, physical structures, physicochemical properties and physiological effects linked with fibre sources (Dikeman and Fahey Jr, 2006). One definition that is fairly widely accepted is to define dietary fibre (DF) as carbohydrate polymers with 10 or more monomeric units, which cannot be hydrolyzed in the small intestines by endogenous enzymes (Howlett *et al.*, 2010; De Vries *et al.*, 2012; Bach Knudsen, 2001). Dietary fibre can also be viewed as the sum of dietary non-starch polysaccharides (NSP) and lignin compounds of plant cell walls (Wenk, 2001; Banino, 2012). Non-starch polysaccharides (NSP) are partially digested in the gut whilst lignin is a complex indigestible polymer deposited in cell walls. The NSPs are further classified as soluble or insoluble in water or weak alkali. Figure 2.1 shows an illustration of DF as a total of resistant starch, non-digestible oligosaccharides (NDOs), NSP and lignin.

2.3 Use of fibrous agro-industrial by-products as ingredients for pig feeds

The animal feed industry as a whole has been challenged by successive decrease of raw materials over the last decades, owing to the increased demands for cereal grains and oil seeds by emerging markets and their usefulness in energy production (De Vries *et al.*, 2012; FAO, 2012). The increase in demand for grain has led to high feed costs; hence, this has constrained pig production. Prices for maize and soybean have almost doubled the 2011 prices world-wide (Van der Westhuizen, 2012). The competition mainly as a result of direct human consumption demands, is progressively challenging and raising concerns about the unsustainable commercial pig production. Utilization and introduction of agro-industrial by-products and crop residues in pig diets reduce competition of grain (Ndindana *et al.*, 2002). Several studies (Esteban *et al.*, 2007; Mirzaei-Aghsaghali and Maheri-Sis, 2008) have also reported the introduction of fibres in diets of pigs to reduce environmental pollution.

<table>
<tr><td colspan="7">Dietary carbohydrates</td><td>Lignin</td></tr>
<tr><td>Digestible carbohydrates</td><td colspan="7">Dietary fibre (non-digestible carbohydrates)</td></tr>
<tr><td>Starch and sugars</td><td>Resistant starch</td><td>NDOs</td><td colspan="4">NSP (FIBRE)</td><td>Lignin</td></tr>
<tr><td colspan="3"></td><td>Pectins</td><td>Fructans
β-glucan</td><td colspan="3">NDF</td></tr>
<tr><td colspan="5"></td><td>Hemi-cellulose</td><td colspan="2">ADF</td></tr>
<tr><td colspan="6"></td><td>Cellulose</td><td>ADL</td></tr>
<tr><td colspan="7"></td><td>Lignin</td></tr>
</table>

← Highly fermentable Poorly fermentable →

NDOs - non-digestible oligosaccharides; **NSP** - Non-starch polysaccharides; **NDF** – neutral detergent fibre; **ADF** – acid detergent fibre; **ADL** – acid detergent lignin

Figure 2.1: Classification of dietary carbohydrates and fibre components

Source: De Leeuw *et al.* (2008)

Dietary fibre sources are readily available cheap by-products from food production and are well accepted by pigs (Bakare *et al.*, 2013; Ndou *et al.*, 2013). Dietary fibre has traditionally been considered as an anti-nutritional factor in pig diets, mainly due to its effects of diluting dietary metabolisable energy and nutrient concentration, decrease ileal and faecal digestibility of energy and nutrients, and depressing growth performance (Canibe and Bach Knudsen, 2002; Serena *et al.*, 2008). The benefits of incorporating dietary fibre in pig diets are, slowly being recognised (Bindelle *et al.*, 2008). Some of the benefits of fibre include gut health stimulation, suppression of stereotypic behaviours, attainment of early satiety in sows, and improved well-being and reproduction performance (Wenk, 2001; De Leeuw *et al.*, 2008). On the hand, too high inclusion levels could depress metabolisable energy content and digestibility of the diet, consequently leading to imbalances in GIT physiological functions (Noblet and Le Goff, 2001; Le Goff *et al.*, 2003).

2.4 Physicochemical properties of dietary fibre matrices

The principal physicochemical properties of dietary fibre with physiological effects that are important during passage of the digestive tract and their nutritional significance are shown in Table 2.1. Hydration properties are, arguably, more important. Water holding capacity (WHC), viscosity, solubility and swelling capacity (SWC) are the most important properties to define the hydration capacity of DF. They determine the physiological effects and fate of DF along the GIT and are important for effective digestion (Guillon and Champ, 2000).

Table 2.1: Important physicochemical properties of DF in the gut

Property	**Influence**
Digestibility	Extent of fibre digestion
Particle size	Surface area available for digestion
Hydration	Digesta mixing and flow
Viscosity	Digesta flow and nutrient availability
Porosity	Nutrient availability
Ion exchange, absorption	Nutrient availability
Solubility	Viscosity, mixing, availability

Source: (Robertson, 1988)

2.4.1 Water holding capacity

Water holding capacity reflects the ability of fibre to incorporate or immobilise water within its matrix, swell and form gels with high water contents (Kyriazakis and Emmans, 1995; Canibe and Bach Knudsen, 2002). Technically, WHC describes the amount of water that can be held or taken up by a known amount of fibre under known or used conditions (Guillon and Champ, 2000; Elleuch *et al.*, 2011). The term WHC is often used in relation to swelling capacity and viscosity of the material under investigation (Elhardallou and Walker, 1993; Takahashi *et al.*, 2009).

Fibre polymers bind water at differing strengths and in different quantities. Water in digesta can be held by dietary particles or remain unbound as either trapped or free water (Chaplin, 2003; Anguita *et al.*, 2006). Water holding capacity of fibre matrix along the gut depends on the conditions of each particular GIT segment (Canibe and Bach Knudsen, 2002). It is of high importance that when an investigation on physicochemical implications of fibre source and inclusion level is conducted, samples for measurements be taken from representable sites of the GIT. Common methods for measuring WHC include filtration, centrifugation and use of dialysis bags (Elhardallou and Walker, 1993; Kyriazakis and Emmans, 1995).

2.4.2 Swelling capacity

Swelling capacity is the volume occupied by a known weight of fibre as it absorbs water within its matrix under known or used conditions (Guillon and Champ, 2000). Swelling of fibre within the aqueous medium of the gut affects digesta water uptake and mineral absorption, and determines diffusion rate and the response of intestinal smooth muscles to bulky diets (Elhardallou and Walker, 1993). Swelling forms the first phase of fibre solubilisation process in which the incoming water from the upper intestinal tract spreads the macromolecules of fibre matrix components until they are fully extended and disseminated (Bach Knudsen, 2001; Knudsen, 2011).

2.4.3 Viscosity

Viscosity refers to the direct relationship between the flow of fibre matrix and the force applied to move it (Dikeman and Fahey Jr, 2006). Viscosity depends on the ability of the porous matrix structure formed by polysaccharide chains to hold water through hydrogen bonding, dietary concentration and solvent characteristics (Borchani *et al.*, 2011). The inclusion of polysaccharides imposes non-Newtonian flow of the digesta, and the increased shear rate can affect viscosity in different ways (Sanderson, 1981). It defines the relationship between the shear rate and the shear stress.

Water soluble fibres retain an ability to increase digesta viscosity (Abdul-Hamid and Luan, 2000). Viscosity of the digesta increases with an increase in fibre concentration in the diet (Elleuch *et al.*, 2011). Viscosity reduces gastric emptying rate and delay absorption of nutrient in the small intestine (De Leeuw *et al.*, 2008). Other factors affecting viscosity involve fibre intrinsic factors, the solvent and the temperature of surrounding medium (Guillon and Champ, 2000). The extent with which viscosity of DF physicochemical properties of digesta changes along the gut is unclear.

2.4.4 Water binding capacity and absorption

Water binding capacity of fibre describes the actual amount of fibre that will bind to the surrounding water in a particular medium under known or defined conditions (Guillon and Champ, 2000). It is determined by chemical composition and physical structure of molecules, and by the pH and electrolyte concentration of the surrounding aqueous medium (Bach

Knudsen, 2001). Thus, during gut transit, fibre sources may swell to variable extents and so as the dynamics from gut segment to segment. Water binding capacity provides detailed information about the fibre sources, more especially its substance porosity and volume (Elleuch *et al.*, 2011).

2.4.5 Solubility

Solubility is a reliable predictor of fibre fermentability and has profound effects on fibre physiological implications and functionality (Guillon and Champ, 2000). It is defined as "the portion of the polysaccharide which can homogenously mix in solvents such as cold water, hot water, dilute acid or dilute alkali" (Urriola *et al.*, 2010). Differentiation between soluble and insoluble fibre is solely based on their behaviour when mixed with water. Soluble dietary fibres form a solution when mixed with water, whilst insoluble fibres behave otherwise. Factors like glycosidic link between monosaccharides and functional groups such as sulphates and carboxyl (COOH) are the main determinants of fibre solubility (Elleuch *et al.*, 2011). These groups partly explains why fibre sources such as brans or husks from different crops may have the same constituent monosaccharide but yet differ in solubility strengths (Banino, 2012).

2.5 Effects of physical properties of fibrous diets on feed intake

The bulking capacity of dietary fibre increases retention in the stomach which influences the stomach wall to elongate leading to earlier satiety (Bindelle *et al.*, 2008). An increase in inclusion level of dietary fibre suppresses digestibility of nutrients, transit time throughout the gastrointestinal tract, and decreases the time exposure of host's digestive microbial enzymes (Bach Knudsen, 2001; Wenk, 2001; Bindelle *et al.*, 2008). Feed intake is compromised when high dietary fibre is incorporated. For sows, however, early satiety is desired and important for welfare and health (Meunier-Salaün *et al.*, 2001). In growing pigs, incorporation of DF in diets compromises voluntary feed intake as a consequence of gut fill (Anguita *et al.*, 2007).

Bulkiness of DF can be a result of particle structure and size or high water holding capacity (Bindelle *et al.*, 2008; De Leeuw *et al.*, 2008). The bulking properties of dietary fibre increases time of mastication and stimulate mechanoreceptors in the GIT, leading to a reduction in feeding motivation (De Leeuw *et al.*, 2008). Dietary fibre, like any other diet ingredient, consists of water as its primary constituent. Most of this water is free water. During digestion, this water is used for mixing of digesta and solubilisation of nutrients in digesta solution before absorption (Robertson, 1988). Water holding capacity slows down emptying of the stomach, due to its function to prolong digesta retention time (Bindelle *et al.*, 2008). As the WHC of dietary fibre increases, more space is required, thereby reducing feed intake (Tsaras *et al.*, 1998).

Viscous soluble fibre, therefore, have higher impact in depressing voluntary feed intake compared to insoluble fibre sources (Bach Knudsen, 2001; Wenk, 2001). Depending on the WHC of the feed, viscosity of the digesta slows down enzymatic action and the diffusion rate of solubilised components through the mucosal surface (Asp, 1996; Wenk, 2001; Bindelle *et al.*, 2008). Less is known about the effect of DF swelling capacity on feed intake and changes in the hydration properties of the digesta. The WHC and SWC are often correlated (Takahashi *et al.*, 2009).

Despite the negative impact of DF on digestibility, Ndindana *et al.* (2002), Kanengoni *et al.* (2004) and Chimonyo *et al.* (2001) observed no effect on feed intake in pigs fed on graded levels maize cob-meal. In summary, the relationship between hydration properties of the digesta with feed intake in growing and finishing pigs is still unclear. Investigating dynamics of the digesta during gut transit in conjunction with degradability potential of the gut segment is critical for predicting feed intake and digestion.

2.6 Influence of physical properties of fibrous diets on digestion

Digestion and fermentation of carbohydrates in pigs mainly occurs in the small and large intestines (Wenk, 2001). The digestion site, rate and the extent of release of nutrients during gut transit, and whether the polymers will be degraded by enzymes or microbes are determined by the chemical composition, physical structure, and physicochemical properties of NSPs (Robertson, 1988; Canibe and Bach Knudsen, 2002). Other factors affecting degradability and fermentation of dietary fibres are shown in Table 2.2. Although there is no enzymatic action taking place in the stomach and small intestines, microflora colonizing the foregut digest small fractions of fibre components through fermentation mechanisms (Bach Knudsen *et al.*, 2001). It is, however, established that dietary fibre leaves the stomach and small intestine nearly intact, and much degradation occurs in the large intestine through microbial fermentation (Montagne *et al.*, 2003).

Effects of dietary fibre on the physiology of the GIT can be direct or indirect. Direct effects remain important throughout the GIT, but are particularly relevant in the stomach and the small intestines (Ellis *et al.*, 1995; Mikkelsen *et al.*, 2004). These effects involve modification of physicochemical properties of the digesta, mainly the hydration properties (Anguita *et al.*, 2007; Molist *et al.*, 2009).

Table 2.2: Factors affecting digestion and fermentation of dietary fibre

Factor	**References**
Restricted or *ad libitum* feeding	Cunningham *et al.*, 1962; Henry and Etienne, 1969; Gargallo and Zimmerman, 1981
Adaptation	
Age and body weight of pigs	
Fibre source	Gargallo and Zimmerman, 1981; Canibe and Bach Knudsen, 2002; Ndindana *et al.*, 2002; Kanengoni *et al.*, 2004
Inclusion level	
Non-fibrous component (e.g. fat, glucose, antibiotics)	Skipitaries *et al.*, 1957; Gargallo and Zimmerman, 1981; Bindelle *et al.*, 2008
Environmental conditions (e.g. temperature)	Whittemore *et al.*, 2001
Degree of lignification	Bach Knudsen *et al.*, 2001; Williams *et al.*, 2001; Montagne *et al.*, 2003; Anguita *et al.*, 2006; Banino, 2012
Processing technique	
Solubility	
Microbial composition	
Intestinal transit time	

Digestion of fibre in the small intestine varies from 10 to 62 %, depending on the source and level of inclusion of fibre in the diet, and age of a pig (Bach Knudsen *et al.*, 2001). In the hindgut, caecal and colonic microflora yield short chain fatty acids (SCFAs), lactic acid, water, gases (carbon dioxide, hydrogen, methane), bacterial biomass and heat (Gdala *et al.*, 1997; Bach Knudsen, 2001; Montagne *et al.*, 2003; Anguita *et al.*, 2006).

Absorption of the SCFA in growing pigs occurs rapidly in the large intestine and contributes up to 24 % of the maintenance energy supply (Canibe and Bach Knudsen, 2002; Montagne *et al.*, 2003). Digestive and physiological effects of fibre, depending on the source and solubility of dietary fibre incorporated in pig diets are different (Table 2.3). Solubility of NSP plays a major role during fermentation along the gut. Soluble dietary fibre generally ferment easily, rapidly and completely in the large intestine when compared to insoluble dietary fibre (Bach Knudsen, 2001). Noblet and Shi (1993) reported that insoluble fibres take a long time to degrade and ferment. As a result, fermentation for such fibre occurs along the full length of the large intestines. Soluble fibre sources are easily digestible compared to insoluble fibrous ingredients, and consequently play an important role in the regulation of digestion and absorption in the small intestine (Banino, 2012).

2.7 Effects of physical properties of fibrous diets on gut size development

High fibre content in pig diets enhances gut segment development, more particularly the stomach and large intestine, relative to low-fibre diets (Freire *et al.*, 2000; Gomes *et al.*, 2006). Factors affecting gut size development include fibre source, age of pig, inclusion level, and the ratio between soluble and insoluble components of fibre (Len *et al.*, 2009; Ngoc *et al.*, 2012). Elongated retention time due to fibre bulkiness in the gut is associated with an increase in gut segment weights.

Table 2.3: Effects of soluble and insoluble NSPs during digestive passage

Soluble NSP	Insoluble NSP
Decrease viscosity of the digesta	Decrease transit time
Increase intestinal transit time	Enhance water holding capacity
Delay gastric emptying	Increase dilution of colonic contents
Delay glucose absorption	Increase faecal bulk
Increase pancreatic secretion	
Lower absorption rate	

Slow emptying of the gut gives the fibre matrix more time to stimulate mucosa size development and gut hypertrophy (Ngoc *et al.*, 2012). Bulk properties, particularly physicochemical properties, of dietary fibre are related to hypertrophy of the visceral organs (Stanogias and Pearce, 1985). Another possible cause for gut size development is the production of SCFAs, which influences intestinal growth through stimulation of epithelial cell proliferation (Jørgensen *et al.*, 1996; Freire *et al.*, 2000).

2.8 Gut health and welfare

Dietary fibre has a significant role in gut health maintenance. Depending on source and inclusion level of fibre incorporated, the diet may have both beneficial and harmful effects by providing substrate that either prohibits or enhance the proliferation of the pathogenic bacteria (Banino, 2012). An illustrative picture of gut health ecosystem is shown in Figure 2.2. Gut health is attained through the balance between the interaction of the diet, commensal bacteria and gut mucosa (Montagne *et al.*, 2003; Banino, 2012).

2.9 Summary

The pig, physicochemical properties of diet and digesta, as well as the environment all affect performance. Common fibre sources with potential of being used in growing pig diets were identified and their usefulness in relation to changes in digesta properties and feed intake were reviewed. The objective of the present study was to identify the most accurate physicochemical properties that best describe bulkiness of a feed and digesta, such that intake can be accurately predicted using that parameter. It is, therefore, of paramount importance to characterise physicochemical properties of feeds and digesta so that pig producers can have a comprehensive understanding of their effects on bulkiness, and consequently their effects on the maximum amount of feed that can be consumed to support potential growth.

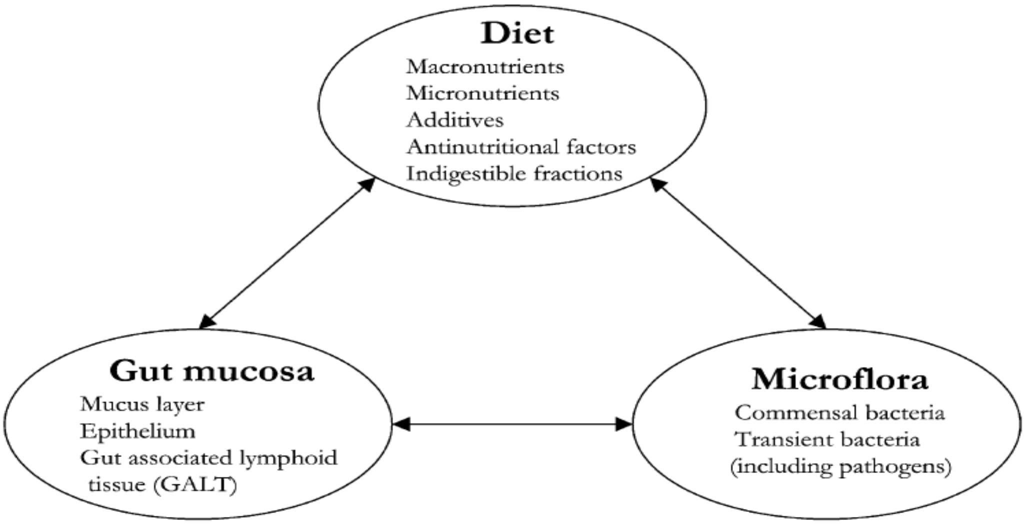

Figure 2.2: The interrelationship between the effective factors in the gut

Sources: Montagne *et al.* (2003) and Banino (2012)

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CHAPTER THREE: Effects of feeding incremental levels of maize cob meal on physicochemical properties of digesta in growing pigs

Submitted to Livestock Science (under review)

Abstract

The objective of the current study was to determine the effects of incorporating graded levels of maize cob meal in diets on the physicochemical properties of digesta and sizes of gastrointestinal organs in growing pigs. Three pigs were allocated to each of six diets containing maize cob levels at 0, 80, 160, 240, 320 and 400 g/kg DM inclusion levels. A completely randomized design was used. The initial body weight (BW) was 14 ± 1.2 kg and the pigs were fed *ad libitum*. After four weeks, weights of the GIT compartments were recorded and the contents of digesta from the stomach and intestines were sampled for analyses of water concentration, water holding capacity (WHC) and swelling capacity (SWC). The WHC of digesta in the stomach, ileum and caecum decreased ($P< 0.05$) with maize cob inclusion level. The SWC in the stomach decreased with the inclusion level of maize cob meal. The SWC of caecal digesta increased with maize cob inclusion level ($P< 0.05$). Physicochemical properties of digesta increased ($P< 0.05$) from the stomach to ileum then decreased as the digesta moved through the hindgut, except for SWC which increased ($P< 0.05$) for diets below 400 g/kg along the hindgut. Maize cob inclusion level had no effect on pH of other segments except in the distal colon. It can be concluded that changes in the physicochemical characteristics of the digesta along the gut is influenced by maize cob inclusion level in the diet.

Keywords: dietary fibre, digesta, physicochemical properties.

3.1 Introduction

There is a growing need for exploring the use of fibrous feedstuffs in pig diets due to increasing prices of cereal grains. The grains are utilized for human consumption and in the production of biofuels (Wenk, 2001; Högberg and Lindberg, 2006; Metzler and Mosenthin, 2008). Fibrous feedstuffs have multiple benefits. They promote pig welfare, gut health and some fibre sources are fermentable (Ndou *et al.*, 2013a). Better knowledge of how pigs utilize fibrous feedstuffs increase the ability of nutritionists to identify alternative ingredients for feeding pigs. For example, it is crucial to determine the changes in the physicochemical properties of digesta as fibre level is increased.

Physicochemical properties of dietary fibre (DF) are expected to change as the digesta passes along the gut (Anguita *et al.*, 2007). The extent of fibre fermentation depends on the type and inclusion level of fibre (Montagne *et al.*, 2003). For example, Canibe and Bach Knudsen (2002) reported that barley and pea fibres had different effects on hydration properties of digesta from segment to segment, thus different ileal digestibility and ceacal fermentation. Besides influencing voluntary feed intake, physicochemical properties affect the feeding behaviour of pigs (Asp, 1996; Bindelle *et al.*, 2008; Bakare *et al.*, 2013). To fully understand the influence of dietary fibre on pig performance, health and welfare, it is necessary to investigate changes in the physicochemical properties of the digesta as it moves along the gut. In addition, weight of gut segment should be estimated, so as to understand the physiological and anatomical responses of pigs fed on fibrous feeds. The information assists in providing explanations to the effects of dietary fibre on the wellbeing of the pig. The need to understand the dynamics with which physicochemical properties of digesta change during transit in the gut enables feed compounders to appropriately formulate fibrous diets to maximize nutritional benefits and physiological responses of pigs. Assessment of digesta has, thus far, received little attention because of the need to sacrifice many animals for research purposes.

Ndou *et al*. (2013a, b) assessed a number of fibrous sources for inclusion in pig diets. These included sunflower husk, grass hay, maize cobs, lucerne hay and maize stover. Of these, maize cobs had the least influence on depressing feed intake at high inclusion levels. Maize cob meal, a by-product of maize is produced in great quantities across most parts of Southern Africa, where maize is the staple crop. It has a low water holding capacity (WHC) and is a highly soluble fibrous source. As a result, when included in pig diets, it does not greatly depress feed intake and growth performance (Ndou *et al.*, 2013b). Maize cob is also a ready source of available non-starch polysaccharides for microbial fermentation (Ndou *et al.*, 2013a). The influence of these fibre sources on changes in the physicochemical properties of digesta was not determined. Water holding capacity, viscosity and swelling capacity (SWC) induce direct effects of dietary fibre that influence availability of nutrients during transit in the gut (Högberg and Lindberg, 2004; Anguita *et al.*, 2007). The response in weight of the different gut segments, as well as the digesta, to increasing fibre inclusion also assist in explaining the role of dietary fibres to gut health and pig welfare (Ngoc *et al.*, 2012). The objective of the study was to determine effect of feeding incremental levels of maize cob on physicochemical properties of digesta and the size of gut segments in growing pigs. It was hypothesized that the physicochemical properties of digesta are influenced by inclusion of maize cobs.

3.2 Materials and Methods

3.2.1 Ethical consideration

The trial was performed according to the conduct by the Certification of Authorization to Experiment on Living Animals provided by the University of KwaZulu-Natal Animal Ethics Committee (Reference Number 082/12/Animal).

3.2.2 Study site

The study was carried out at Ukulinga Research Farm, UKZN, Pietermaritzburg. The farm is located in the subtropical hinterland. Ukulinga Research Farm lies at 30° 24`S, 29° 24` E and is approximately 700 m above sea level. Climatic conditions are characterized by an annual rainfall of 735 mm, and mean annual maximum and minimum temperatures of 25.7°C and 8.9°C, respectively.

3.2.3 Pigs and housing

Eighteen clinically healthy male pigs of the PIC group (Large White × Landrace) with an initial body weight (BW) of 14 ± 1.2 kg were used in the experiment. The weaner pigs were purchased from Chiltern farm, Cramond, KwaZulu-Natal Province, South Africa. Pigs were ear-tagged and housed in individual cages (1.5 m × 1 m). Each cage had a plastic self-feeder trough (Big Dutchman Lean Machine®) and a low-pressure nipple drinker to provide feed and water, respectively. Automated HOBO TEMPERATURE, RH©, 1996 ONSET data loggers were used to record ambient temperature and relative humidity at 15 min intervals throughout the experiment. The average temperature and relative humidity were maintained at 21.1 ± 1.89 ^{o}C and 41.4 ± 1.45 %, respectively, by use of a single heating, lighting and ventilation system. Period of darkness and lighting were controlled at 12 h cycles. A complete randomized design was used.

3.2.4 Experimental diets and feeding management

Six experimental diets containing different incremental levels of maize cob were formulated. A low DF (50 g/kg DM of total dietary fibre) high quality commercial feed (Express Weaner, Meadow Feeds Ltd, Pietermaritzburg, South Africa), formulated to meet the nutritional requirements of growing pigs was used as a control feed. The basal diet contained 425.6, 175.6, 83.8, 100.0, 100.0,75, 20 and 20 g/kg DM of yellow maize, soybean, soybean oil cake, whole wheat, wheat bran, sunflower oil cake, cape fish and additives, respectively. Based on Ndou *et al*. (2013), the basal diet was diluted with maize cob at 80, 160, 240, 320 and 400 g/kg DM. Three pigs were allocated to each diet. Data collection continued after 10 days of acclimatization and continued for 28 d. Feed and water were provided *ad libitum*.

3.2.5 Measurement of digesta and pig performance

The amount of feed consumed every week was estimated by measuring the weight of feed at the beginning and end of each week. Feed refusals and spillages were measured and subtracted from weekly intakes. Average daily feed intake (ADFI) was calculated by dividing the difference between the feed offered and total of refusals and spillages by seven. The body weight (BW) of each pig was determined every week, before feeding, to determine average daily gain (ADG). Feed conversion ratio (FCR) for each pig was calculated as the ratio of the amount of feed consumed to ADG.

After 28 d of successive feeding, each pig was weighed, euthanized by intravenous injection of sodium pento-barbitone (200 mg/kg BW) and eviscerated. The GIT (from cardias to rectum) was immediately removed and segmented into different parts namely stomach, ileum, caecum, and the colon by means of double ties at the beginning and end of each section. The ileum was recognized by the presence of the Peyer's patches. The hindgut segments namely caecum and colon were considered as part of the gut entering the pelvic cavity and reaching the rectum part of gut that is attached to the anus. The colon segment was unravelled and divided into two equal parts; proximal and the distal colon. The stomach, caecum and colon were weighed with and without the intestinal contents to determine their weights and digesta weight in each segment. Sampling was done according to the procedure described by Anguita *et al.* (2007) and Molist *et al.* (2009).

3.2.6 Determination of physicochemical properties of diets and digesta

Proximate analyses and determination of physicochemical measurements of feed bulk were performed, in triplicate, in the Animal and Poultry Science Laboratory at the University of KwaZulu-Natal, Pietermaritzburg. Table 3.1 shows the chemical composition and physical properties of the experimental diets used in the study. Dry matter (DM) (2001.12), Ash (942.05), and crude protein (CP) (990.03) were determined according to the method of Association of Official Analytical chemists (AOAC, 1984; 2005) standard procedures. Gross Energy (GE) was determined using a bomb calorimeter. Analysis of WHC of the digesta was performed on wet materials, while SWC was performed on freeze-dried materials. Water concentration of digesta was determined in all the digesta samples as the amount of water lost during the preparative step of freeze-drying and the drying of the freeze-dried samples at 103°C until constant weight. Neutral detergent fibre (NDF) and acid detergent fibre (ADF) contents were determined using ANKOM Fibre Analyser (Ankom, Macedon, NY, USA) according to Van Soest *et al.* (1991). The NDF content was assayed using heat stable α-amylase (Sigma A3306; Sigma Chemical Co., St. Louis, MO, USA). Both NDF and ADF were expressed with residual and ash content. Diet Bulk density was measured according to the water displacement method, as described by (Kyriazakis and Emmans, 1995).

Table 3.1: Chemical composition and physical properties of experimental diets

	Maize cob inclusion level (g/kg DM)					
Component (DM basis)	0	80	160	240	320	400
Chemical composition						
Dry matter (g/kg)	90.1	90.1	90.4	90.7	90.9	90.8
Ash (g/kg)	5.52	5.28	5.04	4.55	4.36	4.38
[1]calc Digestible energy (MJ/kg)	10.8	10.6	10.6	9.98	9.51	9.39
Ether extract (g/kg)	5.45	4.88	3.73	3.40	3.00	2.91
Crude protein (g/kg)	24.8	21.9	20.8	19.9	16.9	18.5
Physical properties						
Crude fibre (g/kg)	81.3	96.4	110	126	142	153
Neutral detergent fibre (g/kg)	431	454	470	477	505	507
Acid detergent fibre (g/kg)	68.4	171	186	236	257	326
Density (g/ml)	1.75	1.52	1.45	1.37	1.29	1.25
Water holding capacity (g/g)	4.60	4.50	4.80	5.71	5.93	5.94
Swelling capacity (ml/g)	2.54	3.00	3.11	3.10	3.24	3.61

DM: dry matter

[1]calc Digestible energy = 949 + (0.789 x GE) - (43 x % Ash) - (41 x % NDF) (Noblet and Perez, 1993)

Digesta samples were first collected in plastic paper and pH was assessed in triplicate through an insertion of Crison 52 02 glass pH electrode. Samples from different segments of the GIT were collected within 90 minutes of slaughter and were immediately frozen at -20°C. Half of the collected samples were first freeze-dried, and then dried at 103°C for dry matter (DM) analysis. The other half was divided into aliquots for WHC and SWC analyses. Water holding capacity of diets and fresh digesta samples was determined by centrifugation following the method by Anguita *et al.* (2006), in triplicate. The intestinal content samples collected in plastics were thawed and then 4.5 to 5 g was measured into previously weighed plastic centrifuge tubes and then centrifuged at 2500 ×g for 25 minutes, the supernatant was discarded. The tubes were then inverted and left to drain for a period of 30 minutes to allow for the completion of water removal. Water holding capacity of the digesta samples was determined as the weight lost after the samples have been dried at 103 °C for 20 hours. The results were expressed as g water held per g dry residue.

Swelling capacity was measured using the modified bed volume technique as described by Canibe and Bach Knudsen (2002), in triplicate. Experimental diets and digesta samples (2 g) were weighed into 15 ml measuring plastic tubes, a solution of 9 g/l NaCl containing 0.2g/l NaN_3 was added to a final volume of 10 ml, where samples were incubated at 39 ^{o}C in a water shaking bath overnight. After 16 hours, the shaker was stopped and samples were left in the water for 1 hour before being taken out to measure the volume occupied by the fibre and digesta. The results were expressed as ml of swollen sample per gram of dry residue.

3.2.7 Statistical analyses

The PROC REG (SAS, 2008) was used to determine the relationships between maize cob inclusion level and ADFI, ADG and FCR. A PROC GLM procedure of SAS (2008) was used to determine the effect maize cob inclusion level on physicochemical properties of digesta across segment. Regression analysis was also used to determine the relationship between maize cob inclusion level and the physicochemical properties (pH, water concentration, WHC and SWC) of digesta in each segment. Stepwise regression in SAS (2008) was used to identify physicochemical properties of the digesta which influenced the weights of the segments.

3.3 Results

3.3.1 Pig performance, segment contents and segment weights

Relationships between pig performance (ADFI, ADG and FCR) with the inclusion level of maize cob are shown in Table 3.2. Increase in maize cob meal inclusion was associated with a quadratic decrease in ADFI ($P < 0{\cdot}05$). There was a linear decrease in ADG and FCR with incremental levels of maize cob meal in the diet ($P < 0.05$).

There was a positive quadratic relationship ($P < 0.05$) between maize cob inclusion and the weight of the digesta in the stomach (Table 3.2). There was a quadratic decrease in colonic intestinal content as maize cob level increased ($P < 0.01$). As the maize cob inclusion level increased, the weight of the stomach increased linearly ($P < 0.01$). Changes in stomach weights were positively related with increases in WHC ($P < 0.01$) and SWC ($P < 0.05$) in maize cob diets and digesta.

Table 3.2: Effect of maize cob inclusion level on ADFI, ADG and FCR, digesta weight across GIT segments and on the weight of segments

Item	Maize cob inclusion level (g/kg DM)						SEM	Regression coefficient		*P*-value
	0	80	160	240	320	400		Linear	Quadratic	
Performance										
ADFI	1.22	1.28	1.31	1.36	1.26	0.95	0.15	0.014	-0.0008	*
ADG	0.80	0.87	0.48	0.60	0.79	0.45	0.25	-0.023		*
FCR	0.57	0.65	0.31	0.46	0.58	0.44	0.14	-0.022		*
Digesta										
Stomach	21.6	19.3	16.8	14.8	23.5	43.2	5.10	-1.32	0.04	*
Caecum	20.2	20.1	23.3	14.2	20.8	29.1	5.10			*NS*
Colon	19. 9	26.4	30.6	39.4	31.5	34.3	5.10	1.09	-0.02	**
Segment										
Stomach	7.69	8.10	8.31	8.65	10.3	10.9	3.00	0.005		**
Caecum	10.4	4.09	3.00	3.50	6.35	3.86	3.00			*NS*
Colon	20.1	20.6	23.9	14.3	21.0	30.6	3.00			*NS*

SEM is for n=3

NS- not significant (P > 0.05); *P < 0.05; **P< 0.01

ADFI- average daily feed intake; ADG – average daily gain; FCR; feed conversion ratio

3.3.2 Physicochemical characteristics of the digesta

The effect of maize cob-based diets on the pH of digesta along the gut segments is shown in Table 3.3. The pH increased linearly ($P < 0.01$) with the increase in maize cob inclusion level in the distal colon. Maize cob inclusion level had no effect on digesta pH in the stomach, ileum, caecum, and proximal colon ($P > 0.05$).

The effect of maize cob inclusion on digesta swelling capacity is shown in Table 3.4. There was a quadratic increase in SWC of digesta in the stomach and ileum as the level of inclusion was increased ($P < 0.05$). The swelling capacity of digesta in the caecum increased linearly with incremental levels of maize cob ($P < 0.001$). An increase in maize cob inclusion was related with a quadratic increase in digesta SWC in the proximal colon ($P< 0.01$). The WHC of digesta in the stomach, ileum and caecum decreased ($P< 0.05$) with maize cob incremental levels (Table 3.5). Water concentration decreased with maize cob incremental levels in the stomach and distal colon (P < *0.01*) (Table 3.5). An increase in maize cob inclusion had a linear increase on water concentration in the ileum, caecum and proximal colon (P < *0.01*).

Water holding capacity of the digesta from different gut segments is shown in Figure 3.1. As digesta moved along the gut, WHC was lowest in the stomach (2.57 g/g DM) and highest in the ileum (4.66 g/g DM), however, the amount of water held declined during each successive section of the hindgut as shown in distal colon (3.03 g/g DM) and caecum (4.12 g/g DM) ($P< 0.05$). During gut transit from the stomach to the ileum, WHC of the digesta of pigs feeding on a basal diet increased at higher rate compared to maize cob-based diets with inclusion level below 320 g/kg.

Table 3.3: Effect of maize-based diets on digesta pH in the stomach, ileum, caecum, proximal colon and distal colon

Digesta Segment	Maize cob-based diets (g/kg DM)						SEM	Regression coefficient	P *-value*
	0	80	160	240	320	400		Linear	
Stomach	3.76	4.18	3.87	4.15	3.74	4.2	0.13		NS
Ileum	5.35	5.67	5.27	6.03	6.19	6.03	0.22		NS
Caecum	5.37	5.56	5.51	5.67	5.38	5.32	0.07		NS
Proximal colon	5.64	5.84	5.7	5.66	5.49	5.49	0.07		NS
Distal colon	5.96	6.04	6.03	6.15	6.21	6.19	0.08	-0.002	***

SEM: standard error of the mean (n=3)

NS- not significant; *** *P*< 0.001

Table 3.4: Swelling capacity of digesta samples from gut segments of pigs fed maize cob-based diets

Digesta Segment	Maize cob inclusion level (g/kg DM)						SEM	Regression coefficient		P-*value*
	0	80	160	240	320	400		Linear	Quadratic	
Stomach	3.92	3.45	3.26	3.42	3.28	3.76	0.097	-0.051	0.001	***
Ileum	4.59	3.86	3.81	3.89	4.34	4.63	0.097	-0.069	0.002	***
Caecum	3.23	3.25	3.72	3.61	4.13	4.22	0.097	0.021		***
Proximal colon	3.15	3.27	3.25	3.83	3.82	4.37	0.097	0.003	0.001	**
Distal colon	3.59	3.7	3.12	4.32	4.4	3.54	0.097			NS

SEM: standard error of the mean (n=3)

NS- not significant; **P < 0.01; ***P < 0.001

Table 3.5: Relationship between maize cob inclusion levels and the physicochemical properties of the digesta across the gut

Item	Regression coefficient		P-value
	Linear	Quadratic	
Water holding capacity			
Stomach	-0.015		*
Ileum	-0.13	0.0036	***
Caecum	-0.016		*
Proximal colon	0.03		***
Distal colon	0.058		*
Water concentration			
Stomach	-0.016		**
Ileum	0.32		***
Caecum	0.04		**
Proximal colon	0.33		**
Distal colon	-0.07		***

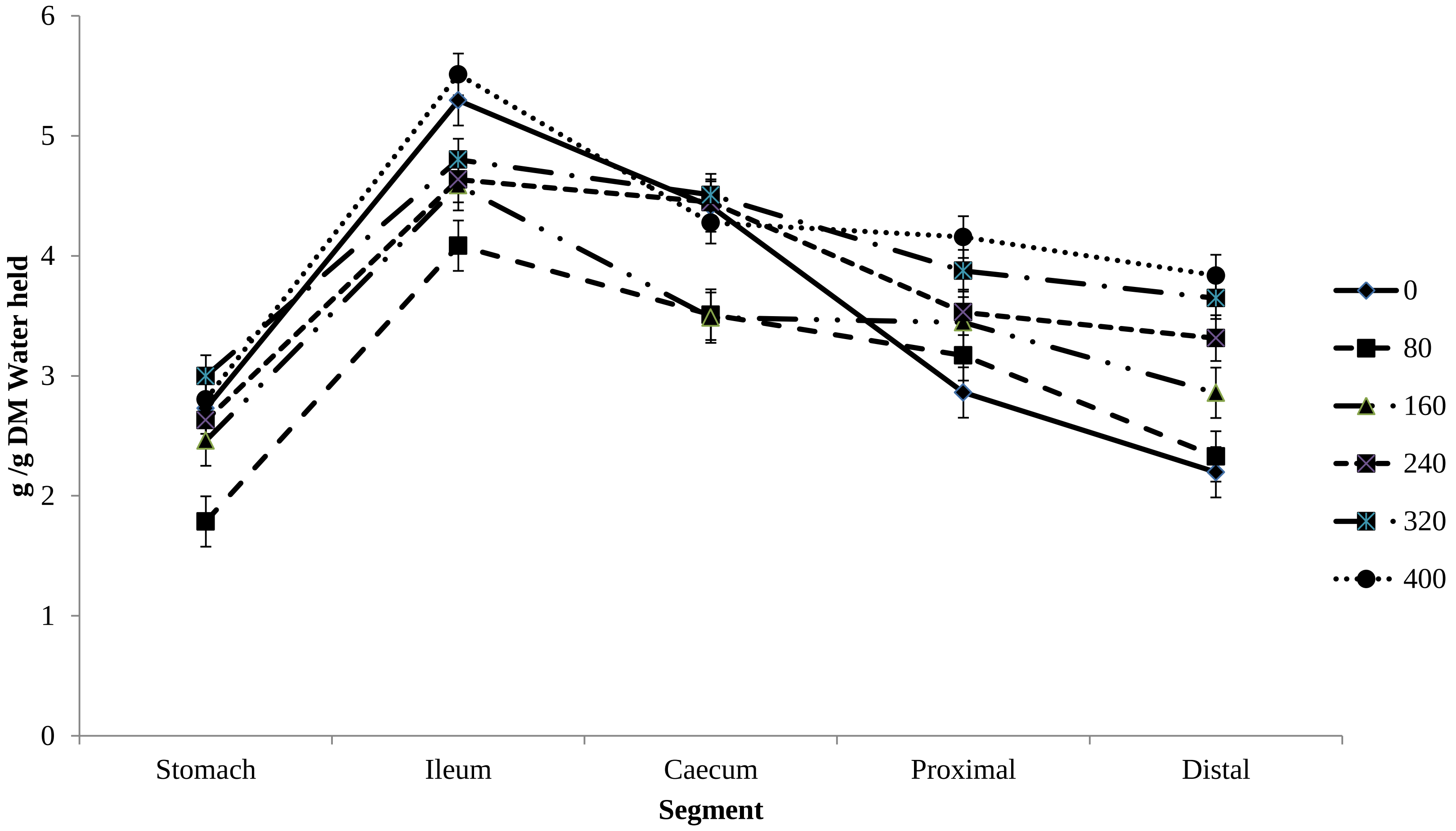

Figure 3.1: Effect of maize cob meal inclusion on water holding capacity of digesta from different GIT segments

Maize cob inclusion influenced water concentration of the digesta, as shown in Figure 3.2. The water concentration of digesta during transit from the stomach to the ileum of pigs fed on the control diet increased at a higher rate compared to that of pigs fed on 80 and 160 g/kg maize cob meal-based diets.

3.4 Discussion

All the pigs remained healthy throughout the experiment. The diets used in the current study were based on maize cob meal in order to stimulate a range of fibre content possible to use in the pig industry. Feed bulk affects feed intake (Kyriazakis and Emmans, 1995). The observation that ADFI initially increased as maize cob meal level increased, before it started to decline could be related to the physicochemical properties and limitations of the size of the stomach. These findings concur with (Ndou *et al.*, 2013a). The increase in weights of the stomach segment reflects the adaption pigs make when fibre levels in the diet are increased.

The caecum and colon weights were not influenced by maize cob inclusion levels in the diet. Studies in poultry (Borin *et al.*, 2006) suggested that inclusion of fibre at high levels may increase the digestive capacity as a result of an increased volume of the GIT segment such as the colon. This was, however, in contrast with findings from the current study. Ingestion of maize cob diets higher than 240 g/kg decreased the weight of the colon. Only the stomach content weights increased with maize cob inclusion level, as expected. Pigs given high fibre diets have been reported to have heavier GIT segment weights compared to those given low fibre diets (Jørgensen *et al.*, 1996; Nyachoti *et al.*, 2000; Len *et al.*, 2009). In the current study, no significant effects of maize cob meal were observed in the weights of caecum and colon. Whitney *et al.* (2006) observed that the response of gut weights is fibre source-specific. For example, diets containing distillers’ grain increased the large intestine weight.

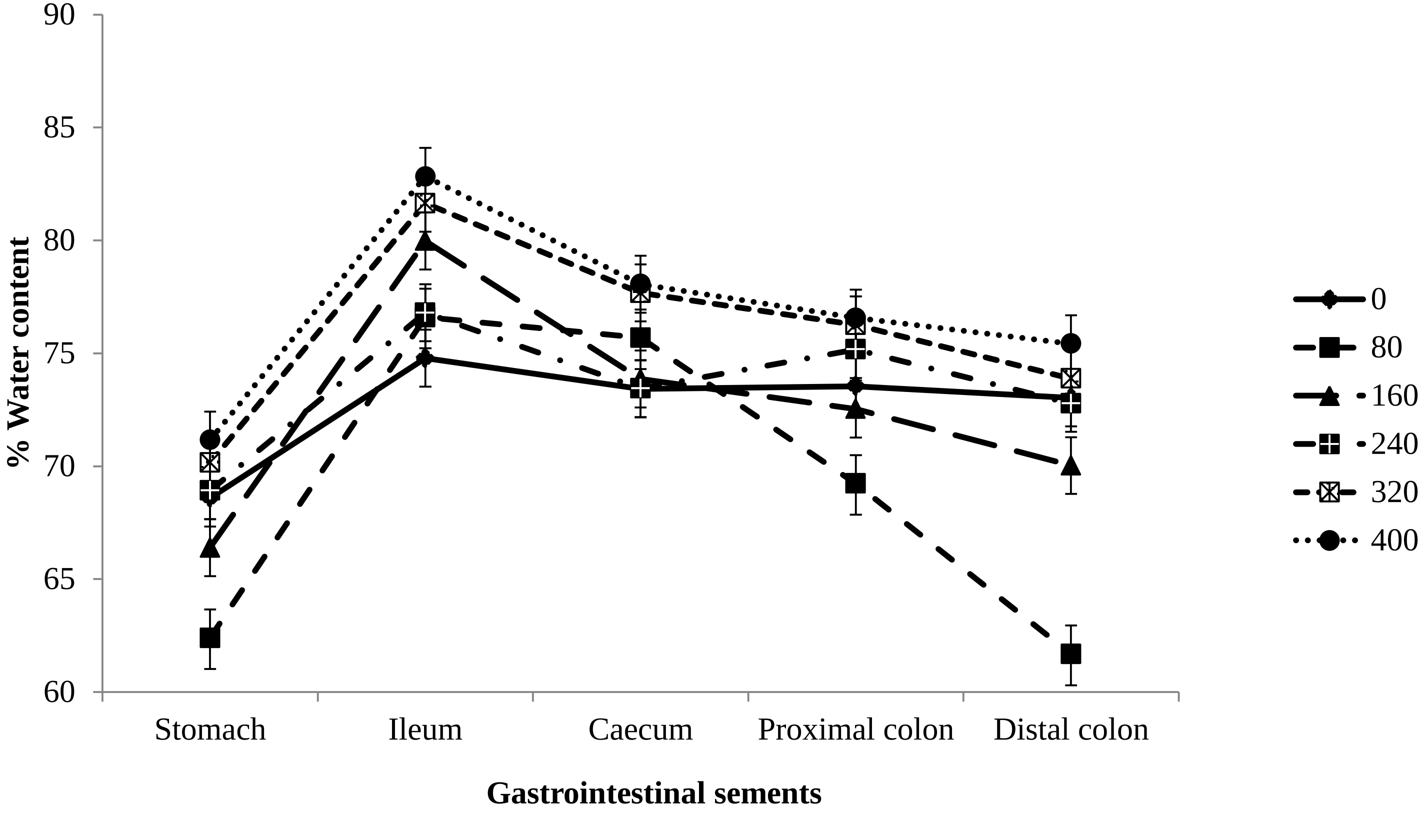

Figure 3.2: Effect of maize cob inclusion levels on water concentration of gastrointestinal content

In contrast, diets containing bean hulls, similar to maize cobs in the current study, did not. Bean hulls had a higher WHC and SWC than the distiller's grain.

The decrease in pH in the distal colon as maize cob level increased could have health benefits to the pigs. Diets that maintain low pH levels beyond the proximal colon lower the risks of colon cancer (Glitsø *et al.*, 1998). In contrast, no relationship was found between pH and maize cob inclusion level in the stomach, ileum, caecum, and proximal colon. As reported by Högberg and Lindberg (2006), the continuous secretion of hydrochloric acid in the stomach could have maintained the pH at lower levels thus suppressing the effect of fibre inclusion level. Lack of a relationship in maize based diets and pH in other segments in not clear. The overall digesta pH depends on the rate at which the acids are produced, absorbed and utilised, and on the overall concentration of short-chain fatty acids (Pluske *et al.*, 1998). The buffering capacity of the digesta and its constituents also affect pH (Newmark and Lupton, 1990). Moreover, the incremental maize cob levels may have influenced the size of microbiota and stimulated different species of microflora (Anguita *et al.*, 2007). It is also possible that the observed pH could be due to the interaction of other physicochemical properties of the digesta. Viscosity of the digesta, for example, could not be measured in the current study.

Swelling forms the first part of the solubilisation process whereby the incoming water spreads the macromolecules of dietary fibre components until they fully extend and get disseminated (Bach Knudsen, 2001; Knudsen, 2011). High fibre content is expected to increase the volume and the extent to which the fibre component expands (Bach Knudsen, 2001). Inclusion of maize cob level increased the SWC of the digesta in the stomach and ileum at a higher rate than in the proximal colon. Ndou *et al.* (2013b) described maize cob-meal as a highly soluble fibre source. Soluble fibres are generally highly fermentable due to their physiological effects to increase the surface area of the substrate for easy colonisation and effective degradation (Bach Knudsen, 2001). The decrease in SWC of the digesta with incremental levels of maize cob could have been due to increased susceptibility of the digesta to microbial action (Canibe and Bach Knudsen, 2002).

The finding that WHC of the digesta decreased as it moved through the hindgut agrees with Anguita *et al.* (2007). High levels of dietary fibre were expected to increase WHC of the digesta during gut transit (Canibe and Bach Knudsen, 2002; Anguita *et al.*, 2007; Molist *et al.*, 2009). Findings from the current study, however, contrasted these earlier reports. Maize cob inclusion level decreased the WHC of the digesta in the stomach, ileum, and caecum. It is not clear whether viscosity, particle size and transit time could have interacted with the digesta properties (Banino, 2012). This could also reflect high levels of disappearance of nutrients (Canibe and Bach Knudsen, 2002). As expected, incremental levels of physicochemical properties in the diets increased WHC of the digesta in the proximal and distal colon (Molist *et al.*, 2009) and provide a slowly fermentable substrate (Freire *et al.* (2000). The observation that WHC of digesta for pigs fed on the basal diet increased sharply in the foregut and rapidly decreased in the hindgut is probably due to the higher WHC of dietary fibre (Fardet *et al.*, 1997; Anguita *et al.*, 2007). The basal feed was also expected to more highly digestible.

Dietary fibre binds water at varying strengths and in different quantities, consequently, water in the digesta can be held by dietary components or remain unbound as either trapped or free water in the GIT segment (Chaplin, 2003; Anguita *et al.*, 2007). High-fibre diets had the highest water concentration as the digesta moved across the gut segments. Water concentration in the stomach in relation with maize cob inclusion level showed the same pattern as WHC. An increase in maize cob levels decreased water concentration in the distal colon probably due to the primary function of the colon to actively absorb water and sodium ions against the electrochemical gradient (Williams *et al.,* 2001; Anguita *et al.,* 2007). The increase of water concentration along the gut in pigs on the basal diet reflected a high digestibility of starch fraction in the foregut compared to the hindgut (Bach Knudsen, 2001; Molist *et al.,* 2009). Interestingly, 80 and 160 g/kg maize cob diets decreased water concentration in the hindgut rapidly compared to the basal diet.

3.5 Conclusions

Stomach weights increased with the inclusion level of maize cob. Maize cob inclusion level had no effect on pH of other segments except in the distal colon. It can be concluded that changes in the physicochemical characteristics of the digesta along the gut of growing pigs is influenced by the maize cob inclusion level in the diet. Digesta physicochemical properties need to be considered when developing models to predict voluntary feed intake of fibrous feeds in pigs.

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CHAPTER FOUR: Effects of physicochemical properties of fibrous diets on hydration properties of digesta from finishing pigs

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Abstract

The objectives of the study were to determine the relationship between the hydration properties of fibrous diets with the digesta along the gut in finishing pigs, and to predict feed intake from stomach digesta hydration properties. A total of 84 pigs weighing 80.9 ± 8.15 kg body weight were given, *ad libitum*, each of the 21 diets containing a diet diluted with 0, 80, 160, 240, 320 and 400 g/kg of maize cob, lucerne hay, sunflower husk and citrus pulp. After 30 days of the trial, the pigs were slaughtered and weighed, intestinal contents sampled and the gut segments weighed. The stomach weights increased linearly with an increase in dietary NDF but increased with quadratic functions with an increase in SWC of the diet (P <0.05). An increase in WHC of the fibrous diets linearly increased the WHC of the proximal colon (P <0.01) at a faster rate compared to the WHC of the distal colon (P <0.001). As the SWC of the diets increased, linear increases in SWC of the digesta in the stomach (P <0.01) and caecum (P <0.001) were observed. The WHC of the digesta was negatively correlated to SWC ($P < 0.001$) in the stomach. The SFI linearly decreased with an increase in SWC of the diet (P < 0.001). There was no relationship between WHC of the diet and SFI (P > 0.05). There was a negative linear relationship ($P < 0.01$) between SFI of finishing pigs and the SWC of the digesta. The swelling capacity of the diets and digesta in the stomach are accurate descriptors of scaled feed intake. Swelling capacity has great influence in the stomach weights whilst other bulking properties such as WHC and NDF had an effect on weight and digesta properties in the caecum, proximal and distal colon.

Keywords: dietary fibre; finishing pigs; swelling capacity; water holding capacity.

4.1 Introduction

Changes in hydration properties of digesta in finishing pigs are poorly understood. Such changes depend on the interaction between age of the pig, physical structure and physicochemical properties of the diet, among other factors (Canibe and Bach Knudsen, 2002; Bindelle *et al.*, 2008).

Previous studies on digesta kinetics have been based on a limited number of fibrous sources with a narrow range of physicochemical properties (Anguita *et al.*, 2007; Molist *et al.*, 2009; Banino, 2012). In Chapter 3, inclusion of dietary fibre (DF) in growing pigs influenced the water holding capacity (WHC) and swelling capacity (SWC) of the digesta. These changes are likely to be different from those of finishing pigs. Fermentation ability, the size of the gut and experience to utilising fibrous diets is expected to be higher in finishing than growing pigs. It is, therefore, imperative to determine the effects of the physicochemical properties of diets on hydration properties of digesta in finishing pigs. Such digesta properties can then be used to estimate voluntary feed intake of pigs.

The objectives of the study were to determine the relationships between the hydration properties of the feed and the digesta along the gut in finishing pigs, and to predict feed intake using these hydration properties of digesta in the stomach. The hypothesis tested was that hydration properties of the digesta affect feed intake of finishing pigs.

4.2 Materials and Methods

4.2.1 Study site

The study was carried out at Ukulinga Research Farm, in the University of KwaZulu-Natal, Pietermaritzburg. Details on the site description are given in Section 3.2.

4.2.2 Pigs and housing

A total of 84 clinically healthy male pigs (Large White × Landrace) with body weight (BW) of 80.9 ± 8.15 kg were used. Before the experiment started, each pig was ear-tagged and was allocated to individual concrete-floored pens (2.0 m × 1.1 m). Each pen had a plastic self-feeder trough (Big Dutchman Lean Machine®) and a low-pressure nipple drinker. Feed and water were provided ad libitum. The pens were cleaned daily.

The trial on pigs was performed according to the conduct by the Certification of Authorization to Experiment on Living Animals provided by the UKZN Animal Ethics Committee (Reference Number 082/12/Animal). Automated HOBO TEMPERATURE, RH©, 1996 ONSET data logger was used to record ambient temperature and relative humidity at 15 min intervals throughout the experiment. The average temperature and relative humidity within the pig house were maintained at 22.10 ± 1.79 ^{o}C and 42.45 ± 1.50 %, respectively, by use of a single heating, lighting and ventilation system.

4.2.3 Diets

The diets were based on maize cob (MC), sunflower husk (SH), citrus pulp (PU) and lucerne hay (LH) as fibrous ingredients. A low-fibre high quality commercial feed (Supreme Grower, Meadow feeds LTD, Pietermaritzburg, South Africa) was used as a basal feed. The basal diet contained 500 g yellow maize, 158 g soybean, 20.2 g soybean oil cake, 163 g wheat bran, 85 g sunflower oil cake, and 48.8 g of additives per every kg on dry matter (DM) basis. Each fibrous ingredient was ground using a 2 mm sieve through a mill (Thomas Wiley$^{(R)}$ Mill, New Jersey, USA). Following the assumption that pigs will consume more to satisfy the requirements of the most limiting nutrient, the basal feed was diluted with each of the fibre sources at inclusion levels of 0, 80, 160, 240, 320 and 400 g/kg to make a total of 21 complete diets. Tables 4.1 and 4.2 show the chemical composition and physical properties of the experimental diets used. The diets were not supplemented with any growth promoters and antibodies. Four individually-penned pigs were randomly allocated to each diet for 30 days, following an adaptation period of 10 d. A completely randomized design was used.

4.2.4 Measurements

Pigs were weighed weekly. The body weight (BW) of each pig was divided by 7 to determine average daily gain (ADG). Feed intake was recorded on daily basis. The FCR was determined for the whole trial by dividing ADFI by ADG.

During the last day of the trial, pigs were given their last meal at 0600 h. After a 4 hour (h) fasting period, each pig was euthanized by intravenous injection of sodium pento-barbitone (200 mg/kg BW) and eviscerated. The GIT (from *cardias* to rectum) was immediately removed and segmented into stomach, ileum, caecum, and proximal colon and distal colon. The colon segment was unravelled and divided into two equal sections. Empty segments (stomach, caecum, proximal and distal colon) of digestive tract were weighed separately. Digesta was collected into plastic bags from all five GIT segments within 90 min of slaughter, and the samples were immediately frozen at -20 °C. Sampling of intestinal contents was done according to the procedures described by Anguita *et al.* (2007) and Molist *et al.* (2009).

4.2.5 Determination of physicochemical properties of diets and digesta

Proximate analysis and determination of physicochemical measurements of feed bulk for all the diets and digesta samples were performed, in triplicate, in the Animal and Poultry Science Laboratory at the UKZN, Pietermaritzburg.

Table 4.1: Chemical composition of experimental fibre diets (g/kg)

Fibre sources	Level (g/kg)	Chemical composition				
		DM (g/kg)	[1]calc DE (MJ/kg DM)	Crude protein (g/kg DM)	Diethyl ether extract (g/kg DM)	Ash (g/kg DM)
B	0	90.14	10.70	24.78	3.73	5.52
MC	80	90.05	10.50	21.85	4.88	5.28
MC	160	90.91	10.30	20.79	5.45	5.04
MC	240	90.35	9.99	19.91	3.40	4.55
MC	320	90.79	9.50	16.87	3.00	4.36
MC	400	90.69	9.41	14.52	2.91	4.38
LH	80	87.59	9.84	17.88	5.09	5.75
LH	160	88.23	8.64	17.78	5.14	5.60
LH	240	88.07	8.00	17.94	3.46	6.80
LH	320	88.59	9.54	17.62	4.49	6.62
LH	400	88.25	9.57	17.31	3.61	6.41
PU	80	87.75	9.35	18.02	4.48	5.07
PU	160	91.61	10.00	16.06	4.94	5.34
PU	240	88.53	10.20	14.76	2.75	5.13
PU	320	88.07	10.50	14.35	4.36	5.17
PU	400	87.95	11.00	13.96	3.25	5.23
SH	80	88.02	8.40	16.87	4.68	4.84
SH	160	87.78	8.90	15.89	4.45	4.71
SH	240	88.17	9.64	15.16	4.26	4.38
SH	320	90.09	8.93	13.46	4.60	3.90
SH	400	88.78	8.49	12.46	3.13	4.18
[2]SEM		1.28	0.82	2.70	0.83	0.78

B – basal diet; MC – maize cob; LH – lucerne hay; PU - citrus pulp; SH – sunflower husk

DM – dry matter

[1]calc DE = 949 + (0.789 x GE) - (43 x %Ash) - (41 x %NDF) (Noblet and Perez, 1993)

[2]SEM – standard error of means

Table 4.2: Physical properties of experimental fibre diets (g/kg)

Fibre source	Level (g/kg)	Physical property				
		Bulk Density (g/ml)	NDF (g/kg)	ADF (g/kg)	WHC (g /g)	SWC (ml/g)
B	0	1.83	430.93	68.39	4.60	2.54
MC	80	1.75	454.44	170.57	4.50	3.00
MC	160	1.65	470.30	185.59	5.71	3.11
MC	240	1.64	477.09	236.12	4.80	3.10
MC	320	1.47	505.41	325.75	5.94	3.61
MC	400	1.44	506.83	256.96	5.94	3.24
LH	80	1.75	450.62	126.02	4.06	2.81
LH	160	1.69	537.03	183.50	5.61	2.99
LH	240	1.65	548.06	205.97	5.28	2.94
LH	320	1.47	476.99	285.88	6.60	3.19
LH	400	1.44	471.05	303.55	7.32	3.81
PU	80	1.86	475.35	165.91	4.07	2.56
PU	160	1.77	434.68	202.89	6.39	3.73
PU	240	1.75	411.00	229.59	6.34	2.99
PU	320	1.73	404.67	306.99	6.36	2.97
PU	400	1.73	362.00	277.17	7.42	2.75
SH	80	1.76	541.69	164.32	4.58	2.90
SH	160	1.69	511.54	310.24	4.20	2.76
SH	240	1.61	475.99	285.43	4.08	2.86
SH	320	1.54	535.81	452.44	4.87	2.98
SH	400	1.47	565.81	457.06	4.80	3.27
SEM		0.13	51.20	93.85	1.04	0.33

B – basal diet; MC – maize cob; LH – lucerne hay; PU - citrus pulp; SH – sunflower husk NDF- neutral detergent; ADF – acid detergent fibre; WHC – water holding capacity; SWC – swelling capacity

[1]SEM – standard error of means

Chemical composition, determined according to the method of Association of Official Analytical chemists (AOAC, 1984; 2005) standard procedures, and the physical properties of the experimental diets were determined as described in chapter 3. Analyses of WHC and SWC of digesta samples were performed on wet materials and freeze-dried materials, respectively.

Fresh digesta pH was assessed, in triplicate, through an insertion of Crison 52 02 glass pH electrode. The collected samples were divided into aliquots for WHC and SWC analyses. Water holding capacity was determined by centrifugation following the method described by Anguita *et al.* (2006). The procedure was also performed in triplicate. The values were expressed as g water held per g dry residue (g/g). Swelling capacity was measured based on the modified bed volume technique as described by Canibe and Bach Knudsen (2002). The values were expressed as ml of swollen sample per gram of dry residue (ml/g). All analyses were performed in triplicate.

4.2.6 Statistical analyses

Effects of source of fibre, fibre inclusion level, and their interactions on ADFI, ADG and FCR were determined using the GLM procedures (SAS, 2008). The model used was:

$Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha \times \beta)_{ij} + \varepsilon_{ijk;}$

where:

Y_{ijkl} is the performance parameter (ADFI, ADG and FCR);

μ is the overall mean response common to all observations;

α_i is the effect of fibre source (i = MC, SH, PU, LH);

β_j is the effect of fibre inclusion level (j = 0, 80, 160, 240, 320 and 400 g/kg);

$(\alpha \times \beta)_{ij}$ is the interaction between the fibre source and its inclusion level and

ε_{ijk} is the residual error.

The relationships between the fibre source and inclusion level with performance parameters were analyzed using the quadratic response-surface model procedures (PROC RSREG) of SAS (2008). Stepwise regression in SAS (2008) was used to identify physicochemical properties of the diets which influenced gut segment weights. The quadratic response surface model (PROC RSREG) procedure of SAS (2008) was used to determine the relationship between stomach, ileum, caecum, proximal colon and distal colon weights and each of the diet physicochemical properties selected using stepwise regression.

The PROC RSREG of SAS (2008) was used to determine the relationship between hydration properties in the diet and in the digesta along the gut segments. The correlation between WHC and SWC of the digesta in each gut segment was analyzed using Pearson's correlation (PROC CORR) of SAS (2008). The stepwise regression of SAS (2008) was used to identify hydration properties of digesta that influence scaled feed intake (SFI). RSREG (SAS, 2008) was used to determine the type of relationship between SFI with each of the selected hydration properties.

4.3 Results

4.3.1 Effect of inclusion level of fibre on pig performance

The effects of inclusion level of fibre in pig diets on performance parameters are shown in Table 4.3. Although ADFI increased linearly with the inclusion levels of citrus pulp and lucerne hay ($P < 0.01$), it was reduced linearly with increase in incremental levels of MC ($P < 0.001$). Intake of SH-based diets initially increased with inclusion level and then decreased gradually. Across all fibre sources, ADG decreased linearly only with increase in inclusion

Table 4.3: Effect of fibre source and inclusion level on pig performance

Item	Fibre source	Inclusion level (g/kg)						SEM	Regression coefficient		P-value
		0	80	160	240	320	400		Linear	Quadratic	
ADFI	PU	3.41	3.23	3.12	3.29	2.89	2.59	0.24	0.01		**
	LH	3.75	2.92	3.61	3.26	2.26	2.38	0.25	0.08		***
	MC	3.43	3.31	2.98	3.21	2.04	2.8	0.24	-0.04		**
	SH	3.00	3.26	3.43	3.34	2.67	2.61	0.23	0.04	-0.001	*
ADG	PU	0.59	0.95	0.88	0.87	0.97	0.97	0.86			NS
	LH	0.90	0.76	1.10	0.87	0.77	0.67	0.84			NS
	MC	0.85	0.70	1.22	0.90	0.70	0.74	0.85			NS
	SH	0.53	1.29	0.83	0.80	0.83	0.91	0.86	-0.0007		*
FCR	PU	0.17	0.30	0.29	0.27	0.34	0.37	0.29			NS
	LH	0.25	0.27	0.32	0.29	0.38	0.28	0.30			NS
	MC	0.26	0.22	0.42	0.31	0.38	0.27	0.31			NS
	SH	0.17	0.42	0.24	0.26	0.33	0.37	0.30			NS
SFI	PU	34.9	31.1	33.3	34.7	32.3	31.0	0.45			NS
	LH	33.2	30.4	34.0	35.0	25.6	28.8	0.38	0.002		*
	MC	34.6	31.9	32.0	28.6	22.2	31.4	0.49	-0.006		**
	SH	33.8	31.0	35.7	32.5	29.6	28.9	0.36	0.002		*

NS – Not significant, *P<0.05, P< 0.01, ***P<0.001

ADFI – average daily feed intake (kg), ADG, average daily gain (kg), FCR, feed conversion ratio; for the whole trial

SFI – scaled feed intake; for the last week of the trial

SEM – standard error of means

level of SH, and then gradually increased ($P < 0.05$). Incremental levels of all fibre sources had no influence on FCR ($P > 0.05$).

4.3.2 Effects of physicochemical properties of the diet on segment weights

The effects of physicochemical properties of diets on gut segment weight are shown in Table 4.4. The stomach weights increased linearly with increase in NDF but increased quadratically with an increase in SWC ($P < 0.05$). Other physicochemical properties, including ADF and WHC, had no significant effects on stomach weights. All physicochemical properties of the diets did not influence ileal weights ($P > 0.05$). A linear decrease ($P < 0.05$) in caecum weight was observed as the SWC the diets increased. Among all physicochemical properties, only an increase in NDF content of the diet linearly increased the proximal colon weights ($P < 0.05$).

4.3.3 Effects of hydration properties of the diet on hydration properties of digesta in each gut segment

Table 4.5 shows the relationships between hydration properties of the diet with digesta. Water holding capacity of the diet had no effect on WHC of the digesta in the stomach, ileum and caecum ($P > 0.05$). An increase in WHC of the fibrous diets caused linear increase in the WHC of the proximal ($P < 0.01$) and distal ($P < 0.001$) colonic digesta, however, rate of fibre matrix to take up and hold water was faster in the distal colon. As the SWC of the feed increased, linear increases in SWC of the digesta in the stomach ($P < 0.01$) and caecum ($P < 0.001$) were observed. The SWC of the diet did not influence the SWC of the digesta in the ileum, proximal colon and distal colon. Rates of swelling rate were faster in the stomach than in caecum ($P > 0.05$).

Table 4.4: Effect of the physicochemical properties of the diet on segment weights

Item	Model [segment weight = $ax^2+bx+c+e$]			R^2 value	*P* – value
	A	B	c		
Stomach weight					
NDF		5.48±3.59	-507±835	0.0612	*
SWC	159±91.2	-945±577	204±904	0.0615	*
Caecum weigh					
SWC		-114±277	325±434	0.0841	*
Proximal colon weight					
NDF		0.86±11.02	156±256	0.129	*

NDF – neutral detergent fibre; SWC – swelling capacity; ADF – acid detergent fibre; *a*, *b* and *c* are regression coefficient; x – physicochemical property of the diet; *e* – residual error
* $P<0.05$

Table 4.5: Effect of physicochemical properties of the diet on hydration properties of the digesta

Item	Model [hydration property $=ax^2+bx+c+e$]		R^2 value	P - value
	B	c		
Water holding capacity				
Proximal colon				
WHC	0.0435±0.487	3.10±1.33	0.0791	**
Distal colon				
WHC	0.377±0.483	1.62±1.32	0.21	***
Swelling capacity				
Stomach				
SWC	2.57±2.40	-1.49±3.75	0.068	**
Caecum				
SWC	1.01±1.37	0.984+2.13	0.273	***

$^{**}P < 0.01$, $^{***}P < 0.001$.

WHC – Water holding capacity, SWC – swelling capacity
a, b and *c* are regression coefficient; x – hydration property of the digesta; *e* – residual error

4.3.5 Correlations between hydration properties of the digesta in gut segments

Table 4.6 shows the correlation coefficients among WHC and SWC of digesta from different segments of the gut. The WHC was negatively correlated to SWC ($P < 0.001$) in the stomach. In the ileum and proximal colon, WHC was positively correlated with SWC ($P < 0.001$). There were no significant correlations between WHC and SWC of the digesta in the caecum and distal colon.

4.3.6 Prediction of scaled feed intake from the physicochemical properties of the diets and digesta

The effects of physicochemical properties of digesta from the different gut segments on feed intake of pigs are shown in Table 4.7. The SFI linearly decreased with an increase in SWC of the diet (P < 0.001). There was no relationship between WHC of the diet and SFI (P > 0.05). There was a linear decrease ($P < 0.01$) in SFI of finishing pigs as the SWC of the digesta increased. No relationship was observed between WHC of the digesta and SFI in the stomach ($P > 0.05$).

4.4 Discussion

The study was designed to determine how physicochemical properties of fibrous diets relate to the hydration properties of digesta as well as intake of finishing pigs. To have a comprehensive understanding of the effects of the physicochemical properties of bulky diets, a variety of fibre sources were used to dilute the basal feed at varying inclusion levels. The fibrous feedstuffs used had different WHC, SWC, NDF and ADF. These fibre sources were used to formulate diets with a wide range of physicochemical properties. The fibre sources used in the current study were also chosen due to their availability and abundance, especially in the tropics and sub-tropics.

Table 4.6: Correlation coefficients among hydration properties of the digesta in each gut segment

	SWC_{st}	SWC_{il}	SWC_{ca}	SWC_{pc}	SWC_{dc}
WHC_{st}	-0.267***	-	-	-	-
WHC_{il}		0.341***	-	-	-
WHC_{ca}			0.118^{NS}	-	-
WHC_{pc}				0.438***	-
WHC_{dc}					0.165^{NS}

NS – not significant ($P > 0.05$), ***$P < 0.001$.

WHC – water holding capacity, SWC – swelling capacity

Subscripts: $_{st}$- stomach, $_{il}$ – ileum, $_{ca}$ – caecum, $_{pc}$ – proximal colon and $_{dc}$ – distal colon

Table 4.7: Prediction of feed intake from the physicochemical properties of digesta from the different gut segments

Item	Model [SFI = bx+c+*e*]		R^2 value	P-value
	B	C		
Diet				
SWC	-3.5 ± 13.9	46.1 ± 22.8	0.1382	***
Stomach				
SWC	-0.501 ± 4.57	38.8 ± 7.46	0.0781	**

**$P < 0.05$, **$P < 0.01$.

SWC – swelling capacity

a,*b* and *c* are regression coefficient; x – SWC; *e* – residual error;

The observation that ADFI increased with inclusion levels of PU and LH could be ascribed to the notion that pigs consume feed to compensate for decrease in the energy content, so that they could meet their requirements for growth (Whittemore *et al.*, 2001). The finding that incremental levels of MC depressed ADFI was unexpected and contradicts (Kanengoni *et al.*, 2004) and (Ndou *et al.*, 2013a). The observation that ADFI initially increased with incremental levels of SH up to a point where it then decreased indicates that pigs tolerate low levels of WHC, SWC and NDF, probably due to increase in both the size of the gut segments and fermentation ability but decreases when optimum inclusion levels are exceeded. The observation that ADG of pigs decreased with SH inclusion can be attributed to the masking effects of dietary fibre on the bio-availability of non-fibrous feed components to enzymatic degradation (Le Goff *et al.*, 2003; Whittemore *et al.*, 2003). The lack of differences in ADG of pigs fed on diets based on PU, LH and MC suggests that the pigs adapted differently to the utilization of the different fibrous feeds. The observation that FCR was not affected by fibre sources and inclusion levels is difficult to explain, but indicates that fibrous diets are, to a great extent, utilized for meeting the growth requirements of pigs. The contribution of each fibre source to the nutrient requirements of pigs, however, warrants further investigation.

The observation that the stomach weight increased with an increase in NDF content and SWC of the diets implies that feed bulk led to the expansion and distension of stomach tissues. Another plausible explanation could be that the physiological effects of fibrous diets may trigger a secretion of digestive fluids for catabolizing dietary fibre, leading to organ hypertrophy (Wenk, 2001; Agyekum *et al.*, 2012). Our findings agree with (Gomes *et al.*, 2006) who reported that empty stomach weight increased when dietary NDF content exceeded 80 g/kg. In their study, ADF and WHC had no effect on stomach weights. Caecum and the colon are both the most active gut segments in the degradation of fibre (Bach

Knudsen, 2001). The observation that the caecum weight decreased with SWC of the diet suggests that during transit of digesta in the gut, various biochemical changes occur in the foregut. Therefore, the capacity of digesta which escapes enzymatic digestion to swell is limited. The biochemical changes that influence physicochemical properties of digesta during gut transit warrants further investigation. The increase in the proximal colon weight with an increase in NDF content was consistent with literature (Len *et al.*, 2009; Ngoc *et al.*, 2012). The digesta which escape enzymatic digestion in the foregut has high NDF content, which could have triggered hypertrophy to support microbial fermentation and the subsequent absorption of volatile fatty acids (Stanogias and Pearce, 1985; Bindelle *et al.*, 2008).

The finding that WHC of the diet had no relation with WHC of the digesta in the stomach, ileum and caecum was not expected. The swelling capacity feed is expected to increase with the ability of the feed components to hold water (Canibe and Bach Knudsen, 2002; Knudsen, 2011). The findings from the current study could indicate that the affinity for the hydrophilic binding sites of fibrous matrices to hold water molecules will be reduced. The reduction in the ability to bind water is caused by saturation of these sites by drinking water during mastication. Feeding and drinking behaviours of the pigs were, however, not observed. Pigs on fibre based diets are expected to drink more water than those on low-fibre diets (De Leeuw *et al.*, 2008). Water holding capacity measures the ability of NPS matrix to hold or takes up water. The WHC of the diet and that of the digesta in the proximal and distal colon were positively correlated. These findings agree with (Molist *et al.*, 2009). The observed faster increase on the ability of the digesta to hold water in the distal colon than in the proximal colon may be associated with the physiological function of the colonic epithelium to absorb water against the electrochemical gradient of sodium ions (Williams *et al.*, 2001). As the concentration of water around the digesta is reduced, more hydrophilic binding sites within the fibrous matrices become vacant, thus their ability and affinity to water molecules is revived, and consequently increasing WHC of digesta in the distal colon.

The finding that an increase of SWC in the diet increased the SWC of digesta in the stomach indicates that mastication, the ability of the non-starch polysaccharides, to trap water within its matrices, swell and form ‘bulky’ gels with high water contents, is enhanced (Knudsen, 1997; 2011). By the time digesta reaches the caecum, their capacity to swell is observed to be less effective due to that the fibrous matrices would have reached a certain elastic limit or optimum capacity to absorb water. High SWC and WHC determines fermentability of fibre along the gut segments (Canibe and Bach Knudsen, 2002). The observed slight increases in SWC of the digesta could be a mechanism to increase the surface area of the digesta to microbial degradation. The lack of relation that was observed in SWC of the diets and SWC digesta in the ileum, proximal colon and distal colon could be explained by the interaction of other effective hydration properties along the gut (Banino, 2012).

The negative correlation observed between WHC and SWC in the stomach contradicts previous studies by Takahashi *et al.* (2005) and Takahashi *et al.* (2009) but supports the notion that bulking properties changes during transit in the gut depending on biochemical as well as physical activities that occur in each gut segment (stomach and small intestine) (Glitsø *et al.*, 1998; Mikkelsen *et al.*, 2004; Anguita *et al.*, 2007). For a fibre to swell, it has to take up water first (Elhardallou and Walker, 1993; Guillon and Champ, 2000). In the stomach drinking water saturates all water binding sites with the digesta thereby reducing the capacity to hold more water molecules. Concurrently, as water molecules gather they tend to repel each other, thereby initiating a tendency of the feed molecules to occupy more space (Elhardallou and Walker, 1993).

The findings that WHC positively correlated (r = 0.438) with SWC in the ileum and proximal colon were in agreement with the reports by Canibe and Bach Knudsen (2002) and Takahashi *et al.* (2009). The SWC and WHC are often related because for a feed to increase in size it has to have a high capacity to retain water within its matrices. The relationship between WHC and other chemical properties of fibres can be explained by the prevalence of hydrogen bonds within the fibre matrix and the extent with which these bonds are exposed as possible binding sites (hydroxyl groups) with water (Oakenfull, 2001). The lack of correlation between WHC and SWC in the caecum and distal colon could be attributed to the fact that digesta would have gone through a plethora of biochemical and physical processes that induce direct and indirect effects. Direct effects such as modifications viscosity, WHC or digesta passage rate during enzymatic digestion, absorption and mixing due to churning actions of the gut muscle, are more relevant in the stomach and small intestines (Ellis *et al.*, 1995; Glitsø *et al.*, 1998; Mikkelsen *et al.*, 2004). On the other hand, indirect effects gain more relevance in the hindgut where fermentation processes occurs, as well as releases of short chain fatty acids, organic acids and gases (Anguita *et al.*, 2007; Bindelle *et al.*, 2008). Therefore, each or a combination of either of the aforementioned mechanisms will which change particle size and chemical composition, thereby leading to paradoxical relationships between physicochemical properties of digesta.

The SFI decreased as the feeds swelled. As the feed components absorbs water, its components swell and increase in size. As a result, ingestion will be suppressed due to limitation of space in the stomach. Our findings are contrary to previous studies by Tsaras *et al.* (1998), Whittemore *et al.* (2003) and Ndou *et al.* (2013b), who repeatedly reported that WHC, NDF and ADF are the most accurate descriptors of feed intake. Unlike in the previous studies, swelling capacity was the accurate measure in the current study and the dietary treatments had physicochemical properties that were widely spread.

The reduction in SFI observed with increase in SWC of digesta in the stomach also supports that the postulation that the volume was constrained due to gut fill as digesta expand. The realization that rates of decrease in SFI were pronounced when swelling capacity of the diet increased than that of stomach digesta confirms that physicochemical properties of digesta change from one segment to the other. The difference in these rates of decrease further indicates that the limit of elasticity with which feed molecules swell decrease along the gut.

4.5 Conclusions

Swelling capacity has great influence in the stomach weights whilst other bulking properties such as WHC and NDF had an effect on weight and digesta properties in the caecum, proximal and distal colon. The segment weights and digesta properties are influenced by different physicochemical properties. The swelling capacity of the diets and stomach digesta in the stomach are accurate descriptors of scaled feed intake.

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CHAPTER FIVE: General discussion, conclusions and recommendations

5.1 General discussion

Use of fibrous diets is receiving increasing interests among feed compounders to reduce feed costs and, more importantly, reduce competition for grain between humans and livestock. Physicochemical properties of alternative feed resources, therefore, need to be explored and characterized. The physicochemical measures feed components which define the bulkiness of the feed and digesta, and hence the amount of fibrous feed that can be consumed by growing and finishing pigs. Among these, hydration properties of digesta need to be determined, as they influence the functional, nutritional and physiological effects of dietary fibre. It is imperative to determine the physicochemical measurements of bulkiness of diets and digesta so that consumption of sufficient nutrients by growing and finishing pigs is achieved without restricting nutrients to achieve potential growth and reduce nutrient losses to the environment.

The effects of varying inclusion levels of dietary fibre in growing pigs were determined in Chapter 3. The physicochemical characteristics of the digesta along the gut were influenced by the maize cob inclusion level. The physical properties of feed ingredients varied widely with incremental levels of maize cob. The variation in the physicochemical nature of digesta within each segment indicated that monomeric composition and structural arrangements of building blocks is not uniform and might impose complex physiological effects on gut fill, digestibility and performance. To understand the influence of bulkiness on digesta properties, and subsequently feed intake, it is essential that a variety of fibre sources are used so that conclusions on relationships between digesta properties within each gut segment intake and bulkiness can be made over a wide range of physicochemical properties.

It was hypothesised that the relationship between physicochemical properties of diets and digesta in growing pigs would be different from that in finishing pigs. Unlike in growing pigs, maize cob, sunflower husk, citrus pulp and lucerne hay were used as the fibre sources for finishing pigs (Chapter 4). The mechanisms with which physicochemical properties of digesta in growing pigs could be different for finishing pigs. Scaled feed intake (SFI), defined as ADFI expressed as a proportion of the body weight of the pig, decreased as the SWC increased. As the feed components swell, it absorbs water and increase in size, inevitably reducing bulk density of the feed. As a result, ingestion will be suppressed due to limitation of space in the stomach. In literature, it was argued that WHC, rather than SWC, influences SFI. In the current study, SWC was an accurate measure of SFI.

Reduction in SFI with increase in SWC of digesta in the stomach also supports the postulations that the volume was constrained due to gut fill as digesta expand. The realization that rates of decrease in SFI were pronounced when swelling capacity of the diet increased than that of stomach digesta confirms that physicochemical properties of digesta change along the gut.

5.2 Conclusions

Incorporation of fibre ingredients induces variable physical properties that additively influence feed bulk and subsequently digesta properties along the gut. Changes in physicochemical characteristics of the digesta along the gut was influenced by maize cob level. The swelling capacity of the diets and stomach digesta in stomach are accurate descriptors of scaled feed intake. Swelling capacity influenced stomach weights whilst WHC and NDF had an effect on weight and digesta properties in the caecum, proximal and distal colon. The influence of physicochemical properties of diets and digesta in growing pigs is different to that in finishing pigs.

5.3 Recommendations and further research

Physicochemical measurements of digesta and feed bulk provide predictive relationships describing changes in feed intake with bulkiness that could be used to estimate the gut capacity of growing pigs. Feed compounders should also consider the influence that physical properties of feed ingredients have on changes in digesta properties when formulating diets. If pig producers decide to make use of bulky ingredients when they are available at a reasonable cost, selecting fibrous ingredients with low SWC, such as maize cob and sunflower husks, is recommend for these are occupy likely to occupy less space in the GIT. Furthermore, due to that inclusion of dietary fibre reducing bulking density and increases feed spillages, pelleting the bulky feeds would help to reduce these effects.

There is need to investigate further how specific non-starch polysaccharides of digesta change during transit in the gut. There is need, therefore, for further research to characterize physicochemical properties of digesta in different sections of the gut. Furthermore, the mucosal nature of gut walls of finishing pigs given fibrous feeds with a wide range of physicochemical properties need to be measured. These properties should be measured in conjunction with transit time and concentration of short chain fatty acids within each section of the gut. Research on the effects of hydration properties of bulky diets with enzymatic additives on feeding, drinking and stereotypic behaviours of pigs is recommended to establish the effects of satiety levels on pig welfare. It is of paramount importance also to assess the influence of feed bulk on water intake and nutrient excretion from a wide of variety fibrous sources.