THE EFFECT OF HIGH-FIBER DIETS ON NUTRIENT UTILIZATION AND INTESTINAL MORPHOLOGY OF GROWING PIGS

by

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CHAPTER I

INTRODUCTION

Within the past decade, there has been a revival of interest in the potential benefits of high-fiber intakes in man and animals. In humans, experimental and epidemiological evidence suggests that increased fiber intakes may be effective in protecting against or treating a variety of gastrointestinal and metabolic diseases, most notably colon cancer, atherosclerosis and coronary heart diseases, diabetes and hypercholesterolemia (Eastwood and Passmore, 1983).

The use of greater amounts of high-fiber feedstuffs in swine diets may have both economic and physiological benefits. To a limited degree, by-product feedstuffs which contain large amounts of fiber represent a source of less expensive dietary energy. However, other reasons have also been proposed for increasing dietary intakes of fiber by swine. Early studies by Teague and Hanson (1954) and Gorrill et al. (1960) showed that modest dietary additions of fiber increased growth in pigs. A later study by Corley et al. (1978) also showed that high-fiber diets increased growth, and they proposed that certain

fiber sources had an 'antibiotic-like' growth-promoting effect when fed to pigs.

Numerous studies using weanling pigs have not demonstrated that cereal grain or oilseed fibers increase growth rate or decrease the incidence of scours (Wahlstrom et al., 1977; Kong et al., 1980; Kornegay et al., 1980,1981). However, Brumm and Peo (1985) have recently shown that alfalfa hay and alfalfa meal reduce the incidence and severity of scours in feeder pigs, while neither fiber source affected growth.

Studies have also suggested that the consumption of alfalfa hay by gestating sows increases piglet survival percentage and increases sow longevity over a three-parity period, although subsequent studies have failed to confirm the benefit on piglet survival of feeding alfalfa meal to sows (Calvert et al., 1985; Pond et al., 1985). Zoiopoulos et al. (1982,1983) suggested that oat hulls or oat straw increased fat content of sow milk, although no subsequent effect of this on piglet survival was demonstrated. A series of recent studies indicates that high-alfalfa diets protect gestating sows and gilts from zearalenone and T-2 mycotoxicoses, apparently by decreasing the absorption of these toxins from the intestine (Smith, 1980; Carson and Smith, 1983; Stangroom and Smith, 1984).

However, the inclusion of fiber in the diet may also have negative effects on the nutritional status of the animal. Although this aspect of fiber nutriture has received less attention, evidence suggests that high fiber intakes may decrease mineral balance to an extent that acute or chronic mineral deficiencies could be created (Reinhold et al., 1976). Despite considerable research, a clear picture has not developed on the impact of high-fiber diets on mineral balance, and the physiological consequences of any fiber-induced reduction in mineral balance.

A number of factors contribute to the poor understanding of the relationship between fiber intake and mineral utilization. Foremost, is the fact that a number of proposed mechanisms exist, which alone or in combination, may be involved in a fiber-induced decrease in mineral utilization. At the present time, these include:

1. binding or sequestering of metal ions by the fiber matrix within the gastrointestinal lumen,

2. decreased bioavailability of minerals contained in the fiber source,

3. increased transit rate of digesta through the gastrointestinal tract, and

4. damage to the intestinal absorptive surface or an alteration in surface structure which limits mineral access to the epithelial cells or decrease intestinal transport capacity.

Because the ability of purified or native fibers to alter digestive function may result from one or more of the above mechanisms, it has been difficult to design and conduct experiments able to account for all possible mechanisms. The information available at the present time is fairly limited in scope, since most studies have been conducted in humans and experimental animals and have used protocols which used relatively small amounts of dietary fiber, were conducted over short time periods, and have used relatively high mineral intakes.

It has been difficult to adapt these results for practical use in swine diets, since the types and levels of fiber, and the durations of feeding, are quite different in swine feeding systems. Therefore, at the present time there is insufficient information available to determine whether different fiber sources would have a negative impact on mineral utilization in swine, particularly when fed at the high levels being contemplated, and for the long time periods which would be encountered in a practical feeding situation.

Although much is known about the effects of certain high-fiber diets on protein and energy utilization by swine, only recently have reports been presented which indicate that fiber may also impair mineral utilization in pigs. Thus, if the beneficial uses of fiber are to be exploited successfully, it is crucial that an understanding be developed of the effects of different fiber sources on mineral utilization, so that those fiber sources or feeding conditions which might limit mineral utilization, can be avoided or overcome.

The experiments reported herein were conducted to provide information on the effect of dietary fiber on nutrient utilization in pigs, and to provide descriptive data on the effects of high-fiber diets on intestinal structure in the pig. Specific objectives were:

1. to determine the effect of high-fiber diets on mineral balance. A collateral objective was to compare the effects of different fiber sources, which differed in their susceptibility to degradation within the gastrointestinal tract of the pig, on mineral and nutrient utilization in growing pigs,

2. to determine if the ability of dietary fiber to influence mineral utilization is dependent on

the duration of feeding or the level of mineral intake, and

3. to obtain descriptive data on intestinal morphology and ultrastructure of pigs fed conventional low-fiber diets or diets containing high-fiber feedstuffs.

CHAPTER II

REVIEW OF THE LITERATURE

Definition and properties of dietary fiber

Defining what constitutes 'dietary fiber' remains a controversial subject, however considerable effort has been directed in recent years to developing a definition which could be used in explaining the diverse range of nutritional and physiological responses attributed to the consumption of high-fiber diets. Most definitions of dietary fiber originated from Trowell's (1972) definition of fiber as the plant cell wall components resistent to digestion by human or animal digestive enzymes.

However, arguments have been presented to include components not found in the cell wall, but which are resistent to digestive enzymes, in a more comprehensive definition of dietary fiber (Spiller and Fasset-Cornelius, 1976). Thus, current concepts of dietary fiber are based on Cummings' definition (1981), which defines dietary fiber as the sum of the non-starch polysaccharides present plus lignin. It should be noted that this definition may be excessively restrictive, since many chemical constituents excluded by this

definition probably contribute to the measured amount of dietary fiber but are not non-starch polysaccharides or lignin. A scheme based on the outline of Asp and Johansson (1984) identifies those constituents which might be included in a definition of dietary fiber, and is presented in table 1. Southgate et al. (1978) have objected to definitions of dietary fiber which include indigestible proteins, lipids, waxes, cutins and inorganic compounds. They suggest that these substances be placed in a separate category of substances which 'modify' the properties of the major fiber components included in Cumming's definition. Whether the use of such a restrictive definition may be misleading is a subject of current debate, and ultimately, different descriptions of fiber may need to be developed in order to describe the diverse functional properties of natural fiber sources (Heaton, 1983).

Analysis.

The analytical method used to measure dietary fiber is a key factor in the interpretation and comparison of different studies, because the definition of dietary fiber is an end-product of the analytical method used in a particular study. Because of the complex and variable nature of the substances included in any definition of dietary fiber, the development of methods to quantify the

Table 1. Chemical constituents of dietary fiber and those which may modify the action of dietary fiber

Components included in definition of dietary fiber
Cellulose
Hemicellulose
Pectins
Gums
Mucilages
Lignins
Components excluded from definition of dietary fiber
Cutins and waxes
Indigestible proteins and lipids
Insoluble starches
Inorganic elements
Silicates
Trace amines or polyamines
Lignans
Phenolic monomers

Adapted from Asp and Johannsen (1984)

fiber content of feedstuffs has been an active area of research. The following discussion outlines the principle methods currently in use, but it should be noted that numerous modifications of each method are available. Comprehensive reviews on methodologies available for fiber analysis have been published (Southgate et al., 1978; Monte and Vaughan, 1982; Asp and Johansson, 1984).

The crude fiber or Weende procedure, has been extensively used for over a century to quantify the insoluble fiber residue component of human and animal feedstuffs. The method utilizes sequential extractions of acid and alkali to isolate an insoluble residue, which is primarily composed of cellulose and lignin. This method gives results similar to those obtained by the methods outlined below for many fiber sources which contain small amounts of soluble fiber substances (Monte and Vaughan, 1982).

Detergent methods. Methods designed to extract soluble components in acid- or neutral-detergent solutions were developed by Van Soest and co-workers (Goering and Van Soest, 1970). The acid-detergent fiber (ADF) and neutral-detergent fiber (NDF) residues obtained have been widely used to estimate dietary fiber in human and animal feedstuffs. The ADF residue provides an

estimate of cellulose and lignin content, while estimates of hemicellulose content are obtained by difference using the amounts of ADF and NDF present. The method is not able to measure soluble substances such as pectins, which are extensively removed by the NDF extractions, since it is virtually impossible to recover soluble components from the extraction solutions. Although the method provides a rapid estimation of plant cell wall material, it probably underestimates the total dietary fiber (Southgate et al., 1978). Modified methods incorporating amylase in the NDF extraction steps have largely overcome the problem of incomplete starch removal (Robertson and Van Soest, 1977).

Enzyme-insoluble fiber. Two widely used enzyme methods have been reported. The method of Hellendoorn et al. (1975) involves collection of an insoluble residue obtained following digestion with pepsin-pancreatin. Furda (1981) has suggested a similar method, except that soluble polysaccharides are precipitated with ethanol; total dietary fiber represents the sum of enzyme-insoluble fiber and the ethanol-precipitable soluble fibers. Although these and other enzymic methods result in some protein contamination, a refined enzyme-based method has been suggested as the AOAC approved method for the determination of total dietary fiber (Prosky et al., 1984).

Fractionation of soluble-insoluble polysaccharides. A number of methods have been developed which involve the separation and quantification of non-cellulosic polysaccharides, cellulose and lignin and their component sugars (except for lignin). Most of these methods have evolved from the original method developed by Southgate (1969) which combined chemical and enzymatic steps. The modified methods are described in detail in the review of Monte and Vaughan (1982).

To a certain extent, all of the currently available methods provide useful estimates of dietary fiber in feedstuffs. However, it must be remembered that the ability to relate compositional properties of high-fiber feedstuffs to physiological events resulting from the consumption of that feedstuff will depend upon the quantity and biochemical composition of both soluble and insoluble fiber consumed. In this regard, the estimates of dietary fiber obtained by the different methods will vary considerably for different feedstuffs, and the method used should be carefully selected based on comparative studies of different methods (Heckman and Lane, 1981; reviewed in Southgate et al., 1978).

In the following sections, the term 'dietary fiber' represents measures of insoluble polysaccharides and lignin. Where used, the term 'total dietary fiber'

refers to measures which include both soluble and insoluble polysaccharides and lignin.

Chemical and physical properties of dietary fiber.

The physiological effects attributed to high-fiber intakes result from both the chemical composition and the physical properties of the fiber source consumed. Because dietary fiber represents a heterogenous mixture of chemical constituents, a detailed treatise on the chemistry of dietary fiber is beyond the scope of this review, and only a brief overview of this topic is presented.

A summary of the major chemical components of dietary fiber is given in table 2. Although variable depending on botanical origin, the major fiber components present in terrestrial plants are cellulose, hemicellulose, pectins and lignins, and most published studies consider only these substances (Eastwood and Kay, 1979). However, more effort is being directed at quantifying the effects on health and nutrition of trace constituents present such as phenolic monomers (Jung and Fahey, 1983) and lignans (Horwitz and Walker, 1984; Adlercreutz, 1984). A detailed description of the chemical make-up of dietary fiber has been presented by Salvendran (1983).

Table 2. Structural features of the components of dietary fiber

Major grouping	Principle structural type	Main structural variations
Structural		
Non-cellulosic polysaccharides	galactouronans	methoxy groups, side chains
	xylans, arabino-glucurono-	branched and linear xylan chains, number and distribution of side chains
	mannans, gluco-galacto-	Number and distribution of side chains
	galactans, arabino-	Branching and side chains
Cellulose	β-D-glucan	degree of polymerization, crystaline structure
Lignins	aromatic polymers	type of polymer, functional groups
Non-structural		
Pectins	galactouronans	methoxy groups, side chains
Gums	β-glucans, arabino xylans, gluco- and galactɔ-mannans	side chains, branching, degree of polymerization
Algal polysaccharides	sulfated galactans glucuronic-mannuronans	degree of sulfation distribution of uronic acids
Modified celluloses	ethers, esters	cross-linking

Adapted from Southgate (1978)

Table 3. Possible physiological actions of fiber components in the nonruminant gastrointestinal tract

Physiological property	Fiber type	Physiologic effects
Gel formation	Pectin, mucilages	gastric emptying, mouth-cecum transit, small intestine absorption
Water-holding capacity	Polysaccharides, lignins	mouth-rectum transit, fecal weight, intralumenal pressure, fecal electrolytes
Matrix formation	all types	cecal bacterial metabolism
Cation-exchange capacity	acidic polysaccharides	fecal minerals, bile acids, pH
Antioxidant	lignins	free radical formation and action
Digestibility	polysaccharides	energy availability, chemical environment of cecum-colon, enzyme activity

Adapted from Eastwood and Kay (1979)

Eastwood and Kay (1979) have proposed that many physiological effects of dietary fiber depend on the ability of fiber to form a 'sponge matrix' in the gastrointestinal tract. Although the relationships between chemical and physical properties, and proposed physiological actions of dietary fiber remain largely unknown, proposed relationships between these three items are given in table 3 (Eastwood and Kay, 1979). Although many factors may influence the ability of fiber to alter mineral absorption, three characteristics of dietary fiber may be of somewhat more importance. These three characteristics are: 1) cation-exchange capacity, 2) water-holding capacity, and 3) adsorption properties (Eastwood and Passmore, 1983).

In vitro fiber-mineral interactions.

The ability of polysaccharides and cations to interact chemically is well known, and the basic principles involved have been described (Rendleman, 1978). However, whether there are physiologically-relevant interactions within the gastrointestinal tract which could influence mineral utilization by animals is unknown. Within the past 10 years, a number of investigators have used in vitro systems in order to define the physical and chemical properties of dietary fiber which might be related to the ability of dietary

fiber to influence bowel function and nutrient utilization. Properties of fiber which could influence mineral availability have been identified as cation-exchange capacity (CEC), adsorptive properties and water-holding capacity (WHC) (Eastwood and Passmore, 1983), although other factors are probably involved (Kelsay, 1978; Southgate, 1978).

The properties of native and purified fiber sources which may enable a high-fiber feedstuff to interact with mineral elements have been investigated using in vitro model systems. Generally, plant constituents able to bind minerals are associated with the cell wall fraction of plant tissue (Rees, 1975). Farago and Pitt (1977) reported that the pectate fraction within the cell wall was the primary site of Zn accumulation in plants which accumulate unusually large amounts of Zn in their cell walls. However the sites identified were not specific for Zn since Ca and Cu would exchange for Zn. Studies of the grass Halcus lanatus have shown that a large portion of cell wall Ca is bound by the pectate-lignin complex, while Mg is bound only by lignin (Molloy and Richards, 1971). Although these studies suggest that pectates may be the most important cation-binding component in cell walls, the functional binding sites may vary for different mineral elements (Peterson, 1969).

The functional groups believed to complex metal ions are the carboxyl in uronic acids (i.e. pectin), carboxyl and hydroxyl in phenolic compounds (i.e. lignin, ferulic acid) and the surface hydroxyls of cellulose and other polysaccharide polymers (Jones, 1978; Rees, 1975). It has also been suggested that amorphous silica present in plant tissues may also bind minerals due to the presence of surface silanol groups (Jones, 1978).

The level of unsubstituted uronic acid residues in hemicelluloses is highly correlated with the ability of hemicellulose to bind Ca ions in vitro (Branch et al., 1975; James et al., 1978). Davies (1978) showed that binding of ^{65}Zn to purified fiber components at pH 6.5 was related to the uronic acid content of the fiber. Cellulose (2.3% uronic acids) did not bind Zn, whereas acidic hemicellulose (11.3% uronic acids), pectin (86% uronic acids) and de-esterified pectin (polygalacturonic acid; 96.4% uronic acids) bound 69%, 67% and 86%, respectively, of the available Zn present in solution.

The cation-exchange capacity (CEC) of a number of 'native' fiber sources was studied by Rasper (1979). Using enzyme-insoluble residues, he found that CEC was highly variable for different fiber sources (figure 1). He also reported that CEC was more highly correlated to hemicellulose content expressed as glucose (r=.43) or

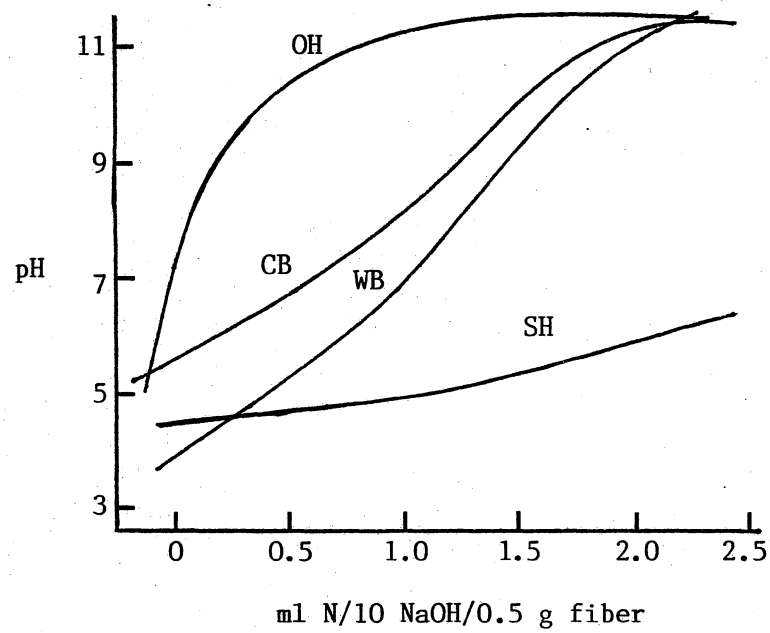

Figure 1. Ion-exchange properties of enzymatically prepared fibers from oat hulls (OH), hard-red spring wheat bran (WB), corn bran (CB) and soybean hulls (SH). Adapted from Rasper (1979).

galacturonic acid (r=.49) than to cellulose content (r=.17). McConnell et al. (1974) reported that CEC of vegetable fiber was correlated to acid-detergent fiber content (r=.39), but not to lignin content (r=-.04). Childs and Abajian (1976) showed that peanut hulls, which have a high lignin content, had a lower CEC than did the vegetable fibers tested by McConnell et al. (1974), suggesting that lignin does not contribute substantially to CEC of many fibers. However, McBurney et al. (1983) reported that sulfuric acid-lignin from oats, hay or sugar beet had CEC values within the range of many vegetable fibers. Even though these studies suggest a marginal role for lignin in ion-exchange properties of high-fiber feeds, lignin has a high capacity to adsorb bile acids in vitro (Story and Kritchevsky, 1976), and the exact relationship between CEC and mineral binding ability of different fibers remains unclear.

Reinhold et al. (1975) showed that purified cellulose was able to bind Ca and Zn ions in vitro from solutions maintained at physiological pH, even though purified celluloses appear unable to adsorb bile acids in vitro (Story and Kritchevsky, 1976) and have a low CEC capacity (McBurney et al., 1983). Because dietary fiber represents a heterogenous mixture of different chemical constituents, a number of studies have attempted to

identify the ability of native feedstuffs or semi-purified fiber fractions to bind minerals, and the physical and chemical conditions which influence mineral binding.

Thompson and Weber (1979) determined the effect of pH on the ability of six fiber sources to bind minerals. Their results showed that endogenous Cu, Zn and Fe were retained by the fiber sources at pH 6.85, but that these minerals were readily released when the fiber sources were maintained at pH 0.65. However, this response was variable for different combinations of fiber sources and minerals (figure 2); iron retention appeared to be less affected than Zn retention. A subsequent study showed that native and enzyme-insoluble fibers were able to bind exogenous minerals in vitro (Thompson and Weber, 1981a).

Although the above experiments demonstrate that dietary fiber is able to bind cations, they do not demonstrate whether binding ability would remain intact under the conditions present in the gastrointestinal tract; the most important factors influencing the in vivo response are probably ionic strength, pH, digestion processes (both enzymatic and microbial) and the presence of competitive binding ligands.

Rasper (1979) demonstrated that the method used for the isolation of dietary fiber affected CEC. He reported

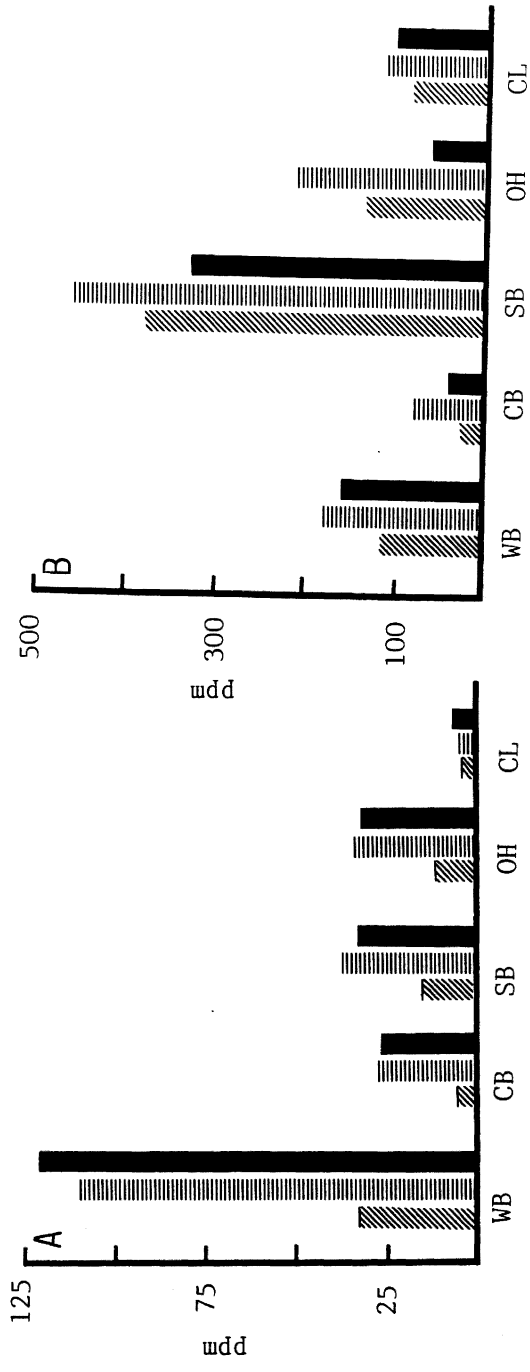

Figure 2. Contents of Zn (A) and Fe (B) in wheat bran (WB), corn bran (CB), soy bran (SB), oat hulls (OH) and cellulose (CL) after treatment at pH 0.65 (▨), pH 6.8 (≣) or pH 0.65 followed by pH 6.8 (■). Adapted from Thompson and Weber (1979).

that the preparation of an enzyme-insoluble residue did not change the CEC of oat hulls, but increased CEC of corn bran and soybean hulls. Similar results were reported by Thompson and Weber (1981a) who showed that the preparation of an enzyme-insoluble residue increased Cu and Zn binding by soy bran, decreased binding by oat hulls, but did not affect binding by wheat bran or purified cellulose. Overall, the CEC of the six fiber sources tested by Thompson and Weber (1979) were decreased by treatment of the native fiber sources with digestive enzymes.

A modest correlation (r=.51) exists between CEC and WHC by dietary fiber (Rasper, 1979). Schimberni et al. (1982a,b) have also demonstrated a positive relationship between CEC and WHC in different dietary fibers, although correlation coefficients were not reported. The effects of digestion on WHC may be similar to the effects of digestion on ion-binding capacity of dietary fiber. In vitro digestion of fiber sources with human fecal inoculums (McBurney et al., 1985) decreases WHC of the isolated fiber fractions, but it is not known if the lower WHC results from a change in physical retention of water or by a reduction in ionic water binding, or both. Regardless, the available data suggests that the partial degradation of fiber by microbial and animal enzymes may

increase or decrease cation binding, depending on the fiber source (Thompson and Weber, 1981a).

The magnitude of the enzyme-induced changes in ion binding may be related to the chemical nature of the interaction between the metal ion and the binding site, and whether the bond formed is susceptible to animal and/or microbial enzymes. Mod et al. (1981, 1982) investigated the interaction of Ca, Mg, Mn, Cu, Zn and Fe with hemicelluloses isolated from rice bran. All minerals were bound by hemicellulose, but binding capacity was highly variable between the water- and alkali-soluble hemicelluloses at similar and different pH levels. The actions of hemicellulase, trypsin and pepsin (applied separately) released the bound minerals, but the extent of release was variable for the different cations, and was somewhat dependent on the protein content of the incubation media. These results suggest that ion binding by some fiber components is more complex than can be explained by simple ion-carbohydrate interactions.

The extent to which the carbohydrate components of dietary fiber contribute to the binding of ions by dietary fiber is controversial. Studies by Rendleman (1982) and Rendleman and Grobe (1982) have suggested that less than 10% of the cation-binding capacity of wheat bran can be attributed to the polysaccharide components.

These studies showed that cellulose isolated from bran did not bind Zn or Ca, and that hemicelluloses accounted for most of the Ca and Zn binding capacity attributable to the bran fiber components (excluding phytate). These results are in contrast to earlier reports by Reinhold et al. (1975) and Ismail-Beigi et al. (1977) which showed that bran and cellulose were able to complex cations in vitro.

The different results of these two groups are difficult to explain. Part of the reason for the greater overall binding observed by Reinhold and co-workers may be that they used a phosphate-buffered system, which is known to alter mineral solubility, regardless of the presence of fiber (Rendleman and Grobe, 1982). Alternatively, both groups used different fiber sources and fractionation schemes to isolate their fiber fractions, which could have altered the binding capacity or characteristics of the fibers. A substantial amount of evidence indicates that fiber isolation methods influence CEC and cation-binding properties of different fibers (Rasper, 1979; Thompson and Weber, 1979, 1981a; Frolich et al., 1984).

The ability of native fiber sources or fiber fractions to bind minerals is dependent on the ionic strength and pH of the reactions solutions used. Parrott

and Thrall (1978) reported that the WHC of most fibers decreased as the ionic strength was raised from 0.01 M to 1.0 M (as NaCl or $CaCl_2$), while increasing the pH tended to increase WHC. In general, in vitro studies indicate that mineral binding progressively increases as the pH of the test solutions approach neutrality (Camire and Clydesdale, 1981; Rendleman, 1982; Rendleman and Grobe, 1982; Thompson and Weber, 1979, 1981a; Reinhold et al., 1981; Fernandez and Phillips, 1982a). However, at least in the case of Fe, ligands which compete for Fe with the fiber matrix appear to alter Fe solubility, and subsequently decrease the negative effects of fiber on Fe solubility (Leigh and Miller, 1983).

Although evidence indicates that fibers possess the necessary chemical characteristics which would permit interactions with mineral ions, the data do not identify specific fiber components or levels of fiber which may behave in a similar fashion in vivo. The conflicting nature of the data prevents the accurate selection of fiber sources which may have in vivo effects.

Utilization of fibrous feedstuffs

The ability of dietary fiber to complex minerals is only one mechanism by which high-fiber diets may impair mineral utilization. Alternatively, the ability of high-fiber diets to decrease mineral balance may be a secondary response to effects which fiber has on growth rate and feed intake, and on energy and nitrogen utilization, which subsequently alter metabolic mineral demand. The following sections examine the current body of information which pertains to the effects of high-fiber diets on growth and nutrient utilization of swine; pertinent human and experimental animal studies are included where data on swine are unavailable. General reviews have been published which discuss the applied and economic aspects of the use of high-fiber ingredients in animal diets (Fahey, 1979; Laplace and Lebas, 1981; Pond, 1981; Fahey and Holzgraefe, 1982), and on the general effects of high-fiber diets on nutrition and physiological processes of humans and animals (Losowsky, 1978; Ali et al., 1981).

Effect of dietary fiber on the intestinal microflora.

The ability of swine to utilize fiber as an energy source results from the fermentation of cellulosic and

non-cellulosic polysaccharides to short-chain volatile fatty acids (VFA) and lactic acid by the gastrointestinal microflora (Cranwell, 1968; Rerat, 1978, March, 1979). Although the gastrointestinal flora is poorly defined, limited evidence shows that the normal indigenous microflora has a significant impact on nutrient utilization by the pig.

In suckling pigs, the predominant flora consists of strains of Lactobacillus fermentum and Streptococcus salivarius (Barrow et al., 1980) which are attached to the epithelium of the entire gastrointestinal tract. Conversely, in weaned pigs the primary flora consists of L. acidophilus and S. bovis (Fuller et al., 1978). It is believed that the association of lactic acid bacteria is a primary means of maintaining gastrointestinal pH low enough to prevent colonization by pathogenic strains of E. coli (Barrow et al., 1977).

Salanitro et al. (1977) studied the composition of the bacteria present in the feces of adult swine and reported that 90% of the bacteria present were facultative organisms; the predominant organisms were Eubacterium sp., Clostridium sp. and Propionibacterium acnes. However, bacterial numbers and the relative distribution of bacterial species were variable between pigs, and were influenced by external factors such as sex, diet composition and environmental conditions.

Allison et al. (1979) reported that the composition of the bacterial flora of individual pigs (32 kg bodyweight) was not a constant trait. Their study demonstrated that large differences existed between the bacterial populations of the cecum and colon of the same pigs, between the cecums of littermates, and between the lumenal and epithelial habitats. The cecal epithelial bacterial population was estimated to be 2.67×10^7 bacteria/cm^2.

Contrary to the reports suggesting that the fecal bacteria were facultative organisms, Robinson et al. (1981) showed that the cecal flora of weaned pigs consisted primarily of gram-negative strict anaerobes; the predominant organisms present were B. ruminicola (35%), Selenomona ruminatium (21%), Butyrivibrio fibrisolvens (6%) and B. uniformus (3%). The major gram-positive bacteria present were L. acidophilus (7.6%), Peptostreptococcus productus (3%) and Eubacterium aerofaciens (2.5%). These results conflict with the findings of Russell (1979) who reported that gram-positive bacteria were the predominant organisms (>90% of the total organisms present) present in the large intestine of pigs at 25 weeks of age; the predominant species were Lactobacillus sp., Clostridium sp. and Eubacteria sp. His distribution studies indicated that

populations on the colon cell surface, intestinal cell surface and in the colon contents were 14 x 10^{10}/g dry weight, 5.1 x 10^{10}/g dry weight and 13.3 x 10^{10}/g dry weight, respectively.

The presence of VFA and lactate in the small intestine demonstrates that the microflora influence the metabolism of nutrients in this region of the gastrointestinal tract of the pig (Friend et al., 1963a). However, there has been little research on defining bacterial populations, or the effects of high-fiber diets on bacterial numbers in the gastrointestinal tract of pigs.

Varel et al. (1984a) studied the fecal and large intestine microflora of pigs fed a low-fiber diet or a diet containing 35% alfalfa meal. Although total bacterial numbers in the feces were not affected by alfalfa meal, the numbers of cellulytic bacteria present were greater in pigs fed the alfalfa meal diet. Surprisingly, cecal and colon bacterial numbers or population profiles were not affected by diet composition, suggesting that in the pig, high-fiber diets do not exert the same effect on bacterial populations in all sections of the gastrointestinal tract. These researchers also identified the predominant cellulytic species in the pig as B. succinogenes and R.

flavefaciens. These are also the predominant bacterial species in rat cecum (Montgomery and Macy, 1982), which suggests that there may be some justification for making inter-species comparisons on the effect of fiber on the intestinal flora. Varel et al. (1982) reported that alfalfa meal diets increase fecal cellulytic bacteria numbers 80% and 71% between 0 and 3 weeks, and 3 and 8 weeks, respectively in lean-genotype pigs, but had no effect on the number of cellulytic bacteria in obese-genotype pigs.

In a subsequent study, Varel et al. (1984b) studied the long-term effect of high alfalfa meal diets on fecal bacterial numbers of swine. They reported that alfalfa meal initially increased the number of cellulytic bacteria (from 0 to 32 days), but that bacterial numbers declined by 70 days to levels comparable to those found in pigs fed a low-fiber diet. However, fecal cellulase levels did not increase until 32 days, but remained higher at 70 days in pigs fed the high-fiber diet. Cecal and colon bacterial numbers and level of cellulase activity were not different at slaughter between pigs fed the low- or high-fiber diets. Bedbury and Duke (1983) reported similar results in turkeys. They showed that high-fiber diets increased total bacterial numbers, and that cellulytic activity in both pure cellulytic cultures

and mixed cultures was greater for birds fed the high-fiber diets.

Berghouse et al. (1984) reported that the consumption of a high-fiber diet (containing a mixed fiber source) by humans increased ileal bacterial numbers, but did not change the relative bacterial composition of the flora. Taken together, the available data indicate that high-fiber diets affect bacterial metabolism and populations differently. But, it is not clear whether different dietary fibers have similar quantitative and qualitative effects on the intestinal flora, and what (if any) physiological consequences result from the affects of fiber on the microflora. This point is emphasized by the studies of Pond et al. (1980) and Pekas et al. (1983) which showed that 20% alfalfa meal diets depressed growth rate of lean- and obese-genotype pigs equally, even though a related report by Varel et al. (1982) was able to show different effects of alfalfa meal on the intestinal microflora of these two pig types.

Effect of dietary fiber on growth of pigs.

It has been known for almost four decades that the major site of fiber digestion in the pig is the large intestine. Woodman and Evans (1947) showed that most of

the digestion of diets containing 25% cellulose (isolated from wheat straw) occurred in the large intestine, and that fiber decreased the apparent digestibility of crude protein and ether extract. Bohman et al. (1955) showed that dietary alfalfa (10, 30 or 50% of the diet) increased the weights of the stomach and large intestine and decreased rate of growth in a linear fashion as dietary alfalfa levels increased. However, earlier studies showed that 10% or 30% alfalfa meal did not decrease weight gain, but 50% alfalfa meal did decrease weight gain (Bohman et al., 1953). Axelsson and Eriksson (1953) reported that relatively low levels of wheat straw (3.7 or 7.4% of the diet) did not affect weight gain in pigs, but high levels (11.0% of the diet) decreased weight gain. The ability of different dietary fiber sources to depress growth rate has been reported by others (Merkel et al., 1958; Jensen et al., 1959; Pond et al., 1962).

However, not all fiber sources decrease growth rate to the same degree. Hochstetler et al. (1959) showed that the inclusion of 20% or 40% oats in the diet had no effect on weight gain, whereas wheat bran decreased weight gain when fed at 40% of the diet, and alfalfa depressed growth rate when fed at 10% or 20% of the diet. Crampton et al. (1954) reported that 25% wild oats or

wheat bran in the diet did not affect weight gain in pigs. However, when mixtures of alfalfa meal and either oats or wheat bran (12.5% of each fiber source) were fed, weight gains were decreased. Agrawal et al. (1982) has reported that up to 60% of the corn in swine rations can be replaced by wheat bran (up to 52% of the total diet) without depressing weight gains.

The growth-depressing effect of fiber is primarily due to the dilution of the digestible energy content of the diet. Jensen et al. (1959) showed that the decrease in growth rate caused by feeding 30% oat hulls could be overcome by adding 14% corn oil to the diet. Troelson and Bell (1962) noted that if the rate of gain were adjusted for digestible energy intake, there was no decrease in weight gain when pigs were fed diets containing corn cobs, wheat bran, alfalfa, cellulose or oat hulls. More recent studies by Baird et al. (1970, 1975) have shown that at a constant dietary metabolizable energy level, the inclusion of rice mill feed, wheat bran or cottonseed hulls had no effect on weight gain.

Recent research confirms that the depression in weight gain caused by fibrous feeds is a result of energy dilution of the diet, and a subsequent inability of the pig to consume enough feed to maintain adequate energy intakes. Kornegay (1978, 1981) reported that soybean

hulls could be included in swine diets up to 12% of the diet without affecting performance, while greater amounts (24% of the diet) depressed weight gain. Powley et al. (1981) showed that increasing dietary levels of alfalfa meal from 0% to 20%, 40% or 60% caused an incremental decrease in weight gain and feed intake, which suggested that the growth depression was a result of the inability of the pig to maintain energy intake. Drewry (1981) reported that pigs reached market weight at an older age when fed diets containing high levels of fiber (5% wheat bran, 19.9% oats and 15% dehydrated alfalfa). Moser et al. (1982a) reported that 4% or 8% solka-floc decreased weight gain in growing-finishing pigs, although the effect could be attributed to depressed feed intake in only one of two trials. The inclusion of tallow in the diets alleviated the growth-depressing effect of cellulose.

However, modest levels of dietary fiber supplied as oats (Kornegay et al., 1981) or soybean hulls (Kornegay et al., 1980) had no effect on weight gain of nursery pigs. Kennelly and Aherne (1980a) demonstrated that 22% oat hulls depressed weight gain in pigs up to 63 kg body-weight, but had no effect on growth of pigs from 63 kg to 92 kg bodyweight. They also reported that feed efficiency was improved if energy and protein levels were increased in the high fiber diets, but not if only

protein levels were raised. Similarly, Robles and Ewan (1982) reported that rice bran (which contains a substantial amount of fat) could be fed up to 2% of the bodyweight without influencing feed efficiency.

Effect of dietary fiber on nitrogen and energy utilization.

The inclusion of fiber in the diet decreases the apparent digestibilities of dry matter, energy, ether extract, nitrogen-free extract and crude protein (Woodman and Evans, 1947; Forbes and Hamilton, 1952; Teague and Hanson, 1954; Glover and Duthie, 1958; Friend et al., 1962; Boenker et al., 1969; Keys et al., 1970; DeGoey and Ewan, 1975; Stanley and Ewan, 1981). Detailed discussions of the effects of diet and other factors on nutrient utilization in pigs have been published by others (Rerat, 1978,1981; Low, 1980).

Just (1982a,b) has studied the effect of dietary fiber on energy utilization in pigs. His data indicate that inclusion of oat bran or wheat bran in the diet shifts the site of energy absorption from the small intestine to the large intestine. When pigs were fed a synthetic diet, digestible energy was 89%, with 17% occurring in the large intestine. However, when fiber was added to the diet, the total digestible energy was

81%, but 29% occurred in the large intestine. He reported that dietary fiber decreased the level of deposited energy and the net energy value of the diet (as a percentage of metabolizable energy). The latter response was associated with an increase in urinary energy excretion with increased fiber intake, which he attributed to the absorption of non-utilizable energy sources produced by microbial fiber fermentation.

The mechanism by which dietary fiber contributes usable energy to the pig is through fermentation of the polysaccharides to VFA and lactate by the intestinal microflora. The large intestine of the pig is the site of greatest absorption of VFA, and most VFA absorbed are metabolized rapidly during absorption (Imoto and Namioka, 1978a), although hepatic portal blood VFA levels have been reported to be substantial (Topping et al., 1985).

Considerable effort has been directed at determining the site of VFA production in the gastrointestinal tract of the pig, and the proportion of the energy requirement which VFA can supply. Both the large and small intestine contain bacteria capable of converting free sugars and complex carbohydrates to lactate and VFA. Although the microflora of the stomach have the ability to ferment carbohydrates, fermentation in this organ does not contribute significantly to the energy needs of the pig (Braude et al., 1970; Vervaeke et al., 1979).

The concentrations of VFA are relatively low in the proximal intestine, but gradually increase proceeding distally (Friend et al., 1963b; Clemens et al., 1975; Sambrook, 1979). Energetically, it is more efficient to produce VFA and lactate in the distal portion of the intestine since large intestine VFA absorption is more efficient (Argenzio and Southworth, 1975; Imoto and Namioka, 1978a). The contribution of VFA to the energy requirement of the pig has been estimated to be approximately 10%, dependent upon diet composition and other factors (Friend et al., 1963b; Imoto and Namioka, 1978b; Kennelly et al., 1981; Gargallo and Zimmerman, 1981a).

The inclusion of fiber in the diet influences the ratios of the various VFA formed. Friend et al. (1963a) showed that the inclusion of wheat bran in the diet arrested lactate production in the hind gut of pigs. Gargallo and Zimmerman (1981a) reported that the inclusion of sunflower hulls in the diet did not influence acetate production, but decreased the production of propionate and butyrate in the cecum and colon. Friend et al (1962) showed that the inclusion of cellulose or wheat bran in the diet increased the proportion of acetate and decreased the proportions of propionate and butyrate in the feces of pigs. However,

Gargallo and Zimmerman (1980) failed to find any influence of dietary cellulose (at 2, 10 or 18% of the diet) on the quantity or pattern of VFA produced in the cecum of growing pigs. Kass et al. (1980b) reported that increasing the level of alfalfa meal in the diets of weanling pigs resulted in an increase in VFA concentrations in the cecum and colon, and also increased the proportion of acetate:propionate and butyrate.

There is conflicting evidence as to the major site of fiber digestion in the hind gut, and the relative importance of the different sections of the large intestine on energy production. Several studies indicate that the cecum plays a minor role in energy utilization. Lloyd et al. (1958) reported that the ability of the pig to utilize fiber was not affected by cecectomy. A recent study by Gargallo and Zimmerman (1981b) also indicates that cecectomy does not alter cellulose digestibility in growing pigs. Farrell and Johnson (1972) concluded that the cecum played a minor role in energy utilization in intact pigs fed diets containing 8% or 26% cellulose. It is unclear whether the distal large intestine is able to compensate for the absence of the cecum in cecectomized animals. Gargallo and Zimmerman (1981b) suggested that there was greater distension of the gut, and a subsequent slowing of digesta flow, which allowed greater microbial

fermentation of the fiber in the colon of cecectomized pigs.

Small amounts of cellulose and hemicellulose are degraded in the stomach of pigs (Keys and DeBarthe, 1974a; Sambrook, 1979), although the amount would appear to be nutritionally insignificant. The botanical origin of the fiber source also influences the extent of microbial degradation of fibrous components in the small intestine; but again, the quantitative disappearance in the small intestine is small (Keys and DeBarthe, 1974a; Sambrook, 1979). A recent report by Millard and Chesson (1984) suggests that small intestine fermentation may be substantial for certain fiber sources which contain relatively high proportions of hemicellulose or soluble non-starch polysaccharides. Thus, although the exact significance and extent of fiber digestion in the various segments of the intestine are not fully understood, it appears that the colon may be of more relative importance than the other segments. It has been shown that the concentrations of VFA is lower in the colon of pigs than in the cecum (Ehle et al., 1982; Topping et al., 1985), but whether this reflects differences in the rates of production, absorption, or both, is not known.

Whiting and Bezeau (1957a) reported that the ability of dietary fiber to decrease apparent and true protein

digestibility resulted from an increase in fecal metabolic nitrogen, although fiber did not change urinary nitrogen excretion (Whiting and Bezeau, 1957b). Bell et al. (1983) showed that metabolic fecal nitrogen increased two-fold when the level of barley hulls in the diet was increased from 0% to 30%. Boenker et al. (1969) indicated that dietary corn cobs increased fecal nitrogen about 10%, although no effect on nitrogen retention was seen. The increase in fecal nitrogen is primarily a result of an increase in fecal bacterial nitrogen (Farrell, 1973).

From 15% to 50% of the nitrogen which enters the large intestine disappears during transit through this segment of the gastrointestinal tract (Holmes et al., 1974; Ivan and Farrell, 1976; Mason et al., 1976). It is generally believed that the disappearance of alpha-amino nitrogen in the large intestine results from the deamination and decarboxylation of these compounds, with the subsequent formation of amines and ammonia (Michel, 1966), which are then used for bacterial amino acid and protein synthesis (Niiyama et al., 1978). Although absorption of ammonia, amines and amino acids by the large intestine has been documented, nitrogen absorbed from the large intestine is poorly utilized for metabolic purposes (Rerat, 1978; Just et al., 1981), and most is

excreted in the urine as urea (Wunsche et al., 1982). However, a small portion of this nitrogen is incorporated into tissue protein (Grimson et al., 1971; Deguchi et al., 1978; Niiyama et al., 1978). Krawielitzki et al. (1982) reported that when ^{15}N-lysine was infused into the cecum, 78-88% was excreted in the urine as urea, 3-5% appeared in the feces unchanged, and 5% was incorporated into bacterial protein. Only about 1.6% of the infused lysine was absorbed intact.

Sauer et al. (1980) reported that crude protein digestibility only decreased slightly when barley straw was added to swine diets at 7.5% or 15%. They also showed that as the ileal and rectal crude protein digestibilities decreased, the values became more similar to each other. They attributed this response to net amino acid synthesis in the large intestine at the higher diet fiber levels, and they demonstrated net synthesis of lysine and methionine in the large intestine of pigs fed the highest fiber level. Just (1980) has reported that increasing the level of straw fiber in the diet from 5% to 9% of the diet dry matter depressed both ileal and rectal nitrogen and amino acid digestibilities, and almost completely arrested apparent nitrogen absorption from the large intestine.

Fahey et al. (1980) demonstrated that nitrogen balance was decreased by the addition of solka-floc or alphacel to diets containing 16% crude protein, but that no effect was observed with diets containing 9% crude protein. This is in contrast to other reports which demonstrated that nitrogen retention was increased by modest levels of dietary cellulose (Corley et al., 1978; Sherry et al., 1981).

Whiting and Bezeau (1957b) reported that solka-floc, oat hulls and methacel had different effects on fecal nitrogen excretion, which may reflect the ability of the microflora to ferment the fiber components. Despite decreases in apparent and true crude protein digestibility resulting from high fiber intakes, fiber does not appear to decrease nitrogen retention (Boenker et al., 1969).

In general, fiber appears to increase fecal nitrogen excretion only if adequate amounts of readily fermentable carbohydrates and nitrogen are available to support bacterial protein synthesis (Gargallo and Zimmerman, 1981c). The effects of fiber on urinary nitrogen excretion are also contradictory; in some experiments fiber increases urine nitrogen levels (Gargallo and Zimmerman, 1981c), while in other experiments fiber decreases urine nitrogen levels (Fahey et al., 1980;

Sherry et al., 1981; Malmlof and Hakansson, 1984). Kennelly and Aherne (1980b) have suggested that if the fiber source contributes only small amounts of protein to the diet, there will not be a large effect on nitrogen utilization. Additionally, high-nitrogen fiber sources (i.e., alfalfa) would also make it difficult to distinguish between effects of the fiber source on nitrogen digestibility and effects resulting from changes in the composition or availability of the diet protein sources (Bach Knudsen et al., 1982).

Digestion of fiber components.

The overall digestibility of fiber sources and the constituent fiber components contained in them varies considerably in pigs. Factors such as level of fiber intake, fiber source and the level of other dietary constituents may exert an influence on fiber component digestibility, and these factors have been reviewed elsewhere (Laplace and Lebas, 1981).

In a general sense, fiber sources derived from legumes are more digestible than are those derived from cereal grains and grasses (Stanogias and Pearce, 1985). However, this is somewhat dependent on botanical species within these major groups, since many legume-derived fiber sources such as peanut and pea hulls have a low

digestibility (Stanogias and Pearce, 1985; Lindemann et al., 1986). Large cultivar differences have also been reported for some fiber sources. Bell and Shires (1982) showed that Tower rapeseed hulls decreased NDF digestibility from 40% to 14% when included in the diet at 30%, whereas R-500 rapeseed hulls only decreased NDF digestibility from 44% to 38% when included in the diet at a comparable level.

There do not appear to be any adaptive changes over time in the ability of the pig to digest dietary fiber. Cunningham et al. (1962) reported that the apparent digestibility of cellulose did not change over the course of a 15 week feeding trial in pigs fed diets containing 40% solka-floc. Similarly, Kennelly et al. (1981) reported that VFA production remained the same throughout a 15 week experiment for pigs fed diets containing 52% alfalfa meal. Partridge et al. (1983) showed that diet NDF and ADF digestibilities were similar in pigs at 35 kg and 65 kg bodyweight when fed diets containing 15% solka-floc from 20 kg bodyweight.

DeGoey and Ewan (1975) have reported that the young pig (6 kg bodyweight) cannot utilize cellulose. In this respect, pigs may 'adapt' to dietary fiber as far as the ability to utilize fiber develops with chronological age of the animal. Although large variations have been

reported in the ability of individual pigs to digest fiber (Keys et al., 1970; Farrell, 1973), a relationship does not appear to exist between fiber digestion and the growth response of individual pigs to high-fiber diets; e.g. pigs which have a greater ability to digest fiber do not have a greater resistence to the growth depressing effects of fiber (Frank et al., 1983).

Effect of dietary fiber on mineral absorption.

Despite considerable research, the exact relationship between fiber intake and mineral utilization remains obscure. The present review makes no attempt to cover all of the published data, but presents a summary of reports which illustrate the complexity of this relationship.

Interest in the possible ability of fiber to decrease mineral balance began with a report by Ismail-Beigi et al. (1977) which showed that 10 g cellulose/d added to the diet over a 20 d period decreased plasma Ca and Zn levels, and induced negative Ca and Zn balances in three human subjects. Also, an earlier report by Heaton and Pomare (1974) had showed that consumption of wheat bran caused a decrease in plasma Ca levels in humans. Drews et al. (1979) reported that 14.2 g/d of hemicellulose, but not cellulose or citrus pectin,

decreased Zn, Cu and Mg balances in eight human subjects. However, this study only used a 3 d adjustment period and a 4 d balance period, and in view of the fact that serum and urine mineral levels did not change, it is difficult to conclude whether the changes in mineral balance represent transient adjustments to the diets or permanent alterations in mineral balance.

Although a number of studies have shown that fruit and vegetable fibers and wheat fibers increase fecal Ca losses (Kelsay et al., 1979; Robertson et al., 1979; Cummings et al., 1979a), other studies using pectin or wheat bran have not demonstrated that the higher fecal losses reduce Ca balance (Cummings et al., 1979b).

Although fiber source is an important variable, the amount of fiber fed and the duration of feeding may determine if a particular fiber source has an effect on mineral balance in man. Van Dokkum et al. (1982) fed 12 male subjects a diet containing 9 g NDF/d (as white bread) followed by a diet containing 22 g NDF/d (coarse bran bread), each for a 20 d period. Although the coarse bran increased intakes and fecal excretion of Ca, Mg, Fe, Zn and Cu, only Ca balance was decreased by the bran (from 14 mg/d to -42 mg/d). The same subjects were then fed diets supplying 22 g NDF/d as coarse or fine bran, or 35 g NDF/d as coarse bran, for an additional 20 d period.

The higher-fiber bran diet decreased Mg and Fe balance to negative values, and caused Ca and Zn balance to remain negative, whereas the two medium fiber diets tended to increase the balances of Ca, Mg and Zn to positive values. Andersson et al. (1983) measured mineral balances in six human subjects fed diets containing 6, 19 or 33 g total non-starch polysaccharides for 21 d and 28 d, and showed that Ca, Zn, Fe and Mg balances were unaffected. These studies indicate that insoluble dietary fibers such as wheat bran have a small, and inconsistent effect on mineral balance in humans.

However, Sandberg et al. (1982) studied the effect of feeding 16 g wheat bran per day (for 7 d) on small intestine mineral absorption in six patients with ileostomies. Bran decreased small intestine absorption of Zn during a 3 d collection period, but increased Fe absorption, and had no effect on Ca or Mg absorption. These observations are in contrast to a report by Partridge (1978b) which showed that increasing the diet cellulose level from 3% to 9% decreased large intestine Zn absorption in pigs, but did not alter small intestine Zn absorption measured over a 24 h period following a 6 d adaptation period. Although the results from these two studies could reflect a species difference in the site of Zn absorption in pigs and humans, it may also indicate

that the intestinal site of fiber-mineral interactions may vary for different fiber sources.

Although Van Dokkum et al. (1982) showed that the fractional absorption of minerals appeared to be lower for subjects fed bran diets than for those fed white bread diets, the relationship between mineral availability and absorption in bran diets is unclear. Simpson et al. (1981) fed each of 60 human subjects a meal containing 12 g bran and a meal containing no fiber (on two consecutive days), and then measured blood levels (14 d later) of extrinsic labels of ^{59}Fe or ^{55}Fe. Their results indicate that whole bran decreased Fe absorption (measured as the percentage of the extrinsic label present in the blood) from 2.39% to 0.62%, but that dephytinized bran had no effect (1.39% vs. 1.29%). Additionally, Fe absorption from diets containing insoluble bran components was 3.12%, and the addition of the soluble fiber components (excluding phytate) decreased Fe absorption to 2.33%.

Fairweather-Tait (1982) studied Fe absorption by rats fed diets containing breads of similar composition to the breads used in the human studies of Van Dokkum et al. (1982). Iron balance was measured for 14 d while rats consumed a fiber-free synthetic diet (0.4% dietary fiber; DF), or diets containing white bread (1.6% DF), brown

bread (3.8% DF) or whole-meal bread (7.2% DF). Compared with rats fed the control diet, all breads decreased Fe balance and blood Fe levels but did not affect the apparent absorption (as a percentage) of an extrinsic Fe label. The observation that Fe balance, apparent Fe absorption and blood Fe levels were similar for all rats fed the different bread diets suggests that bran fiber per se does not affect Fe utilization, but that the overall diet composition matrix resulting from the inclusion of the breads in the diets does alter Fe availability or Fe utilization.

A number of studies have investigated the effect of soluble fibers on Fe absorption in animals. Wolbling et al. (1980) showed that 10% guar gum or Na-alginate decreased ^{59}Fe absorption by 40% in Fe-replete rats, but neither fiber source had an effect on Fe absorption in Fe-deficient rats. Similar results were obtained in experiments using ligated intestinal loops in situ; alginate and guar decreased Fe absorption by 60% in Fe-replete animals, but by only 15% in Fe-deficient animals. These authors concluded that the fiber sources were unable to compete successfully for available Fe with intestinal Fe receptors or Fe-binding ligands in the deficient animals. Fernandez and Phillips (1982b) reported that 0.15 mg/ml of pectin or psyllium mucilage

(but not 1.6 mg cellulose /ml) decreased ^{59}Fe absorption from thiry-vella fistulae perfusion solutions in dogs by 30 to 50%, and the effect of each fiber source occurred regardless of whether the dogs were Fe-replete or anemic.

However, feeding studies offer less conclusive evidence of an effect of fiber on Fe utilization. Baig et al. (1983) fed rats for 30 d diets containing 2% citrus pectin, and measured ^{59}Fe absorption and turnover. Regardless of diet Fe level (10 or 150 mg/kg), pectin had no effect on Fe utilization.

The above studies indicate that both fiber and mineral level in the diet, and the nature of the fiber source, may interact to determine whether a fiber source will decrease mineral utilization. It would appear that there may be 'critical' fiber and mineral levels, as well as mineral status, which need to be met before an observable effect of fiber on Fe utilization or the utilization of any other mineral can be seen.

In vivo studies are in general agreement with in vitro studies which suggest that the soluble fiber components have a greater ability to bind minerals than do insoluble fibers (Bagheri and Gueguen, 1983; Rendleman, 1982). At the same time, the in vivo studies also support those in vitro studies which indicate that native fibers and semi-purified fractions are able to

complex minerals (Thompson and Weber, 1979; 1981a; Reinhold et al., 1981). However, the often conflicting nature of the data appears to result from a set of complex interactions between mineral status, the presence of factors other than carbohydrates in the fiber source, the processing of the fiber source, and the level of fiber fed. Most human studies have fed bran fiber in the form of bread. The fermentation undergone during the baking process probably influences the physical and chemical nature of the bran, and it has been shown that in vitro cation-binding by fiber sources (Thompson and Weber, 1979; 1981a) and the ability of corn and wheat fiber to depress Fe absorption by intestinal slices in vitro (Reinhold et al., 1983) is altered by enzyme treatment.

A number of studies have been conducted in order to evaluate the in vivo response to dietary fiber consumption under different diet and physiological conditions, and to try to determine what are the physiological consequences resulting from increased fiber intakes. Kelsay and Prather (1983) fed 12 human subjects a low fiber control diet (5.5 g NDF/d) or one of two high-fiber diets which supplied 25 g NDF/d (with or without spinach) from fruits and vegetables. Mineral balances measured after 14 d showed no effect of diet

composition on Ca, Mg or Zn retention. However mineral balances at 21 d showed that the high-fiber diet which contained spinach decreased Ca, Mg and Zn balances. The fecal excretion of NDF (12 g/d) were equal for subjects fed the two high-fiber diets, which suggests that the oxalic acid contained in the spinach was responsible for the effect of the high-fiber spinach diet on mineral balance. Gordon and Chao (1984) investigated the effect of dietary components on hemoglobin (Hb) regeneration in Fe-deficient rats over a 14 d repletion period. This study showed that bran (21%), cellulose (1.7%), pectin, lignin or phytate (all 0.66%) either decreased or did not change Hb regeneration time in rats compared with rats fed a ferrous sulfate control diet. However, spinach (15%) decreased the relative bioavailability of dietary Fe by 53%, but an equal amount of oxalic acid as was supplied by the spinach diet (2.1%) had no effect. These two studies indicate that factors present in a fiber source, but not included in a measure of dietary fiber (such as oxalic acid), may interact to form fiber-mineral-oxalic acid complexes which are then able to impair mineral absorption.

A similar controversy exists concerning the role of phytic acid in fiber-induced depressions of mineral absorption. Davies et al. (1977) used a similar approach

to this question as did Gordon and Chao (1984) for the Fe-oxalic acid interaction. These workers used Zn-deficient rats, and measured the ability of different Zn repletion diets to restore growth rate. Their results indicated that when wheat bran (15%) or phytate were added to the repletion diets, added dietary Zn failed to stimulate growth rate. However, isolated bran fiber (no phytate) did not block the growth response to added dietary Zn. They also showed that Zn added to the drinking water to further increase Zn intake was able to overcome the negative effects of phytate and bran.

Although purified cellulose has a low mineral-binding capacity in vitro (Bagheri and Gueguen, 1983; Rendleman, 1982), Gruden and Buber (1982) showed that cellulose decreased ^{65}Zn absorption from ligated loops of rat intestine in situ, although diet levels of up to 16% cellulose have failed to alter in vivo Zn balance in rats (Tsai and Lei, 1979). Turnland et al. (1984) used a stable isotope method to measure Zn absorption in four human subjects fed 2.34 g phytic acid/d or 0.5 g cellulose/(kg bodyweight · d). Apparent Zn absorption was 34% in the subjects consuming the control and cellulose diets, but only 17.5% in the subjects consuming the phytic acid diet.

The preceeding experiments indicate that dietary fiber has an inconsistent effect on mineral balance. The major problem encountered in comparing the results of different experiments is the difficulty in correlating the significance of depressed mineral absorption seen in studies using in vitro or in situ tissue uptake measures with the relatively milder effects observed using in vivo balance techniques. Additionally, it is difficult to determine using relatively short-term studies, whether the changes seen reflect transient adaptations, or 'true' depressions in mineral absorption or balance.

A number of experiments have been conducted to determine what physiological consequences may arise from the depression in mineral balance occurring with high fiber intakes. Harmuth-Hoene and Schelenz (1980) studied the effect of a number of gum-type fibers on short-term and long-term mineral balance in growing rats. They reported that carrageenan (C), agar-agar (AA), and Na-alginate (NA) decreased fractional Fe absorption (as a percentage of intake), that C and AA decreased Ca absorption, but that only guar gum and carob bean gum decreased Zn absorption; these results suggest that the mechanisms involved in fiber-mineral interactions are quite specific for different fiber and mineral combinations. One interesting observation they reported

was that AA decreased Fe balance at 1, 5 and 21 weeks of a long-term experiment, and that both guar gum and AA decreased Zn balance at the three time periods. However, despite these depressions in mineral balance, carcass Fe and Zn levels were not changed. It would thus appear that compensatory mechanisms were able to prevent a negative effect of these two fibers on body mineral status.

Bagheri and Gueguen (1982a) showed that 10 and 15% dietary wheat bran decreased Mg, P and Zn balance compared with rats fed a low-fiber control diet when measured after 5 and 29 d. However, growth rates were not affected by bran, raising a question as to what physiological significance the fiber-induced decreases in mineral balance had. With the exception of the study by Harmuth-Hoene and Schelenz (1980), these results suggest that the experiments were not of long enough duration to deplete body mineral reserves and elicit a growth response. However, growth is probably a relatively insensitive measure of marginal depressions in mineral absorption.

In their studies using rats, Bagheri and Gueguen (1982a) showed that 10% and 15% bran decreased Mg, P and Zn balances when measured after rats consumed the diets for 5 d and 29 d, although balances were greater at the second time point. This demonstrates that there is no

significant short-term adaptation to fiber intake in rats, and suggests that bioavailability may be the problem in bran diets, and not binding of exogenous minerals by the bran. Other studies by this group have shown that if diet mineral levels are not equalized (i.e. inorganic Zn levels are similar in all of the diets), bran has no effect on mineral balance (Bagheri and Gueguen, 1981). These results are supported by studies which show that the absorption of extrinsic diet labels of ^{45}Ca and ^{65}Zn are not influenced by 5%, 10% or 15% dietary wheat bran (Bagheri and Gueguen, 1982b).

Gordon et al. (1983) measured mineral balance of rats fed diets containing 0, 5, 10 or 20% cellulose for 27, 34 and 41 d. Cellulose (10 and 20%) decreased Mg and Zn balances at all three time periods, however growth rate was not changed. In a 140 d study, growth rate, body Cu and Zn status, Cu and Zn balance, and endogenous excretion of Cu and Zn, were not affected by the consumption of diets containing 7.5% pectin, guar meal or dehydrated carrot fiber (Scheibel and Mehta, 1985). Iron status, evaluated by serum Fe and ferritin levels and serum total iron binding capacity, was not changed in monkeys fed diets containing 9.7% cellulose or psyllium husk for 9 months (Buth and Mehta, 1983).

Thompson and Weber (1981b) fed different fiber sources to add 6% NDF to the diet of 18 d old chicks, and used tibia mineral levels as an indicator of mineral status. Tibia Zn was decreased by cellulose, corn bran, oat hulls and rice bran, tibia Fe by oat hulls and rice bran, and tibia Mn by only rice bran. However, only rice bran decreased growth rate. Although this study indicates that fiber sources are able to affect body mineral status, it also suggests that when this occurs over a relatively short duration of time, the animal may be able to partition available minerals to body needs such as growth, and thus minimize the observable physiological impact. It is unclear if longer-term feeding periods would have eventually produced detectable consequences to growth and health of the birds due to the lower mineral retentions.

Van der Aar et al. (1983) used 8 d old chicks to assess the effect of different purified and native fiber sources on mineral status during an 18 d feeding trial. Only 8% oat bran and 4 or 8% wheat bran decreased tibia Zn levels, although these fiber sources, as well as cellulose and corn bran, decreased serum Zn levels. The more restrictive effect of fiber on chicks in this study may be related to the lower diet levels of fiber used and the different means of expressing mineral content of the

bones (i.e. percentage of bone ash versus percentage of the fat-free dry bone in the previous study).

No clear pattern has emerged on the effect of fiber on mineral utilization in pigs. Partridge (1978a) fed three diets to compare ileal and fecal apparent mineral balances. Apparent Ca, P and Mg absorption were greater at both sites for pigs fed a synthetic diet containing 3% cellulose than for pigs fed a barley-wheat bran diet or a synthetic-peanut meal-cellulose diet. This study indicated that cellulose did not affect mineral balance when compared to conventional type diets. In a subsequent study, he was able to demonstrate that the addition of 6% cellulose to a semi-synthetic diet decreased large intestine absorption of Ca, P, Mg and Zn, but increased small intestine Zn absorption (Partridge, 1978b). Moser et al. (1982a) reported that the addition of 4 or 8% cellulose to corn-based and sorghum-based diets for 104 d did not affect blood Ca or P levels, or the size and weight of metacarpal bones. However, cellulose appeared to increase bone breaking strength and bone stress resistence in pigs fed the sorghum diets; however, no explanation for this response was offered by these authors.

Moser et al. (1982b) also investigated the effect of 10% dietary oat hulls on Ca and P balance of pigs (40 kg)

after a 10 d feeding period. They reported a slight increase in fecal P and Ca levels, but no significant effect on overall mineral balance. Bagheri and Gueguen (1983) reported that 20% coarse wheat bran increased Mg and P balance, while 10% fine bran increased Mg, P and Zn balances. Neither fiber source effected Ca balance; fine bran increased Zn balance from a negative to a positive balance, while Zn balance was negative for pigs fed control or coarse bran diets. These workers also compared the effect of feeding 2.5% pectin (72% methylated or 40% esterified), and showed that methylated pectin decreased Ca and Mg balances, while esterified pectin decreased P balance, and reduced Mg, Ca and Zn balances to negative balances.

Using conventional diets, Ravindran et al. (1984) reported that the addition of 50% ground oats (approximately 6.5% NDF) did not affect the fractional absorption or retention of minerals after an 8 d feeding period. However, their diets contained mineral levels at least three times the requirement of the pig, and it seems unlikely that this modest amount of fiber would have been able to exert a negative effect detectable by balance methods. Similarly, Newton et al. (1983) reported that 20% wheat bran did not affect fractional Fe or Zn absorption in pigs after a 14 d period, but increased Fe

absorption and decreased Zn absorption after 80 d. However, their diets contained high levels of minerals, and the relevance of this depression in Zn absorption is not clear, particularly since mineral balances were not determined.

However, Newton et al. (1983) reported that a fiber fraction recovered from feces of pigs fed the bran diets appeared to accumulate Fe, Zn and Cu. This is in contrast to a report by Dintzis and Watson (1984) which indicated that wheat bran did not accumulate Fe, but that the Fe content of corn bran increased four-fold, following passage through the human gastrointestinal tract. Although the reasons for the different results in these two studies are not clear, part of the reason may relate to the failure of Newton et al. (1983) to adjust the measured mineral concentrations for the amounts of certain bran fractions degraded during passage through the gastrointestinal tract. But, these two studies indicate that certain fiber sources are able to bind or accumulate minerals under in vivo conditions.

Lindemann et al. (1986) studied the effect of peanut hulls on mineral absorption in growing pigs. Peanut hulls were added to a basal diet by substitution at 7.5, 15 and 30%. They reported that the two higher levels of peanut hulls decreased Mn, Zn and Na retention, while the

highest level of peanut hulls also decreased Ca, P and K retention. All levels of peanut hulls increased Fe balance. Although diet mineral levels were high, the decrease in the retention of some minerals (i.e. Zn; decreased from 45 to 14 mg/d with 30% hulls) is greater than would be expected by dilution of the diet with a less available Zn source, which suggests that peanut hulls can interfere with mineral absorption in the pig.

Holzgraefe et al. (1985) fed a very high fiber diet (45.8% of an alfalfa hay:orchardgrass hay mixture) to gestating sows for 80 d, but did not find a negative effect of this fiber source on Ca, P or Mg retention. Although their results are somewhat confounded by unequal diet mineral levels (control, 0.8% Ca and 0.85% P; hay, 0.50% Ca and 1.10% P), this study suggests that the sow can tolerate intakes of this particular fiber source with no detrimental effects on mineral balance.

The study of Lindemann et al. (1986) showed that peanut hulls increased Fe balance. Frolich and Lyso (1983) showed that diets in which all of the Fe was supplied by cereal grains and 20% wheat bran were able to support Hb regeneration in Fe-deficient pigs equally as well as diets in which 80% of the Fe was supplied by ferrous sulfate. Thus, certain high-fiber feedstuffs may be sources of readily available minerals, while at the

same time, they may impair the absorption of other minerals.

Effect of dietary fiber on digesta rate of passage.

It has been proposed that a faster digesta rate of passage may contribute to the decrease in apparent nutrient utilization by animals fed high-fiber diets (Eastwood and Kay, 1979). Although many studies have measured 'rate of passage', due to different methods of demarcating feces and expressing subsequent measures the evidence is difficult to interpret; especially since different fiber sources may affect different components which contribute to whole-tract digesta rate of passage.

In general, the consumption of high-fiber diets by pigs increases apparent rate of digesta passage expressed as the time elapsed for an oral marker dose to appear in the feces (Castle and Castle, 1956, 1957; Seerly et al., 1962; Kass et al., 1980a; Fioramonti and Bueno, 1980; Ruckebusch et al., 1981). In nonruminant animals, the movement of digesta through the gastrointestinal tract appears to represent at least two independent compartments. Thus, diet-induced changes in rate of passage may result from independent changes in either or both compartments (Van Soest et al., 1983).

Luckey et al. (1979) described rate of passage studies in miniature pigs fed three meals daily, which

showed that the fecal appearance of marker exhibited a biphasic pattern, with a large concentration peak at 2-4 d and a small secondary peak at 7-8 d. Other studies have suggested that this excretory pattern reflects the existence of two compartments consisting of the stomach-small intestine and the cecum-colon (Keys and DeBarthe, 1974b; Thielemans et al., 1978).

The relative contribution of each compartment to the faster whole-tract digesta transit rate in animals fed high-fiber diets is unclear. Low et al. (1985) fed pigs (two times daily) diets containing 0 or 10% cellulose, and reported that as diet intake increased, the absolute amount of digesta leaving the stomach increased proportionally; however the rate of stomach emptying (as a percentage of intake) was not influenced by level of intake or diet cellulose content. Although Riottot et al. (1984) suggested that stomach emptying of polyethylene glycol (PEG) was delayed in rats fed wheat bran diets, it is not clear if both liquid and solid phases responded in a similar manner, since PEG is a fluid phase marker.

Digesta transit through the small intestine of the pig is rapid; maximal ileal flow occurs by 4-6 h post-feeding and total passage occurs by 14 h (Alimon and Farrell, 1980; Darcy et al., 1980). The digestibility of nutrients at the terminal ileum exhibits a circadian

variation which is influenced by frequency of feeding and diet composition (Livingstone et al., 1980). These workers, and Moore (1957), have suggested that this response reflects different rates of stomach emptying at different times. Using different methods, both Seerly et al. (1962) and Hutcheson et al. (1983) showed that the rate of passage of meals consumed in the morning was slower than of meals consumed during the evening; the latter group suggested that this was due to different rates of gastric emptying. However, Brown et al. (1979a) reported that 18% wheat bran or pectin did not influence gastric emptying in the rat.

Takeda et al. (1982) reported that the inclusion of fiber in rat diets increased jejunoileal digesta transit rate. Although Laplace (1978) reported that synthetic diets slowed digesta movement through the small intestine of the pig, there is no convincing evidence to show that dietary fiber has an affect on small intestine digesta transit rates.

In animals and man, whole-tract rate of passage measures exhibit large amounts of variation, but most studies indicate that fiber sources which are resistent to degradation decrease digesta transit time (Cummings et al., 1978, 1979a). However, the response to different fiber sources varies. Lebas and Laplace (1977) reported

that digesta rate of passage in rabbits was influenced to varying degrees by fiber sources which resisted degradation to different degrees. These workers ranked the fiber sources in descending order of transit rate as barley straw, oak sawdust and wood cellulose.

The effect of different fiber sources does not appear to be dependent on the presence of bacterial fermentation end-products. Studies have shown that wheat bran increased whole-tract rate of passage equally in germ-free and conventional rats (Riottot et al., 1984). Studies using pigs showed that wheat bran increased rate of passage, but intracecal infusions of antibiotics or VFA did not further change the rate of passage (Bardon and Fioramonti, 1983). Cherbut and Ruckebusch (1985) have shown that the inclusion of 10% indigestible plastic discs in the diet decreased retention time from 129 h to 94 h; these studies argue against a major role of bacterial fermentation as a contributing factor or prerequisite to different rate of passage patterns in animals fed diets containing high fiber ingredients.

The effect of different fiber sources on rate of passage appears closely related to the 'bulking' characteristics of the fiber source. Those fibers which increase fecal output (and hence are less digestible) appear to increase rate of passage most consistently.

Hillman et al. (1983) showed that cellulose and lignin, but not pectin, increased rate of passage and stool weight in human subjects. Ehle et al. (1982) reported that fecal marker appearance was generally earlier in pigs fed alfalfa meal, wheat bran or cellulose, although the response of individual animals was variable.

Bell (1960) showed that different fiber sources (fed at 8%, 16%, 24% and 32%) influenced rate of passage to different degrees, in a fashion somewhat related to their physical and chemical composition. Wheat straw, alfalfa and beet pulp diets had the slowest relative transit rates, wheat bran the fastest, and corn cobs and cellulose intermediate transit rates.

Stanogias and Pearce (1985) reported that the rate of passage response was dependent on both source and level of fiber in the diet. Certain degradable fiber sources such as soy hulls, lupine hulls and wheat bran did not affect rate of passage when fed at 7.5% or 15% of the diet, but increased rate of passage (ROP) when fed at 22 or 30% of the diet. Other sources such as alfalfa stems or corn cobs showed a linear increase in ROP with increasing diet levels, while other fiber sources such as oat hulls had equal effects on ROP at all four diet levels. Fleming and Lee (1983) showed that navy bean hulls (Phaseolus vulgaris L.) increased ROP in rats, but

that the cell wall fraction from these beans had no effect.

Part of the explanation for the different results obtained with different fiber sources may be related to the retention site of the fiber particles in the gastrointestinal tract. Ehle et al. (1982) reported that coarse particles are retained in the 'cecum' compartment longer than fine particles, which results in a longer digesta turnover time. Similar results have been reported by Farrell and Johnson (1972) who showed that 26% cellulose increased the residence time of digesta in the cecum. Additionally, Hecker and Grovum (1975) reported that rate of passage was slowest in the proximal section of the large intestine.

Most swine studies have used protocols which included meal-feeding patterns and limited feed intakes. High fiber intakes increase intestinal volume and size, which in part reflects the higher feed intakes by pigs fed high-fiber diets ad libitum. Thus, it would seem that observations on the effects of fiber on rate of passage obtained using restricted feed intakes may not accurately reflect the response which would be expected under ad libitum feeding conditions. This contention is supported by studies which have shown that 30% peanut hulls initially decrease transit time, but that the

effect is not maintained over a 14 d feeding period in which the pigs were limit-fed the diets twice daily (Lindemann et al., 1986).

Effect of dietary fiber on gastrointestinal structure and function

Some effects of dietary fiber on nutrient utilization may be mediated by lumenal interactions between fiber components and other nutrients, or by the ability of fiber (or by-products of fiber fermentation) to alter lumenal chemical and physical conditions such that subsequent absorption is impaired. Until recently, it has been overlooked that a major portion of the effect of dietary fiber on nutrient utilization may be mediated by direct and indirect effects of fiber on intestinal structure and/or function. Although definitive evidence that fiber alters absorptive function is somewhat lacking, recent reports support three potential actions of fiber on absorptive function: 1) changes in the epithelial cell mucin layer, 2) physical damage to the epithelium and 3) alteration in epithelial cell membrane structure and/or function.

Intestinal epithelial cell diffusion barrier.

The surface epithelium of the gastrointestinal tract is covered by a mucopolysaccharide coating called the

epithelial cell mucin layer (ECML). The mucus which is the main structural component of the ECML is formed from large molecules which consist of four subunits joined by disulfide bridges, linked together to form large polymers (Marshall and Allen, 1977; Mantle et al., 1981). The in vivo polymerizing ability, in combination with the concentration of mucus present, allows the mucus to form a viscous gel at the surface of swine intestine (Allen et al., 1976). Under the chemical conditions present in the intestinal tract, diffusion through the ECML is dependent in part on the solute size, molecular charge, hydration radius and ability to form hydrogen bonds with the sialic acid and ester-sulfate residues present in the mucus (Allen, 1978; Braybrooks et al., 1975).

Nimmerfall and Rosenthaler (1980) proposed that the ECML was the primary barrier limiting the rate of passage of ergot peptide alkaloids from the intestinal lumen to the cell surface. Smithson et al. (1981) have identified the ECML as a barrier to nutrient absorption, and demonstrated that the ECML is synonymous with the so-called 'unstirred water layer' (USL). In vitro studies using intestine preparations have shown that the ECML is the major barrier limiting the rate of absorption of sugars, amino acids and minerals (King et al., 1981; Karasov and Diamond, 1983).

The thickness of the ECML is somewhat species-dependent. The thickness of the ECML has been estimated to be 4.3 um in rats (Smithson et al., 1981), 500-1000 um in dogs (Ryu and Grim, 1982), and 700-1400 um in rats when measured as the pH gradient layer (Flemstrom and Kivilaakso, 1983). A common feature of the ECML is the presence of a bicarbonate-pH gradient across the mucin layer. The structural and rheological properties of the mucus, and the integrity of the pH gradient are dependent upon the lumenal pH and ionic strength (Forstner, 1978; Lewis, 1976; Bahari et al., 1982).

The presence of the ECML presents both a physical and a chemical barrier through which nutrients (minerals) must pass in order to reach the intestinal surface. A number of studies have shown that gastrointestinal mucins are able to bind Zn, Ca, Fe and Mg ions (Forstner and Forstner, 1975; Bella and Kim, 1973; Rendleman, 1982; Rendleman and Grobe, 1982). Williams and Turnberg (1980) suggested that the viscous nature of the ECML, in combination with the ion-binding properties of the mucus, retards the movement of ions through the layer. Alternatively, it has been proposed that the ECML may enhance mineral absorption by trapping lumenal minerals in close proximity to the cell absorptive surface (Quarterman, 1984).

It is not known if a thicker mucus layer, or greater lumenal mucin concentrations, would be beneficial or detrimental to mineral absorption. However, several lines of evidence suggest that high-fiber diets alter the amounts of mucin present in the gastrointestinal tract. Schneeman et al. (1982) reported that the consumption of a 20% wheat bran diet for 14 d increased villus goblet cell numbers in rat duodenum, but did not change the number of epithelial cells present in small intestine or the number of goblet cells in ileum. However Jacobs and Huber (1982) reported that dietary pectin decreased goblet cell numbers in rat colon. Similarly, Gentle and Savory (1975) demonstrated that the feeding of 20% oak sawdust increased goblet cell numbers only in the ceca of chicks.

Fiber may alter lumenal osmolarity or pH by increasing the amount of water retained in the digesta or by increasing VFA levels (Van Dokkum et al., 1983; Jacobs and Lupton, 1982). Sakata and Engelhardt (1981) reported that lumenal osmolarity has a marked effect on the pattern of mucin release in rat colon. Hypertonic solutions caused a dose-dependent increase in mucin release in both proximal and distal colon, while hypotonic solutions only stimulated mucin release in proximal colon. Whether changes in mucin levels or

release occur when animals are fed high-fiber diets has not been investigated.

Shiau and Chang (1983) and Gyory and Chang (1983) reported that the consumption of fermentable fiber sources decreased fecal mucinase and B-glucuronidase activities in a dose-dependent fashion. Theoretically, this would reduce mucin degradation and decrease toxin exposure due to lower degradation rates of toxin-conjugates. However, no data has been presented to show any physiological consequence of these altered enzyme patterns. Although cecal and colon mucinase levels are lower in rats fed wheat bran diets, it is not known whether this results in a thicker ECML, greater digesta mucin levels, or both (Gyory and Chang, 1983).

Effect of dietary fiber on intestinal structure and function.

Intestinal transport capacity is able to adapt to different conditions such as the frequency and quantity of food intake, diet composition, disease and changes in the gut microflora (Abrams, 1977; Williamson, 1978a,b). The epithelial cells which line the intestinal tract are constantly renewed, and the turnover time of villus epithelial cells has been estimated to range from 2-4 d (rodents) to 3-6 d (humans). Studies using young pigs have reported cell turnover times of 2-4 d (Moon, 1971; Dauncey et al., 1983).

The factors which regulate the rate of cell renewal are not known, although a combination of endogenous (neural and endocrine) and exogenous (lumenal nutrients, pressure, etc.) factors are believed to be involved. Dowling and Gleeson (1973) suggested that 'topical nutrients' were required to stimulate the intestinal hyperplasia observed in rats following intestinal resection. Stragand and Hagemann (1977) have suggested that both physical and chemical stimulants are required in order for a 'hyper-proliferative' state to occur. Using a fast-feed mouse model system, they showed that sugars, amino acids and minerals were required in the diet in order to elicit a mucosal growth response. However, the presence or absence of fiber in the diet did not affect the response.

A number of studies have used 'elemental' diets (highly purified, synthetic, fiber-free diets) in order to identify possible roles for dietary fiber in the maintenance of normal intestinal structure and cell proliferation rates. Ryan et al. (1979) reported that mucosal mass was greater in rats fed a conventional 'chow' diet than in rats fed a liquid elemental diet. Although these workers suggested that both physical bulk of the chow, as well as the fiber content were responsible for this response, Sircar et al. (1983)

presented evidence that bulk, at least when fed in the form of cellulose, had a relatively small role in the maintenance of normal mucosal mass and cell proliferation rates. The latter workers reported that dietary cellulose (10 or 15%) did not alter DNA synthesis in colon of rats 18 h after feeding compared with rats fed a fiber-free synthetic diet, and that the DNA synthetic rates were less than those in rats fed a chow-type diet.

Goodlad and Wright (1983) showed that 30% cellulose exerted relatively large effects on cell proliferation and intestinal mass in mice fed these diets for a 7 d period. Cellulose increased mucosal weight and cell proliferation rates, and the number of cells per crypt in colon when added to a fiber-free diet. However, cellulose did not change any measured parameters in the small intestine. Ecknauer et al. (1981) showed that 24% cellulose increased cell proliferation, but not to levels equal to cell proliferation rates in rats fed a chow diet. However, cellulose was not able to overcome the reduction in villus size which occurred with the feeding of a fiber-free diet.

Biol et al. (1984) reported that microvilli were longer and narrower in jejunum from rats fed a chow diet than in rats fed a synthetic diet. Tasman-Jones et al. (1982) reported that villi maintained a leaf-like

morphology at weaning in rats fed a fiber-free or 10% cellulose diets, but assumed a broad-leafed or ridge-like appearance in rats fed a chow or pectin-based diet. Intestinal protein synthesis and cell proliferation were greater in ileum than in proximal small intestine of rats fed a chow diet than in rats fed a fiber-free synthetic diet (Southon et al., 1985). These workers also reported that villi were shorter, crypts were more numerous and crypt cell production rate was greater in ileum of the rats fed the chow diet, although there were few changes in the jejunum.

These studies indicate that at least part of the stimulatory effect of dietary fiber on enteric growth may be mediated by bacterial fermentation end-products, particularly VFA. This hypothesis would be consistent with the established stimulatory effect of VFA on intestinal cell proliferation (Sakata and Engelhardt, 1983). Additionally, the consumption of high-fiber diets reduces large intestine pH in rats (Jacobs and Lupton, 1982), and recent evidence indicates that a lower large intestine pH stimulates cell proliferation under diet conditions which lower pH without dietary fiber additions (Lupton et al., 1985). However, it should be noted that other chemical substances contained in the fiber source or diet may have direct effects on cell proliferation or morphology (Dembinski et al., 1984).

The intestinal response to natural fiber sources varies considerably, and reports indicate that fiber may have effects on intralumenal enzyme activity, as well as effects on intestinal morphology and function. The consumption of natural fiber sources increases intestinal weight in pigs (Coey and Robinson, 1954; Bohman et al., 1955; Kass et al., 1980a), although some studies have failed to detect a response to high fiber intakes (Pond et al., 1980). Kuan et al. (1983) showed that alfalfa cell wall material increased small intestine, cecum and proximal colon weights and increased length of cecum and proximal colon, but had no effect on distal colon. However, Pekas et al. (1983) reported that 50% alfalfa increased small intestine length and weight, and colon weight in lean-genotype pigs but not in obese-genotype pigs. When examined below the gross anatomical level, the effects of native and purified fibers on intestinal structure and function present a more confused picture.

Because the effect of fiber on mucosal structure and morphology may be related to microbial action, some studies have evaluated dietary fiber effects on morphology and cell population kinetics at the light microscopy level in germ-free (GF) and conventional (CV) animals. It is generally accepted that the effects of the microflora on morphology agree with the findings of

Rolls et al. (1978). They showed that mitotic index and cell migration rate, crypt depth and villus height were greater in CV chicks than in GF chicks. Brown et al. (1979b) showed that 18% pectin increased the weights of whole intestine, muscle layer and mucosa throughout the rat small intestine, but that crypt depth was only increased in the distal small intestine. Additionally, pectin decreased mucosal alkaline phosphatase and leucyl-B-naphthylamidase activities, but this response was greater in proximal than in distal small intestine.

The localization of the effects of fiber in different intestinal sites has been reported by others. Jacobs and White (1983) showed that 20% wheat bran caused a hyperplasic response in colon and cecum, but had no effect in jejunum after a 28 d feeding period in rats. The mitotic index was not affected by bran, but the incorporation of tritiated-thymidine into DNA was greater in large intestine, which corresponded to an increase in the number of cells per crypt in distal colon. This suggests that proliferative activity was unchanged by bran, and bran increased only the size of the proliferative cell compartment. Cell migration times measured by autoradiography indicated a longer cell transit time in cecum (decreased exfoliation), a shorter transit time in proximal colon (increased exfoliation), and no change in migration time in distal colon.

The complexity of this response has been reported in subsequent studies by this group. Jacobs (1983) fed diets containing 20% oat bran, 10% pectin or 10% guar gum to rats for 28 d. He showed that although mitotic index was not altered, the labelling index was decreased by oat bran, primarily as a result of a reduction in crypt cell populations. However, pectin increased crypt depth and decreased villus height, which increased villus cell turnover rate; the magnitude was less for rats fed the guar diet.

Komai et al. (1982) reported similar results in rats fed 20% pectin diets. They reported that pectin increased jejunal crypt and villus cell populations, and cell migration rate, but only in CV rats. In contrast, they reported that cellulose increased cell turnover rate in GF rats but not in CV rats (Komai and Kimura, 1980). This suggests that only part of the response to fiber is dependent on fermentation end-products, and that bulk may exert a direct physical effect on the mucosa, or elicit a hormonal response from the animal.

The effects of fiber on intestinal cell size and cell numbers varies; some studies suggest that fiber results in intestinal hyperplasia (Jacobs and White, 1983; Jacobs, 1983) or hypertrophy (Farness and Schneeman, 1982; Brown et al., 1979b), or no effect

(Schneeman et al., 1982). However, dietary fiber seems to increase cell proliferative activity, although cell numbers may not necessarily be increased because of a greater turnover rate. Jacobs (1984) and Clapp et al. (1984) reported that a number of cereal brans result in a hyper-proliferative intestinal response in rats and mice which increases chemically-induced colon tumour yields. This type of response indicates that the proliferative response to fiber may have an impact on the ability of the cell to respond to different nutrient loads or environmental conditions.

Morphological changes observed at the light microscopy level have been inconsistent. Scheibel and Mehta (1985) reported that pectin and guar caused blunting and fusion of ileal villi, but they only observed this response in six of 16 rats. Gordon et al. (1983) reported that cellulose increased the neutrophil infiltrate in lamina propria, but they were unable to correlate this change with effects of the cellulose on growth or nutrient utilization. Mercurio and Behm (1981) showed that villus surface area was greater in rats fed high fiber diets. Similarly, Sigleo et al. (1981) reported that fiber increased villus height and width, and that the rate of influx of 3-O-methyl-glucose and a-amino-isobutyric acid was greater for fiber-fed rats,

suggesting that absorptive capacity may be greater in rats fed high-fiber diets which increase intestinal surface area. However, Johnson et al. (1984) showed that although guar gum increased mucosal growth in rats, the uptake of 3-O-methyl-glucose was decreased. They indicated that this probably resulted from a decrease in cellular enzyme levels and not from a decrease in cell numbers, since the level of transport and the level of enzyme activity were lower when expressed per unit of DNA.

The gross changes seen in rat intestine in response to dietary fiber parallel the gross intestinal changes described earlier for pigs. Younoszai et al. (1978) reported that fiber increases the weight and length of the colon in rats. Other studies have reported that dietary fiber increases colon muscle thickness (Dowling et al., 1967) or intestinal wall tensile strength (Araujo, 1978). Jacobs (1985) reported that wheat bran increased muscle mass in rat proximal and distal colon, exclusively as a result of muscle cell hypertrophy. However, oat bran and pectin decreased muscle size and mass in jejunum, and oat bran also decreased muscle size and mass in distal and proximal colon. These results further demonstrate that the physical bulking properties and fermentation characteristics of different fiber

sources can result in completely different intestinal responses to dietary fiber.

Increased villus transit rate may affect the maturity of the enterocytes present on the villus. Farness and Schneeman (1982) reported that cellulose and pectin decreased leucine-aminopeptidase activity but not sucrase activity in rat mucosal homogenates. Similar results were reported by Brown et al. (1979b) who showed that pectin decreased alkaline phosphatase and leucine-aminopeptidase activities in rat intestines. The synthesis of leucine peptidase occurs as the cells migrate up the villus, which suggests that certain fibers may alter cell maturation as it migrates up the villus. Others have reported that fiber decreases levels of calcium-binding protein (Oku et al., 1982b) and rates of phospholipid and cholesterol biosynthesis in rat intestine (Schwartz et al., 1983). However, the changes in intestinal enzyme levels and cell proliferation are reversible if the fiber source is removed from the diet, although the time course has been variable in different experiments (Jacobs, 1984; Oku et al., 1982a). Gentle and Savory (1975) have also reported that 20% oak sawdust increased intestinal length in Japanese quail with no effect on villus length or submucosal thickness. However, they also reported that the larger gut size resulting

from fiber consumption in quail is reversible upon removal of the fiber from the diet, and the rate of recovery is similar to the rate of onset of the gross changes (Savory and Gentle, 1976). Thus it is unclear whether the changes observed in the intestine in response to dietary fiber represent transient adaptive changes or if they represent alterations in function which persist as long as the fiber is consumed.

A limited number of studies indicate that changes in villus shape and morphology are visible at the electron microscopic level but are not visible at lower magnifications. Knehans and O'Dell (1980) fed diets containing alfalfa, cabbage or alfalfa holocellulose to guinea pigs for 28 d. They showed that alfalfa resulted in villus areas devoid of microvilli, and villi with evidence of physical damage such as puncture holes. Although the other two fiber sources had relatively small effects on intestinal morphology, intestinal surface debris was greater in guinea pigs fed the three high-fiber diets than in guinea pigs fed conventional low-fiber diets. Both cabbage and alfalfa holocellulose resulted in a number of 'indentations' in the villus surface which appeared to be associated with the presence of a novel fusiform-type microorganism. However, since all three fiber sources increased growth rate, it is

unclear whether these effects of fiber are beneficial or detrimental.

Cassidy et al. (1981) reported that pectin, cellulose and alfalfa caused surface epithelium damage in rats, although the effect of each fiber source was somewhat site specific within the intestinal tract. In jejunum and colon, alfalfa resulted in areas of microvilli exfoliation, cellular swelling and a decrease in microvilli density (restricted to colon). Pectin increased the amount of cellular swelling and microvillar disarray in jejunum, while both cellulose and pectin decreased microvillus density in colon, although the effects were less severe than those in the rats fed the alfalfa. Wheat bran did not effect epithelial morphology, and a subsequent study revealed no ultrastructural damage to the epithelium due to the consumption of wheat bran or cellulose (Cassidy et al., 1982).

The functional significance of any morphological changes remain to be elucidated. However, separate studies indicate that fiber may alter intestinal transport function and permeability. Studies indicate that although pectin alters mitotic activity and intestinal morphology, the uptake of glucose from perfusion solutions in situ is not impaired by the previous feeding of pectin (Brown et al., 1979b).

However, when glucose uptake is measured with pectin present in the perfusion solution, glucose uptake is diminished (Flourie et al., 1984). These workers showed that the measured USL thickness increased from 667 um to 1219 um and 1873 um when pectin was added to the perfusion solution at 6 or 10 g/l, respectively. The increase in USL thickness may be due to increased mucus secretion and/or inclusion of pectin in the USL, however, the mechanical removal of USL effects in vitro (using everted gut sacs or intestinal rings) abolishes the negative effects of soluble fibers such as pectin and guar gum on glucose and amino acid transport and on the apparent depressions in surface enzyme activities (Elsenhans et al., 1980,1981).

The ability of soluble fibers such as pectin and gums to decrease sugar absorption and improve glucose tolerance in patients or animals fed these fiber sources (or other insoluble fiber sources) may result from their ability to form a thicker, less permeable USL (Wolever et al., 1979; Ebihara and Kiriyama, 1982; Nygren and Hallmans, 1982). Rainbird et al. (1984) showed that the depressive effect of guar gum on glucose uptake from jejunal perfusion solutions in pigs increased as the length of the perfusion increased from 1 to 6 h, which tends to support in vivo and in vitro observations that

these substances are incorporated into the USL and decrease solute access to the intestinal surface.

Schwartz and Levine (1980) showed that rats chronically fed 10% cellulose or 5% pectin had lower blood glucose levels than rats fed a fiber-free diet, but glucose absorption was not altered when fiber sources were included in an acute glucose tolerance test. Although neither fiber source affected villus morphology, in situ glucose uptake from perfusion solutions was lower for rats chronically fed either fiber source; inclusion of cellulose or pectin in the perfusion solution had no effect on glucose uptake. This study suggests that fiber consumption may alter intestinal transport capacity.

In a subsequent study, Schwartz et al. (1982) studied in vitro Na and Cl transport capacity by intestines from rats fed 10% cellulose or 5% pectin diets for 28 d. Using strips of intestine in a Ussing chamber, they reported that the net flux of Na and Cl was lower in intestines from the rats fed the fiber diets, and that the decrease in electrolyte flux could be accounted for by a decrease in the mucosal to serosal flux of each element. They suggested that fiber modifies membrane structural components associated with transport functions, although the mechanism is unknown. Freeman (1984) has reported similar results in rats fed diets

containing 4.5% alfalfa leaf powder, cellulose powder or slippery elm bark for 49 d. They reported that in situ jejunal uptake of L-leucine from perfusion solutions was decreased in rats fed the alfalfa leaf meal and elm bark diets, but not the cellulose diets. They also showed that only elm bark decreased intestinal uptake of the peptide L-leu-gly (but not L-gly-leu), which indicates that fibers can alter different transport systems independently.

Other studies by Schwartz et al. (1983) using rats fed pectin and cellulose showed that in vitro glucose and leucine uptake by intestinal rings is impaired by prolonged consumption of fiber (42 d). This study also showed that intestinal phospholipid and cholesterol synthesis, but not triglyceride synthesis, decreased in rats fed the high-fiber diets. The effects on synthesis were greater in ileum than jejunum, and were greater in crypt than in villus cells. Together, these observations and those of Freeman (1984) indicate that fiber may alter cell synthetic and transport functions in a manner dependent on anatomical site, cell population and cell function, but somewhat independent of one another.

It is worthwhile to note that the overall effect of fiber on intestinal transport is somewhat ambiguous, because some unusual results have been reported using

perfusion techniques. Dryden et al. (1985) used a perfusion technique to study the effects of consumption of 5% guar and 32% coarse or fine wheat bran diets on glucose transport by rat duodenum and jejunum. In this study, duodenal glucose uptake was decreased in rats previously fed coarse bran when measured after 35, 50 and 60 minutes of perfusion, but only after 60 minutes in rats previously fed guar gum. In jejunum, glucose transport was lower after 20 and 35 minutes, but not after 50 or 60 minutes of perfusion in rats previously fed coarse bran. Although this study was conducted using fasted rats and incorporated a fairly extensive preliminary perfusion period, it is not clear whether these observations reflect possible USL effects or adaptations to the perfusion technique. Regardless, these results suggest that caution may need to be exercised in the interpretation of studies using in situ and in vitro techniques.

A report by Fairweather-Tait and Wright (1985) indicates that a mixed plant fiber source may alter intestinal transport capacity for Zn and Ca, but not Fe in rats. When measured by in situ uptake of extrinsic labels, rats fed the fiber source for 3 or 28 d had lower absorptive capacities for Ca and Zn. Similar to the results for organic nutrients, this study indicates that

transport systems for different minerals may be altered independently by a particular fiber source.

The in vivo perfusion and in vitro transport studies indicate a negative impact of fiber on transport capability of intestine, however these studies have not examined if changes in the site of absorption may also have occurred. Although studies have not been conducted to determine if other intestinal sites are able to compensate for the altered transport rates observed in small intestine, studies using an intestinal resection model have shown that other intestinal sites can compensate for reduced small intestine transport resulting from partial or total small intestine enterectomies. Urban and Michel (1983) showed that following 70% small intestine resection, remnant duodenum and ileum adapted by increasing mucosal mass and by assuming certain transport functions. They showed that duodenum increased absorption of water and electrolytes, while ileum became able to transport galactose; the mucosal growth and transport adaptations occurred as separate phenomena. However, Urban et al. (1983) have also shown that although small intestine resection increased mucosal growth in colon, induction of sugar transport could not be demonstrated. Antonson and Vanderhoof (1982) showed that after distal small bowel

resection, the proximal remnant was able to increase Zn absorption, but that distal Zn transport was unable to adapt to proximal resection. These studies indicate that if fiber impairs nutrient absorption in the small intestine (or large intestine), the overall metabolic consequence could be attenuated by corresponding increases in absorption by other intestinal sites; however the response would depend on the particular nutrient affected, and the ability of other sites to take over these functions.

The preceeding studies provide only a cursory overview of the potential of the gastrointestinal tract to adapt, and illustrate that adaptation to dietary fiber may vary depending not only the nutrient involved, but on the mechanism by which fiber is able to impair nutrient absorption. The mechanisms and signals involved in the adaptation of intestinal transport systems are not known, but are probably somewhat different for the various nutrients (Karasov and Diamond, 1983).

Summary

Feedstuffs which contain high amounts of dietary fiber have characteristics which enable them to influence

bowel function and nutrient utilization when included in the diet. However, it is not possible to accurately predict which characteristics of dietary fiber cause these responses, because adequate in vitro systems have not been developed which are able to mimic the effects of digestive and microbial enzymes on the physical and chemical characteristics of dietary fiber. Under controlled in vitro conditions, dietary fiber is able to bind minerals, but evidence to show that fiber retains this ability within the lumenal environment of the gastrointestinal tract is equivocal.

In vivo studies present a confused picture on the ability of dietary fiber to influence mineral balance. A number of factors probably contribute to the variable responses reported, including duration of feeding, diet mineral levels, diet fiber level and processing of the fiber prior to feeding. Although the data available supports a negative effect of dietary fiber on mineral absorption, a number of unanswered questions remain. It is unclear what physiological consequences (if any) result from a fiber-induced depression in mineral balance, and whether the animal can adapt metabolically, to the altered supply or availability of minerals in high-fiber diets. The question of what effect duration of feeding has on the ability of fiber to alter mineral

balance remains of special importance, particularly since adequate body reserves may mask any negative effect of fiber on short-term mineral nutriture.

A number of putative mechanisms exist which may explain how fiber is able to decrease mineral absorption. Although each may assume relatively more importance under different conditions, all are probably involved to some degree in most feeding situations. These mechanisms include cation binding by the fiber matrix within the intestinal lumen, modification of intestinal transport capacity or intestinal permeability, increased unstirred-layer thickness or resistence, increased digesta rate of passage through one or more sections of the gastrointestinal tract, and increased digesta water contents which may alter the lumenal environment thereby changing mineral concentrations or solubilities.

At the present time, insufficient evidence is available to speculate on the relative importance of each putative mechanism, and which characteristics of different fiber sources may be related to each mechanism. Finally, serious questions remain on how experimental protocols may affect the response obtained by feeding high-fiber diets. It should not be unexpected that factors such as previous diet composition, duration of adaptation and collection periods, and frequency and

level of feeding may confound responses, and along with the variable composition of different lots of the same fiber source, may account for the different responses obtained by different research groups up to the present time.

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CHAPTER III

EFFECT OF SALINOMYCIN ON NUTRIENT ABSORPTION AND RETENTION BY GROWING PIGS FED CORN-SOYBEAN MEAL DIETS WITH OR WITHOUT OAT HULLS OR WHEAT BRAN

Summary

Four balance trials were conducted to determine the effect of the antibiotic salinomycin (SM) on nitrogen (N) and energy utilization and fiber component digestibility by swine fed low- or high-fiber diets. Treatments were corn-soybean meal control (C), 10% oat hull (OH) and 20% wheat bran (WB) diets, each with or without SM (82 mg/kg). In trial 1A, 12 female pigs (34.6 kg) were fed the C or WB diets with or without SM for a 9-d adaptation period followed by a 5-d feces and urine collection period. In trial 1B, the same pigs (50.5 kg) were fed the C or OH diets with previous fiber and SM levels reversed. Trial 2 was conducted in a similar fashion with the order of the fiber sources fed reversed (OH in trial 2A, 32.3 kg; WB in trial 2B, 44.7 kg). SM increased apparent N digestibility and N absorption ($P<.01$) in the WB trials, but also increased ($P<.05$) urine N and thus SM did not affect N retention. Although apparent N absorption was decreased ($P<.06$) by SM in the OH trials, this largely reflected a lower N intake ($P<.02$) and SM did not alter N retention. SM did not alter apparent energy utilization

by pigs fed the C or OH diets, but increased the coefficients for D.E. and M.E. ($P<.01$) and dry matter (DM) digestibility ($P<.05$) of pigs fed the WB diets. Both OH and WB decreased apparent N digestibility ($P<.01$), but did not affect N retention ($P>.10$). OH and WB decreased ($P<.01$) energy digestibility. Digestion coefficients for DM, acid-detergent fiber, neutral-detergent fiber, cellulose and hemicellulose were not affected by SM, but were decreased by OH and WB ($P<.01$). Estimated DM digestibilities (calculated by difference) for OH and WB were 4.9% and 61.3%, respectively. The data indicate that SM may influence energy and N utilization in pigs fed a degradable source of fiber (WB), but not in pigs fed a low fiber diet (C) or a diet containing a high-fiber ingredient resistant to fermentation (OH). This suggests that SM may alter microbial fermentation in the gastrointestinal tract of the pig.

Introduction

The ability of the pig to utilize high-fiber feedstuffs is dependent on many factors, one of which is the presence of an active microflora in the gastrointestinal tract (Cranwell, 1968). The consumption of high-fiber diets by pigs depresses apparent nitrogen (N) digestibility, although this effect of fiber is

dependent in part on its chemical composition and susceptibility to fermentation (Bach Knudsen et al., 1982).

Studies have shown that antibiotics are able to increase apparent N absorption in the small intestine (Eggum et al., 1982) and to increase the apparent digestibility of energy and fiber (Ravindran et al., 1984) in pigs fed high-fiber diets; however, it is not known whether these effects result from the action of the antibiotics on the composition or metabolism of the intestinal microflora. The data of De Wilde (1984) suggests that salinomycin (which improves growth rate and feed efficiency when fed to pigs-Schneider et al., 1979; Blair and Shires, 1981; Leeson et al., 1981; Lindemann et al., 1985) exerts a direct effect on microbial metabolism in the gastrointestinal tract of the pig. De Wilde (1984) found that salinomycin decreased fecal total N and bacterial N outputs when fed to pigs. However, his work did not indicate whether salinomycin affected N retention or apparent energy utilization, or if the effect of salinomycin on gut fermentation was related to the amount of fermentable substrate present in the diet.

The present experiment was conducted to determine the effect of salinomycin on apparent N and energy utilization and on fiber component digestibility by pigs

fed a conventional low fiber corn-soybean meal diet or diets containing supplements of high fiber feedstuffs. Two fiber sources (oat hulls and wheat bran) were used which differed in their susceptibility to degradation within the gastrointestinal tract of the pig.

Materials and Methods

Diets.

Experimental diets were formulated to contain 13% crude protein (table 1). The six diets were a corn-soybean meal control diet (C), a diet with 10% oat hulls (OH) and a diet with 20% wheat bran (WB), each with or without 82 mg salinomycin (SM)/kg diet. The amounts of OH (10%) and WB (20%) used were calculated to increase the neutral-detergent fiber (NDF) level of the diets 6 percentage units above that level present in the C diets. Diets were supplemented with minerals and vitamins as described in table 1.

The analyzed composition of the the two fiber sources was (as-is basis): oat hulls - 92.8% dry matter (DM), 0.64% nitrogen (N), 16.7 MJ/kg gross energy, 70.0% NDF, 37.7% acid-detergent fiber (ADF), 29.2% cellulose, 32.3% hemicellulose and 6.7% lignin; wheat bran - 89.2% DM, 2.68% N, 17.2 MJ/kg gross energy, 36.7% NDF, 12.7% ADF, 8.7% cellulose, 24.0% hemicellulose, and 4.1% lignin.

Table 1. Ingredient composition of experimental diets

Ingredient	Dietary Treatment[1]		
	Control	Oat hulls	Wheat bran
	(%)	(%)	(%)
Ground corn	83.50	72.58	67.82
Soybean meal	14.03	14.90	10.28
Oat hulls	---	10.00	---
Wheat bran	---	---	20.00
Dicalcium phosphate	0.88	1.00	---
Limestone	0.91	0.84	1.37
Iodized salt	0.23	0.23	0.23
Vitamin-Se premix[2]	0.15	0.15	0.15
Zinc premix[3]	0.30	0.30	0.15
Nutrient Analysis (as-fed basis)			
Dry matter, %	89.8	89.6	89.6
Nitrogen, %	2.00	2.04	2.08
Gross energy, kcal/kg	3896	3896	3944
Neutral-detergent fiber, %	8.02	13.94	14.52
Acid-detergent fiber, %	3.22	6.38	4.78
Cellulose, %	2.50	4.84	3.54
Hemicellulose, %	4.80	7.56	9.74
Lignin, %	0.82	1.16	0.96

[1]Salinomycin was added to the diet as a premix (0.12%) at the expense of corn and supplied 82 mg salinomycin/kg diet.

[2]Vitamin-Se premix provided (per kg diet): 2.6 mg riboflavin, 13.2 mg pantothenic acid, 13.2 mg niacin, 13.2 µg B_{12}, 264 mg choline chloride, 2640 IU vitamin A, 264 IU vitamin D, 6.6 IU vitamin E, 660 µg vitamin K (as menadione sodium bisulfite complex), and 0.06 mg Se.

[3]Zinc premix provided (elemental Zn from $ZnCO_3$ per kg diet): Control, 20 mg; Oat hull, 20 mg; Wheat bran, 10 mg.

Animals and dietary treatments.

In trial 1A, 12 female pigs (34.6 ± 1.1 kg bodyweight) were placed in stainless steel metabolism cages for a 7-d adjustment period after which one of four diets (control or WB, with or without SM) was fed for a 9-d adaptation period and a 5-d feces and urine collection period. Pigs were fed two equal portions (0600 and 1200 h) of feed daily in meal form to total 9.99% x kg bodyweight $^{.75}$. Deionized water was available ad libitum from nipple waterers. Animal rooms were maintained at 21 C with a 13 h light:11 h dark schedule.

In trial 1B, the same 12 pigs as in trial 1A (50.5 ±1.3 kg body weight) were fed diet C (without SM) for 7 d, followed by the C or OH diets with or without SM. Pigs were reassigned to diets so that both previous fiber and SM treatments were reversed. The adaptation period to the experimental diets and the collection period were of the same durations as in trial 1A.

Trial 2 was conducted similarly to trial 1, only the order of the fiber sources fed was reversed (oat hulls in trial 2A, wheat bran in trial 2B). The twelve female pigs used weighed 32.3 ± 0.5 kg and 44.7 ± 0.5 kg for trials 2A and 2B, respectively. In trial 2A, pigs were allowed an initial 8-d adjustment period to the cages. The adaptation period to the experimental diets was 7 d and the collection period was 5 d for trials 2A and 2B.

Sample collection and analysis.

In all trials, total feces and urine collections began (and terminated) following appearance in the feces of a marker (.5% chromic oxide added to the morning feed) administered 5 d apart. During the collection periods, feces were collected and weighed at 3-h intervals for d 1 to 2, at 4-h intervals for d 3 to 4, and at 6-h intervals for d 5, followed by collections at 3-h intervals until appearance of the second marker dose in the feces. The feces were dried 24 hours in a forced-draft oven (60 C), weighed, and ground to pass a 1 mm screen using a cyclone-type sample mill (U-D Corp., Boulder, CO). The ground samples were pooled for each pig for the entire collection period. Urine samples were collected in plastic containers and stored at room temperature until analyzed at the end of each collection period. Urine pH was maintained below 4.0 with appropriate additions of 6 N HCl.

Dry matter content was determined on feed and fecal samples by drying at 105 C for 18 h. Nitrogen was determined on all samples by the micro-kjeldahl method, and caloric content of feed, feces and lyophilized urine samples was determined by bomb calorimetry. Cellulose, lignin and ADF were determined by the methods of Goering and Van Soest (1970), and NDF by the amylase method of

Robertson and Van Soest (1977). Hemicellulose was calculated as the difference between NDF and ADF.

Oat hull and wheat bran trials were analyzed separately by the general linear models procedure of SAS (SAS, 1982), using a model which contained the effects of fiber (high or low), SM (with or without), trial (1 or 2), and all two-way interactions. Within a given fiber source (C, OH or WB), the effect of SM was tested using Student's t-test.

The absolute amounts of nutrients consumed differed between trials based on the differences in body weights of the pigs used. Data corresponding to absolute amounts of nutrient/day were adjusted by dividing the absolute amount by the metabolic body size ($kg^{.75}$) of the animal to facilitate a more accurate interpretation of the results. Only the adjusted data are presented in the accompanying tables.

Results

Energy and nitrogen utilization.

In the OH trials, N intake ($P<.02$) and apparent N absorption ($P<.06$) were lower for pigs fed the diets containing SM, however N retention was not influenced by SM ($P>.10$). In the WB trials (table 2), SM increased apparent N absorption and digestibility ($P<.01$).

However, because SM increased (P<.05) urine N excretion, apparent N retention was unaffected (P>.10). The effect of SM was more pronounced in pigs fed the WB diets than in those pigs fed the C diets. Pigs fed the WB diet with SM had a greater (P<.01) apparent N absorption and greater (P<.05) urine N excretion than did pigs fed the WB diet without SM. Subsequently, N retention did not differ between pigs fed the diets with or without SM, regardless of fiber content. Apparent N digestibility was lower (P<.01) for pigs fed the diets containing OH or WB compared to pigs fed the C diets, however there was no effect (P>.10) of either fiber source on apparent N absorption or retention (table 2).

The addition of SM to the C or OH diets did not influence apparent energy absorption or retention (P>.10). In the WB trials, SM increased apparent energy absorption (P<.01) and retention (P<.05) by pigs fed the WB diet, but did not influence apparent energy absorption or retention by pigs fed the C diets. The WB x SM interaction was significant for energy retained (P<.08), and coefficients for digestible (P<.05) and metabolizable (P<.10) energy. The addition of either OH or WB (table 2) to the control diet decreased (P<.01) apparent energy absorption and retention and decreased (P<.01) the coefficients for digestible and metabolizable energy, but did not affect urine energy losses (P>.10).

Table 2. Effect of salinomycin (SM) on nitrogen and energy utilization by pigs fed diets with or without 10% oat hulls (OH) or 20% wheat bran (WB)

Criteria	Oat Hull Trials[1] Diet Group					Main effect P-values		Wheat Bran Trials[1] Diet Group					Main effect P-values	
	C	CSM	OH	OHSM	SEM	OH	SM	C	CSM	WB	WBSM	SEM	WB	SM
n	(6)	(6)	(6)	(6)				(6)	(5)	(6)	(6)			
Nitrogen[2]														
Intake	2.02	1.95†	2.04	1.97†	0.03	NS	.02	2.02	1.98**	2.06	2.10**	0.01	.01	NS
Feces	0.25	0.23	0.29	0.26	0.01	.01	.05	0.26	0.23*	0.40	0.29**	0.01	.01	.01
Urine	0.66	0.67	0.60	0.61	0.05	NS	NS	0.68	0.70	0.63	0.75*	0.03	NS	.05
Absorbed	1.76	1.72	1.75	1.71	0.02	NS	.06	1.76	1.75	1.66	1.81**	0.01	NS	.01
Retained	1.11	1.05	1.16	1.10	0.04	NS	NS	1.09	1.05	1.03	1.06	0.03	NS	NS
Digestibility, %	87.5	88.3	85.9	86.6	0.4	.01	.10	87.0	88.5†	80.6	86.0	0.6	.01	.01
Retained, %	54.9	54.2	56.6	55.5	2.3	NS	NS	53.9	53.1	50.0	50.3	1.6	.06	NS
n	(6)	(6)	(6)	(6)				(6)	(5)	(6)	(6)			
Energy[3]														
Intake	388.3	366.0	382.6	386.1	7.6	NS	NS	389.4	388.9	394.1	395.1	0.4	.01	NS
Feces	41.6	35.5	72.7	69.3	2.5	.01	NS	42.2	43.4	70.2	64.5*	1.6	.01	NS
Urine	7.1	6.8	6.5	7.0	1.0	NS	NS	9.1	8.4	8.3	9.2	0.5	NS	NS
Absorbed	346.7	330.5	309.8	316.8	6.0	.01	NS	347.2	345.6	323.9	330.6*	1.7	.01	NS
Retained	339.6	323.7	303.4	309.8	6.2	.01	NS	338.1	337.2	315.6	321.4*	1.7	.01	NS
D.E., %	89.3	90.1	81.3	81.9	0.4	.01	NS	89.2	88.8	82.2	83.7*	0.4	.01	NS
M.E., %	87.5	88.2	79.3	80.2	0.5	.01	NS	86.8	86.7	80.1	81.4*	0.4	.01	NS
$M.E._N$, %	84.4	85.1	76.0	76.9	0.7	.01	NS	83.0	83.4	76.6	78.1*	0.5	.01	.08

[1]Probability values represent significant least-squares differences between diets with salinomycin compared with the appropriate diets without salinomycin (†P<.10, *P<.05, **P<.01).

[2]Values for N intake, feces, urine, absorbed and retained as g $N/(kg^{.75}$ bodyweight·d).

[3]Values for energy intake, feces, urine, absorbed and retained as kcal/($kg^{.75}$ bodyweight·d).

Table 3. Effect of salinomycin (SM) on dry matter and fiber component digestibility by pigs fed diets with or without 10% oat hulls (OH) or 20% wheat bran (WB)

Criteria[2]	Oat Hull Trials					Main effect P-values		Wheat Bran Trials					Main effect P-values	
	Diet Group[1]							Diet Group[1]						
	C	CSM	OH	OHSM	SEM	OH	SM	C	CSM	WB	WBSM	SEM	WB	SM
n	(6)	(6)	(6)	(6)				(6)	(5)	(6)	(6)			
Dry Matter														
Intake	89.6	88.0	87.2	88.6	1.16	NS	NS	89.8	89.4	89.5	90.1	0.09	NS	NS
Feces	8.8	8.8	15.6	15.4	0.41	.01	NS	9.1	9.1	14.8	13.8*	0.34	.01	NS
Digested	80.8	79.2	71.6	73.2	0.93	.01	NS	80.7	80.2	74.7	76.3**	0.38	.01	NS
Digested, %	90.2	90.0	82.1	82.6	0.36	.01	NS	89.9	89.8	83.4	84.7*	0.38	.01	NS
Acid-detergent fiber														
Intake	3.21	3.18	6.14	6.45	0.06	.01	NS	3.22	3.22	4.79	4.76	0.01	.01	NS
Feces	1.11	1.21	4.38	4.58	.11	.01	NS	1.08	1.21	2.93	3.02	0.07	.01	NS
Digested	2.10	1.95	1.77	1.87	0.09	.04	NS	2.14	2.01	1.85	1.74	0.07	.01	.10
Digested, %	65.4	61.5	28.8	29.0	1.70	.01	NS	66.4	62.4	38.7	36.5	1.66	.01	.08
Neutral-detergent fiber														
Intake	8.00	7.88	13.49	14.02	0.15	.01	NS	8.03	8.00	14.43	14.60	0.01	.01	NS
Feces	3.68	3.94	9.50	9.75	0.26	.01	NS	3.73	4.05	7.60	7.67	0.20	.01	NS
Digested	4.33	3.94	3.98	4.26	0.19	NS	NS	4.30	3.95	6.84	6.93	0.21	.01	NS
Digested, %	54.1	50.0	29.6	30.4	1.80	.01	NS	53.5	49.3	47.4	47.4	3.03	.07	NS
Cellulose														
Intake	2.46	2.49	4.64	4.88	0.05	.01	NS	2.46	2.53	3.56	3.53	0.01	.01	NS
Feces	0.96	1.06	3.36	3.51	0.10	.01	NS	0.89	0.96	2.08	2.14	0.06	.01	NS
Digested	1.49	1.43	1.28	1.37	0.07	.10	NS	1.57	1.56	1.47	1.38	0.06	.05	NS
Digested, %	60.8	57.4	27.8	28.1	2.10	.01	NS	63.8	61.8	41.4	39.3	2.13	.01	NS
Hemicellulose														
Intake	4.79	4.70	7.34	7.56	0.08	.01	NS	4.80	4.77	9.64	9.84	0.01	.01	.01
Feces	2.59	2.82†	5.30	5.37	0.16	.01	NS	2.79	2.99	4.88	4.90	0.15	.01	NS
Digested	2.20	1.88†	2.04	2.19	0.12	NS	NS	2.02	1.78	4.76	4.94	0.15	.01	NS
Digested, %	46.0	40.2†	27.9	29.0	2.00	.01	NS	42.0	37.2	49.4	50.2	2.58	.01	NS
Lignin														
Intake	0.87	0.77	1.09	1.20	0.01	.01	NS	0.87	0.78	1.00	0.92	0.01	.01	.01
Feces	0.14	0.12	0.78	0.78	0.02	.01	NS	0.18	0.19	0.79	0.84	0.02	.01	NS
Digested	0.73	0.64	0.31	0.42	0.02	.01	NS	0.70	0.59	0.21	0.08	0.02	.01	.01
Digested, %	83.9	82.9	28.5	34.6	1.78	.01	NS	79.9	76.1	21.2	8.4	2.59	.01	.01

[1]Probability values represent significant least-squares differences between diets with salinomycin compared with the appropriate diets without salinomycin (†P<.10; *P<.05; **P<.01).

[2]Values for intake, feces and digested as g/(kg$^{.75}$ bodyweight·d).

Fiber component digestibility.

Salinomycin increased (P<.05) dry matter digestibility by pigs fed the WB diet, but did not influence DM digestibility by pigs fed the C or OH diets (table 3). Salinomycin did not greatly influence NDF, cellulose or hemicellulose digestibility in either the OH or WB trials, while it decreased the apparent digestibility of ADF (P<.08) and lignin (P<.01) by pigs in the WB trials, but not in the OH trials.

The addition of OH or WB (table 3) to the C diet decreased apparent DM digestibility (%) (P<.01). Wheat bran decreased (P<.01) the percentage DM in the feces (32.9% to 26.4%), whereas OH did not alter the DM percentage of the feces (31.7% to 33.4%; P>.10). Fecal water increased (P<.01) from 18.6 to 40.2 and from 19.2 to 31.2 g/(kg ^{75} bodyweight d) by pigs fed the WB and OH diets, respectively. Salinomycin did not influence (P>.10) fecal DM percentage or fecal water output.

The digestion coefficients of all fiber components were lower (P<.01) for pigs fed the OH diets than for pigs fed the C diets. However, the amount of each fiber component digested during transit through the gastrointestinal tract varied. Pigs fed the OH diets digested less cellulose (P<.10), ADF (P<.04) and lignin (P<.01) than pigs fed the C diets, with no difference in the amount of NDF or hemicellulose digested (P>.10).

The apparent digestibilities of NDF ($P<.07$), and ADF, cellulose and lignin ($P<.01$) were lower, but hemicellulose digestibility was higher ($P<.01$), by pigs fed the WB diets than by pigs fed the C diets. The absolute amounts of hemicellulose and NDF digested were greater ($P<.01$), while the amounts of ADF and lignin ($P<.01$) and cellulose ($P<.05$) digested were less by pigs fed the WB diets than by pigs fed the C diets.

The apparent digestibility of the fiber components in WB and OH were estimated by a difference method, assuming that the apparent digestibility of the fiber components contained in the basal ingredients (corn and soybean meal) did not differ between the low and high fiber diets. Digestion coefficients for OH were: DM, 4.9%, ADF, 0%, NDF, 3.1%, cellulose, 0.7% and hemicellulose, 8.8%. Digestion coefficients for WB were: DM, 61.3%, ADF, 6.4%, NDF, 43.0%, cellulose, 11.6% and hemicellulose, 56.8%.

Discussion

Both oat hulls and wheat bran decreased apparent N digestibility in our experiments. The decrease in apparent N digestibility by pigs fed high fiber diets has been attributed to increases in bacterial protein synthesis and endogenous N losses (Farrell, 1973).

Fibrous feedstuffs susceptible to fermentation have a greater impact on fecal N excretion than those resistant to bacterial degradation (Bach Knudsen et al., 1982). The greater DM digestibility, which reflects the extent to which it was fermented, of WB (61.3%) compared to OH (4.9%) may partially explain the large effect of WB on N digestibility compared with OH in our experiment. Other studies have also shown that OH are resistant to degradation (Moser et al., 1982) and have a minimal effect on N digestibility when fed to pigs (Kennelly and Aherne, 1980; Zoiopoulos et al., 1983).

Beames and Eggum (1981) reported that the depression in N digestibility caused by high fiber feedstuffs may reflect differences in the availability of the N in the fiber source. The greater effect of WB on N digestibility in our experiments could also reflect the greater contribution of a less available source of N from WB (2.68% N) compared with OH (0.68% N).

The inclusion of fiber in the diet decreases large intestine ammonia levels and urine N excretion, effects which correspond to an increase in fecal N output (Malmlof and Hakansson, 1984; Varel et al., 1984). Conversely, antibiotics reduce cecal ammonia levels and increase urine N excretion, while reducing fecal N excretion (Gargallo and Zimmerman, 1980; Just et al.,

1981). In the present study, SM increased apparent N digestibility and urine N excretion by pigs fed the WB diet, but not the OH or C diets. These observations are similar to those of De Wilde (1984) who reported that SM decreased fecal total and bacterial N contents. Together, these observations suggest that SM may alter the extent or pattern of gastrointestinal fermentation in the pig. However, since SM did not increase N retention, it is unclear whether the effect of SM on bacterial N metabolism has any nutritional benefit to the pig.

Both OH and WB decreased the apparent digestible energy content of the diets which is in agreement with previous reports showing that high fiber diets have a lower digestible energy content for swine (Just et al., 1983; Morgan et al., 1984). Salinomycin did not influence energy utilization by pigs fed the C or OH diets, but did increase apparent energy absorption by pigs fed the WB diets. The amount of fermentation was probably quantitatively less in the pigs fed the OH and C diets than that in the pigs fed the WB diets, and although SM may have altered energy utilization in pigs fed these diets also, our methods may not have been sensitive enough to detect any effects which SM may have exerted.

Dietary antibiotics have been shown to increase the apparent absorption of N from the small intestine (Just

et al., 1981; Eggum et al., 1982), and although the present data suggests that SM may alter fermentation in the gastrointestinal tract of the pig, the site of this action is not known. The effect of SM on energy and N availability appears to be related to the amount and degradability of the substrate available. Although SM is able to promote growth in pigs fed low-fiber diets (Leeson et al., 1981; Blair and Shires, 1981), we did not detect any effect of SM on energy or N retention in pigs fed low-fiber diets. More sensitive measures of energy and nitrogen metabolism will be needed to identify the site(s) of action of SM and to clarify the physiological significance of the interaction between SM, microbial fermentation in the gastrointestinal tract, and nutrient utilization in the pig.

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CHAPTER IV

EFFECT OF DIETARY OAT HULLS OR WHEAT BRAN ON MINERAL UTILIZATION IN GROWING PIGS FED DIETS WITH OR WITHOUT SALINOMYCIN

Summary

Four balance trials were conducted to determine the effect of dietary fiber (oat hulls or wheat bran) and salinomycin on mineral absorption and balance in growing pigs. The experimental diets were a corn-soybean meal control diet (C), a diet containing 10% oat hulls (OH), a diet containing 20% wheat bran (WB), each with or without salinomycin (SM; 82 mg/kg). The inclusion of OH decreased Ca ($P<.06$) and Zn ($P<.01$) balance, largely as a consequence of decreased fractional absorption (absorbed as a percentage of intake), and decreased ($P<.10$) P balance and efficiency of P retention ($P<.04$). OH did not influence Mg balance. WB did not affect Ca, Zn or P balance, but increased ($P<.02$) Mg balance, primarily due to an increase in Mg intake. Both OH and WB depressed absolute and fractional Na absorption ($P<.01$), with only nonsignificant reductions in Na balance. OH depressed K absorption ($P<.01$), but apparent K absorption was slightly increased ($P<.08$) by WB due to a greater K intake. Neither fiber source affected K balance. Pigs fed the OH and WB diets were in positive Mn balance, in

contrast to the negative Mn balance in pigs fed the C diets. OH and WB increased (P<.01) Cu intake, and despite a decrease in fractional Cu absorption in pigs fed the OH (P<.03), balance was not affected. WB increased (P<.01) Cu balance. The apparent and fractional absorption of P was improved by SM (P<.05) only in pigs fed the WB diets. SM decreased apparent and fractional Cu absorption and Cu balance in the OH trials (P<.05) and WB trials (P<.01) for pigs fed the C diets only. SM did not influence Ca, Mg, Na, K, Zn or Mn absorption and balance. The results indicate that OH, and to a lesser extent WB, decreases mineral balance in pigs. The greater effects of OH suggest that differences in the chemical and physical properties, and susceptibility to degradation, may be as important as level in the diet in determining the impact of dietary fiber on mineral balance.

Introduction

The consumption of diets containing high levels of fiber has been shown to exert a negative effect on mineral absorption in humans and animals (Kelsay, 1981; Ali et al., 1981). Studies conducted with pigs have shown that 20% dietary wheat bran decreases apparent Ca and Zn absorption (Bagheri and Gueguen, 1983). In addition, increasing the dietary cellulose content of a

semi-synthetic diet from 30 to 90 g/kg reduced the apparent absorption of P, Mg, Ca, K and Zn by pigs, with most of the reduction occurring in the large intestine (Partridge, 1978). The complex polysaccharides which comprise dietary fiber are able to bind trace minerals in vitro (Thompson and Weber, 1981a), and Newton et al. (1983) reported that an indigestible bran residue recovered from the feces of pigs fed a 20% wheat bran diet accumulated Cu, Fe, Ca and Zn.

The ability of a fiber source to decrease mineral balance is partially related to the number of cation binding sites available in the fiber matrix. Thus, the extent to which a fiber source is degraded within the digestive tract may influence the ability of that fiber source to decrease mineral balance. The present experiment was conducted to determine the effects of a degradable fiber source (wheat bran) and a fiber source which is resistent to degradation (oat hulls) on mineral balance in pigs. Since the level of microbial activity in the gut may be an important factor influencing the ability of a fiber source to interfere with mineral absorption, these diets were fed either with or without an antibiotic (salinomycin) which has been shown to influence gut fermentation in the pig (De Wilde, 1984).

Materials and Methods

Four balance trials were conducted using 24 crossbred female pigs in order to examine the effects of two fiber sources (oat hulls and wheat bran) on apparent mineral absorption in growing pigs. Dietary treatments and experimental procedures were described by Moore et al. (1986) and will only be briefly summarized.

Diets.

The six dietary treatments (table 1) consisted of a corn-soybean meal control diet (C), a diet containing 10% oat hulls (OH) and a diet containing 20% wheat bran (WB), each with or without salinomycin (SM; 82 mg/kg). Each fiber source was added at a level calculated to supply 6 percentage units neutral-detergent fiber above that level present in the control diet. Supplemental Zn was added to the C, OH and WB diets (20, 20 and 10 mg Zn/kg diet, respectively) in order to equalize intakes. With the exception of Ca, P and Na, no other minerals were added to the diets. The mineral composition of the diets and fiber sources are given in table 2.

Trial conduct and sample collection and analysis.

Two trials were conducted, each with 12 female pigs. In trial 1A, a 5-d fecal and urine collection period followed a 9-d adjustment period to the C and WB diets (mean pig weight of 34.6±1.1 kg). The same pigs (50.5±1.3

Table 1. Ingredient composition of experimental diets

Ingredient	Dietary Treatment[1]		
	Control	Oat hulls	Wheat Bran
	(%)	(%)	(%)
Ground corn	83.50	72.58	67.82
Soybean meal	14.03	14.90	10.28
Oat hulls	---	10.00	---
Wheat bran	---	---	20.00
Dicalcium phosphate	0.88	1.00	---
Limestone	0.91	0.84	1.37
Iodized salt	0.23	0.23	0.23
Vitamin-Se premix[1]	0.15	0.15	0.15
Zinc premix[1]	0.30	0.30	0.15

[1]See table 1 (Chapter 3) for complete premix descriptions and diet descriptions.

Table 2. Nutrient analysis (as-is basis) of experimental diets, oat hulls and wheat bran

Component	Diet Group			Fiber Source	
	Control	Oat hulls	Wheat bran	OH	WB
Dry Matter,%	89.8	89.6	89.6	92.8	89.2
Acid-detergent fiber,%	3.22	6.38	4.78	37.7	12.7
Neutral-detergent fiber,%	8.02	13.94	14.52	70.0	36.7
Cellulose	2.50	4.84	3.54	29.2	8.7
Hemicellulose	4.80	7.56	9.74	32.3	24.0
Lignin	0.82	1.16	0.96	6.7	4.1
Calcium	0.62	0.62	0.60	0.17	0.19
Phosphorus, %	0.47	0.47	0.50	0.10	1.18
Magnesium, %	0.125	0.124	0.210	0.15	0.17
Sodium, %	0.094	0.093	0.096	0.017	0.015
Potassium, %	0.596	0.618	0.730	0.52	1.32
Zinc, mg/kg	51.7	46.7	55.5	22.7	114.0
Copper, mg/kg	5.7	8.0	8.0	9.1	14.2
Manganese, mg/kg	9.6	13.2	34.5	35.4	150.9

kg) were used in trial 1B, with the exception that they were fed the C or OH diets, with previous fiber and salinomycin treatments reversed. Trial 2 was conducted in a similar fashion, but the order of fiber sources fed was reversed; OH in trial 2A (mean pig weight of 32.3±0.5 kg), and WB in trial 2B (mean pig weight of 44.7±0.5 kg).

Feed and fecal samples were prepared for mineral analysis by charring (350 C for 36 h), followed by digestion with nitric acid and hydrogen peroxide (E. R. Morris, personal communication). The residue remaining was dissolved in 6 N HCl (5 ml) and diluted to an appropriate volume. Calcium, Mg, Zn, Cu and Mn were determined in urine samples, and in feed and fecal digests by atomic absorption spectrophotometry using a Perkin-Elmer Model 403 spectrophotometer (Perkin-Elmer Corp., Norwalk, CT). Sodium and K were determined by atomic emission spectroscopy using the same instrument. Phosphorus contents were determined colorimetrically (Fiske and Subbarow, 1925).

Data for the OH and WB trials were analyzed separately using the general linear models procedure of SAS (SAS, 1982), using a model which contained the effects of fiber (high or low), salinomycin (with or without), trial (1 or 2), and all two-way interactions. The data corresponding to absolute amounts of mineral/day are reported as mg mineral/(kg $^{.75}$ bodyweight · day).

Results

Fiber sources.

The addition of OH to the diet (table 3) decreased apparent Ca absorption ($P<.05$) and retention ($P<.06$). Although urine Ca output was greater (P,.07) for pigs fed the WB diets, apparent Ca absorption and retention were not different between pigs fed the C or WB diets ($P>.10$). Apparent P absorption (table 3) was not different between pigs fed the C or OH diets ($P>.10$). But OH increased urine P excretion ($P<.01$) which tended to reduce P balance ($P<.09$). The OH x trial interaction was significant for apparent P retention ($P<.05$), with apparent P retention decreased ($P<.02$) by OH in trial 2A, but not in trial 1B. Although WB increased ($P<.01$) fecal P output, apparent P absorption and retention were not different between pigs fed the WB and C diets ($P>.10$). There was no effect of OH on Mg utilization (table 3). Magnesium intake was greater ($P<.01$) by pigs fed the WB diets, and despite greater ($P<.01$) fecal and urine losses of Mg, pigs fed the WB diets absorbed ($P<.01$) and retained ($P<.02$) more Mg than did pigs fed the C diets.

Apparent and fractional Na absorption were lower (table 4; $P<.01$) for pigs fed either high fiber diet than for pigs fed the C diets. But due to lower urinary

Table 3. Effect of oat hulls (OH) or wheat bran (WB) and salinomycin (SM) on Ca, P and Mg balance in growing pigs

Criteria	Oat Hull Trials[1] Diet Group					Main effect P-values		Wheat Bran Trials[1] Diet Group					Main effect P-values	
	C	CSM	OH	OHSM	SEM	OH	SM	C	CSM	WB	WBSM	SEM	WB	SM
n	(6)	(6)	(6)	(6)				(6)	(5)	(6)	(6)			
Calcium[2]														
Intake	634	600**	614	601	8.0	NS	.01	636	609**	600	594**	0.6	.01	.01
Feces	280	237*	290	275	13.0	.09	.04	289	276	280	257	18.2	NS	NS
Urine	11	13	10	8	1.5	NS	NS	9	9	20	13	3.9	.07	NS
Absorbed	354	363	323	325	15.7	.05	NS	347	333	320	337	18.4	NS	NS
Retained	343	351	313	317	15.5	.06	NS	344	323	300	324	19.2	NS	NS
Absorbed, %[3]	55.8	60.5	52.8	54.2	2.2	.06	NS	54.5	54.6	53.3	56.7	3.0	NS	NS
Retained, %[3]	54.1	58.3	51.1	52.7	2.2	.07	NS	54.1	53.1	50.0	54.6	3.1	NS	NS
Phosphorus[2]														
Intake	468	458	466	465	6.1	NS	NS	469	465	499	500	0.5	.01	NS
Feces	232	218	232	227	6.5	NS	NS	254	240	299	262*	10.5	.01	.01
Urine	14	18	30	27	3.4	.01	NS	7	21**	3	13**	2.4	.01	.01
Absorbed	236	241	234	238	7.1	NS	NS	216	225	199	237*	10.7	NS	.05
Retained	222	222	205	211	7.8	.09	NS	214	204	197	225	12.3	NS	NS
Absorbed, %[3]	50.4	52.4	50.3	51.2	1.3	NS	NS	45.9	48.4	40.0	47.5	2.2	NS	.05
Retained, %[3]	47.4	48.5	43.9	45.3	1.4	.04	NS	45.4	43.8	39.4	45.0	2.6	NS	NS
Magnesium[2]														
Intake	127	121*	124	121	1.6	NS	.01	127	123	210	209	0.2	.01	NS
Feces	87	81	81	85	4.0	NS	NS	85	86	155	148	3.2	.01	NS
Urine	23	24	20	23	2.2	NS	NS	18	22	24	30*	1.8	.01	.02
Absorbed	40	40	44	36†	3.7	NS	NS	42	37	55	61	3.3	.01	NS
Retained	17	16	24	13†	3.8	NS	NS	23	15	32	32	3.8	.02	NS
Absorbed, %[3]	31.7	33.5	35.3	29.6†	3.0	NS	NS	32.6	29.7†	26.2	29.3	1.8	.08	NS
Retained, %[3]	13.2	13.6	19.1	10.4†	3.0	NS	NS	18.2	11.9†	15.0	15.1	2.4	NS	NS

[1]Symbols represent significant least-squares differences between diets with salinomycin compared with the appropriate diets without salinomycin (†P<.10; *P<.05; **P<.01).

[2]Values for intake, feces, urine, absorbed and retained as mg element/(kg$^{.75}$ bodyweight·d).

[3]Expressed as percentage of intake.

Table 4. Effect of oat hulls (OH) or wheat bran (WB) and salinomycin (SM) on Na and K balance in growing pigs

Criteria	Oat Hull Trials Diet Group[1] C	CSM	OH	OHSM	SEM	Main effect P-values OH	SM	Wheat Bran Trials Diet Group[1] C	CSM	WB	WBSM	SEM	Main effect P-values WB	SM
n	(6)	(6)	(6)	(6)				(6)	(5)	(6)	(6)			
Sodium[2]														
Intake	94	92	94	88	1.2	NS	NS	94	93†	94	98	0.1	.01	NS
Feces	18	16	28	24	2.9	.01	NS	16	22†	37	40	2.4	.01	.06
Urine	37	35	33	29	4.4	NS	NS	35	29	18	18	3.4	.01	NS
Absorbed	76	76	66	64	1.8	.01	NS	78	70*	57	58	2.4	.01	NS
Retained	39	40	34	35	3.7	NS	NS	43	42	39	40	3.2	NS	NS
Absorbed, %[3]	80.8	82.8	70.6	72.4	2.2	.01	NS	83.4	75.8†	61.0	59.5	2.5	.01	.09
Retained, %[3]	41.5	44.4	35.3	39.3	4.1	NS	NS	45.7	45.0	41.6	40.8	3.4	NS	NS
Potassium[2]														
Intake	589	592	601	618	7.9	.03	NS	591	600	730	728	0.6	.01	NS
Feces	128	124	176	177	6.5	.01	NS	130	120	243	235	10.0	.01	NS
Urine	293	323	285	296	22.1	NS	NS	283	283	261	284	18.8	NS	NS
Absorbed	462	468	426	441	10.1	.01	NS	461	481	487	493	10.0	.08	NS
Retained	169	145	141	145	15.3	NS	NS	179	198	225	209	16.6	NS	NS
Absorbed, %[3]	78.4	79.0	70.8	71.4	1.1	.01	NS	78.0	80.0	66.6	67.7	1.5	.01	NS
Retained, %[3]	28.6	24.8	23.6	23.5	2.8	NS	NS	30.3	32.8	30.8	28.7	2.4	NS	NS

[1]Symbols represent significant least-squares differences between diets with salinomycin compared with the appropriate diets without salinomycin (†P<.10; *P<.05; **P<.01).

[2]Values for intake, feces, urine, absorbed and retained as mg element/($kg^{.75}$ bodyweight·d).

[3]Expressed as percentage of intake.

(significant only for WB diets, P<.01) Na losses, Na retention was not different between pigs fed the high fiber or C diets. Oat hulls decreased apparent and fractional K absorption (P<.01), but did not influence K balance (table 4). Although WB decreased (P<.01) fractional K absorption, pigs fed the WB diets had a greater apparent K absorption (P<.08), but not K retention, than did pigs fed the C diets.

Pigs fed the OH diets absorbed and retained less Zn (table 5; P<.01) and had a lower fractional Zn absorption (P<.01) than did pigs fed the C diets. The addition of WB to the diet did not effect apparent Zn absorption or retention (P>.10), although fractional Zn absorption was slightly lower (P<.09) for pigs fed the WB diets compared with pigs fed the C diets.

Fractional Cu absorption was lower (table 5; P<.03) for pigs fed the OH diets, however the absolute amounts of Cu absorbed and retained were not affected by OH additions to the diet (P>.10). Copper intake, and apparent Cu absorption and retention were greater (P<.01) for pigs fed the WB diets than for pigs fed the C diets. In both trials, pigs fed the C diets were in negative Mn balance, while pigs fed either the OH or WB diets were in positive Mn balance (Table 4; P<.01 and P<.05, respectively).

Salinomycin.

There was no effect of SM on Ca, Mg, K or Zn utilization (tables 3, 4 and 5) by pigs fed the C, OH or WB diets ($P>.10$). Salinomycin decreased ($P<.09$) fractional Na absorption in the WB trials, but did not influence Na retention ($P>.10$). Apparent Na absorption and retention were not influenced by SM in the OH trials ($P>.10$).

Salinomycin did not influence P absorption or retention by pigs during the OH trials (table 3). In the WB trials SM increased ($P<.05$) apparent P absorption (table 3), but because pigs fed the diets with SM excreted more P in the urine ($P<.01$), P retention was unaffected ($P>.10$). The effect of SM on apparent and fractional P absorption was largely confined to pigs fed the WB diets ($P<.05$), although the effect of SM on urine P output was equally apparent for pigs fed the C or WB diets ($P<.01$).

Salinomycin decreased apparent Cu absorption and retention (table 5) by pigs fed the C diets, but not the high fiber diets in both the OH ($P<.05$) and WB trials ($P<.01$). The OH x SM and WB x SM interactions were significant for apparent Cu absorption and retention ($P<.02$ and $P<.08$, respectively). Salinomycin did not influence apparent Mn absorption and retention by pigs

Table 5. Effect of oat hulls (OH) or wheat bran (WB) and salinomycin (SM) on Zn, Cu and Mn balance in growing pigs

Criteria	Oat Hull Trials[1] Diet Group					Main effect P-values		Wheat Bran Trials[1] Diet Group					Main effect P-values	
	C	CSM	OH	OHSM	SEM	OH	SM	C	CSM	WB	WBSM	SEM	OH	SM
n	(6)	(6)	(6)	(6)				(6)	(5)	(6)	(6)			
Zinc[2]														
Intake	5.00	5.23**	4.74	4.47*	0.06	.01	NS	5.01	5.33**	5.69	5.41**	0.01	.01	NS
Feces	3.58	3.49 †	3.84	3.71	0.17	NS	NS	3.93	3.86	4.47	4.48	0.15	.01	NS
Urine	0.070	0.100†	0.100	0.070	0.010	NS	NS	0.071	0.055	0.061	0.067	0.013	NS	NS
Absorbed	1.42	1.74	0.90	0.76	0.14	.01	NS	1.08	1.45	1.21	0.93	0.15	NS	NS
Retained	1.34	1.64	0.80	0.68	0.15	.01	NS	1.00	1.39	1.15	0.86	0.16	NS	NS
Absorbed, %[3]	28.4	33.2	19.0	17.0	3.1	.01	NS	21.6	27.2	21.4	17.2	2.8	.09	NS
Copper[2]														
Intake	0.58	0.55**	0.78	0.79	0.01	.01	NS	0.58	0.56†	0.80	0.79	0.01	.01	NS
Feces	0.32	0.36	0.54	0.52	0.02	.01	NS	0.32	0.35†	0.48	0.48	0.01	.01	NS
Urine	0.008	0.011	0.013	0.009	0.002	NS	NS	0.009	0.008	0.009	0.008	0.002	NS	NS
Absorbed	0.26	0.19*	0.24	0.27	0.02	NS	NS	0.26	0.21**	0.32	0.31	0.01	.01	.01
Retained	0.25	0.18*	0.22	0.26	0.02	NS	NS	0.25	0.20**	0.31	0.30	0.01	.01	.02
Absorbed, %[3]	44.3	35.4*	30.8	34.6	2.8	.03	NS	44.6	37.9**	39.9	39.0	1.5	NS	.02
Manganese[2]														
Intake	0.96	0.93	1.33	1.27**	0.02	.01	NS	0.96	0.95	3.52	3.38	0.01	.01	NS
Feces	1.14	1.06 †	1.23	1.29	0.05	.01	NS	1.05	1.16	3.36	3.43	0.08	.01	NS
Urine	0.011	0.024†	0.022	0.016	0.005	NS	NS	0.013	0.019	0.030	0.034	0.007	.05	NS
Absorbed	-0.18	-0.12	0.10	-0.02†	0.05	.01	NS	-0.09	-0.21	0.16	-0.05†	0.08	.02	.05
Retained	-0.19	-0.14	0.08	-0.04†	0.04	.01	NS	-0.10	-0.23	0.13	-0.09	0.08	.05	.06

[1]Symbols represent significant least-squares differences between diets with salinomycin compared with the appropriate diets without salinomycin (†P<.10; *P<.05; **P<.01).

[2]Values for intake, feces, urine, absorbed and retained as mg element/(kg$^{.75}$ bodyweight·d).

[3]Expressed as percentage of intake.

fed the C or OH diets in the OH trials (table 5). However, SM decreased apparent Mn absorption ($P<.05$) and retention ($P<.06$) of pigs during the WB trials.

Discussion

The present experiments indicate that the inclusion of OH in the diet of growing pigs may impair mineral absorption, most notably that of Ca and Zn, whereas the inclusion of WB in the diet at a level supplying comparable amounts of neutral-detergent fiber is without great effect. The mechanism by which dietary fiber interferes with mineral absorption is not known, however the NDF fraction of OH and WB is able to bind minerals in vitro (Thompson and Weber, 1979, 1981a). Additionally, in vitro binding capacity of different fiber sources can be altered by the action of digestive enzymes (Thompson and Weber, 1981a).

The OH used in our study were more resistent to degradation (4.9% dry matter digestibility) than was the WB (61.3% dry matter digestibility), and subsequently pigs fed the OH diets excreted more ADF, NDF and cellulose in the feces than did pigs fed the C or WB diets (Moore et al., 1986). Indirectly this would suggest that the OH contributed a greater number of potential mineral binding sites to the digesta, thereby making it

more effective in removing minerals from an absorbable pool. The non-degradable character of OH could depress mineral balance two ways: 1) reduced release by microbial fermentation of minerals bound to the fiber matrix, or 2) reduced availability of minerals present as a constituent of the OH.

Van der Aar et al. (1983) have suggested that the interaction of different minerals with various fiber sources occurs by independent mechanisms and is related to fiber particle size, fiber level in the diet, and the physical and chemical properties of the fiber source. These factors, along with differences in susceptibility of different fiber sources to degradation, may partially explain why fiber sources fed to animals to supply equal amounts of NDF differ in their ability to reduce mineral absorption (present study and Thompson and Weber, 1981b). Although the relative importance of fiber and phytate in depressing mineral absorption remains controversial (Reinhold et al., 1975; Davies et al., 1977), it is unlikely that phytate is a factor in the depression of Ca and Zn absorption caused by OH since the amount of phytate contributed to the diet by OH would be negligible, even if all of the P present in OH (0.10%) had represented phytate-P.

Previous studies with swine have reported that comparable levels of fiber as used in the present experiment from WB (Newton et al., 1983), but not OH (Ravindran et al., 1984), decrease the fractional absorption of minerals. However, these studies used dietary levels of minerals considerably above the current recommended levels (NRC, 1979) and any deterimental effect of fiber on mineral balance may have been masked by the high mineral intakes or the insensitivity of the balance technique at mineral intakes in excess of metabolic demand (Kirchgessner and Weigand, 1983). It is relevant to note, that as in the present study for Cu, Mn, K and Mg, others have noted that high fiber diets increase mineral intakes which result in increased fecal mineral losses and a decrease in fractional absorption, but no change or an increase in mineral balance (Sandberg et al., 1982; Bagheri and Gueguen, 1982; Van Dokkum et al., 1982). Together, these observations indicate a need for further study in order to clarify the physiological relevance of fiber-induced changes in mineral balance under conditions of varying fiber and mineral intakes.

Salinomycin appears to alter the composition or metabolism of the intestinal microflora in pigs (De Wilde, 1984; Moore et al., 1986). Although studies indicate that mineral utilization is different between

germ-free and conventional laboratory animals (Cecil-Smith et al., 1972; Reddy et al., 1972), it is not clear whether the depression in Cu absorption by pigs fed the C diets with SM in the present study is due to a direct effect of SM on the ability of the intestine to transport Cu or an indirect effect on microbial utilization of Cu.

In contrast to the response it exerted on Cu absorption, SM increased apparent and fractional P absorption by pigs fed the diets containing wheat bran. But because SM also increased urine P output, net P balance was not improved. The ability of the pig to hydrolyze phytate is dependent on the microflora since the pig has low levels of intestinal phytase (Moser et al., 1982). Moore et al. (1984) reported that the antimicrobial compound sulfaguanidine enhanced phytate degradation by the rat, which they attributed to a shift in the composition or metabolism of the intestinal microflora which enabled increased phytate hydrolysis. Yoshida et al. (1982) found that under conditions which promoted increased phytate hydrolysis by mice, urine P output increased also. These observations suggest that the effect of SM on P utilization by pigs fed the WB diets may be due to an enhancement of phytate degradation.

In summary, our observations indicate that both fiber sources, as well as salinomycin, possess characteristics which are able to influence mineral absorption and balance. The relatively greater ability of oat hulls to influence Ca and Zn balance indicates that differences in the chemical and physical properties of fiber sources and their relative susceptibility to degradation in the gastrointestinal tract may be involved in the extent to which a fiber alters mineral balance. Further studies are needed on the effect of different fiber sources on mineral balance, as well as the significance of these effects under conditions of varying metabolic demand and mineral intake.

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CHAPTER V

EFFECT OF DIETARY MINERAL LEVEL AND DURATION OF FEEDING ON NUTRIENT UTILIZATION BY GROWING PIGS FED HIGH-FIBER DIETS

Summary

Four balance trials (48 female pigs, mean bodyweight 50.1 kg) were conducted to determine the effect of diet mineral level and duration of feeding on nutrient utilization by pigs fed high-fiber diets. In experiment 1 (2 trials) pigs were fed a corn-soybean meal basal diet (B), a 15% oat hulls diet (OH) or a 15% soybean hulls diet (SH), each with or without mineral supplements (per kg diet: 50 mg Fe and Zn, 3 mg Cu, 2 mg Mn, 0.4 g Mg and 0.51 g Na). Balance trials were conducted after pigs had been fed the diets for 5 d or 26 d. In experiment 2 (2 trials) dietary treatments were the same as in experiment 1, except Ca and P levels were increased by 50%. OH and SH decreased energy digestibility coefficients ($P<.01$) and apparent N absorption ($P<.01$), but not N retention, with the effect of OH greater than the effect of SH. Apparent N absorption did not change over time ($P>.10$), but energy digestibility was greater at 26 d for pigs fed the B ($P<.08$) and SH ($P<.05$) diets. SH increased Fe balance ($P<.01$) compared with pigs fed the B or OH diets. Fe balance was greater at 26 d, but only for pigs fed the

SH diets (P<.01). Fiber source did not affect Zn balance (P>.10), but Zn balance was lower at 26 d for pigs fed the OH diet (P<.05). SH increased Mg absorption (P<.01), but not Mg balance compared with pigs fed the B or OH diets. Mg balance was higher at 26 d (P<.01), which was due to lower urine Mg excretion by pigs fed the OH (P<.05) and SH (P<.01) diets, but greater Mg absorption (P<.05) by pigs fed the B diet. Fiber source did not effect Na balance (P>.10), but OH decreased (P<.01) K balance. The addition of minerals to the diet increased Zn and Na balance (P<.01), but Fe balance was increased by mineral supplementation only in pigs fed the B (P<.05) or SH diets (P<.01). There were no effects of fiber source or duration of feeding on Ca or P balance at either level of Ca or P intake (P>.10). Dietary fiber supplied as OH or SH did not have a major negative impact on mineral utilization by growing pigs. However, the results suggest that fiber sources such as SH may be sources of available Fe and Mg, and may enhance mineral availability from cereal grain-oilseed meal diets.

Introduction

Evidence indicates that high levels of dietary fiber interfere with mineral utilization in humans and animals (Kelsay, 1981; Ali et al., 1981). Recent reports indicate that the addition of high-fiber feedstuffs to

conventional cereal grain-oilseed meal diets may impair mineral utilization in pigs.

Reports indicate that cellulose (Partridge, 1978), pectin (Bagheri and Gueguen, 1983), wheat bran (Newton et al., 1983), peanut hulls (Lindemann et al., 1986) and oat hulls (Moore et al., 1986a) depress Ca and Zn absorption in growing pigs. However, studies in rats and human subjects indicate that there is no effect of duration of feeding on the ability of dietary fiber to depress mineral utilization (Bagheri and Gueguen, 1982; Van Dokkum et al., 1982). Conversely, Newton et al. (1983) showed that 20% wheat bran increased fractional Fe absorption but decreased Zn absorption in pigs fed the diets for 80 days; however bran did not affect apparent mineral absorption in the same pigs after consumption of the diets for only 14 days.

Moore et al. (1986a) reported that 10% oat hulls decreased Zn and Ca balance in growing pigs fed the diets for a 7-d period, but Ravindran et al. (1984) and Moser et al. (1982) were unable to demonstrate an effect on fractional mineral absorption or mineral balance of comparable amounts of oat hulls. The diets used by Ravindran et al. (1984) contained higher dietary mineral levels than the diets used by Moore et al. (1986a), which suggests that higher mineral intakes may overcome the

ability of high fiber intakes to decrease mineral balance.

The objective of the work reported here was to determine the effect of diet mineral level and duration of feeding on mineral balance of pigs fed high-fiber diets. Two fiber sources which differ in their susceptibility to degradation within the gastrointestinal tract (oat hulls and soybean hulls) were used to formulate the high-fiber diets.

Materials and Methods

Diets.

Experiment 1. The six dietary treatments were a corn-soybean meal basal diet (B), a 15% oat hulls diet (OH; LaCrosse Milling Co., Cochrane, WI) and a 15% soybean hulls diet (SH; A. E. Staley Manufacturing Co., Decator, IN), each with or without supplemental minerals (table 1). Each fiber source was added to the diet at a level calculated to supply 8 percentage units neutral-detergent fiber (NDF) above the level of NDF present in the B diet. The mineral supplemented diets received a premix which supplied (per kg diet): 50 mg Fe, 50 mg Zn, 3 mg Cu, 2 mg Mn, 0.4 g Mg and 0.51 g Na.

Experiment 2. The diets used in experiment 2 were similar to the diets used in experiment 1, except dietary

Table 1. Ingredient and nutrient composition of diets (as-is)[1,2]

Ingredient	Diet Fiber Source		
	Basal	Oat hulls	Soybean hulls
	(%)	(%)	(%)
Ground corn	80.96	68.60	70.15
48% soybean meal	16.75	13.92	12.65
Oat hulls	---	15.00	---
Soybean hulls	---	---	15.00
Dicalcium phosphate	0.746	0.897	0.930
Ground limestone	0.863	0.753	0.591
Zinc premix[3]	0.30	0.45	0.30
Iodized salt	0.23	0.23	0.23
Vitamin-Se premix[4]	0.15	0.15	0.15
Nutrient analyses (without/with mineral supplements)			
Dry matter, %	91.5/91.7	92.1/91.8	91.7/91.5
Neutral-detergent fiber, %	9.5/ 9.2	16.3/16.7	17.4/17.2
Acid-detergent fiber, %	3.4/ 3.4	7.7/ 7.8	9.9/ 9.9
Cellulose, %	2.7/ 2.6	5.7/ 5.8	8.3/ 8.3
Hemicellulose, %	6.1/ 5.7	8.7/ 8.9	7.5/ 7.4
Lignin, %	.85/.92	1.54/1.64	1.96/1.81
Nitrogen, %[5]	2.34/2.34	2.18/2.15	2.18/2.16
Calcium, %[6]	.471/.516	.539/.534	.512/.528
Phosphorus, %	.478/.489	.492/.498	.473/.480
Magnesium, %	.119/.144	.113/.144	.117/.150
Sodium, %	.102/.148	.109/.143	.101/.151
Potassium, %	.579/.584	.558/.559	.654/.652
Zinc, mg/kg	54.7/106.8	65.4/112.5	59.0/110.4
Iron, mg/kg	61.9/113.1	84.9/131.1	120.9/170.3
Copper, mg/kg	4.8/7.9	5.0/8.1	4.9/8.2
Manganese, mg/kg	13.8/15.9	20.7/21.3	13.6/16.7

[1]The mineral supplemented diets received a premix (0.12%) which provided per kg of diet: 3 mg Cu as $CuSO_4$, 50 mg Fe as $FeSO_4$, 50 mg Zn as $ZnSO_4$, 2 mg Mn as $MnSO_4$, 0.4 g Mg as (1:1:1) $MgO:MgCO_3:MgSO_4$. Sodium (0.51 g/kg) was supplied as NaCl (1.27 g/kg) at the expense of corn.

Table 1, continued

[2]Dietary Ca and P were increased to 50% above the recommended requirement (NRC, 1979) in experiment 2 by the addition of ground limestone (0.02%) and dicalcium phosphate (1.216%) to the amounts already present in the diets (at the expense of corn).

[3]Zinc premix provided (elemental Zn per kg diet as $ZnSO_4$): basal, 20 mg, oat hulls, 30 mg, and soybean hulls, 20 mg.

[4]Vitamin-Se premix provided per kg of diet: 2.6 mg riboflavin, 13.2 mg niacin, 13.2 mg pantothenic acid, 13.2 µg B_{12}, 264 mg choline chloride, 2640 IU vitamin A, 264 IU vitamin D, 6.6 IU vitamin E, 660 µg vitamin K (as menadione sodium bisulfite complex), and 0.06 mg Se.

[5]In experiment 2, diet Ca levels were (%): basal, 0.775, oat hulls, 0.775, and soybean hulls, 0.795.

[6]In experiment 2, diet P levels were (%): basal, 0.690, oat hulls, 0.705, and soybean hulls, 0.702.

Table 2. Nutrient composition of fiber sources (as-is basis)[1]

Criteria	Oat hulls	Soybean hulls
Dry matter, %	93.0(93.1)	92.8(93.0)
Neutral-detergent fiber, %	55.1(63.2)	61.4(60.1)
Acid-detergent fiber, %	31.7(36.0)	47.0(48.4)
Cellulose, %	22.3(25.5)	40.5(40.6)
Hemicellulose, %	23.4(27.2)	14.4(11.7)
Lignin, %	6.1(7.8)	6.4(8.2)
Nitrogen, %	1.14(0.94)	1.50(1.60)
Calcium, %	0.249(0.098)	0.627(0.554)
Phosphorus, %	0.226(0.198)	0.126(0.126)
Magnesium, %	0.224(0.094)	0.270(0.220)
Sodium, %	0.030(0.016)	0.010(0.013)
Potassium, %	0.701(0.467)	1.381(1.063)
Zinc, mg/kg	41.7(29.6)	47.0(86.3)
Iron, mg/kg	289.3(72.3)	473.5(444.2)
Copper, mg/kg	4.1(6.8)	6.8(8.9)
Manganese, mg/kg	67.9(41.4)	14.5(32.8)

[1]Analyzed composition for oat hulls and soybean hulls fed in trials 1, 2 and 3. Values in parentheses are for fiber sources fed in trial 4.

Ca and P were increased to levels calculated to be 50% greater than the NRC (1979) requirements (table 1). The analyzed nutrient contents of the diets and fiber sources are given in tables 1 and 2, respectively. Complete diet nutrient contents are given in appendix table 1.

Animals and trial protocols.

In each trial, 12 crossbred female pigs were used (2 pigs/treatment in each trial). Following a 4- or 5-d adaptation period to the stainless steel metabolism cages and diets, a 5-d feces and urine collection period was conducted (time 1). A second 5-d balance period (time 2) was conducted after pigs had been fed the diets for 24 or 25 d (experiment 1) or 28 d (experiment 2). Initial bodyweights of the pigs used in trials 1 through 4, respectively, were: 45.4 $\pm$.4 kg, 68.7 $\pm$.5 kg, 45.9 $\pm$ .4 kg, and 40.5 $\pm$ .4 kg. Weight gains of animals were similar in all trials (appendix table 2).

Pigs were fed twice daily (0600 and 1800 h) equal portions of dry feed in meal form to give daily intakes equal to 9.99% of metabolic bodyweight (kg $^{.75}$). Actual intakes varied from 9.47% to 9.99%. One pig fed the B diet (without supplemental minerals) did not complete trial 2 (removed after completion of time 1 collection).

Feces and urine collection periods began at first fecal appearance of a marker (.5% chromic oxide

administered in the 0600 h feed), and terminated at first fecal appearance of a second marker dose administered in the 0600 h feed on day 6 of the collection period. Feces were collected at 3-h intervals on d 1 to 2, 4-h intervals on d 2 to 3, and at 6-h intervals thereafter. No collections were made between 1800 h (1600 h for 4 h collections) and 0600 h.

The feces were collected and weighed (wet weight) and dried for 20 h (60 C) in a forced-air oven and re-weighed. Individual samples were ground in a cyclone-type sample mill (Cyclotec 1093, Tecator, Inc., Hoganas, Sweden) equipped with a 1 mm screen, and combined for each pig over the entire collection period. Urine was collected in plastic containers and acidified with 6 N HCl to maintain pH < 3.

Chemical analyses.

Dry matter contents of feed and fecal samples were determined by drying 18 h at 105 C. Neutral-detergent fiber contents of feed and feces were determined by the modified amylase method of Robertson and Van Soest (1977). Acid-detergent fiber (ADF), cellulose and permanganate-lignin contents were determined by the methods of Goering and Van Soest (1970). Hemicellulose was calculated as the difference between NDF and ADF contents. Nitrogen contents of all samples were

determined by the micro-kjeldahl method, and gross energy contents of feeds and feces were determined by bomb calorimetry.

Feed and fecal samples were prepared for mineral analysis by charring at 350 C (36 h), followed by wet digestion with nitric acid/hydrogen peroxide. Calcium, Fe, Zn, Mn, Cu, and Mg contents were determined on fecal digests and urine samples by atomic absorption spectrophotometry (Model 403 atomic absorption spectrophotometer, Perkin-Elmer Corp., Norwalk, CT), and Na and K contents were determined by flame emission spectroscopy using the same instrument. Phosphorus was determined by the colorimetric method of Fiske and Subbarow (1925).

Statistical methods

The data were analyzed with the general linear models procedure of SAS (1982), using a model which contained the class effects of fiber source, mineral level, duration of feeding (time), trial and all two-way interactions. Three-way interactions were not significant ($P>.10$) in a preliminary analysis and were removed from the model. Class effects and interactions which involved duration of feeding (time) were tested using the mean square of Pig (fiber source x mineral level x trial), while all other tests used the residual error mean

square. Least-squares means were generated using this model. Least-squares differences were used to compare individual class or treatment means. Tabular data corresponding to absolute amounts (i.e. intake, absorbed, retained, etc.) are expressed as the amount per $kg^{.75}$ bodyweight/d, using the bodyweight obtained at the beginning of each collection period.

Results

Nitrogen and energy utilization.

Nitrogen intake was greater for pigs fed the B diet than for pigs fed the OH or SH diets (table 3; $P<.01$). Compared to pigs fed the B diets, both fiber sources decreased apparent N absorption ($P<.01$) but neither fiber source affected apparent N retention ($P>.10$). Apparent N digestibility was decreased by OH and SH ($P<.01$), but apparent biological value (ABV; N retained/N absorbed) was increased by both OH ($P<.05$) and SH ($P<.01$) because both fiber sources decreased urine N excretion ($P<.01$). Compared with pigs fed the OH diets, pigs fed the SH diets excreted more N in the feces ($P<.01$) and less N in the urine ($P<.05$), and apparent N absorption (but not retention) was less for pigs fed the SH diets ($P<.01$).

Both fiber sources decreased apparent energy absorption and the coefficient for digestible energy

Table 3. Effect of dietary fiber source and duration of feeding on nitrogen and energy utilization and rate of passage in growing pigs

Criteria	Fiber Source[3]			SEM	Fiber P-value	Basal[4]		Oat hulls[4]		Soybean hulls[4]		Time	
	B	OH	SH			1	2	1	2	1	2	SEM	P-value
Nitrogen[1]													
Intake	2.30	2.15	2.16[a]	0.01	.01	2.28	2.32*	2.12	2.18*	2.15	2.18**	0.02	.01
Feces	0.31	0.37	0.42[b]	0.01	.01	0.32	0.31	0.37	0.37	0.44	0.41**	0.01	.05
Urine	0.87	0.70	0.63[c]	0.03	.01	0.84	0.89*	0.73	0.68**	0.63	0.63**	0.04	NS
Absorbed	1.98	1.77	1.74[b]	0.01	.01	1.96	2.01*	1.75	1.80**	1.70	1.77**	0.01	.01
Retained	1.12	1.07	1.11[b]	0.03	NS	1.11	1.12	1.02	1.12*	1.08	1.14**	0.04	.09
Digestibility, %	86.4	82.6	80.3[b]	0.3	.01	86.0	86.7	82.4	82.8	79.4	81.3**	0.4	.01
Retained/Absorbed,%	55.9	60.4	63.8[d]	1.4	.01	56.6	55.2	58.3	62.4	63.1	64.5	2.0	NS
Energy[2]													
Intake	392.7	393.6	390.5[b]	2.0	NS	388.4	397.1*	388.5	398.8**	387.8	393.1	2.9	.01
Feces	47.4	81.2	58.3[b]	0.8	.01	48.2	46.6*	80.4	82.0*	59.4	57.3*	1.1	NS
Absorbed	345.4	312.4	332.2[b]	1.9	.01	340.2	350.5†	308.0	316.7*	328.4	335.9*	2.8	.01
Absorbed, %	87.9	79.3	85.1[b]	0.2	.01	87.6	88.3†	79.3	79.4	84.7	85.5*	0.3	.03
Rate of passage hours	27.4	22.8	26.0[b]		.06	25.1	29.8*	21.4	24.1	27.9	34.8**	1.2	.01

[1] Values for intake, feces, urine, absorbed and retained expressed as g N/(kg$^{.75}$ bodyweight · d).

[2] Values for intake, feces and absorbed expressed as kcal/(kg$^{.75}$ bodyweight · d).

[3] Letters denote significant differences for comparisons between fiber sources:
[a] B vs OH and SH P<.01.
[b] All comparisons P<.01.
[c] B vs OH and SH P<.01, OH vs SH P<.05.
[d] B vs OH P<.05, B vs SH P<.01, OH vs SH P<.09.

[4] Symbols denote significant differences between time periods within fiber source: †P<.10, *P<.05, **P<.01.

(table 3; P<.01). Oat hulls had a greater impact on apparent energy utilization than did SH (P<.01).

Apparent N digestibility was greater at time 2 than at time 1 (P<.01), although this response was restricted to pigs fed the SH diets (P<.01). Although apparent N absorption was greater at time 2 than at time 1 for pigs fed the B (P<.05) and OH and SH (P<.01) diets, this reflects a greater N intake at time 2 by the pigs fed the B (P<.07) and OH (P<.05) diets. There was a trend (P<.09) for N retention to be higher at time 2 than at time 1, but N retention was greater at time 2 only for pigs fed the OH diets (P<.05).

Apparent energy absorption was greater at time 2 for pigs fed the B, OH, and SH (P<.05) diets. The coefficient for digestible energy was higher at time 2 than at time 1 (P<.03), but this response was restricted to pigs fed the B (P<.10) and SH (P<.05) diets.

The elapsed time to first appearance of marker in the feces was shorter for pigs fed the OH diets than for pigs fed the B or SH (P<.01) diets at both time periods (table 3). Rate of passage was slower in pigs fed the SH diets than in pigs fed the B diets only at time 2 (P<.01). Rate of passage was slower at time 2 than at time 1 (P<.01) although the effect of duration of feeding was only significant for pigs fed the B (P<.05) and SH (P<.01) diets.

Dry matter and fiber component digestibility.

Oat hulls decreased the digestion coefficients for DM and all fiber components measured (table 4; P<.01). Soyhulls decreased DM digestibility (P<.01), but increased apparent digestibility of all fiber components (P<.01) except lignin. The amounts of each fiber component digested were similar for pigs fed the B and OH diets (P>.10), but the amounts were greater for pigs fed the SH diets (P<.01). Fecal excretion of each fiber component was greater by pigs fed either fiber source (P<.01; except hemicellulose excretion by pigs fed the SH diets, P>.10) compared with pigs fed the B diet.

Total fecal output (wet basis) and fecal water output were greater for pigs fed either high fiber diet (table 4; P<.01) than pigs fed the B diets. Fecal water percentage was higher for pigs fed the SH diets (P<.01) compared with pigs fed the B or OH diets. Fecal wet weight output and fecal water output were greater for pigs fed the SH diets than for pigs fed the OH diets (P<.01).

There was no effect of duration of feeding on DM or fiber component digestibility by pigs fed the B, OH or SH diets (P>.10). Cellulose digestibility was slightly greater (P<.07) at time 2 (77.6%) than at time 1 (73.8%) for pigs fed the SH diets. Duration of feeding did not

Table 4. Effect of dietary oat hulls or soybean hulls on diet dry matter and fiber component utilization and fecal water output by growing pigs

Criteria[1]	Diet Fiber Source[2] B	OH	SH	SEM	Fiber P-value
Dry matter					
Intake	89.8	90.5	90.2[a]	0.5	NS
Feces	10.4	18.2	12.5[a]	0.2	.01
Digested	79.5	72.3	77.7[a]	0.4	.01
Digestibility, %	88.5	79.9	86.1	0.2	.01
Neutral-detergent fiber					
Intake	9.32	16.27	17.35[a]	0.07	.01
Feces	4.00	10.84	5.25[a]	0.12	.01
Digested	5.32	5.45	12.10[b]	0.13	.01
Digestibility, %	57.1	33.4	69.7[a]	0.8	.01
Acid-detergent fiber					
Intake	3.42	7.60	9.85[a]	0.03	.01
Feces	1.31	5.30	2.54[a]	0.07	.01
Digested	2.12	2.31	7.31[b]	0.08	.01
Digestibility, %	61.7	30.3	74.2[a]	0.9	.01
Cellulose					
Intake	2.64	5.61	8.19[a]	0.03	.01
Feces	1.03	3.85	1.99[a]	0.07	.01
Digested	1.61	1.76	6.20[b]	0.07	.01
Digestibility, %	60.9	31.5	75.7[a]	1.0	.01
Hemicellulose					
Intake	5.89	8.71	7.54[a]	0.04	.01
Feces	2.69	5.57	2.72[c]	0.06	.01
Digested	3.20	3.15	4.82[b]	0.06	.01
Digestibility, %	54.3	36.2	63.7[a]	0.7	.01
Lignin					
Intake	0.91	1.59	1.86[a]	0.01	.01
Feces	0.23	0.96	0.46[a]	0.01	.01
Digested	0.68	0.63	1.40[d]	0.01	.01
Digestibility, %	74.5	38.4	74.9[c]	0.9	.01
Fecal water excretion					
Total wet feces	30.4	54.5	42.4[a]	0.9	.01
Fecal water	20.0	36.3	29.8[a]	0.8	.01
Fecal water, %	65.1	66.3	69.9[b]	0.6	.01

[1]Values for intake, feces, digested, total wet feces, and fecal water expressed as $g/(kg \cdot ^{.75}$ bodyweight $\cdot$ d).

[2]Letters denote significant least-squares differences between fiber sources:

[a]All comparisons $P<.01$.

[b]B vs SH, OH vs SH $P<.01$.

[c]B vs OH, OH vs SH $P<.01$.

[d]B vs SH, OH vs SH $P<.01$; B vs OH $P<.02$.

influence wet feces output, fecal water output or fecal water percentage (P>.10).

The apparent digestibilities of DM and fiber components of each fiber source were estimated by difference, assuming that the digestibility of each component contributed by the basal ingredients (corn and soybean meal) was similar in the B and high-fiber diets. Estimated digestion coefficients for OH were: DM, 31.0%. NDF, 10.8%, ADF, 12.2%, cellulose, 12.5%, hemicellulose, 9.8%, and lignin, 16.9%. Estimated digestion coefficients for SH were: DM, 73.2%, NDF, 80.8%, ADF, 78.9%, cellulose, 80.6%, hemicellulose, 88.6%, and lignin, 75.8%.

Mineral utilization.

Although the amounts of Ca and P absorbed and retained were different in experiments 1 and 2 (reflecting the different diet levels), the apparent absorption and retention of Ca and P were not affected by fiber source, duration of feeding or level of mineral supplementation (P>.10), and the results for both experiments were combined. The intake, absorption and retention of Ca for pigs fed the B, OH and SH diets, respectively, were (mg/(kg $^{.75}$ bodyweight $\cdot$ d)): intake, 634, 648 and 650; absorbed, 302, 307 and 306; and retained, 288, 297 and 297. Intake, absorption and

retention of P for the three diets, respectively, were: intake, 578, 593 and 584; absorbed, 274, 289 and 287; and retained, 240, 240 and 243. Complete data are given in appendix tables 3 and 4.

Apparent Cu utilization was not influenced by fiber source or duration of feeding (P>.10). For pigs fed the B, OH and SH diets, Cu intake and retention were (mg/(kg $^{.75}$ bodyweight·d)): intake, .60, .61 and .62, and retention, .06, .06 and .07. Oat hulls increased Mn intake and balance (2.09 and .28, respectively; P<.01) compared to pigs fed the B (1.46 and .18) or SH diets (1.45 and .16). Although the effect of time was significant (P<.03) for Mn balance, only OH decreased Mn balance at time 2 (from .34 to .23; P<.04), although Mn balance was greater at time 2 for pigs fed the OH diets than for pigs fed the SH diets (P<.04). Mineral supplementation did not affect Mn utilization (P>.10). Copper supplementation increased Cu balance of pigs fed the B and OH (P<.05) and SH (P<.01) diets, but balance was not different between pigs fed the B, OH or SH diets (P>.10). Complete tabular data for Mn and Cu utilization are given in appendix tables 5 and 6.

Apparent Zn absorption and retention were not affected by fiber source (table 5; P>.10), although Zn intake and fecal Zn output were greater for pigs fed the

Table 5. Effect of dietary fiber source and duration of feeding on Zn, Fe and Mg utilization by growing pigs

Fiber	Basal		Oat hulls		Soybean hulls			P-values		
Criteria[1,2] Time	1	2	1	2	1	2	SEM	F[3]	T	FxT
Zinc										
Intake	7.98	7.94	8.82	8.88*	8.18	8.12	0.07	.01[a]	NS	NS
Feces	6.33	6.27	6.97	7.58†	6.41	6.29	0.19	.01[b]	NS	NS
Urine	0.087	0.114	0.127	0.091*	0.105	0.107	0.013	NS	NS	NS
Absorbed	1.65	1.67	1.85	1.30*	1.77	1.82	0.17	NS	NS	NS
Retained	1.56	1.55	1.72	1.20	1.66	1.72	0.17	NS	NS	NS
Absorbed, %	20.9	20.2	21.2	15.4†	20.3	21.7	2.1	NS	NS	NS
Iron										
Intake	8.42	8.38	10.59	10.64	14.25	14.15**	0.08	.01[c]	NS	NS
Feces	7.32	6.45*	8.94	9.31	11.84	9.18	0.60	.01[d]	.05	.06
Urine	0.062	0.110*	0.110	0.072†	0.124	0.119**	0.016	NS[e]	NS	.05
Absorbed	1.10	1.93	1.65	1.34	2.42	4.97**	0.57	.01[f]	.04	.06
Retained	1.04	1.82	1.54	1.26	2.29	4.86**	0.57	.01[f]	.04	.06
Absorbed, %	10.9	19.0	14.5	12.8	15.9	34.9	4.8	.02[g]	.04	NS
Magnesium										
Intake	130.0	129.5*	127.0	127.7	135.3	134.4	1.0	.01[h]	NS	NS
Feces	101.3	93.1*	96.1	95.5*	95.2	90.8**	2.2	NS[i]	.03	NS
Urine	22.0	14.1*	28.5	14.1*	36.2	19.7**	4.9	NS[j]	.01	NS
Absorbed	28.7	36.4*	31.0	32.1*	40.1	43.5**	2.2	.01[f]	.03	NS
Retained	6.7	22.3*	2.5	18.0*	4.0	23.8**	5.0	NS[f]	.01	NS
Absorbed, %	22.1	28.2	24.4	25.3	29.6	32.2	1.6	.02[f]	.02	NS

[1] Values for intake, feces, urine, absorbed and retained expressed as mg/(kg$^{.75}$ bodyweight · d).

[2] Symbols denote significant differences between time periods within fiber source: †P<.10, *P<.05, **P<.01.

[3] Letters denote significant differences between fiber sources:

[a] B vs OH, OH vs SH P<.01; B vs SH P<.02.

[b] B vs OH, B vs SH P<.01.

[c] All comparisons P<.01.

[d] B vs OH, B vs SH P<.01; OH vs SH P<.03.

[e] B vs SH P<.04; OH vs SH P<.07.

[f] B vs SH, OH vs SH P<.01.

[g] B vs SH P<.04; OH vs SH P<.02.

[h] B vs OH P<.02; B vs SH, OH vs SH P<.01.

[i] B vs SH P<.08.

[j] B vs SH P<.05.

Table 6. Effect of dietary fiber source and mineral level on Zn, Fe and Mg utilization by growing pigs

Fiber	Basal		Oat hulls		Soybean hulls			P-values		
Criteria[1,2] Mineral	-	+	-	+	-	+	SEM	F	M	FxM
Zinc										
Intake	5.38	10.54**	6.39	11.31**	5.71	10.59**	0.07	.01	.01	NS
Feces	4.27	8.32**	5.13	9.42**	4.51	8.19**	0.19	.01	.01	NS
Urine	0.080	0.121**	0.081	0.137**	0.090	0.122†	0.013	NS	.01	NS
Absorbed	1.10	2.21**	1.26	1.89**	1.20	2.40**	0.17	NS	.01	NS
Retained	1.02	2.09**	1.17	1.75*	1.11	2.27**	0.17	NS	.01	.09
Absorbed, %	20.1	21.0	19.7	16.8	19.8	22.2	2.1	NS	NS	NS
Iron										
Intake	5.91	10.88**	8.22	13.02**	11.90	16.50**	0.08	.01	.01	NS
Feces	5.28	8.49**	7.27	10.97**	9.76	11.25†	0.60	.01	.01	NS
Urine	0.083	0.089	0.067	0.116*	0.118	0.125	0.016	NS	NS	NS
Absorbed	0.64	2.39*	0.94	2.04	2.14	5.25**	0.57	.01	.01	NS
Retained	0.55	2.30*	0.88	1.93	2.03	5.12**	0.57	.01	.01	NS
Absorbed, %	8.2	21.8†	11.4	16.0	18.0	32.8*	4.7	.02	.01	NS
Magnesium										
Intake	119.2	140.3**	114.0	140.7**	123.0	146.7**	1.0	.01	.01	.09
Feces	89.8	104.5**	86.1	105.4**	86.0	100.0**	2.2	NS	.01	NS
Urine	14.7	21.5	19.2	23.4	33.4	22.5	4.9	NS	NS	NS
Absorbed	29.4	35.8†	27.9	35.2*	37.0	46.7**	2.2	.01	.01	NS
Retained	14.7	14.3	8.6	11.8	3.6	24.2**	5.0	NS	.10	NS
Absorbed, %	24.8	25.6	24.5	25.2	29.9	31.9	1.6	.02	NS	NS

[1]Values for intake, feces, urine, absorbed and retained expressed as mg/(kg$^{.75}$ bodyweight · d).

[2]Symbols denote significant differences between mineral level within fiber source: †P<.10, *P<.05, **P<.01.

OH diets (P<.01) compared with pigs fed the B or SH diets. Apparent Zn absorption and retention were lower at time 2 than at time 1 for pigs fed the OH diets (P<.05), but not pigs fed the B or SH diets; the effect of duration of feeding and the fiber source x time interaction were not significant (P>.10).

Oat hulls and SH increased Fe intake and fecal Fe output (table 5; P<.01) compared with pigs fed the B diet, but only SH increased apparent Fe absorption and retention (P<.01). The fiber source x time interactions were significant for Fe absorption and retention (P<.06). At time 2, apparent Fe absorption and retention were greater for pigs fed the SH diets (P<.01) compared to pigs fed the B or OH diets, but Fe balance was similar at time 1 for pigs fed the B, OH and SH diets (P>.10).

Soy hulls, but not OH, increased Mg intake (table 5; P<.01) and apparent Mg absorption (P<.01), but Mg retention was not different betweeen pigs fed the B, OH or SH diets (P>.10). At time 2, fecal (P<.03) and urine (P<.01) Mg output decreased. Apparent Mg absorption (P<.03) was greater at time 2, but the increase was significant only for pigs fed the B diet (P<.05). Apparent Mg retention was greater at time 2 for pigs fed the B and OH (P<.05) and SH (P<.01) diets.

Mineral supplementation of the diets (table 6) increased both apparent absorption and retention of Zn and Fe, but increased only apparent Mg absorption (P<.01) in pigs fed the B, OH or SH diets. Zinc supplementation increased Zn retention of pigs fed the B and SH (P<.01) and OH (P<.05) diets. However, Fe supplementation increased Fe balance in pigs fed the B (P<.05) and SH (P<.01) diets, but not in pigs fed the OH diets (P>.10).

Oat hulls increased fecal Na losses (table 7; P<.01) and decreased apparent Na absorption compared to pigs fed the B or SH diets (P<.10). However, Na balance was not greatly affected (P>.10). Overall, Na balance was lower at time 2 than at time 1 (P<.01). This resulted from an increase in fecal Na excretion by pigs fed the OH diets (P<.01), but an increase in urine Na excretion by pigs fed the B diets (P<.01), while no change occurred in pigs fed the SH diets (P>.10). Sodium balance was not different between pigs fed the B, OH or SH diets at time 1. However, at time 2, Na balance was lower for pigs fed the OH diet compared with pigs fed the SH diet (P<.03). Compared to pigs fed the B diet, OH decreased apparent K absorption (table 7; P<.01) and retention (P<.02), while SH increased K absorption (P<.01) but not retention (P>.10). There was only a slight effect of duration of feeding on K utilization (P<.07). At time 2, K balance

Table 7. Effect of dietary fiber source and duration of feeding on Na and K utilization by growing pigs

Criteria[1,2]	Fiber	Basal		Oat hulls		Soybean hulls		SEM	P-values		
	Time	1	2	1	2	1	2		F[3]	T	FxT
Sodium											
Intake		5.33	5.31	5.46	5.49**	5.37	5.34	0.04	NS[a]	NS	NS
Feces		0.87	0.88**	1.19	1.54	0.87	0.97	0.05	.01[a]	.01	.01
Urine		1.37	1.90	1.41	1.57**	1.47	1.58	0.11	NS[a]	.01	NS
Absorbed		4.47	4.42**	4.27	3.94**	4.51	4.36†	0.06	.02[b]	.01	.07
Retained		3.09	2.55	2.86	2.38**	3.03	2.79	0.12	NS	.01	NS
Absorbed, %		83.3	82.7	78.2	70.9	83.7	81.4	1.0	.01	.01	.01
Potassium											
Intake		15.04	14.98	14.42	14.49	16.81	16.71	0.11	.01[c]	NS	NS
Feces		3.28	3.33	4.28	4.28	3.99	4.16*	0.12	.01[d]	NS	NS
Urine		8.03	7.38	7.83	7.67	9.73	7.68	0.64	.04	.06	NS
Absorbed		11.76	11.62	10.14	10.21	12.82	12.54*	0.14	.01[c]	NS	NS
Retained		3.90	4.66	2.58	2.90	3.61	5.25	0.62	.01[e]	.07	NS
Absorbed, %		78.0	78.0	70.2	70.5	76.1	75.1	0.7	.01	NS	NS

[1] Values for intake, feces, urine, absorbed and retained expressed as mmol/(kg$^{.75}$ bodyweight · d).

[2] Symbols represent significant differences between time periods within fiber source: †P<.10, *P<.05, **P<.01;

[3] Letters denote significant differences between fiber sources:
[a] B vs OH, OH vs SH P<.01.
[b] OH vs SH P<.03.
[c] All comparisons P<.01.
[d] B vs OH B vs SH P<.01, OH vs SH P<.10.
[e] B vs OH P<.02, OH vs SH P<.01.

Table 8. Effect of dietary fiber source and mineral level on Na and K utilization by growing pigs

Criteria[1,2]	Fiber: Basal		Oat hulls		Soybean hulls		SEM	P-values		
	Mineral: −	+	−	+	−	+		F	M	FxM
Sodium										
Intake	4.32	6.32**	4.63	6.32**	4.27	6.44**	0.04	NS	.01	.02
Feces	0.84	0.91**	1.26	1.46**	0.74	1.10**	0.05	.01	.01	NS
Urine	1.25	2.01**	1.00	1.98**	0.99	2.06**	0.11	NS	.01	NS
Absorbed	3.49	5.40**	3.36	4.86**	3.53	5.34**	0.06	.02	.01	NS
Retained	2.23	3.43**	2.36	2.88**	2.54	3.28**	0.12	NS	.01	.07
Absorbed, %	80.6	85.4**	72.3	76.8**	82.4	82.7	1.0	.01	.06	NS
Potassium										
Intake	15.03	14.99	14.40	14.51	16.99	16.52**	0.11	.01	NS	NS
Feces	3.34	3.27†	4.30	4.26	4.42	3.73**	0.12	.01	NS	NS
Urine	6.92	8.48†	7.20	8.30	9.23	8.17	0.64	.04	NS	.01
Absorbed	11.69	11.72†	10.10	10.25	12.57	12.79	0.14	.01	NS	NS
Retained	5.03	3.53†	3.23	2.25	3.93	4.94**	0.62	.01	NS	.01
Absorbed, %	77.8	78.2	70.0	70.7	73.9	77.4**	0.7	.01	NS	NS

[1]Values for intake, feces, urine, absorbed and retained expressed as mmol/(kg$^{.75}$ bodyweight · d).

[2]Symbols represent significant differences between mineral levels within fiber source: †P<.10, **P<.01.

was lower for pigs fed the OH diets than for pigs fed the B ($P<.05$) or SH ($P<.01$) diets. Mineral supplementation increased Na balance (table 8) of pigs fed the B, OH and SH diets ($P<.01$). Sodium balance was similar for all pigs fed the low mineral diets. But Na balance was lower for pigs fed the OH diets compared with pigs fed the B ($P<.01$) or SH ($P<.03$) diets with supplemental minerals. There was no effect of mineral supplementation on K utilization ($P>.10$).

Discussion

Both OH and SH decreased apparent N absorption, but neither fiber source affected N retention. Although many high-fiber diets decrease apparent N digestibility in pigs (Rerat, 1978), this does not appear to be an obligate response of pigs to high fiber intakes. Our previous work (Moore et al., 1986b) as well as that of others (Zoiopoulos et al., 1983; Kennelly and Aherne, 1980) have shown that OH have a small effect on N utilization in pigs.

Fibrous feedstuffs susceptible to fermentation have a greater ability to decrease apparent N digestibility than do fiber sources resistant to fermentation (Bach Knudsen et al., 1982), which probably reflects the ability of fermentable fiber sources to support higher rates of bacterial protein synthesis (Farrell, 1973). The

smaller magnitude effect of OH on apparent N digestibility compared with SH indicates that OH have a lower capacity to support bacterial protein synthesis; this is supported by the lower estimated DM digestibility of OH (31%) compared with SH (73%). However, the smaller magnitude of the effect of OH on N digestibility may also reflect a smaller amount of N contributed to the diets by the OH compared with the SH. Beames and Eggum (1981) have suggested that the effect of some fiber sources on N digestibility may only reflect differences in the availability of the N present in the fiber source and in the relative amounts of N contributed to the diet by different fiber sources.

Nitrogen absorbed from the large intestine, largely as ammonia, has little metabolic value to the pig and most is excreted in the urine as urea (Just et al., 1981). The consumption of high-fiber diets decreases large intestine ammonia levels and urine N excretion (Malmlof and Hakansson, 1984; Varel et al., 1984), effects which correspond to greater rates of bacterial incorporation of N into protein by pigs fed high-fiber diets. In the present study, both fiber sources decreased urine N excretion, and although this increased the apparent biological value of the diet protein, it did not increase nitrogen balance. It would therefore appear that

OH and SH have little effect on the overall N economy of the pig.

However, our results do not rule out possible effects of these fiber sources on small intestine N absorption. The digestion of dietary fiber occurs throughout the length of the gastrointestinal tract (Millard and Chesson, 1984), and Fleming and Wasilewski (1984) have reported that addition of 6% corn bran to synthetic diets decreased ileal apparent N digestibility, but did not affect N digestibility measured at the feces. Oat hulls and SH may alter the pattern or site of N utilization in the pig, but it would not be possible to detect these effects using fecal balance trial techniques.

Both fiber sources decreased apparent energy digestibility, which agrees with previous reports which show that high-fiber diets have a lower digestible energy content (Just et al., 1983; Morgan et al., 1984). The less degradable OH had a more negative effect on D.E. than did the SH. Stanogias and Pearce (1985) also reported that increasing levels of OH added to a fiber-free basal diet had a more depressing effect on D.E. than did increasing levels of SH. The relative resistance of OH (Moore et al., 1986b; Moser et al., 1982) and susceptibility of SH (Kornegay, 1981) to digestion has

been previously reported. The difference in relative digestibility of the OH and SH resulted in the apparent digestibilities of diet fiber components being decreased by OH, but increased by SH; similar results were reported by Stanogias and Pearce (1985).

Oat hulls increased, while SH decreased, the apparent rate of passage (ROP). Overall, high-fiber diets seem to have a faster ROP compared to conventional low-fiber diets (Stanogias and Pearce, 1985), although a large amount of animal variation exists. Although the mechanisms by which fiber increases ROP are not known, it appears that physical bulk and the ability of the fiber to maintain its native matrix structure are important factors (Bardon and Fioramonti, 1983). Although water-holding capacity has been suggested to be a factor in the ability of fiber to alter ROP (Van Dokkum et al., 1983), it is unlikely to be involved in the present trial since only SH increased the percentage water in the feces. It is difficult to assign a physiological consequence to the greater ROP in pigs fed the OH diets, since ROP, but not nutrient digestibilities varied considerably between individual animals.

The duration of feeding exerted no effect on the apparent digestibilities of DM or fiber components. Other researchers have reported that there appears to be no

adaptive increase in fiber digestion after extended periods of feeding of high-fiber diets (Cunningham et al., 1962; Kennelly et al., 1981). The apparent digestibility of energy and N increased slightly over time for pigs fed the SH diets, and although this corresponded to a slower ROP at time 2, it is not clear whether these two responses are causally related. Nyman and Asp (1985) have shown that N digestibility was greater at 18 d than at 4 d in rats fed a degradable fiber source (pectin) but not in rats fed a less degradable fiber source (wheat bran). Considering the short adaptation period used in the present trial, the changes in N and energy utilization and ROP may only reflect adaptation to the change from ad libitum feeding to the restricted feed intake and feeding schedule used in the balance trials, and may not reflect a true adaptation to diet composition.

Although Fe intake was increased by both fiber sources, only SH increased Fe balance, which suggests that Fe contained in SH has a high relative bioavailability. Studies by others using rats and pigs indicate that high-fiber feedstuffs may be sources of available Fe (Frolich and Lyso, 1983; Fairweather-Tait and Wright, 1985; Lindemann et al., 1986). Additionally, Fe balance was increased by the addition of supplemental

Fe to the B and SH diets, but not the OH diets. This suggests that OH may impair Fe availability, although the significance of this effect is not apparent since Fe balance was not different between pigs fed the OH and B diets. Others have reported that fiber may impair Fe balance or decrease bone mineral levels, while growth rate or other tissue mineral contents are unaffected, indicating that available minerals may be partitioned to more critical body needs or that body reserves may be selectively depleted, thus minimizing the impact on the animal (Harmuth-Hoene, 1980; Thompson and Weber, 1981a; Van der Aar et al., 1983).

Although fiber source did not effect Zn balance overall, Zn balance was lower at 26 d than at 5 d for pigs fed the OH diet. Studies in rats and human subjects have generally been unable to demonstrate an effect of duration of feeding on mineral balance (Bagheri and Gueguen, 1982; Van Dokkum et al., 1982). However, Harmuth-Hoene and Schelenz (1980) showed that certain soluble fiber sources decreased mineral balance in rats after prolonged feeding, but the response was variable when measured at 1, 5 or 21 weeks. Similarly, Newton et al. (1983) showed that 20% wheat bran decreased fractional Zn absorption in pigs after 80 d, but not after only 14 d of feeding. In the present trials, there

was no adaptation in fiber component digestibility over time, which agrees with previous studies which indicate that the pig is unable to increase fiber digestibility after prolonged feeding of high-fiber diets (Cunningham et al., 1962; Kennelly et al., 1981). Thus, changes in digesta fiber content during the two collection periods do not appear to be a factor in the different Zn balances at times 1 and 2 for pigs fed the OH diets.

It is not clear whether the decrease in Zn balance at 26, and the failure of Fe balance to increase at 26 d in pigs fed the OH diets is due to a negative effect of OH on the absorptive capacity of the intestine, or if the OH diets may have altered mineral requirements at the second balance period. Fairweather-Tait and Wright (1985) showed that consumption of a mixed-fiber source by rats did not alter Zn or Ca availability, but did decrease intestinal Ca and Zn transport capacity after consumption of the diets for 3 d or 28 d. Studies by others indicate that dietary fiber may alter intestinal transport ability, but that the effect of fiber may only affect specific transport systems (Schwartz et al., 1982; Freeman, 1984). Alternatively, the changes in mineral absorption and balance over time could reflect an adjustment by the pig to the change from an ad-libitum to a limited feeding regimen, or the adjustment to diets

which contained a different composition compared to the diets the pigs were fed prior to the study.

In a previous study, we reported that 10% OH decreased Ca and Zn balance in pigs after a 7 d feeding period (Moore et al., 1986a). Two differences may account for the different response to OH in the present trial. First, the OH diets in the present experiments contained 10 mg/kg more Zn than did the OH diets in our previous treatment or the B diet in the present experiments. Secondly, the OH in the present trial were more digestible (35% DM digestibility) than the OH used in our previous trials (5% DM digestibility). Although fecal NDF outputs were similar in both trials, the combination of a higher Zn intake and OH which were more degradable may have allowed more Zn to become available for absorption in the large intestine. Although Sandberg et al. (1982) suggested that wheat bran only decreased small intestinal Zn absorption in humans, Partridge (1978) showed that cellulose decreased large intestine Zn absorption in pigs.

Regardless of the mechanism by which OH might impair mineral utilization, the different response in these two experiments (present experiment and Moore et al., 1986a) to the same fiber source would support observations by others that physical and chemical characteristics of

different fiber sources, independent of fiber content, may be important determinants as to whether high-fiber diet ingredients can impair mineral absorption (Fairweather-Tait, 1982; Kelsay and Prather, 1983).

At the present time, evidence to show that high-fiber diets impair mineral utilization in pigs is contradictory. Although studies using semi-synthetic (Partridge, 1978; Bagheri and Gueguen, 1983) and cereal grain-oilseed meal (Newton et al., 1983; Lindemann et al.,1986; Moore et al., 1986a) type-diets show that high-fiber diets can impair mineral absorption, other studies have failed to demonstrate an effect of high-fiber diets on mineral utilization (Moser et al., 1982; Ravindran et al., 1984; Holzgraefe et al., 1985). Although a number of variables may contribute to the conflicting results of high-fiber diets on mineral availability, differences in diet mineral content and fiber level (and source) probably contribute much of the variation in results.

The Fe and Zn in the basal and high-fiber diets (without minerals) in the present experiments appear to have a low availability, as evidenced by the fact that the addition of minerals to the diets generally increased apparent absorption. Studies in chicks and rats have shown that high-fiber diets decrease mineral balance (Thompson and Weber, 1981b; Gordon et al., 1983). In

comparison to our diets, the low-fiber diets fed in those experiments supplied between 0 and 2.5 g NDF/(kg $^{.75}$ • d), whereas our basal 'low-fiber' diet supplied over 9 g NDF/(kg $^{.75}$ • d). Most of the fiber present in the basal diet is corn bran (ca. 6 g), and thus the basal diet we used may already be, in relative terms, a high-fiber diet, which may have limited the ability of either fiber source to further decrease mineral balance. Corn bran is able to bind minerals in vitro (Thompson and Weber, 1981b; Reinhold et al., 1981) and corn bran isolated from human feces contains four-fold more iron than when fed (Dintzis and Watson, 1984). Thus, replacement of corn (and subsequently corn bran) with certain high-fiber feedstuffs could actually improve mineral availability, if the fiber source does not in itself decrease mineral availability. This may partly explain the higher Mg balance in pigs fed the SH diets than in pigs fed the B diet, even though diet Mg levels were similar in both diets. The high fiber content of the basal diet may also explain the apparently low bioavailability of Fe in this diet. Fairweather-Tait (1982) showed that Fe availability was decreased by equal amounts when breads containing different amounts of fiber were incorporated into a fiber-free rat diet, indicating that fiber sources are able to alter mineral availability independent of their contribution of fiber to the diet.

Both fiber sources increased fecal K excretion, while only OH increased fecal Na excretion, although Na and K balances were not greatly different between pigs fed the B, OH or SH diets. These changes in the pattern of electrolyte excretion probably reflect an attempt to adjust the osmolarity of the digesta due to the higher water contents caused by the fiber sources. Lindemann et al. (1986) have shown a similar shift in K excretion from urine to feces in pigs fed diets containing high levels of peanut hulls.

Our results suggest that some fiber sources such as SH, may be able to improve mineral balance, either by increasing mineral intakes or by altering the diet composition such that minerals are more available. Although the overall effect of OH was small, the data suggest that OH may impair Zn absorption after short-term feeding periods. However, longer-term studies are required to determine if this response is a transient change in mineral requirements or reflects the onset of a malabsorption condition due to the presence of OH. Additionally, diets composed of cereal grains and oilseed meals are not appropriate 'low-fiber' diets for studies aimed at determining the effects of fiber sources on mineral utilization, particularly in studies where the pig is being considered for use as a model for the study

of the effects of fiber on bowel function in humans (Fleming and Wasilewski, 1984). In this respect, more research is required to assess the impact of different fiber sources added to synthetic, fiber-free diets on mineral utilization in the pig.

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CHAPTER VI

GROWTH AND NUTRIENT UTILIZATION BY PIGS FED HIGH-FIBER DIETS

Summary

Two trials (24 and 48 pigs; 9.7 kg bodyweight) were conducted to determine the effects of moderate amounts of dietary fiber on growth and nutrient utilization in young pigs. The four diets were: a basal corn-soybean meal (B), a 15% oat hulls (OH), a 15% soybean hulls (SH), and a 20% alfalfa meal (AM). Fiber source did not affect daily gain or feed intake (P>.10; g/d) of pigs fed the B (483,967), OH (487,966), SH (496,974) or AM (445,959) diets in a 35-d feeding trial. AM reduced feed efficiency (.467) compared with pigs fed the B (.499; P<.07), SH (.511; P<.05) or OH (.509; P<.05) diets. Balance trials (7-d in duration) were conducted 32 d (trial 1) or 6 d (trial 2) after completion of the feeding trials. Feed intakes were equalized at 10% (trial 1) or 11% (trial 2) of bodyweight ($kg^{.75}$). All fiber sources decreased apparent digestibilities of N (P<.05) and energy and dry matter (P<.01). N retention was unaffected by fiber source (P>.10). Apparent digestibilities of neutral- and acid-detergent fiber, cellulose and hemicellulose were reduced by OH and AM

(P<.01) but not SH (P>.10). Fiber sources did not affect apparent Ca, P, Zn or Mn absorption or retention (P>.10). The fiber sources did not affect Mg absorption (P>.10), but decreased Mg retention (P<.05). Apparent Na absorption was decreased by OH (P<.01), increased by AM (P<.03), but unaffected by SH (P>.10). All fiber sources increased K intake (P<.01), but only SH and AM increased apparent K absorption (P<01). Fiber sources did not affect Na or K retention (P>.10). Oat hulls increased Cu balance (P<.01), but this was primarily a result of higher Cu intake. All fiber sources increased Fe intake, but only SH and AM increased (P<.01) Fe balance. Moderate levels of dietary fiber did not affect performance of young pigs, although apparent energy utilization was decreased by OH, SH and AM additions; however, these levels of fiber had a minimal impact on mineral and N utilization by pigs limit-fed practical cereal grain-oilseed meal diets.

Introduction

Recent reports suggest that high fiber diets decrease mineral absorption and retention in pigs (Bagheri and Gueguen, 1983; Newton et al., 1983; Lindemann et al., 1986; Moore et al., 1986a). However, other studies indicate that high fiber diets do not have

a negative impact on mineral utilization in growing pigs or gestating sows (Moser et al., 1982; Ravindran et al., 1984; Holzgraefe et al., 1985).

Most balance studies showing a negative effect of fiber on mineral utilization have been conducted for short periods of time, and as such, may not accurately reflect the ability of the pig to adjust mineral absorption to changes in diet compostion. Moore et al. (1986a) reported that 10% oat hulls decreased Zn and Ca balance in growing pigs fed the diets for a 7 d period. However, a subsequent study failed to show a large negative effect of oat hulls or soybean hulls on mineral utilization in pigs fed the high-fiber diets for 6 d or 26 d (Moore and Kornegay, unpublished data), and in fact suggested that degradable fiber sources such as soybean hulls might enhance mineral availability from corn-soybean meal diets. Although differences in diet fiber and mineral levels may account for the different results in these two trials, the short duration of these experiments may partly explain the different results obtained. Newton et al. (1983) indicated that wheat bran did not affect fractional mineral absorption in pigs after 14 d, but decreased fractional absorption of Zn after feeding of the diets for 80 d. However, Holzgraefe et al. (1985) failed to find an effect of 40%

orchardgrass-alfalfa hay on mineral balance of gestating sows after 5 d or 45 d of feeding. The present experiments were conducted to determine if growth and mineral or nutrient utilization were impaired in young pigs fed conventional corn-soybean meal or high-fiber diets during the early growing period. Three fiber sources which differed in chemical composition and susceptibility to degradation within the gastrointestinal tract (oat hulls, soybean hulls and alfalfa meal) were used to formulate the high-fiber diets.

Materials and Methods

Animals.

In trial 1, 24 crossbred pigs (16 barrows and 8 gilts; 9.7 ± 0.5 kg) were allotted to diet groups by weight, sex and litter using a randomized complete block design. Pigs were housed in elevated cages (1.2 m x 1.2 m; two pigs per cage) and fed ad libitum one of four experimental diets (table 1): basal corn-soybean meal (B), 15% oat hulls (OH), 15% soybean hulls (SH) or 20% alfalfa meal (AM). Pigs were fed the higher protein set of diets (table 1) during the performance period of trial 1 (35-d duration), followed by a 19-d growing period during which they were fed the lower protein diets. In trial 2, 48 crossbred pigs (24 barrows and 24 gilts; 9.7

± 0.3 kg) were allotted to the same diet groups as used in trial 1 by weight and litter and housed (sexes were penned separately) in slotted-floored pens (1.2 m x 0.91 m; 2 pigs per pen). In trial 2, pigs were fed the higher protein set of diets for 33 d, after which they were moved to metabolism cages and fed the lower protein set of diets. Growth rate and feed intake were determined weekly up to 35 d in trial 1 and 33 d in trial 2. Water was available ad libitum from nipple waterers in both trials.

Balance trials.

Following the feeding trials, three pigs from each diet group were placed in stainless steel metabolism cages in order to determine nutrient utilization by pigs fed the four lower protein diets. In trial 1, pigs were fed twice daily (0600 and 1800 h) an amount of feed equal to 10% of $kg^{.75}$ bodyweight (initial weight) for 13 d, followed by a 7-d total fecal and urine collection period. Deionized water was available ad libitum from nipple waterers. In trial 2, a 7-d balance period followed a 6-d adjustment period to the diets and cages. Feed intake was equalized at 11% of initial $kg^{.75}$ bodyweight in trial 2. The different feed intakes and length of the adaptation periods reflect difficulties in getting the pigs to consume their feed and adjust to the

cages in trial 1. The composition of the fiber sources and diets fed in the balance trials are given in table 2.

The methods used for sample collection and analysis have been described elsewhere (Moore et al., 1986a,b). Chromic oxide used to demarcate the feces was determined by the method of Gherke et al. (1950). Estimated bodyweight at 3 d of the collection period was calculated assuming a constant weight gain while pigs were in the metabolism cages. Balance data corresponding to absolute amounts (i.e. absorbed, retained, etc.) are expressed per unit metabolic bodyweight ($kg^{.75}$) per day using this weight.

Statistical analysis.

Performance trial and balance trial data were analyzed by the general linear models procedure of SAS (1982). Individual animals were the experimental units for all measures, except performance trial feed intake and feed efficiency, where the pen was the experimental unit. The model contained the effects of fiber source, trial, and the two-way interaction. Individual means were compared by least-squares differences.

Table 1. Ingredient composition (%) of diets fed during the growing period and during the balance trials

Ingredient	Performance Trials[1]				Balance Trials[1]			
	B	OH	SH	AM	B	OH	SH	AM
Ground corn	72.83	56.70	58.34	59.19	78.20	62.08	63.71	64.79
Soybean meal, 44%	24.06	25.28	23.76	18.42	19.02	20.24	18.73	13.16
Oat hulls	---	15.00	---	---	---	15.00	---	---
Soybean hulls	---	---	15.00	---	---	---	15.00	---
Alfalfa meal	---	---	---	20.00	---	---	---	20.00
Deflourinated phosphate	1.08	1.08	1.19	1.19	0.90	0.91	1.02	1.00
Limestone	0.83	0.74	0.50	---	0.83	0.72	0.49	---
Zinc premix[2]	0.45	0.45	0.45	0.45	0.30	0.30	0.30	0.30
Trace mineral premix[3]	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25
Iodized salt	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25
Vitamin-Se premix[4]	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25

[1]Abbreviations are: B, basal, OH, oat hulls, SH, soybean hulls, and AM, alfalfa meal.
[2]Zinc premix provided per kg diet: performance trials, 30 mg Zn, balance trials, 20 mg Zn as $ZnSO_4 \cdot H_2O$
[3]Mineral premix provided per kg diet: 10 mg Cu as $CuSO_4 \cdot 5H_2O$ and 5 mg Mn as $MnSO_4 \cdot H_2O$.
[4]Vitamin-Se premix provided per kg diet: 4.3 mg riboflavin, 22 mg niacin, 22 mg pantothenic acid, 22 ug B_{12}, 440 mg choline chloride, 4400 IU vitamin A, 11 IU vitamin E, 440 IU vitamin D, 1100 ug vitamin K (as menadione sodium bisulfite complex), and 0.10 mg Se.

Table 2. Nutrient composition of diets (as-is basis) fed during balance trials

Item	Diet[1]				Fiber Source[1]		
	B	OH	SH	AM	OH	SH	AM
Dry matter, %	91.9	92.6	92.4	92.4	91.8	91.4	93.5
Nitrogen, %	2.43	2.55	2.48	2.43	1.24	1.62	2.98
Neutral-detergent fiber, %	9.26	16.21	17.34	14.34	58.9	60.6	34.6
Acid-detergent fiber, %	3.11	7.44	9.62	8.38	33.2	46.9	27.8
Cellulose, %	2.59	5.64	8.04	8.33	23.2	40.0	19.7
Hemicellulose, %	6.10	8.77	7.71	5.96	25.8	13.8	6.8
Lignin, %	0.60	1.43	2.48	2.43	7.0	6.8	6.7
Calcium, %	0.590	0.596	0.602	0.557	0.132	0.477	1.070
Phosphorus, %	0.518	0.513	0.502	0.508	0.252	0.138	0.263
Magnesium, %	0.120	0.128	0.139	0.136	0.122	0.192	0.227
Sodium, %	0.160	0.158	0.164	0.189	0.026	0.022	0.126
Potassium, %	0.654	0.708	0.752	0.970	0.599	1.022	2.590
Zinc, mg/kg	58.0	59.2	61.4	55.0	32.8	73.8	40.7
Iron, mg/kg	115.8	150.5	190.1	174.8	243.0	476.2	307.7
Copper, mg/kg	19.0	22.2	20.6	20.4	22.7	12.8	16.4
Manganese, mg/kg	20.5	28.3	25.0	29.8	55.4	26.4	60.2

[1]Abbreviations are: B, basal, OH, oat hulls, SH, soybean hulls, and AM, alfalfa meal

Results

Performance.

Oat hulls, soybean hulls and alfalfa meal did not affect average daily gain or feed intake (table 3; P>.10). Feed efficiency was lower for pigs fed the AM diets compared with pigs fed the B (P<.07), OH or SH (P<.05) diets. Gain and feed intake were greater in trial 1 than in trial 2 (P<.01), but no highly significant diet x trial interactions were present (P<.08 for feed intake only).

Dry matter, nitrogen and energy utilization.

All fiber sources decreased DM digestibility (table 4; P<.01). Because of higher diet intakes in trial 2 (10.3% of kg $^{.75}$) than in trial 1 (8.7% of kg $^{.75}$), absolute amounts of DM digested were greater in trial 2 (P<.01), but percent DM digestibilities were not different (P>.10). Soybean hulls and AM (P<.01) and OH (P<.05) decreased apparent N digestibility (table 4), but because all fiber sources increased N intake (P<.01), only SH (P<.05) and AM (P<.01) decreased apparent N absorption. Fiber source on did not affect N retention (P>.10).

Apparent energy absorption and the coefficients for digestible energy were reduced by the three fiber sources (table 4; P<.01). Absolute values for energy and N

Table 3. Effect of dietary oat hulls, soybean hulls or alfalfa meal on growth and feed utilization of growing pigs

Criteria	Diet Fiber Source[1]					P-values[2]		
	B	OH	SH	AM	SEM	D	T	DxT
Bodyweight, kg								
Initial	9.7	9.7	9.7	9.7	0.3	NS	NS	NS
Final	26.2	26.3	26.5	24.9	0.7	NS	.01	NS
Gain, kg/d	0.483	0.487	0.496	0.445	0.018[a]	NS	.01	NS
Feed intake, kg/d	0.967	0.966	0.974	0.959	0.035	NS	.01	.08
Feed efficiency, (gain:feed)	0.499	0.504	0.511	0.467	0.012[b]	.08	NS	NS

[1]Letters represent significant least-squares differences:

[a]B vs AM, P<.10; SH vs AM P<.05.
[b]B vs AM P<.07; OH vs AM, SH vs AM P<.05.

[2]Abbreviations represent statistical model main effects: D, diet, T, trial, and DxT, the diet x trial interaction.

Table 4. Effect of dietary oat hulls, soybean hulls or alfalfa meal on dry matter, nitrogen and energy utilization by growing pigs

Criteria[1]	Diet Fiber Source[2]				SEM	P-values		
	B	OH	SH	AM		D	T	DxT
$kg^{.75}$ bodyweight	14.8	14.9	15.1	14.0	0.3			
Dry matter								
Intake	86.1	88.6	88.4	89.4[a]	0.6	.02	.01	NS
Feces	9.8	18.5	14.3	17.2[b]	0.6	.01	.01	NS
Digested	76.3	70.2	74.0	72.2[c]	0.6	.01	.01	NS
Digestibility, %	88.7	79.1	83.9	80.7[b]	0.6	.01	NS	NS
Nitrogen								
Intake	2.27	2.44	2.37	2.34[b]	0.02	.01	.01	.01
Feces	0.34	0.44	0.50	0.55[d]	0.02	.01	.01	NS
Urine	0.68	0.71	0.65	0.59	0.04	NS	NS	NS
Absorbed	1.93	2.01	1.87	1.79[a]	0.02	.01	.01	.04
Retained	1.26	1.29	1.22	1.20	0.05	NS	.01	NS
Digestibility, %	85.2	82.2	78.6	76.5[d]	0.9	.01	NS	.08
Retained/Absorbed, %	64.9	64.3	64.8	66.8	2.5	NS	.08	NS
Energy								
Intake	375.8	391.2	384.0	394.4[c]	2.7	.01	.01	.06
Feces	47.7	85.1	68.3	84.1[b]	2.7	.01	.01	NS
Absorbed	328.1	306.1	315.8	310.4[b]	2.7	.01	.01	NS
Digestibility, %	87.4	78.2	82.3	78.7[b]	0.6	.01	NS	NS

[1]Values for intake, feces, urine, absorbed (digested) and retained for dry matter and nitrogen expressed as g/($kg.^{75}$ bodyweight · d). Energy intake, feces and absorbed expressed as kcal/($kg.^{75}$ boyweight · d).

[2]Letters represent significant least-squares differences:

[a]B vs OH, SH $P<.05$; B vs AM $P<.01$.

[b]B vs OH, SH or AM $P<.01$.

[c]B vs OH, AM $P<.01$; B vs SH $P<.05$.

[d]B vs SH, AM $P<.01$; B vs OH $P<.05$.

Table 5. Effect of dietary oat hulls, soybean hulls or alfalfa meal on fiber component utilization by growing pigs

Criteria[1]	Diet Fiber Source[2]				SEM	P-values		
	B	OH	SH	AM		D	T	DxT
Neutral-detergent fiber								
Intake	8.62	15.40	16.50	13.83[a]	0.09	.01	.01	.01
Feces	3.62	10.55	6.60	7.81[a]	0.31	.01	.01	.02
Digested	5.00	4.86	9.90	6.02[b]	0.29	.01	.01	NS
Digestibility, %	58.3	31.5	60.5	43.7[c]	2.8	.01	.01	NS
Acid-detergent fiber								
Intake	.2.97	7.10	9.20	8.10[a]	0.05	.01	.01	.01
Feces	1.17	5.22	3.73	4.53[a]	0.14	.01	.01	.01
Digested	1.80	1.88	5.48	3.57[d]	0.13	.01	NS	.01
Digestibility, %	61.1	26.2	60.6	44.2 [c]	2.6	.01	.03	.01
Cellulose								
Intake	2.42	5.36	7.66	5.55[a]	0.04	.01	.01	.01
Feces	0.99	3.79	3.16	3.06[a]	0.12	.01	.01	.01
Digested	1.43	1.57	4.49	2.48[d]	0.11	.01	.01	.01
Digestibility, %	59.7	29.3	59.6	45.0 [c]	3.1	.01	.01	.02
Hemicellulose								
Intake	5.64	8.30	7.30	5.73[e]	0.04	.01	.01	.01
Feces	2.44	5.32	2.87	3.28[c]	0.18	.01	.01	NS
Digested	3.20	2.98	4.43	2.45[d]	0.17	.01	.01	NS
Digestibility, %	56.3	35.5	60.6	42.8 [c]	3.1	.01	.01	NS
Lignin								
Intake	0.58	1.38	1.44	2.28[a]	0.01	.01	.01	.01
Feces	0.16	0.92	0.50	1.17[a]	0.03	.01	NS	.01
Digested	0.42	0.46	0.94	1.11[d]	0.02	.01	.01	.01
Digestibility, %	68.3	30.2	60.8	47.0 [a]	1.6	.01	.01	.01

[1] Values for intake, feces and digested expressed as g/(kg$^{.75}$ bodyweight · d).

[2] Letters represent significant least-squares differences:

[a] B vs OH, SH or AM P<.01.

[b] B vs SH P<.01; B vs AM P<.05.

[c] B vs OH, AM P<.01.

[d] B vs SH, AM P<.01.

[e] B vs OH, SH P<.01.

intake, and apparent absorption were greater in trial 2 than in trial 1 (P<.01), but the digestion coefficients for dietary energy and N were similar in both trials.

Fiber component digestibility.

The absolute intake of NDF, ADF, cellulose and hemicellulose were increased (P<.01) when all fiber sources wre added to the diets, with the exception of hemicellulose for the AM diet (table 5). Oat hulls and AM, but not SH, decreased (P<.01) the apparent digestibilities of NDF, ADF, cellulose and hemicellulose. Compared with pigs fed the B diet, SH, which were highly degraded, increased the absolute amounts of all fiber components digested (P<.01), while OH, which were poorly digested, had no effect on the absolute amounts of fiber components digested (P>.10). With the exception of the amount of hemicellulose, AM increased the absolute amount of fiber components digested (P<.01), although the magnitude of the response was less than for SH. Overall, fiber component digestibilities were lower in trial 2 than in trial 1 (all P<.01, except ADF, P<.05). The diet x trial interactions were significant for ADF and cellulose digestibilities (P<.01). This resulted from large decreases in apparent digestibility for pigs fed the B or SH diets in trial 2 compared to pigs in trial 1, while fiber digestion was similar for pigs fed the OH and AM diets in both trials.

Mineral utilization.

Calcium and Mg intakes varied between pigs fed the four diets (table 6), but fiber source did not affect apparent Ca or Mg absorption (P>.10). Fiber source did not affect Ca balance, but Mg retention was reduced by OH (P<.05) and SH and AM (P<.01). Apparent P absorption (table 6) was slightly higher for pigs fed the AM diets compared with pigs fed the B or OH (P<.06) or SH (P<.07) diets, but did not differ between pigs fed the B, SH or OH diets (P>.10). Calcium balance was lower, but P balance higher, for pigs in trial 2 than in trial 1, but within each trial the effect of fiber source was minimal.

Apparent Na absorption was decreased by OH (table 7; P<.01). Although AM increased fecal Na losses (P<.01), because AM increased Na intake (P<.01), apparent Na absorption was higher for pigs fed the AM diet (P<.05) compared with pigs fed the B diet. Apparent Na absorption was not affected by SH. Fiber source did not affect apparent Na retention (P>.10). All fiber sources increased K intake and fecal K losses (table 7; P<.01), but SH and AM increased (P<.01) apparent K absorption, while OH had no effect. Because of large, and variable, urine K losses, apparent K balance was negative for pigs fed the OH and SH diets, although fiber sources did not affect K balance (P>.10).

Table 6. Effect of dietary oat hulls, soybean hulls or alfalfa meal on Ca, P and Mg utilization by growing pigs

Criteria[1]	Diet Fiber Source[2]				SEM	P-values		
	B	OH	SH	AM		D	T	DxT
Calcium								
Intake	553.4	571.8	575.1	537.7[a]	3.9	.01	.01	.01
Feces	313.9	319.4	333.2	302.8	16.1	NS	.01	NS
Urine	29.6	26.3	31.7	38.1	6.3	NS	NS	.01
Absorbed	239.4	252.4	241.9	234.9	15.4	NS	.01	NS
Retained	209.9	226.2	210.1	196.8	14.0	NS	.01	.05
Absorbed, %	44.4	44.7	42.9	44.1	2.7	NS	.01	NS
Phosphorus								
Intake	484.7	491.9	481.3	491.4	3.4	NS	.01	.01
Feces	257.5	276.4	262.4	245.4	12.9	NS	NS	NS
Urine	3.4	7.4	10.5	10.2[b]	4.1	NS	.10	NS
Absorbed	228.2	226.5	229.0	253.6[b]	8.9	NS	.01	NS
Retained	224.7	219.0	218.5	243.4[b]	10.0	NS	.01	NS
Absorbed, %	46.6	45.3	46.7	51.3[b]	1.8	NS	.01	NS
Magnesium								
Intake	112.2	121.5	131.9	131.2[c]	0.9	.01	.01	NS
Feces	79.8	91.5	96.9	98.4[d]	3.4	.01	.01	NS
Urine	14.6	22.8	32.2	25.5[e]	2.9	.01	.01	NS
Absorbed	32.4	30.0	35.0	32.8	3.1	NS	NS	NS
Retained	17.8	7.2	2.7	7.3[d]	2.5	.01	.01	.09
Absorbed, %	28.9	24.8	26.5	25.1	2.4	NS	.09	NS

[1] Values for intake, feces, urine, absorbed and retained expressed as mg/($kg^{.75}$ bodyweight · d).

[2] Letters represent significant least-squares differences:

[a] B vs OH, SH $P<.01$; B vs AM $P<.05$.

[b] B vs AM $P<.10$.

[c] B vs OH, SH or AM $P<.01$.

[d] B vs OH $P<.05$; B vs SH, AM $P<.01$.

[e] B vs OH $P<.08$; B vs SH $P<.01$; B vs AM $P<.02$.

Table 7. Effect of dietary oat hulls, soybean hulls or alfalfa meal on Na and K utilization by growing pigs

Criteria[1]	Diet Fiber Source[2]				SEM	P-values		
	B	OH	SH	AM		D	T	DxT
Sodium								
Intake	6.55	6.59	6.88	7.97[a]	0.05	.01	.01	.01
Feces	1.26	2.27	1.65	2.06[b]	0.17	.01	.01	NS
Urine	2.18	1.61	2.69	2.67	0.33	NS	.03	NS
Absorbed	5.29	4.32	5.23	5.92[c]	0.18	.01	.01	NS
Retained	3.12	2.71	2.55	3.24[d]	0.26	NS	NS	.05
Absorbed, %	81.2	65.6	76.7	74.9	2.6	.01	.01	NS
Retained, %	48.4	41.5	37.1	41.9[e]	3.9	NS	.01	NS
Fecal molarity, mM	0.057	0.065	0.056	0.050	0.005	NS	NS	NS
Potassium								
Intake	15.75	17.46	18.49	24.01[f]	0.14	.01	.01	.01
Feces	3.17	4.48	4.17	5.34[f]	0.22	.01	.01	NS
Urine	9.96	20.15	15.89	8.74	4.82	NS	.06	NS
Absorbed	12.58	12.98	14.32	18.67[a]	0.21	.01	.01	NS
Retained	2.62	-7.17	-1.56	9.93	4.80	NS	NS	NS
Absorbed, %	79.8	74.3	77.4	77.7[g]	1.1	.04	NS	NS
Retained, %	20.1	-31.8	-5.6	39.8	23.4	NS	NS	NS
Fecal molarity, mM	0.155	0.129	0.148	0.139	0.013	NS	NS	NS

[1]Values for intake, feces, urine, absorbed and retained expressed as mmol/(kg$^{.75}$ bodyweight · d).
[2]Letters represent significant least-squares differences:
[a]B vs SH, AM P<.01.
[b]B vs OH, AM P<.01.
[c]B vs OH P<.01; B vs AM P<.03.
[d]B vs OH P<.01; B vs AM P<.10.
[e]B vs SH P<.06.
[f]B vs OH, SH or AM P<.01.
[g]B vs OH P<.01.

Table 8. Effect of dietary oat hulls, soybean hulls or alfalfa meal on Zn and Cu utilization by growing pigs

Criteria[1]	Diet Fiber Source[2]				SEM	P-values		
	B	OH	SH	AM		D	T	DxT
Zinc								
Intake	5.49	5.68	5.88	5.34[a]	0.04	.01	.01	.01
Feces	4.32	4.13	4.71	4.12	0.20	NS	.01	.02
Urine	0.084	0.079	0.111	0.080	0.016	NS	.03	NS
Absorbed	1.17	1.55	1.17	1.22	0.20	NS	.01	NS
Retained	1.08	1.47	1.06	1.14	0.20	NS	.01	NS
Absorbed, %	21.6	26.8	19.3	21.5	3.3	NS	.02	NS
Copper								
Intake	1.78	2.11	1.97	1.98[b]	0.01	.01	.01	.01
Feces	1.12	1.29	1.31	1.31[b]	0.03	.01	.01	NS
Urine	0.021	0.017	0.018	0.018	0.004	NS	NS	NS
Absorbed	0.67	0.82	0.66	0.67[c]	0.03	.01	.01	.06
Retained	0.64	0.81	0.64	0.65[c]	0.03	.01	.01	.04
Absorbed, %	37.4	39.0	33.0	33.7	1.4	.04	.03	NS

[1]Values for intake, feces, urine, absorbed and retained expressed as mg/(kg$^{.75}$ bodyweight · d).

[2]Letters represent significant least-squares differences:
[a]B vs OH, SH $P<.01$; B vs AM $P<.02$.
[b]B vs OH, SH or AM $P<.01$.
[c]B vs OH $P<.01$.

Table 9. Effect of dietary oat hulls, soybean hulls or alfalfa meal on Fe and Mn utilization by growing pigs

Criteria[1]	Diet Fiber Source[2]				SEM	P-values		
	B	OH	SH	AM		D	T	DxT
Iron								
Intake	10.87	14.54	18.26	16.88[a]	0.11	.01	.01	.01
Feces	7.51	11.03	13.51	11.41[a]	0.33	.01	.01	.01
Urine	0.127	0.135	0.219	0.109[b]	0.048	NS	.01	.01
Absorbed	3.36	3.50	4.75	5.47[b]	0.27	.01	NS	.01
Retained	3.23	3.37	4.54	5.36[b]	0.27	.01	NS	.01
Absorbed, %	30.9	23.9	26.4	33.1[c]	1.9	.03	.01	.01
Manganese								
Intake	1.92	2.72	2.40	2.88[a]	0.02	.01	.01	.01
Feces	1.72	2.44	2.17	2.53[a]	0.06	.01	.01	NS
Urine	0.026	0.032	0.037	0.028[d]	0.008	NS	.01	NS
Absorbed	0.20	0.28	0.22	0.35[d]	0.06	NS	NS	.05
Retained	0.18	0.25	0.19	0.32[d]	0.06	NS	NS	.06
Absorbed, %	10.6	10.2	9.2	12.6	2.2	NS	.07	.08

[1]Values for intake, feces, urine, absorbed and retained expressed as mg/(kg$^{.75}$ bodyweight · d).

[2]Letters represent significant least-squares differences:
[a]B vs OH, SH or AM P<.01.
[b]B vs SH, AM P<.01.
[c]B vs OH P<.02.
[d]B vs AM P<.10.

Apparent Zn absorption and retention were not different between pigs fed the different diets (table 8; P>.10). Oat hulls increased Cu intake and apparent Cu absorption and retention compared with pigs fed the B diet (P<.01). Although SH and AM increased Cu intake (P<.01), Cu balance was not different between pigs fed the B, SH or AM diets (P>.10). The significant diet x trial interactions for Cu balance reflected a lower Cu balance for pigs fed the the SH diet in trial 1, but a higher Cu balance in trial 2 compared with pigs fed the B diet.

All fiber sources increased Fe intake (P<.01), but only SH and AM increased Fe balance (table 9; P<.01). The diet x trial interaction was significant for Fe balance (P<.01) reflecting the result that AM increased Fe balance in trial 1 but not in trial 2. Although all fiber sources increased Mn intake (table 9; P<.01), only AM increased Mn balance (P<.10) compared with pigs fed the B diet, but the effect of AM on Mn balance was confined to trial 1 only.

Discussion

The modest levels of dietary fiber fed in the present experiments did not affect growth or feed efficiency. Other studies have shown that modest

additions of cellulose or natural fiber sources to the diets of young pigs do not have a negative effect on growth rate (Kornegay, 1978, 1981; Brumm and Peo, 1985).

All three fiber sources decreased apparent N absorption; however, none affected N retention. Although many high-fiber diets decrease apparent N digestibility in pigs, this is not an obligate response to high fiber intakes. Other studies have shown that OH have a small effect on apparent N absorption in pigs. (Kennelly and Aherne, 1980; Moore et al., 1986b).

The smaller magnitude effect of OH on apparent N digestibility compared with SH and AM probably reflects the smaller contribution of N to the diet by OH compared with SH and AM, as well as the lower ability of this fiber source to support microbial protein synthesis. In general, high protein fiber sources and those more susceptible to fermentation, have a greater depressing effect on N absorption (Beames and Eggum, 1981; Bach Knudsen et al., 1982).

Although dietary fiber sometimes decreases urine N levels (Malmlof and Hakansson, 1984), the present results agree with studies which indicate that high-fiber diets have a small effect on urine N excretion or N retention (Corley et al., 1978; Moore et al., 1986b). However, since fiber digestion occurs throughout the length of the

gastrointestinal tract (Millard and Chesson, 1984), effects of dietary fiber on the pattern of N digestion or absorption cannot be excluded (Fleming and Wasilewski, 1984).

All fiber sources decreased apparent energy digestibility, which agrees with previous reports which show that high-fiber diets have a lower digestible energy (D.E.) content (Just et al., 1983; Morgan et al., 1984). The less degradable OH and AM had a more negative effect on D.E. than did SH. The relative resistance of OH and susceptibility of SH to digestion has been reported by others (Kornegay, 1981; Moser et al., 1982; Stanogias and Pearce, 1985; Moore et al., 1986b).

The large differences in fiber component digestibilities between the two trials were unexpected. Although relatively little is known about factors which affect fiber utilization in pigs, it is possible that trial differences in food intake (higher in trial 2), pig age (younger in trial 2), or duration of feeding (shorter in trial 2) are involved.

Our previous studies show that fiber digestibility by pigs fed diets containing OH or SH is similar after 6 or 26 d of consuming the diets (Moore and Kornegay, unpublished data). Similarly, studies by others indicate that intestinal microbial adaptation to high-fiber diets

is fairly rapid (Varel et al., 1984) and fiber digestibility and VFA production do not adaptively increase after 15 weeks of pigs consuming higher fiber diets (Cunningham et al., 1962; Kennelly et al., 1981). Although carefully controlled studies of the effect of age have not been conducted, longitudinal studies indicate that fiber digestibility does not appreciably increase with age or weight (Partridge et al., 1983), and may even decrease slightly (Kass et al., 1980).

The D.E. content of feeds does not appear to vary greatly in pigs fed at different levels (Morgan et al., 1984), but Cunningham et al. (1962) reported that cellulose digestibility was higher in limit-fed pigs compared with ad-libitum fed pigs. Although a direct comparison is confounded by age, Kornegay (1981) reported that fiber components of SH were more digestible by sows (150 kg) fed at 4.2% of $kg^{\cdot 75}$ than by younger pigs (46 kg) fed at 11% of $kg^{\cdot 75}$ (Kornegay, 1978). Whether these differences reflect intake, fiber source composition, or age is not clear; however, our previous studies with pigs (30-50 kg) fed at 9 to 10% of $kg^{\cdot 75}$ have provided fiber digestibilities within the ranges of those obtained in both of the present trials (Moore et al., 1986b; Moore and Kornegay, unpublished data). Thus, the trial differences in fiber utilization would appear to reflect

animal variation in the ability to digest fiber, and not different management procedures in the two trials.

Regardless, the lower fiber digestibilities did not appear to correspond to growth rate greatly, and although energy digestion coefficients were slightly lower in trial 2 for pigs fed the B (86% vs 88%) and SH (81% vs 83%), the differences were not statistically significant. Frank et al. (1983) have reported that growth rate of pigs fed high-fiber diets is not closely related to the ability of individual pigs to digest fiber.

All fiber sources increased Fe intake, although Fe balance was increased by only SH and AM, which suggests that Fe contained in SH and AM has a high relative bioavailability. Other studies indicate that high-fiber feedstuffs may be sources of available Fe for pigs (Frolich and Lyso, 1983; Lindemann et al., 1986; Moore and Kornegay, unpublished data). With few exceptions, the fiber sources did not greatly affect the absorption and retention of minerals other than Fe in the present trials. This is in contrast to our previous studies indicating that OH and SH may decrease or enhance the availability of some minerals from corn-soybean meal diets (Moore et al., 1986a; Moore and Kornegay, unpublished data). Although no explanation for these different results is obvious, different mineral and fiber

intakes, animal variation, as well as differences in fiber source composition, all probably contribute to the different response of mineral balance to high-fiber diets in different experiments.

Thus, although reports indicate that high-fiber diets may impair mineral absorption by pigs (Bagheri and Gueguen, 1983; Newton et al., 1983; Lindemann et al., 1986; Moore et al., 1986a), the present data and that of others, fail to show large effects of dietary fiber on mineral balance (Holzgraefe et al., 1985; Moore and Kornegay, unpublished data). Most studies conducted with pigs have been of rather short duration, have used restricted feed intakes, and have used moderate dietary levels of fiber (usually less than 20% of the fiber source in the diet). It is unclear whether results obtained under these conditions are applicable to practical feeding conditions. However, the present results, and those of others, suggest that modest amounts of dietary fiber would not be expected to have a significant negative effect on mineral balance in pigs when included in diets which meet the recognized mineral requirements (NRC, 1979) of the pig. It should be recognized that different fiber sources included at higher levels in the diet, and fed ad libitum may have different effects on mineral and nutrient utilization.

This particular aspect of fiber nutriture in the pig needs to be clarified.

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CHAPTER VII

INTESTINAL MORPHOLOGY OF GROWING PIGS FED CORN-SOYBEAN MEAL DIETS WITH OR WITHOUT OAT HULLS, SOYBEAN HULLS OR ALFALFA MEAL

Summary

Surface morphology of jejunum, ileum and colon of eleven pigs fed corn-soybean meals diets with or without 15% oat hulls, 15% soybean hulls or 20% alfalfa meal were evaluated by scanning electron microscopy (SEM). Three pigs (9.7 kg initial bodyweight) were fed each of the diets (only two pigs for oat hulls diet) ad libitum for 54 d, followed by a 20-d limit-fed (9.99% of kg $^{.75}$ bodyweight) period. Villi shape and surface morphology in jejunum and ileum were variable, and were largely independent of diet fed. Tongue- and leaf-like villi were most common in jejunum and ileum, although finger-like villi were present. Two pigs fed alfalfa meal had jejunum villus morphologies characterized by loss of epithelial cells and microvilli at the apical villus surface. Villi in one of these pigs were blunted and exhibited a folded appearance, with extensive loss of epithelium integrity at villus apex. Areas of cellular disarray and interruptions in the epithelium were common in ileum of many pigs, regardless of diet fed. These areas were confined to the apical one-third of the

villus, but not all villi in a given pig were affected. Ileum villi of one pig fed soybean hulls were blunted and frequently folded, and the epithelial surface had a corrugated appearance with extensive loss of epithelial cells and microvilli at the villus apex. Filamentous bacteria were observed in association with ileum villi of this pig. Colon morphology was highly variable between pigs and within individual pigs. Interruptions in the epithelium and areas devoid of microvilli were common regardless of diet fed, but the surface area affected was small. A consistent effect of additions of dietary fiber on intestinal morphology was not detectable by SEM. The observations suggest that some pigs may be susceptible to detrimental effects of dietary fiber on intestinal structure, and that practical swine diets result in an intestinal architecture which could be a factor limiting nutrient utilization from conventional corn-soybean meal diets.

Introduction

Diet composition and the presence of lumenal nutrients influence villus shape and rate of epithelial cell proliferation (Creamer, 1974; Clarke, 1975). Although the relationship between intestinal morphology and function in apparently healthy animals is unclear,

studies indicate that intestinal nutrient uptake is impaired in rats chronically fed diets containing cellulose or native fiber sources (Schwartz and Levine, 1980; Schwartz et al., 1982; Freeman, 1984).

Knehans and O'Dell (1980) reported that interruptions in the intestinal epithelium were more frequent in guinea pigs fed diets containing alfalfa. Epithelial abnormalities have also been observed in intestines from rats fed diets containing pectin or alfalfa (Cassidy et al., 1981). Although Tasman-Jones et al. (1982) reported that intestinal morphology of weanling rats fed chow-type diets was different from that of rats fed fiber-free diets with or without cellulose, neither chow or cellulose-containing diets appeared to damage the epithelial surface. Not all fiber sources exert detectable effects on intestinal structure (Knehans and O'Dell, 1980; Cassidy et al., 1981).

Although the lower nutrient absorption by pigs fed high-fiber diets may result from the different level and availability of nutrients in these diets compared with conventional cereal grain-oilseed meal diets (Laplace and Lebas, 1981), possible detrimental effects of high-fiber diets on intestinal structure and function in pigs have not been investigated. The objective of the present study was to obtain descriptive data on intestinal

morphology of pigs fed conventional corn-soybean meal diets, or diets containing dietary fiber supplied by oat hulls, soybean hulls or alfalfa meal. Nutrient utilization and growth of the pigs used in the present study have been reported elsewhere (chapter 6).

Materials and Methods

Animals and diets.

Twelve crossbred, male-castrate pigs (3 per dietary treatment) were fed one of four diets (table 1): a basal corn-soybean meal diet (B), a 15% oat hulls diet (OH), a 15% soybean hulls diet (SH), or a 20% alfalfa meal diet (AM). Pigs (9.7 kg bodyweight; 40 d of age) were fed ad libitum the higher protein diets for 35 d, followed by the lower protein diets for 19 d. The pigs were transferred to individual cages and limit-fed (9.99% of $kg^{.75}$ bodyweight) the same diets twice daily in equal amounts (0600 and 1800 h) for 21 d. One animal from each treatment was sacrificed on each of three successive days to obtain tissue samples. At sacrifice, pigs had consumed the diets for 76 d (final bodyweight 47.9 kg). One pig fed the OH diet became lame and did not complete the experiment.

Table 1. Ingredient composition (%) of diets fed during the growing period and during the balance trials

Ingredient	Performance Trials[1]				Balance Trials[1]			
	B	OH	SH	AM	B	OH	SH	AM
Ground corn	72.83	56.70	58.34	59.19	78.20	62.08	63.71	64.79
Soybean meal, 44%	24.06	25.28	23.76	18.42	19.02	20.24	18.73	13.16
Oat hulls	---	15.00	---	---	---	15.00	---	---
Soybean hulls	---	---	15.00	---	---	---	15.00	---
Alfalfa meal	---	---	---	20.00	---	---	---	20.00
Deflourinated phosphate	1.08	1.08	1.19	1.19	0.90	0.91	1.02	1.00
Limestone	0.83	0.74	0.50	---	0.83	0.72	0.49	---
Zinc premix[2]	0.45	0.45	0.45	0.45	0.30	0.30	0.30	0.30
Trace mineral premix[3]	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25
Iodized salt	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25
Vitamin-Se premix[4]	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25

[1]Abbreviations are: B, basal, OH, oat hulls, SH, soybean hulls, and AM, alfalfa meal.
[2]Zinc premix provided per kg diet: performance trials, 30 mg Zn, balance trials, 20 mg Zn as $ZnSO_4 \cdot H_2O$
[3]Mineral premix provided per kg diet: 10 mg Cu as $CuSO_4 \cdot 5H_2O$ and 5 mg Mn as $MnSO_4 \cdot H_2O$.
[4]Vitamin-Se premix provided per kg diet: 4.3 mg riboflavin, 22 mg niacin, 22 mg pantothenic acid, 22 ug B_{12}, 440 mg choline chloride, 4400 IU vitamin A, 11 IU vitamin E, 440 IU vitamin D, 1100 ug vitamin K (as menadione sodium bisulfite complex), and 0.10 mg Se.

Tissue collection.

Pigs were fed at 0600 h on the day of sacrifice. Tissue samples were removed from pigs between 0800 and 1100 h, while pigs were maintained under anaethesia (sodium pentabarbital administered via ear vein). Three intestinal sites were sampled: jejunum, 180 cm distal to the pyloric junction; ileum, 15 cm proximal to the ileo-cecal-colic junction; and colon, 15 cm distal to the ileo-cecal-colic junction. Intestinal segments were rinsed briefly with ice-cold buffered saline (.13 M NaCl, .01 M NaH_2PO_4 , .01 M KH_2PO_4, pH 7.4) and immediately fixed (5-7 h) by immersion in ice-cold 4% PGA (paraformaldehyde:glutaraldehyde:acrolein, 1:1:1, in .1 M cacodylate buffer, pH 7.4). The samples were rinsed free of fixative with cacodylate buffer (0.1 M, pH 7.4; 3 changes) and dehydrated through an ethanol series (3 changes each, 20-40-60-80-100%). The dehydrated samples were critical point dried (Model 28000 critical point dryer, Ladd Research Industries, Inc., Burlington, VT), mounted on aluminum stubs, and gold coated (SPI sputter, Structure Probe, Inc., W. Chester, PA). Samples were viewed using a JSM-35C scanning electron microscope (JEOL, Inc., Peabody, MA) at accelerating voltages of 10kV or 15kV.

Results

Morphology of the jejunum surface was variable between different pigs fed the basal diet (figure 1). Villi were mostly tongue- and leaf-like in appearance, but finger-like villi were present in all samples. Individual epithelial cells were arranged in uniform patterns and densely covered with microvilli (figure 1D). Villi in jejunum of some pigs (5 pigs out of 8; figure 2) fed the high-fiber diets were similar in appearance to those of pigs fed the B diet. Although small interruptions in the epithelium were frequently seen (figure 2C), the occurrence and surface area affected were small.

Jejunum morphologies different from those described above were seen in three pigs. Tongue-like villi of one pig fed SH had a mild disaray of microvilli and some loss of cellular material at the villus apex (figure 3). Jejunum villi from one pig fed AM (figure 4) were tongue- and finger-like, and had clefts or crater-like areas near the villus apex, which were characterized by mild cellular disarray, and loss of epithelial cells and microvilli. Villi in jejunum from a second pig fed AM (figure 5) were blunted and exhibited a large degree of folding. There was a marked erosion of microvilli and cells from the apical surface of affected villi, however,

adjacent and lateral areas of surface epithelium were unaffected.

Ileum villus morphology was not different between most pigs (10 pigs out of 11) regardless of diet fed. Villi were predominantly tongue- and finger-like (figures 6 and 7). In pigs fed the B diet, the surface was relatively smooth with surface convolutions, but villus apical surfaces consistently showed a cellular disarray (figure 6). Areas of cellular disarray and epithelial erosion on the upper one-third of many villi were frequently observed (figure 7).

A different morphology of two distinct patterns was observed in the ileum from one pig fed SH (figures 8 and 9). Villi were tongue- and finger-like and had a corrugated surface appearance (figure 8). The second pattern consisted of blunted and folded villi with the same corrugated appearance on the lateral villus surfaces (figure 9). In both instances, the apical villus surface was characterized by cellular disarray with loss of cellular material and microvilli. Filamentous microorganisms were consistently present in ileum samples from this pig.

In general, colon epithelium was smooth in appearance, and crypt and goblet cell openings were prominent (figures 10 and 11). Individual cells or

clusters of cells were present with few or no microvilli present. There was a mild cellular disarry in some colon samples (figure 12), but the pattern of microvillus density was similar to those samples described in figures 10 and 11.

Interruptions in colon epithelium were observed in many samples, but the incidence and extent of occurrence in different pigs varied. Most colon samples had some epithelial interruptions, which generally consisted of small holes inhabited by microorganisms (figure 13).

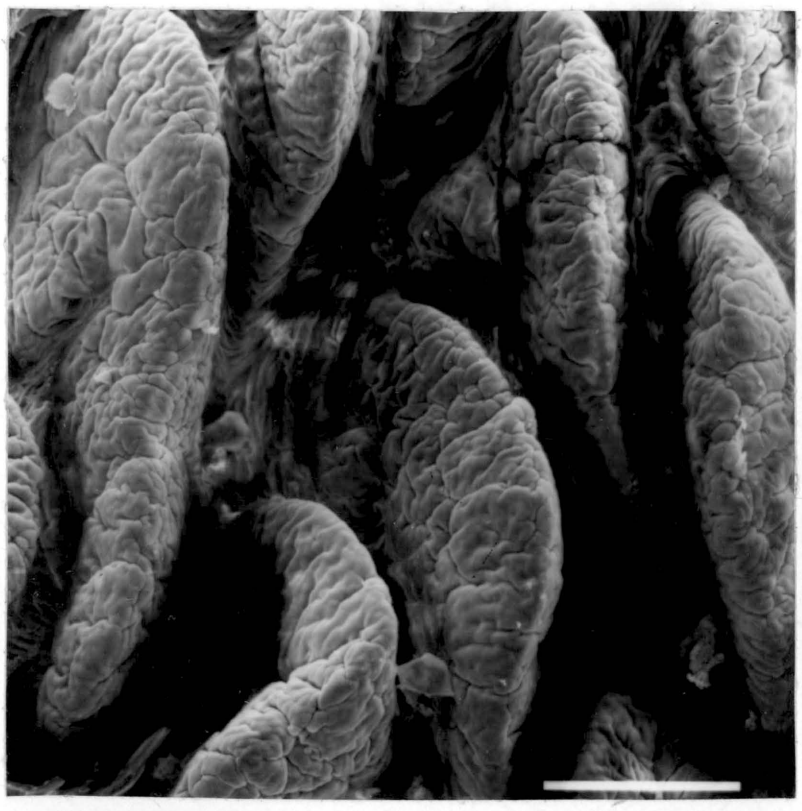
Discussion

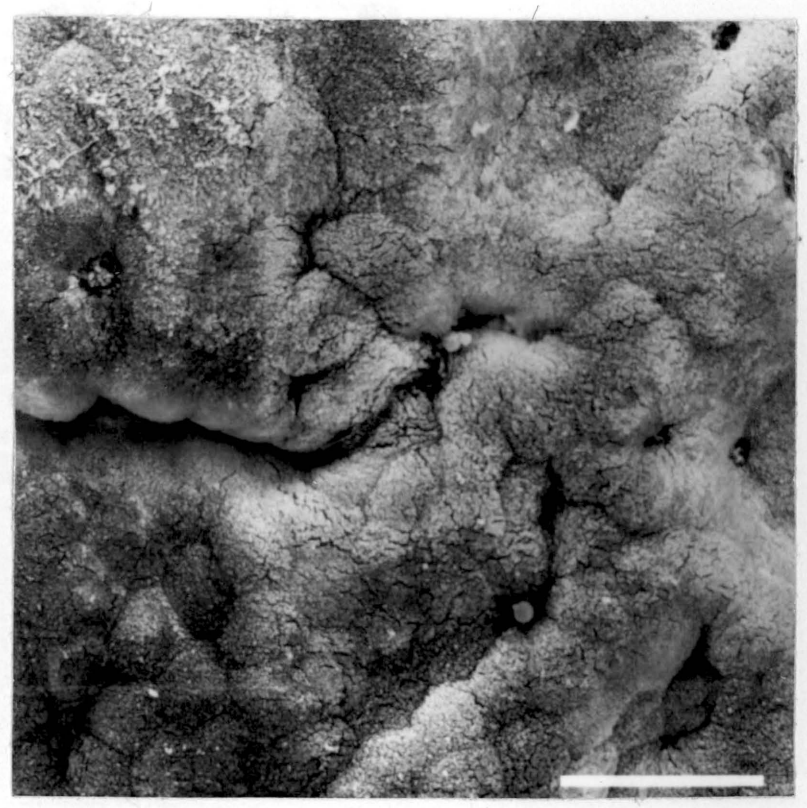
Villus shape and surface morphology differed considerably between pigs used in the present study. Because the different morphologies existed between pigs fed the same diets, it is not possible to conclude whether any, or all, of the variation in morphology which existed was related to diet or environmental influences or simply to animal variation. Jejunal villus populations composed of finger- and tongue-like villi have been described in pigs younger than those pigs used in the present study (Hornich et al., 1973; Bertshingert and Pohlenz, 1983). However, general descriptions of intestinal morphology in pigs are not available, and it is not clear whether any, or all, of the morphologies we observed can be considered 'normal'.

A

B

C



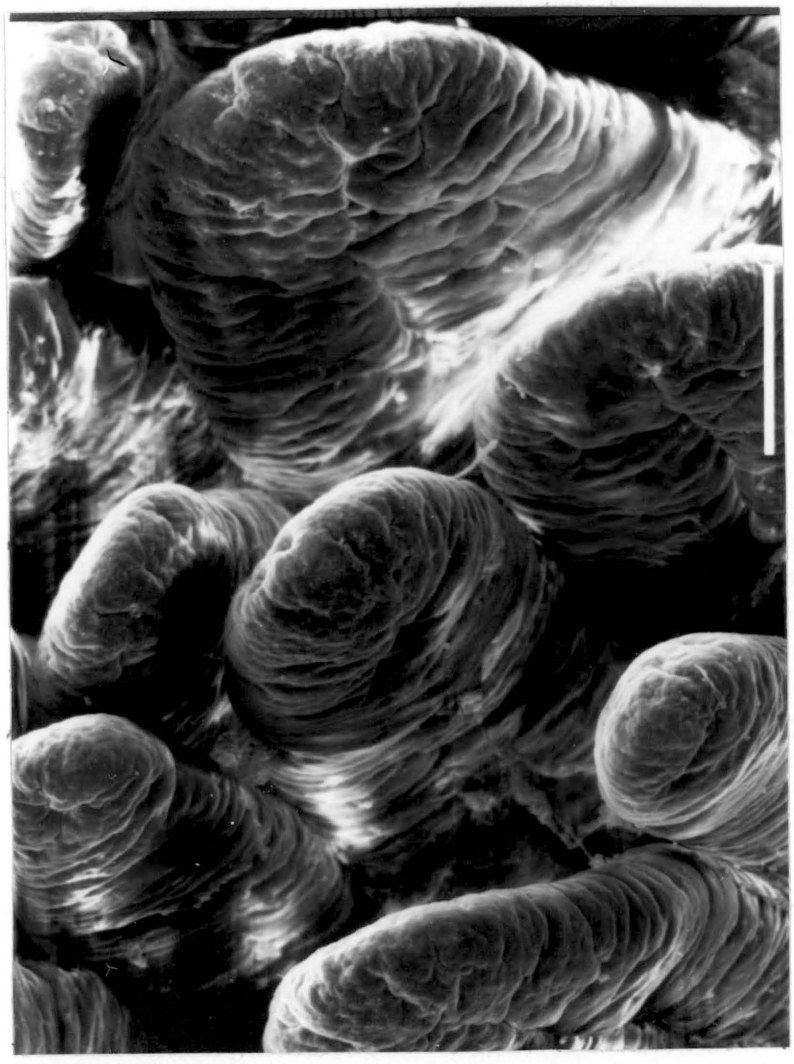


D

Figure 1. Representative jejunum morphology of pigs fed the basal diet. See page 244 for caption.

A

B



C

Figure 2. Jejunum morphology observed in pigs fed the high-fiber diets which resembles that seen in pigs fed the basal diet. See page 244 for caption.

A

B

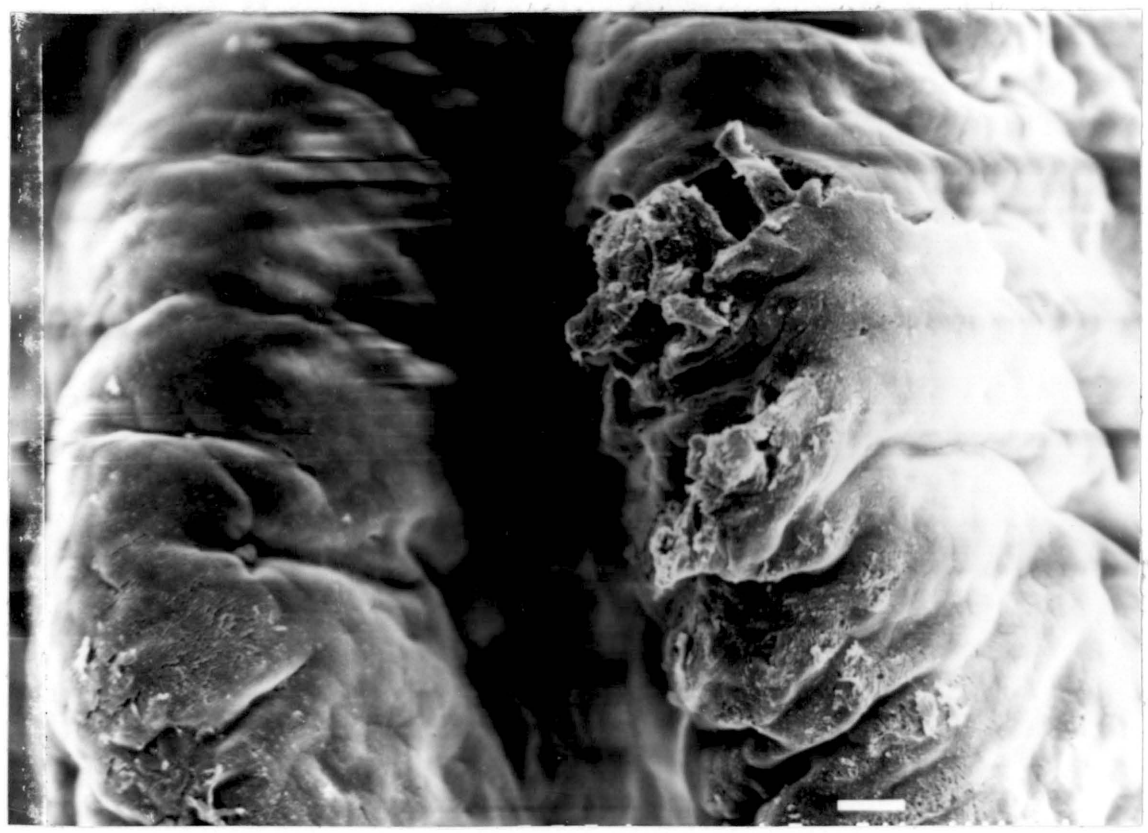
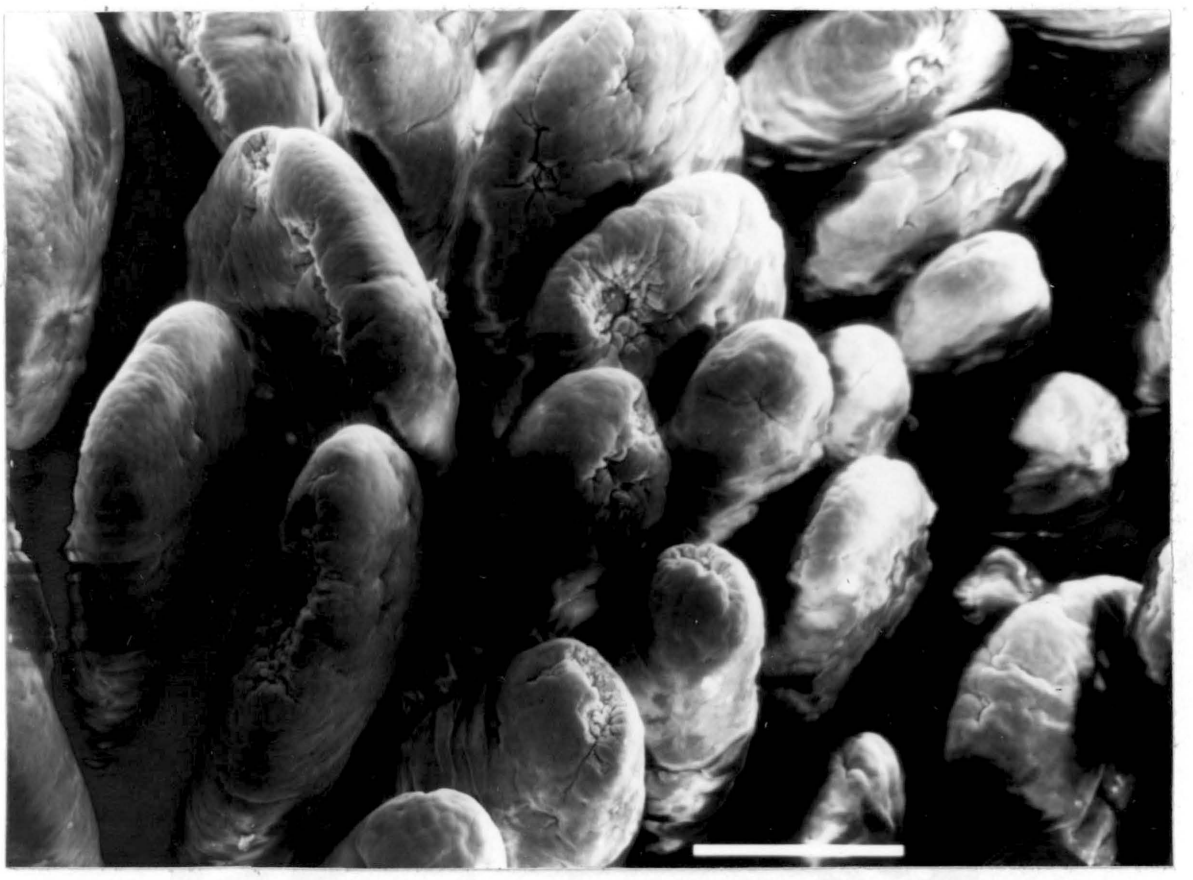


Figure 3. Different jejunum morphology observed in one pig fed the SH diet. See page 244 for caption.

A



B

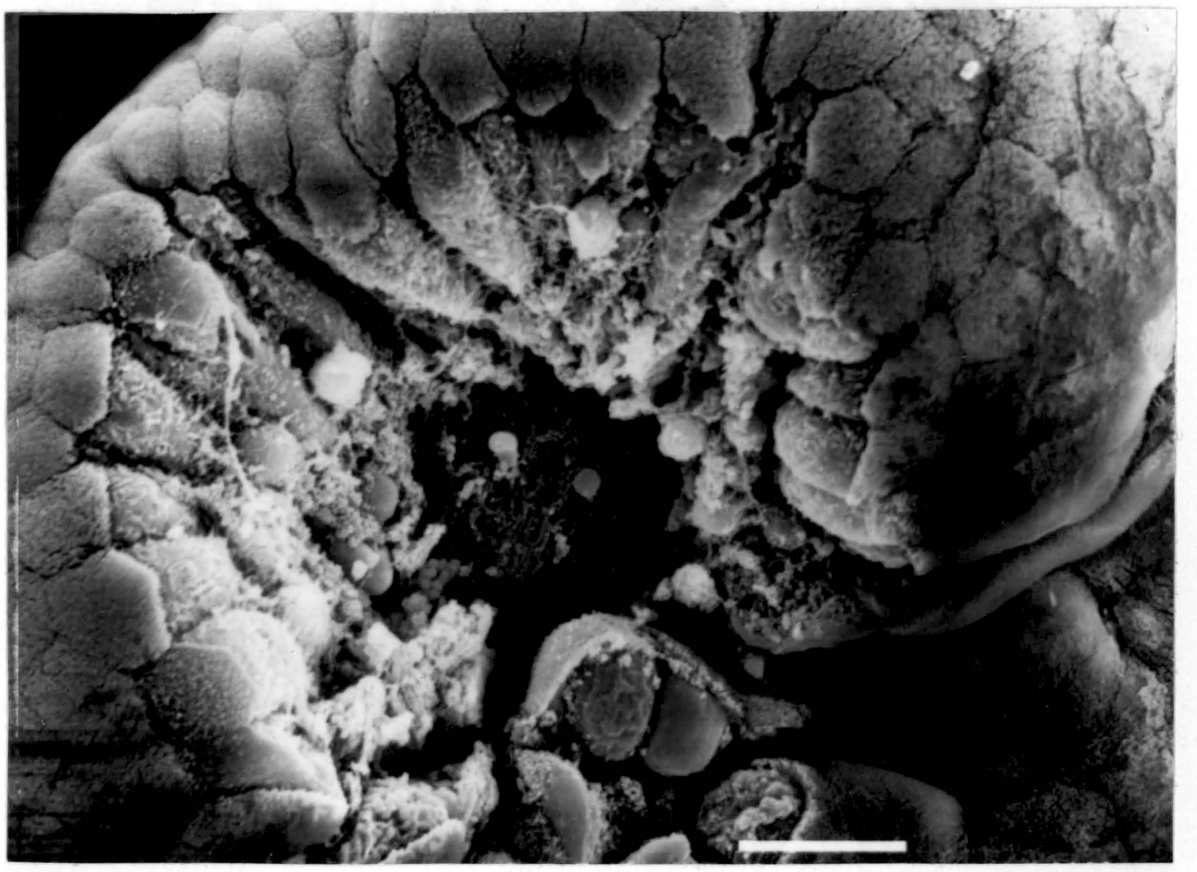
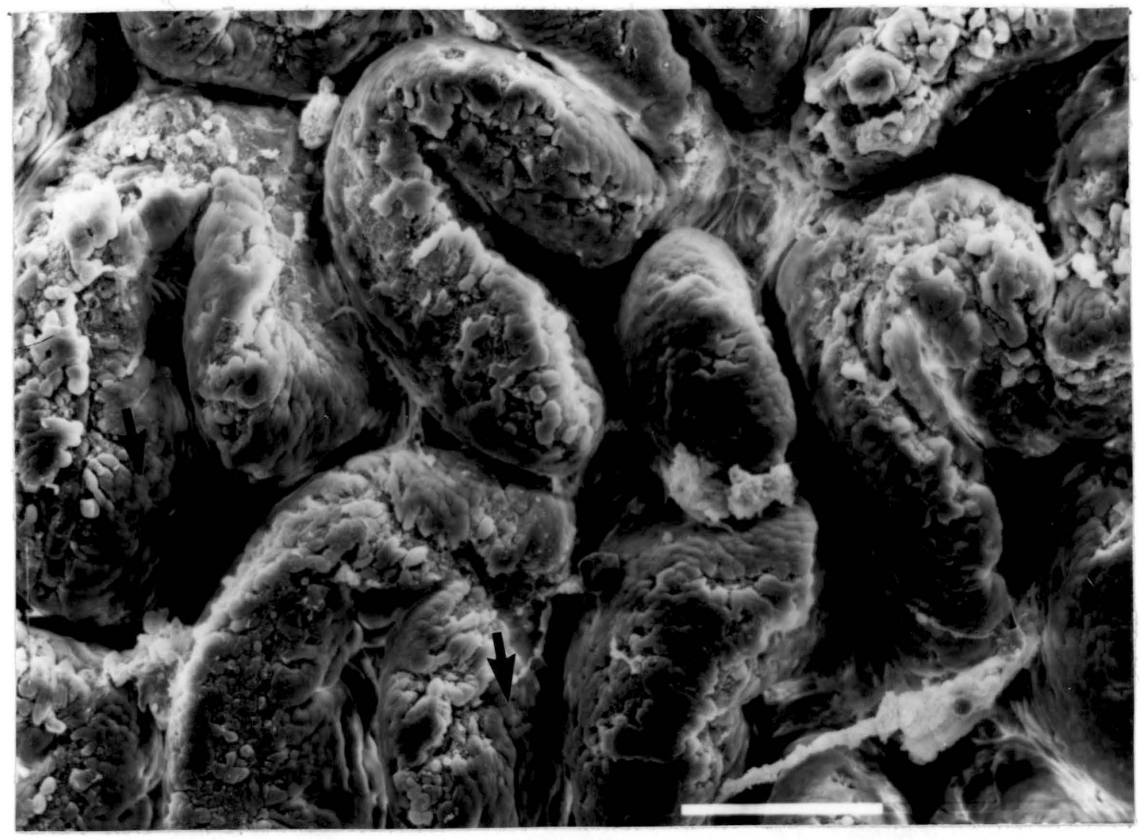


Figure 4. Different jejunum morphology observed in one pig fed the AM diet. See page 244 for caption.

A



B

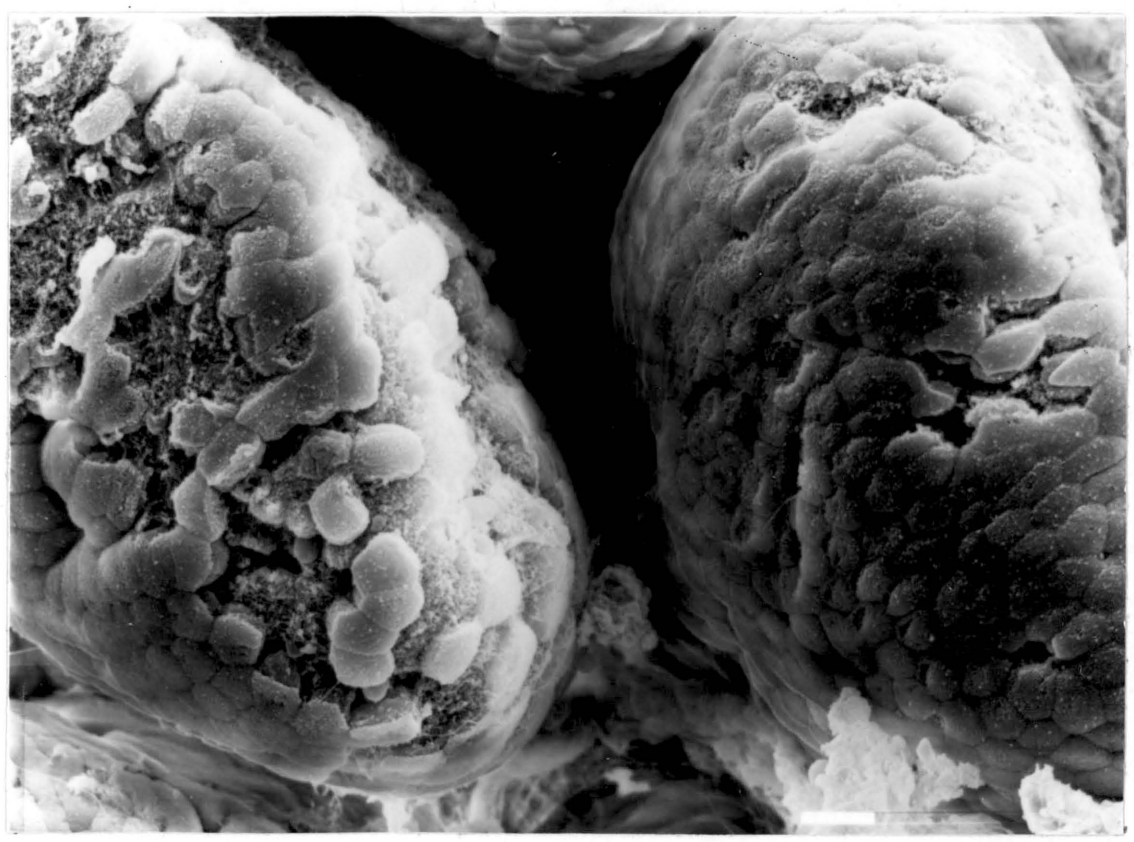


Figure 5. Different jejunum morphology observed in one pig fed the AM diet. See page 244 for caption.

Figure 1. Representative jejunum villus morphologies of pigs fed the basal diet. Villi were tongue- and finger-like in two pigs (A and B), but were mostly leaf-like in the third pig (C). The surface was smooth in appearance, and individual cells were arranged in a uniform pattern, and were densely covered with microvilli (D). A cleft of disorganized cells was present in one sample (A) at the villus apex and probably reflects the cell extrusion zone. Magnification of A through C approximately 200x (bars=100 um). Magnification of D approximately 2000x (bar=10 um).

Figure 2. Representative jejunum villus morphologies of pigs fed the high-fiber diets. In all but three pigs, morphology was not different from that of pigs fed the basal diet. Villi were finger- and tongue-like, and the surface epithelium did not differ from that of pigs fed the B diet. Small areas of cellular disarray (arrows, C) were present, but the incidence and surface area affected were small. Micrographs represent pigs fed the SH (A), AM (B) and OH (C) diets. Magnification of A through C approximately 200x (bars=10 um).

Figure 3. Different jejunum villus morphology was seen in one pig fed the SH diet. Villi were tongue-like (A), and many had areas of mild cellular and microvillus disarray (B) at the villus apex, frequently associated with interruptions of the epithelium. The lateral villus surfaces were normal in appearance. Magnification of A approximately 200x (bar=100 um). Magnification of B approximately 660x (bar=10 um).

Figure 4. Tongue- and finger-like villi were present in jejunum of one pig fed the AM diet. There were clefts of cellular disarray and crater-like areas with loss of epithelial cells at the apical villus surfaces (A). The crater-like areas (B) were bordered by normal appearing epithelium, although some bordering cells lacked a microvillus covering. The lateral villus surfaces were unaffected. Magnification of A approximately 200x (bar=100 um). Magnification of B approximately 1600x (bar=10 um).

Figure 5. Jejunum villi were blunted and irregularly folded with flattened apical surfaces in one pig fed the AM diet (A). The lateral surfaces were mostly unaffected, but some had a corrugated-like appearance (arrows, A). There was a loss of epithelial cells and microvilli at the apical surface, frequently associated with cellular disarray (B). Some villi (right, B) within these areas were not affected, or had small areas of damage. Magnification of A approximately 200x (bar=100 um). Magnification of B approximately 720x (bar=10 um).

A

B

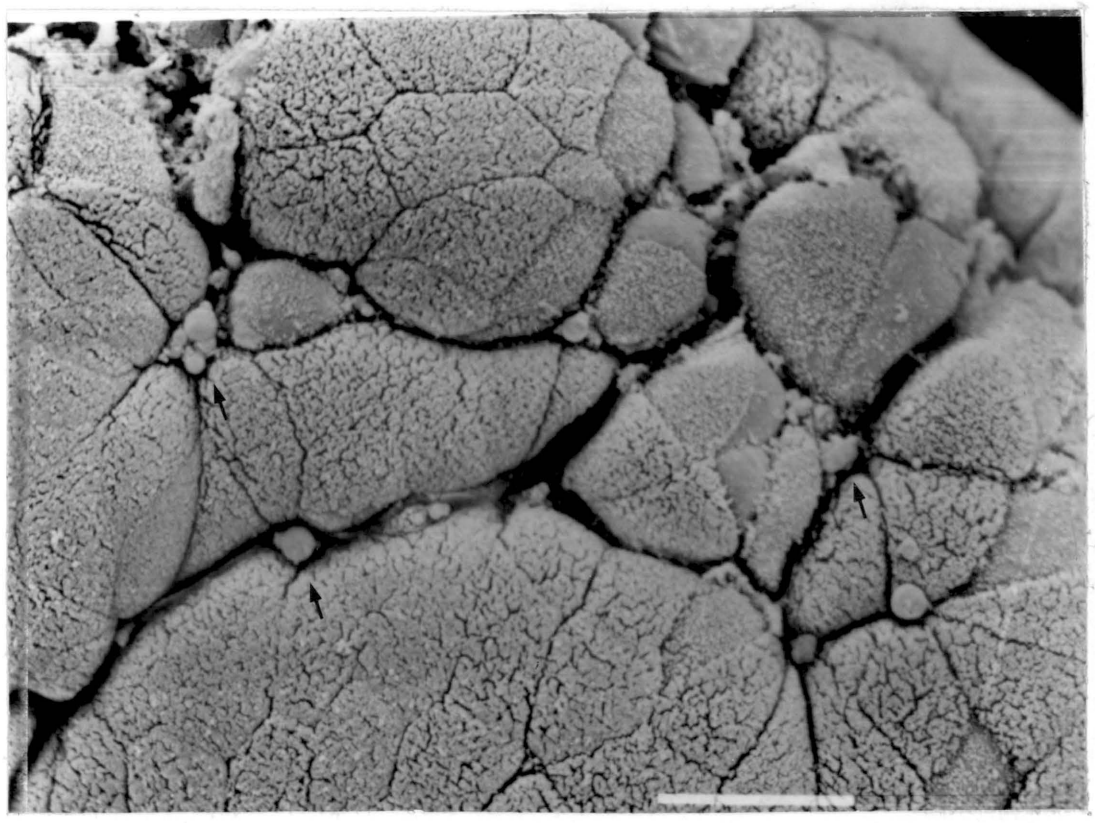


Figure 6. Atypical ileum morphology represented by that observed in pig fed the basal diet. See page 249 for caption.

A

B

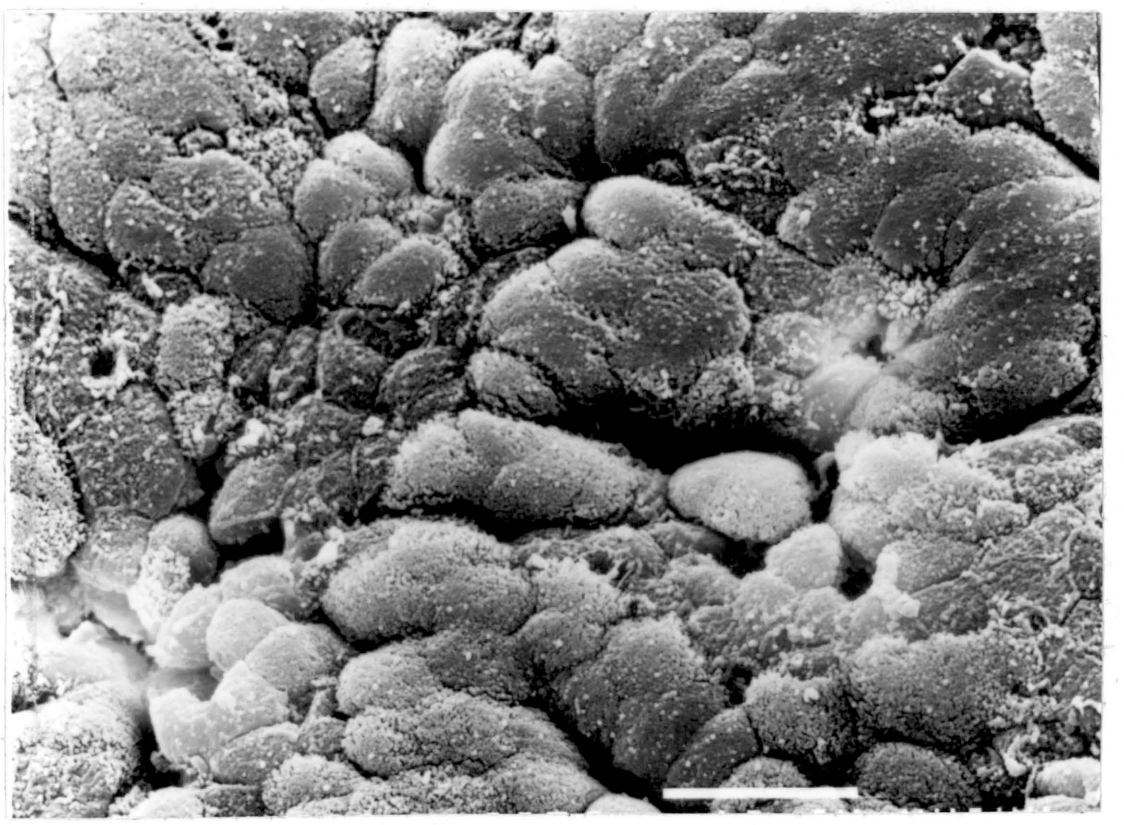
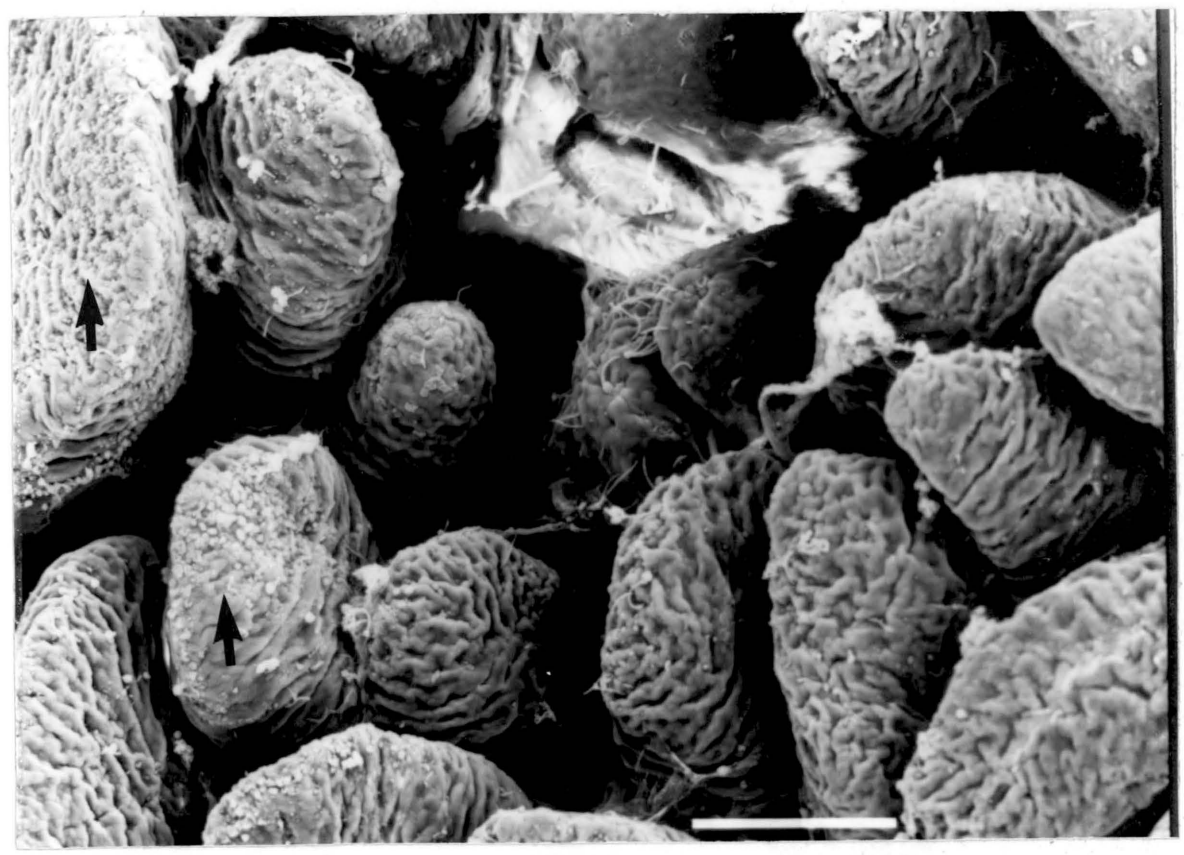


Figure 7. Representative ileum morphology of pigs fed the high-fiber diets which is similar to that observed in pigs fed the basal diet. See page 249 for caption.

A



B

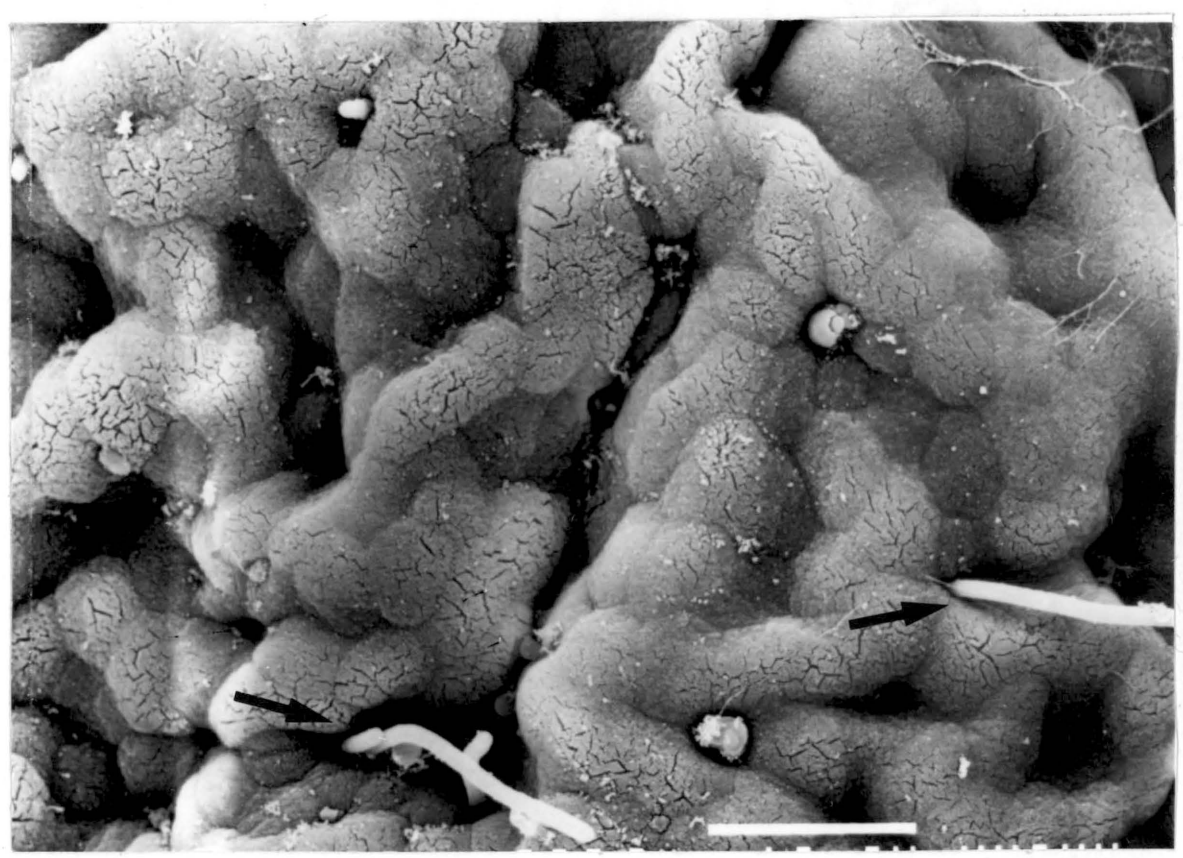
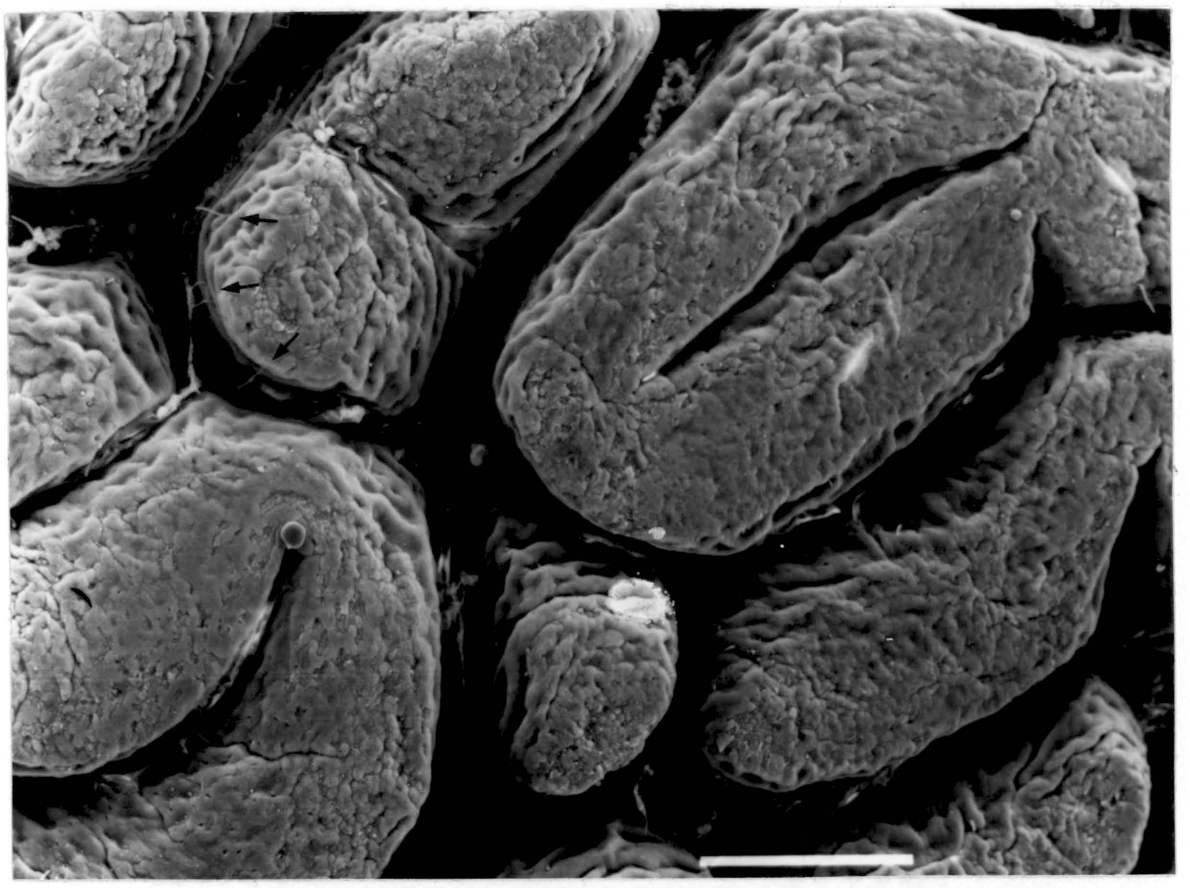


Figure 8. Different ileum morphology observed in one pig fed the SH diet. See page 249 for caption.

A



B

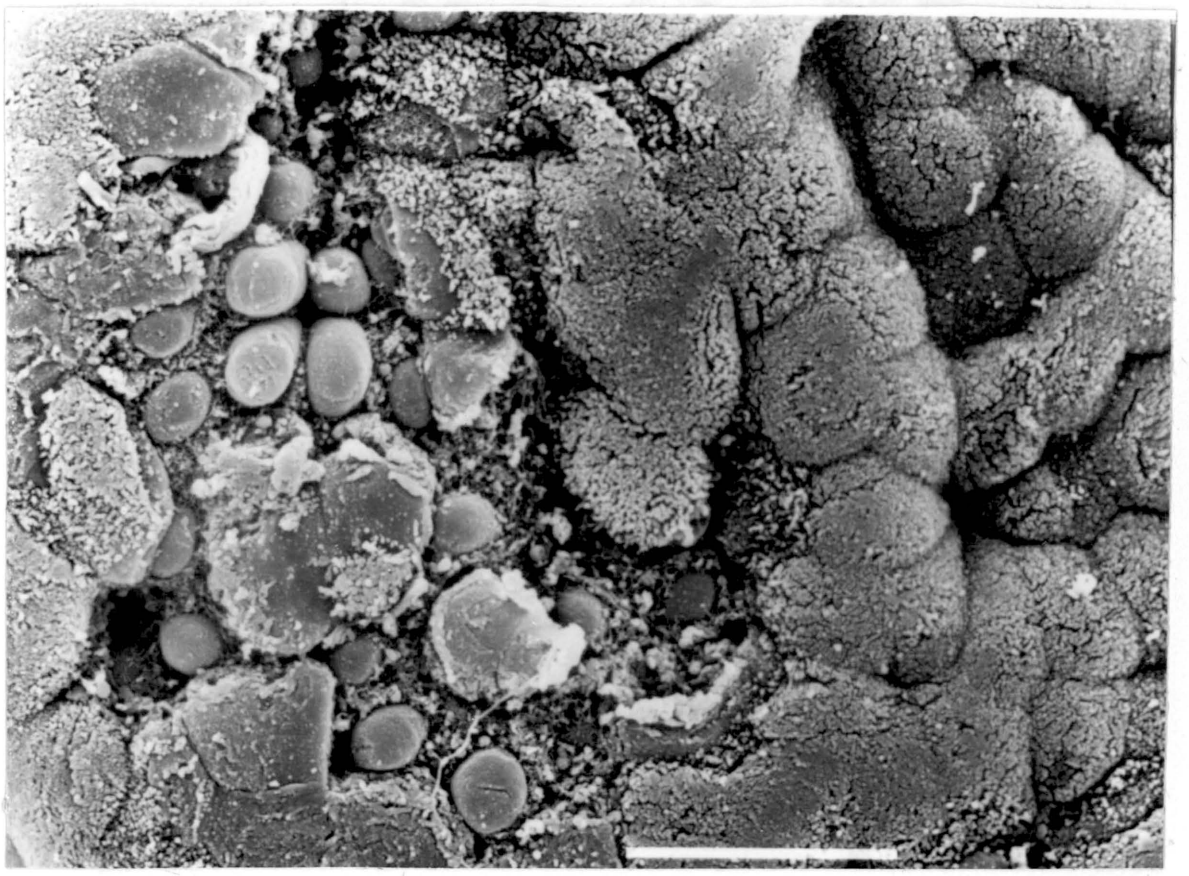


Figure 9. Similar ileum morphology as that shown in figure 8 observed in same pig fed the SH diet. See page 249 for caption.

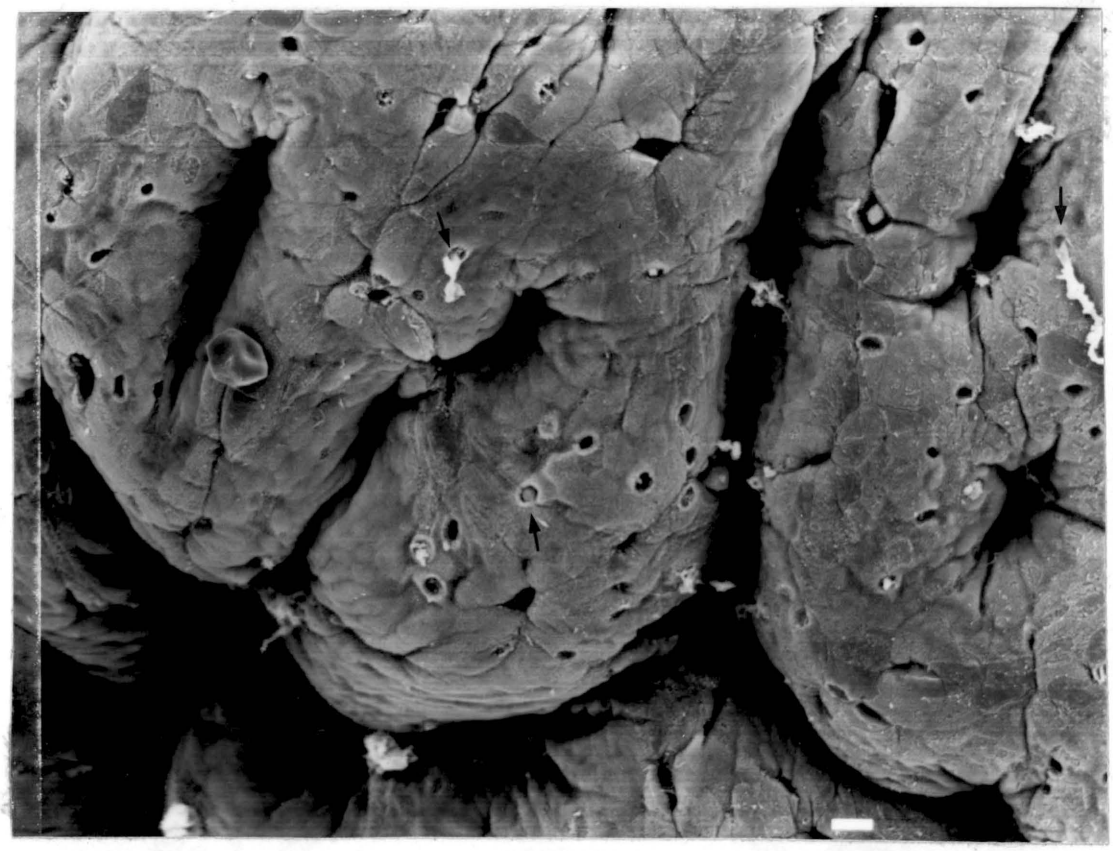
Figure 6. Most ileum villi were finger- and tongue-like. Cellular disarray was common along the apical surface (A), and probably reflects the cell extrusion zone. The lateral surfaces were smooth, and epithelium interruptions were infrequent. The cellular disarray and loss of microvilli on individual cells at the villus apex (B) was not extensive. Areas adjacent to these areas were normal, and are representative of the lateral surface morphology on villi of this type. Some cellular debris is present at the apex (arrows, B). Magnification of A approximately 200x (bar=100 um). Magnification of B approximately 2000x (bar=10 um).

Figure 7. In most pigs, areas of cellular disarray and minor microvillus erosion were seen on the upper one-third of individual villi (arrows, A). The cells lacked the organized pattern and shape commonly seen (figure 6B), and there was loss of microvilli on individual cells (B). The occurrence and extent of this morphology was variable in different pigs. Magnification of A approximately 200x (bar=100 um). Magnification of B approximately 2000x (bar=10 um).

Figure 8. In one pig fed the SH diet, ileum villi were finger- and tongue-like (A), but the surface had a corrugated-like appearance. There was cellular disarray and loss of microvilli at the villus apex (arrows, A). The surface epithelium was otherwise densely covered with microvilli (B). Filamentous microorganisms were observed attached to the epithelium (arrows, B) only in this pig. Magnification of A approximately 200x (bar=100 um). Magnification of B approximately 2000x (bar=10 um).

Figure 9. Some ileum areas from the same pig as in figure 8 had a more disorganized appearance. Villi were blunted and folded, although the lateral surface had a corrugated appearance. The surface showed extensive cellular disarray and loss of microvilli and epithelial cells (B), and cellular debris was visible. Adjacent areas were relatively normal, although the corrugated morphology was evident. The surface in B is representative of damage seen on the villus apex of villi in figure 8A. Filamentous microorganisms can be seen in A (arrows). Magnification of A approximately 200x (bar=100 um). Magnification of B approximately 2600x (bar=10 um).

A



B

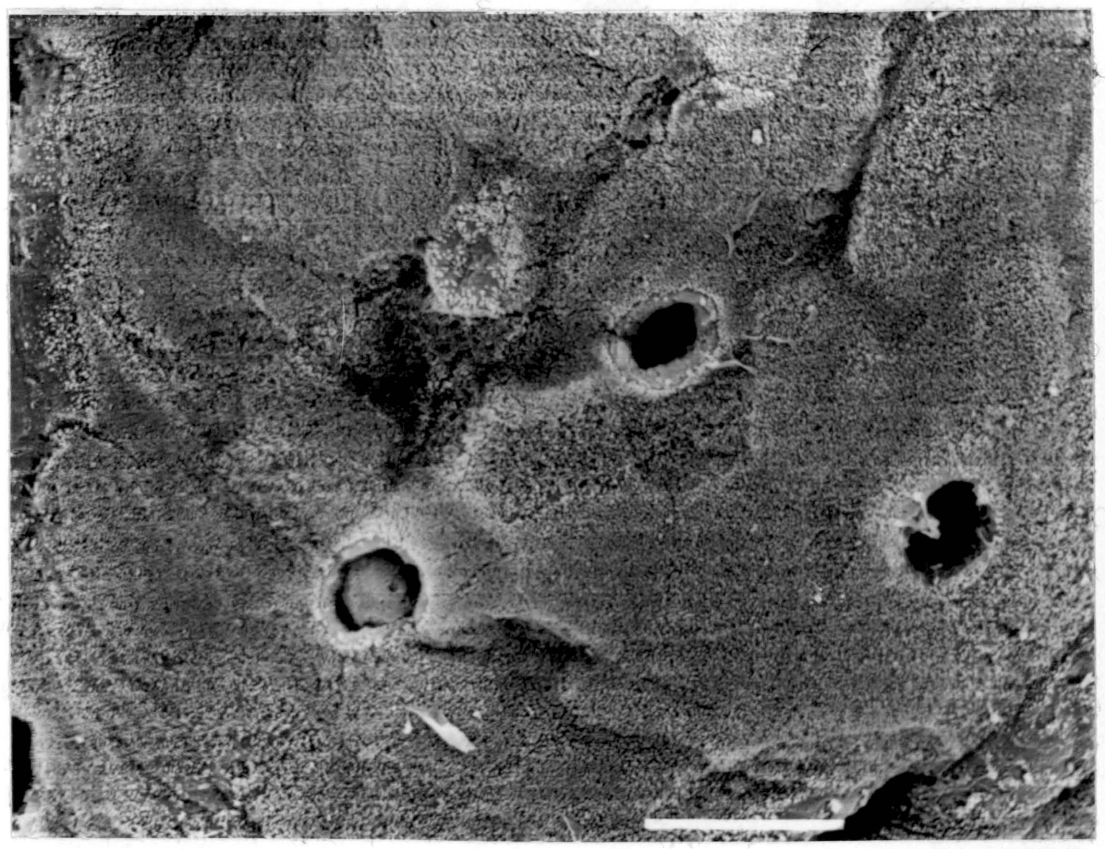
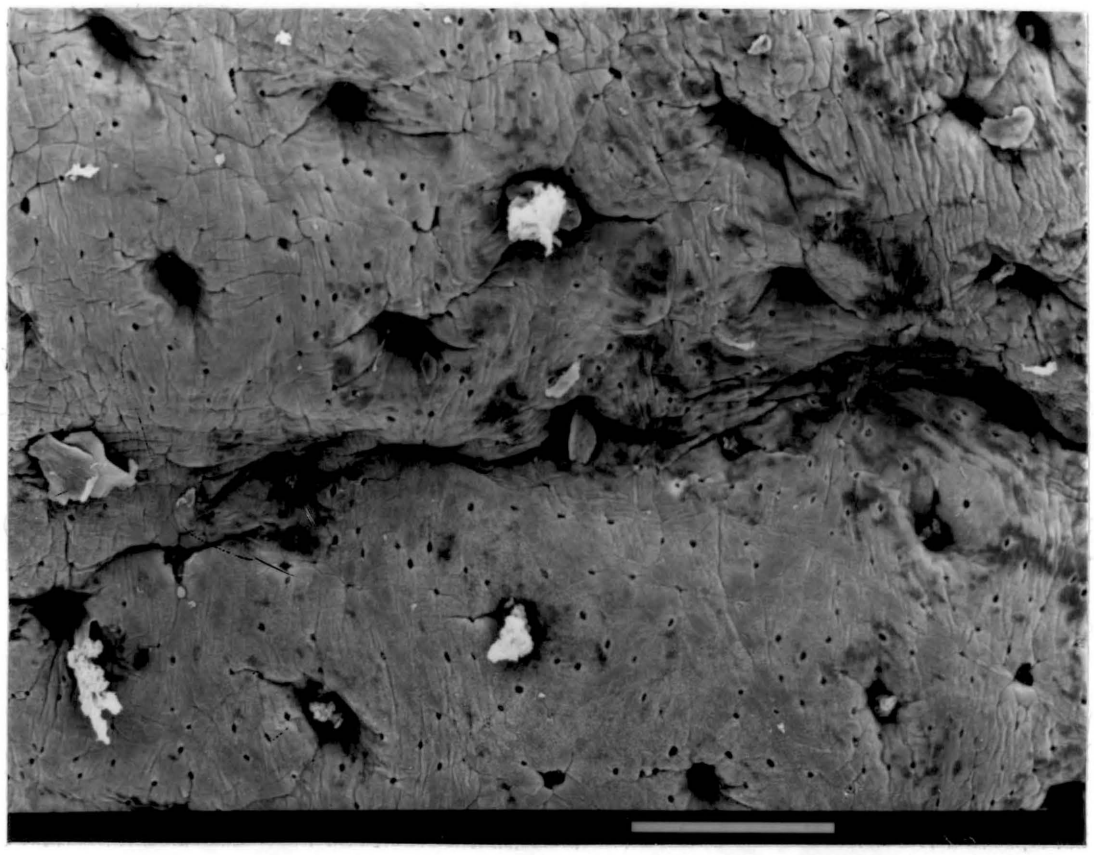


Figure 10. Colon morphology observed in pig fed the basal diet. See page 254 for caption.

A



B

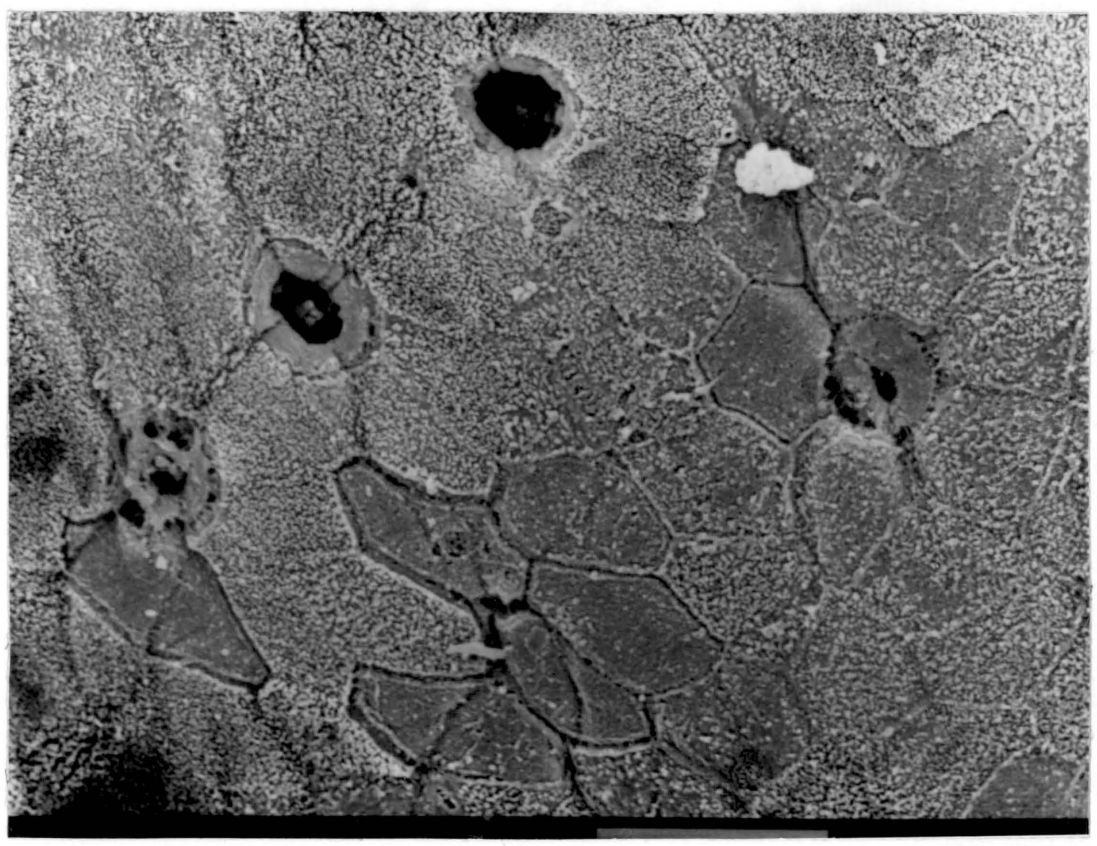
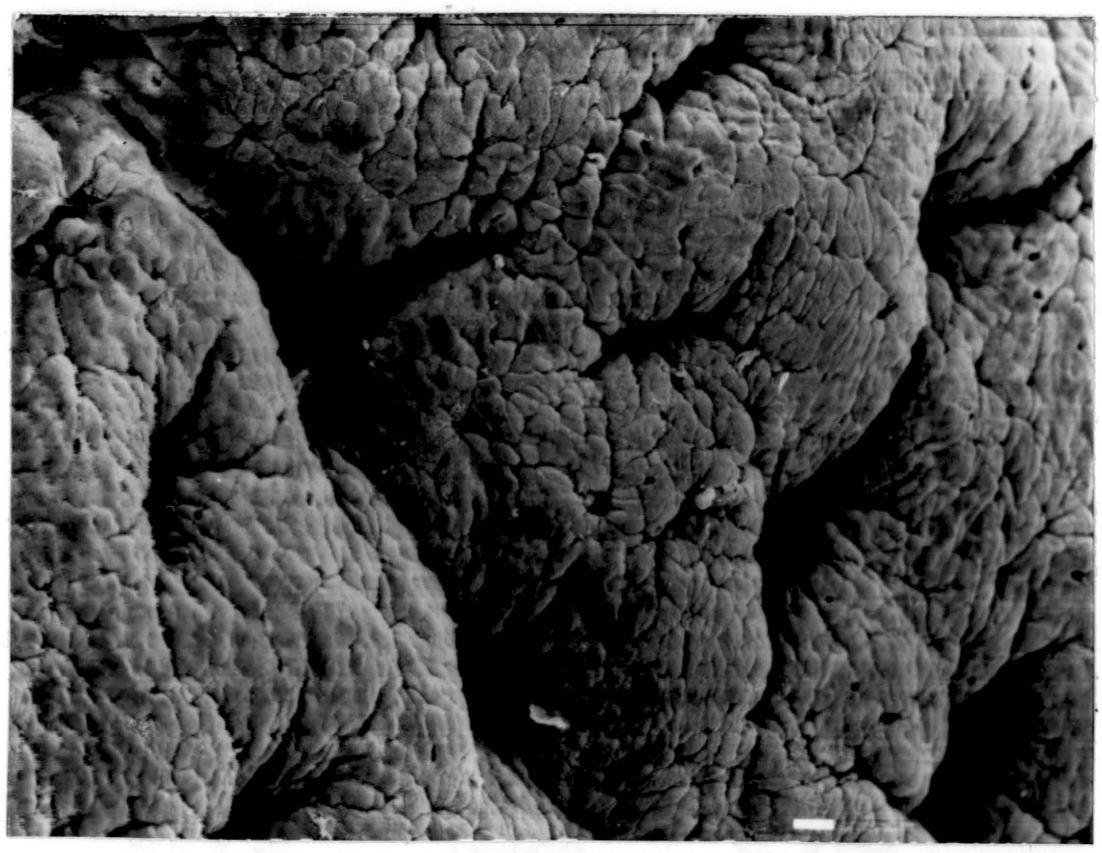


Figure 11. Colon morphology observed in pig fed the AM diet. See page 254 for caption.

A



B

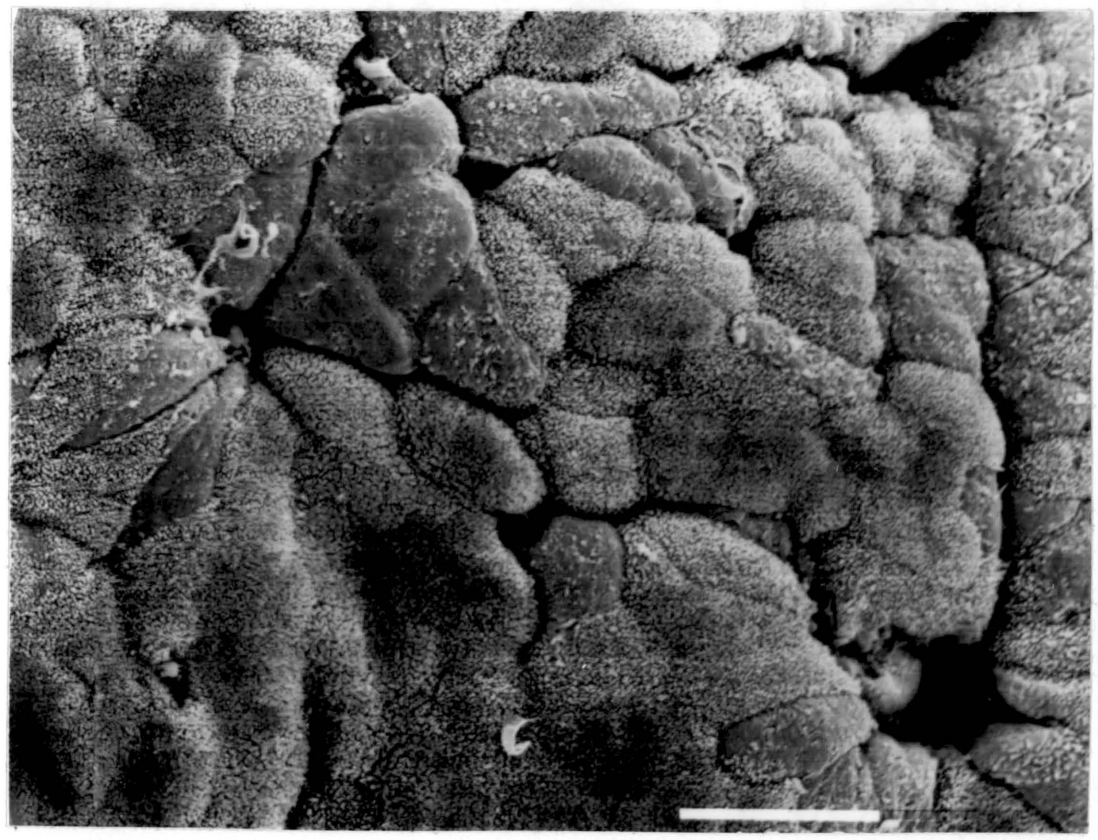
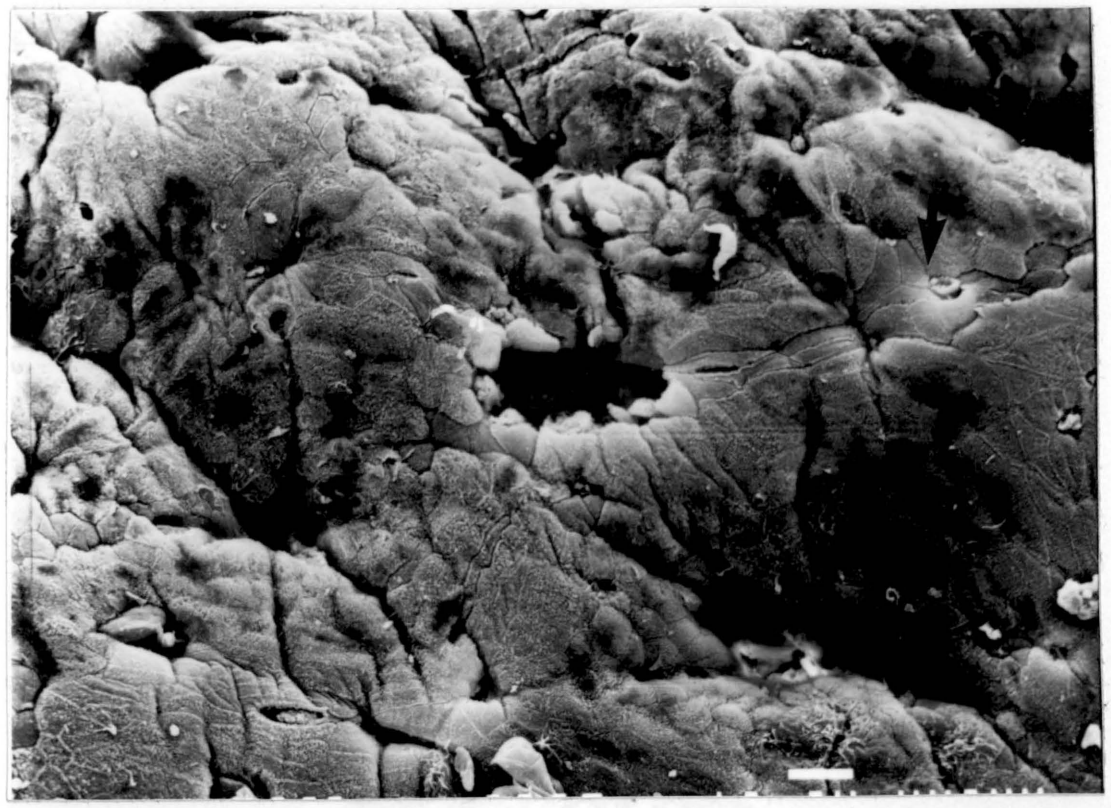
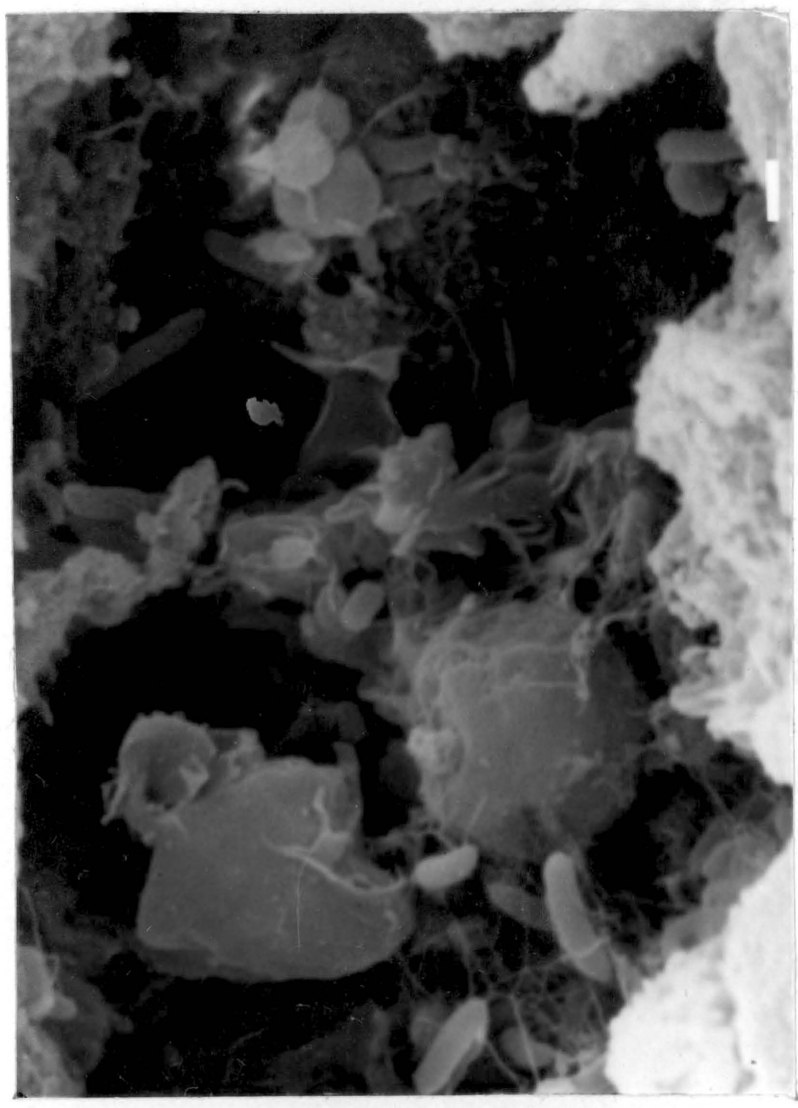


Figure 12. Colon morphology observed in pig fed the OH diet. See page 254 for caption.

A



B



C

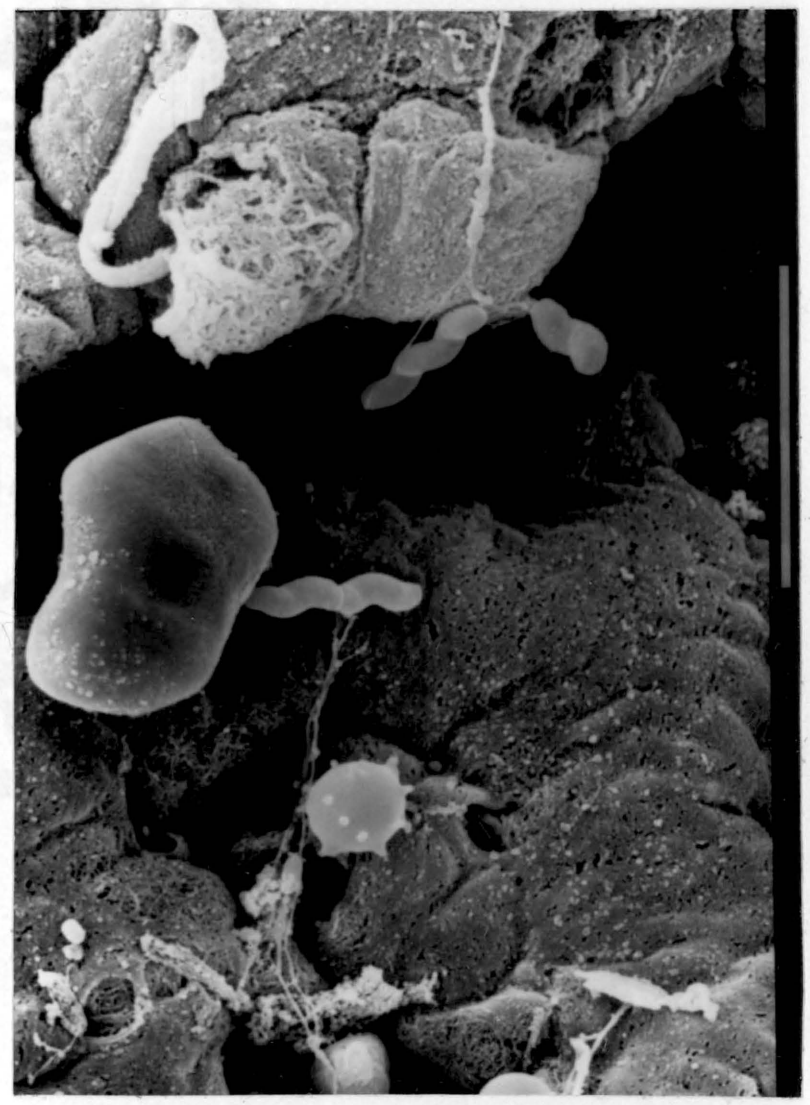


Figure 13. Morphology associated with interruptions in colon epithelium. See page 254 for caption.

Figure 10. Three distinct colon morphologies were present in pigs fed the four diets. Figure 10A represents a typical colon surface observed in many pigs (from pig fed the B diet). The surface was smooth, and crypt and goblet cell openings were prominent. The surface was densely covered with microvilli (B), although small areas comprised of a few cells each were present with few or no microvilli (arrows, B). Mucous strands can be seen at some goblet cell orifices (arrows, A). Magnification of A approximately 400x (bar=10 um). Magnification of B approximately 2000x (bar=10 um).

Figure 11. A second morphology type was frequently seen (A). This sample from a pig fed the AM diet has a similar morphology as that in figure 10A. The density of microvilli was less and the areas of lower microvilli density were extensive (B). However, areas of colon with a microvillus density similar to that in figure 10B were also present. Magnification of A approximately 200x (bar=100 um). Magnification of B approximately 2200x (bar=10 um).

Figure 12. A third morphology observed in some pigs was characterized by an irregular surface (A). There was cellular disarray (B), and the pattern of microvillus was similar to density that of figure 10B. Magnification of A approximately 400x (bar=10 um). Magnification of B approximately 2000x (bar=10 um).

Figure 13. Many colon samples had interruptions in the epithelium, but the occurrence and extent were variable. Figure 13A shows a small hole in the colon epithelium of a pig fed the AM diet. The surface shows an exaggerated version of the morphology shown in figure 12A. There were large areas without microvilli (arrows, A). The interruptions in epithelium were usually inhabited by microorganisms. Figure 13B represents the hole seen in figure 13A. Numerous bacteria were present along with cellular and surface debris. Figure 13C is a view of a colon surface interruption from a pig fed the SH diet. A different type of bacteria are present, along with a food particle and a presumed macrophage. Although the size of these holes were usually small, some areas of colon were present with extensive networks of epithelial interruptions. Magnification of A approximately 660x (bar=10 um). Magnification of B approximately 5400x (bar=1 um). Magnification of C approximately 3200x (bar=10 um).

Villus morphologies consistent with current concepts of abnormal intestinal morphology were observed, although they were restricted to specific intestinal sites, and generally occured in only a single pig (i.e. figures 5, 8 and 9). These morphologies consisted of blunted and folded villi with areas of cellular disarray and erosion of microvilli, or in the case of colon, a lower microvilli density and occasional interruptions in the epithelium. These types of damage have been reported in rats fed different high-fiber diets (Cassidy et al., 1981, 1982). Additionally, small clefts or seams which lacked the integrity of adjacent villar areas were present at the apex of many ileal villi. Although these areas may only reflect the cell extrusion zone, reports indicate that similar types of morphologies are absent in intestines from rats fed conventional chow- or purified diets, but are present in intestines from rats fed various bile-salt binding resins (Cassidy et al., 1980).

Our observations suggest that areas of damage were present in the intestines of pigs used in the present study, although the surface area affected and the incidence were relatively low. Scheibel and Mehta (1985) reported that pectin resulted in a higher incidence of blunted and fused villi in rats, but only a small proportion of rats were affected. Similarly, Knehans and

O'Dell (1980) showed that surface epithelial damage was more frequent in guinea pigs fed alfalfa although all guinea pigs were not affected equally. More importantly, growth was higher for guinea pigs fed the diets containing alfalfa. The physiological significance to the health or nutritional status of the pigs which exhibited epithelial abnormalities in the present study is not clear, since growth or nutrient utilization was not different between the different pigs (chapter 6).

The microbial flora of the intestine is responsible for much of what is considered 'normal' intestinal morphology in animals (Abrams, 1977). The effects of dietary fiber on intestinal morphology may in part reflect the ability of dietary fiber to alter bacterial numbers or metabolism. Since the microbial population in different pigs and in different intestinal sites within individual pigs varies considerably (Salanitro et al., 1977; Allison et al., 1979), particular pigs may be more susceptible to effects of dietary fiber on intestinal structure or function than others.

In ileum of one pig fed SH, villi exhibited a dramatic difference in shape and surface morphology compared with that observed in the other pigs (figures 8 and 9), which was accompanied by a loss of cellular material and microvilli at the villar apex. Additionally,

only in this pig were filamentous bacteria seen attached to the epithelial surface. Although these bacteria have been described in rodent ileum (Erlandsen and Chase, 1974), we are unaware of their description in pigs. We have observed these bacteria associated with a similar corrugated ileal villus morphology in a pig fed rice bran (unpublished observations). Whether there exists a causal relationship between diet composition, the presence of these particular bacteria, and this type of morphology is unknown. Similarly, a variety of microorganisms were associated with interruptions in colon epithelium, and it is not known whether these are opportunistic inhabitants, or are part of the cause of this type of damage. Knehans and O'Dell (1980) reported that a novel fusiform-like organism was associated with unusual epithelium indentations in small intestine of guinea pigs fed alfalfa. Thus, the interrelationships between the intestinal microflora and diet composition, and intestinal structure, deserve additional study.

The potential variation in microbial response to dietary fiber, and the relatively high fiber content of the basal diet (approximately 9% neutral-detergent fiber), preclude our concluding that dietary fiber does not have a significant effect on intestinal morphology in the pig. Fiber intakes by the pigs fed in the present

experiment (on a metabolic bodyweight basis) approach fiber intakes of rats fed high-fiber diets in many studies. Thus, the 'low-fiber' diet we fed may already have resulted in morphologic changes associated with high fiber intakes, above which the fiber supplements were unable to exert a detectable effect. Tasman-Jones et al. (1982) have shown that fiber sources added to a chow-type diet have less effect on post-weaning intestinal morphology in rats than when the fiber sources are added to a fiber-free diet.

The present results indicate that the addition of moderate amounts of high-fiber ingredients to conventional corn-soybean meal diets has a minimal effect on intestinal morphology in the pig. However, evidence of damage to the epithelium was observed in most pigs, but was extensive only in some animals fed the high-fiber diets. Further study is required using fiber-free diets to determine whether the fiber present in cereal grain-oilseed meal diets contributes to the occurrence of intestinal epithelium damage, and to determine whether this type of abnormal morphology may be a factor limiting nutrient utilization by pigs fed these type diets.Since certain pigs appear to be more susceptible to intestinal damage than others, identification and use of these animals may be able to offer insight into some of the

relationships between diet composition, the microflora, and intestinal structure and function.

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CHAPTER VIII

SUMMARY AND CONCLUSIONS

The present experiments indicate that moderate additions of high-fiber feedstuffs to practical swine diets have a minimal negative impact on nutrient utilization by growing pigs. The fiber sources which were fed (wheat bran, oat hulls, soybean hulls, and alfalfa meal) all decreased apparent N and energy absorption, but did not affect N retention. These results are in agreement with the well documented effects of dietary fiber on the utilization of nitrogen and energy.

Viewed as a whole, the mineral balance data obtained from the three sets of balance trials argues against the hypothesis that dietary fiber has a negative impact on mineral utilization of pigs limit-fed corn-soybean meal type diets. Although oat hulls decreased apparent absorption of some minerals in the first set of trials, the effect of oat hulls was inconsistent, and the two subsequent sets of experiments did not offer convincing data to support a negative effect of oat hulls on mineral utilization. Although differences in the composition of the oat hulls used in the different trials, and different mineral levels in the experimental diets probably contribute to the variability of the results, the small

numbers of animals per treatment in each trial were also probably responsible for some of the variation.

However, some characteristics of the present data limit a blanket conclusion minimizing a negative effect of fiber on mineral balance in pigs under practical feeding situations. In all of the present experiments, pigs were limit-fed diets which contained relatively low levels of the fiber sources (20% or less) and had mineral levels at or exceeding the suggested requirements of the pig. It is reasonable to expect that diets fed ad libitum which contain different fiber sources or contain higher levels of fiber than we fed may result in a different response. However, given the ability of intestinal transport capacity to adapt to different nutrient loads and metabolic requirements, it seems unlikely that high-fiber diets will drastically alter nutrient status of pigs, unless other factors or conditions are present which can limit nutrient availability or absorption.

In contrast to the possible negative effects of fiber on mineral utilization, the results of the different trials indicate that some high-fiber feedstuffs may have a beneficial effect on mineral availability. Although all fiber sources increased Fe intake, SH and AM consistently increased Fe balance, which suggests that

some fiber sources could be used as acceptable sources of available minerals in pig diets. Additionally, the results of experiment 2 suggest that replacement of corn and soybean meal with SH could increase Mg absorption. Whether this results from shifts in the proportion of fiber or minerals from the different ingredients is not clear, but the response indicates that the potential exists for improving nutrient availability from practical diets through modifications of diet ingredient formulations.

The variable intestinal morphologies observed in pigs, regardless of diet fed, prevents any definitive conclusions from being made regarding the effect of high-fiber feedstuffs on intestinal structure. However, intestinal morphologies were present in some pigs which, although they were not correlated with growth or nutrient utilization, were obviously undesirable. In agreement with reports in rodents, the fact that only a proportion of pigs showed abnormal intestinal morphologies suggests that certain pigs may be more susceptible to possible negative effects of dietary fiber than others. These observations emphasize that information is needed on what can be considered 'normal' or 'acceptable' intestinal structure in the pig. This particular information is requisite to future studies which are needed in order to

determine the relationship between intestinal structure and function, and how diet compositions may be modified in order to maximize nutrient absorption.

APPENDIX A

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CHAPTER VI

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Appendix table 1. Analyzed nutrient contents of diets fed in trials 1 through 4 (as-is basis)

	Trials 1 and 2						Trial 3						Trial 4					
Fiber source	Basal		Oat hulls		Soybean hulls		Basal		Oat hulls		Soybean hulls		Basal		Oat hulls		Soybean hulls	
Mineral level	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
Dry matter,%	90.3	91.0	91.8	91.3	91.4	89.9	92.3	92.6	92.3	92.5	92.2	92.6	91.9	91.5	92.2	91.7	91.6	92.0
NDF,%	10.01	9.82	16.44	16.52	18.58	18.06	9.03	8.87	15.19	16.15	16.78	16.63	9.54	8.85	17.39	17.40	16.86	17.06
ADF,%	3.74	3.54	7.84	7.49	10.51	9.98	3.19	3.42	7.01	7.46	9.12	9.56	3.35	3.37	8.17	8.42	10.04	10.12
Cellulose,%	2.87	2.71	5.55	5.54	8.71	8.32	2.72	2.65	5.72	5.64	7.93	8.05	2.56	2.44	5.94	6.06	8.16	8.16
Hemicellulose,%	6.27	6.28	8.60	9.03	8.07	8.08	5.84	5.45	8.18	8.69	7.66	7.07	6.19	5.48	9.22	8.98	6.82	6.94
Lignin,%	1.06	1.04	1.89	1.45	1.98	1.78	0.68	0.95	1.11	1.58	1.71	1.70	0.82	0.77	1.61	1.90	2.20	1.94
Nitrogen,%	2.20	2.22	2.15	2.12	2.10	2.17	2.42	2.40	2.22	2.14	2.24	2.20	2.41	2.39	2.16	2.19	2.20	2.10
Ca,%	.471	.516	.539	.534	.512	.528	.770	.787	.777	.778	.774	.774	.753	.779	.774	.772	.780	.852
P,%	.478	.489	.492	.498	.473	.480	.686	.693	.690	.712	.690	.689	.675	.705	.704	.715	.686	.752
Mg,%	.119	.144	.113	.144	.117	.150	.124	.144	.123	.144	.127	.147	.120	.140	.118	.135	.134	.152
Na,%	.096	.150	.109	.156	.090	.151	.108	.165	.113	.164	.114	.167	.102	.128	.105	.109	.099	.136
K,%	.649	.644	.635	.612	.705	.685	.506	.515	.493	.515	.627	.642	.581	.592	.546	.550	.630	.630
Zn, mg/kg	54.2	109.5	65.4	117.7	52.1	106.5	52.4	100.5	63.5	110.6	54.3	101.9	57.6	110.5	67.2	109.2	70.7	122.7
Fe, mg/kg	54.3	104.0	81.4	129.8	115.1	163.0	67.1	118.0	97.3	146.6	124.2	175.2	64.3	117.3	76.0	117.6	123.4	172.8
Cu, mg/kg	3.7	6.7	3.6	6.1	3.9	6.6	5.3	8.5	5.4	8.4	5.0	8.9	5.4	8.4	5.9	9.9	5.8	9.1
Mn, mg/kg	13.9	15.3	21.5	22.3	12.3	14.7	15.0	17.7	21.1	23.1	13.3	16.7	12.5	14.8	19.6	18.4	15.1	18.6

Appendix table 2. Initial and final bodyweights and weight gains of pigs for trials 1 through 4

	Trial 1				Trial 2				Trial 3				Trial 4			
Cage	Diet	Init.	Fin.	Gain	Diet	Init.	Fin.	Gain	Diet	Init.	Fin.	Gain	Diet	Init.	Fin.	Gain
		kg				kg				kg				kg		
1	B-	44.5	61.4	.468	OH+	68.2	91.4	.723	B-	48.2	74.5	.695	SH+	42.3	58.2	.409
2	OH-	47.3	64.1	.468					OH-	47.3	67.3	.527	SH-	42.7	60.4	.454
3	SH-	46.8	63.2	.454	OH-	67.3	88.2	.654	SH-	44.5	65.4	.550	OH+	41.8	56.4	.373
4	B+	45.4	64.5	.532	SH-	67.3	90.0	.709	OH+	44.5	67.3	.600	B-	40.9	57.3	.418
5	OH+	45.4	63.6	.504	SH+	69.5	90.0	.641	B+	44.1	69.1	.659	B+	39.1	61.4	.573
6	SH+	45.9	70.9	.695	B+	67.7	86.4	.582	SH+	43.2	65.9	.600	OH-	43.2	60.9	.454
7	OH+	46.4	63.2	.468	OH-	69.1	86.4	.541	B-	44.5	73.2	.754	B+	41.4	60.9	.500
8	SH+	43.6	60.4	.468	SH-	70.0	92.3	.695	OH-	45.4	68.2	.600	OH-	37.3	51.8	.373
9	B-	46.4	69.5	.645	B+	68.6	93.2	.768	SH+	45.4	71.4	.682	OH+	39.5	55.9	.418
10	OH-	43.6	63.6	.554	B-	70.0	91.8	.682	SH-	48.2	72.7	.645	SH-	38.2	60.0	.559
11	SH-	43.6	64.5	.582	OH+	69.1	95.4	.823	B+	45.9	75.9	.791	B-	36.8	53.6	.432
12	B+	46.4	70.4	.668	SH+	70.0	92.7	.709	OH+	50.0	66.8	.441	SH+	38.2	55.9	.454

Average initial bodyweight (kg):

45.4	68.6	45.9	40.0

Daily gain as % of initial bodyweight:

1.19%	0.99%	1.38%	0.99%

Feed intake (% of $kg^{.75}$):

Collection 1	9.82%	9.64%	9.99%	9.99%
Collection 2	9.99%	9.47%	9.98%	9.93%

Druation of trial:

36 d	32 d	38 d	39 d

Appendix table 3. Effect of dietary fiber source and duration of feeding on Ca and P utilization by growing pigs

Criteria[1]	Fiber / Time	Basal 1	Basal 2	Oat hulls[3] 1	Oat hulls[3] 2	Soybean hulls 1	Soybean hulls 2	SEM	P-values F[2]	P-values T	P-values FxT
Calcium											
Intake		635.6	632.8	647.0	649.0	652.4	648.6	3.5	.05[a]	NS	NS
Feces		338.0	327.3	329.5	351.6	343.9	345.4	9.4	NS[b]	NS	NS
Urine		14.9	13.6	11.7	8.8	9.4	9.1	1.6	NS[b]	NS	NS
Absorbed		297.6	305.5	317.5	297.4	308.5	303.3	8.7	NS	NS	NS
Retained		282.7	291.1	305.9	288.6	299.0	294.2	8.9	NS	NS	NS
Absorbed, %		46.7	48.8	49.6	45.6[†]	47.4	46.9	1.4	NS	NS	NS
Phosphorus											
Intake		579.5	576.9	592.0	593.8	585.7	582.2	3.3	.07[c]	NS	NS
Feces		302.1	307.4	297.6	309.8	292.7	300.3	6.5	NS[d]	NS	NS
Urine		33.5	35.5	53.2	44.2	47.4	42.5	5.2	.03[d]	NS	NS
Absorbed		277.4	269.6	294.3	284.0	292.9	282.0	5.9	NS[e]	.06	NS
Retained		243.9	234.1	241.1	239.8	245.6	239.6	7.2	NS[f]	NS	NS
Absorbed, %		47.7	46.9	50.0	48.0	50.2	48.7	1.1	NS[f]	NS	NS

[1]Values for intake, feces, urine, absorbed and retained expressed as mg/($kg^{.75}$ bodyweight · d).

[2]Superscripts denote significant differences between fiber sources:
[a]B vs OH, B vs SH P<.01.
[b]B vs OH P<.02; B vs SH P<.01.
[c]B vs OH, OH vs SH P<.01; B vs SH P<.09.
[d]B vs OH P<.01; B vs SH P<.06.
[e]B vs OH P<.02; B vs SH P<.03.
[f]B vs SH P<.06.

[3]Symbols denote significant differences between time periods within fiber source: [†]P<.10.

Appendix table 4. Effect of dietary fiber source and mineral level on Ca and P utilization by growing pigs

Criteria[1]	Fiber / Mineral	Basal[2] −	Basal[2] +	Oat hulls[2] −	Oat hulls[2] +	Soybean hulls[2] −	Soybean hulls[2] +	SEM	P-values F	P-values M	P-values FxM
Calcium											
Intake		629.0	639.4*	644.7	651.3	642.4	658.6**	3.5	.05	.05	NS
Feces		341.8	323.5**	344.3	336.7**	345.5	343.8	9.4	NS	NS	NS
Urine		9.3	19.3*	6.9	13.6	9.6	8.9	1.6	NS	.03	NS
Absorbed		287.2	315.9*	300.4	314.5	296.9	314.8	8.7	NS	.06	NS
Retained		277.9	296.6*	293.5	301.0	287.2	306.0	8.9	NS	NS	NS
Absorbed, %		45.6	49.9*	46.7	48.5	45.7	48.6	1.4	NS	NS	NS
Phosphorus											
Intake		572.0	584.4*	583.1	602.7**	578.5	589.4**	3.3	.07	.01	NS
Feces		306.2	303.2	296.5	310.9	286.9	306.1**	6.5	NS	NS	NS
Urine		30.1	38.9	48.2	49.3	52.8	37.1*	5.2	.03	NS	.06
Absorbed		265.8	281.2†	286.5	291.8	291.6	283.3	5.9	NS	NS	NS
Retained		235.7	242.3	238.4	242.5	238.8	246.3	7.2	NS	NS	NS
Absorbed, %		46.6	48.0	49.4	48.6	50.3	48.6	1.1	NS	NS	NS

[1]Values for intake, feces, urine, absorbed and retained expressed as mg/(kg$^{.75}$ bodyweight · d).

[2]Symbols denote significant differences between mineral level within fiber source: †P<.10, *P<.05, **P<.01.

Appendix table 5. Effect dietary fiber source and duration of feeding on Mn and Cu utilization by growing pigs

Criteria[1]	Fiber	Basal[2]		Oat hulls[2]		Soybean hulls[2]		SEM	P-values		
	Time	1	2	1	2	1	2		F[3]	T	FxT
Manganese											
Intake		1.46	1.45	2.09	2.10**	1.46	1.45	0.01	.01[a]	NS	NS
Feces		1.25	1.26	1.72	1.84*	1.25	1.29	0.03	.01[a]	.03	NS
Urine		0.017	0.020	0.032	0.019**	0.021	0.019	0.004	NS[b]	NS	NS
Absorbed		0.21	0.19	0.37	0.25*	0.21	0.16	0.03	.01[a]	.02	NS
Retained		0.19	0.17	0.34	0.23	0.19	0.14	0.03	.01[a]	.03	NS
Absorbed, %		13.5	11.4	16.4	11.1	11.7	9.1	1.9	NS	.04	NS
Copper											
Intake		0.598	0.594	0.605	0.608	0.618	0.613	0.004	.09[c]	NS	NS
Feces		0.518	0.505	0.536	0.529	0.544	0.516	0.012	NS	NS	NS
Urine		0.011	0.015	0.015	0.010†	0.013	0.012	0.002	NS	NS	NS
Absorbed		0.081	0.089	0.070	0.079	0.074	0.097	0.012	NS	NS	NS
Retained		0.069	0.074	0.054	0.069	0.060	0.085	0.012	NS	NS	NS
Absorbed, %		12.3	14.4	11.7	11.4	10.7	14.3	1.9	NS	NS	NS

[1]Values for intake, feces, urine, absorbed and retained expressed as mg/(kg$^{.75}$ bodyweight · d).

[2]Symbols denote significant differences between time periods within fiber source: †P<.10, *P<.05, **P<.01.

[3]Superscripts denote significant differences between fiber sources:

[a]OH vs SH, OH vs B P<.01.
[b]B vs OH P<.09.
[c]B vs OH P<.03, B vs SH P<.01.

Appendix table 6. Effect of dietary fiber source and mineral level on Mn and Cu utilization by growing pigs

Criteria[1]	Fiber / Mineral	Basal[2] −	Basal[2] +	Oat hulls[2] −	Oat hulls[2] +	Soybean hulls[2] −	Soybean hulls[2] +	SEM	P-values F	P-values M	P-values FxM
Manganese											
Intake		1.36	1.55^{**}_{*}	2.04	2.14^{**}_{**}	1.32	1.58^{**}_{**}	0.01	.01	.01	.01
Feces		1.20	1.32	1.71	1.85	1.17	1.37	0.03	.01	.01	NS
Urine		0.017	0.019	0.026	0.025	0.021	0.018	0.004	NS	NS	NS
Absorbed		0.17	0.23	0.33	0.29	0.15	0.21	0.03	.01	NS	NS
Retained		0.15	0.21	0.30	0.26	0.13	0.20	0.03	.01	NS	.07
Absorbed, %		12.2	15.2	16.4	13.7	10.7	12.9	1.9	NS	NS	NS
Copper											
Intake		0.447	0.746^{**}_{**}	0.452	0.761^{**}_{**}	0.463	0.768^{**}_{**}	0.004	.09	.01	NS
Feces		0.387	$0.636^{\dagger}$	0.401	0.664	0.423	0.637	0.012	NS	.01	NS
Urine		0.010	$0.016^{\dagger}_{**}$	0.011	0.014_{**}	0.012	0.013_{**}	0.002	NS	.01	NS
Absorbed		0.060	0.110_{*}	0.052	0.097_{*}	0.040	0.131_{**}	0.012	NS	.01	NS
Retained		0.050	0.094	0.040	0.083	0.028	0.117_{*}	0.012	NS	.01	NS
Absorbed, %		12.0	14.7	10.4	12.7	8.5	16.5	1.9	NS	.02	NS

[1]Values for intake, feces, urine, absorbed and retained expressed as mg/(kg$^{.75}$ bodyweight · d).

[2]Symbols denote significant differences between mineral levels within fiber source: $^{\dagger}P<.10$, $^{*}P<.05$, $^{**}P<.01$.

Appendix table 7. Effect of dietary oat hulls, soybean hulls or alfalfa meal on weight gain, feed intake and feed efficiency of growing pigs in trials 1 and 2

Criteria[1]	Trial 1					Trial 2				
	B	OH	SH	AM	SEM	B	OH	SH	AM	SEM
Bodyweight, kg										
Initial	9.74	9.80	9.61	9.73	0.47	9.66	9.64	9.78	9.74	0.33
Final	28.34	27.95	26.70	26.63	1.19	23.99	24.70	26.31	23.17[a]	0.84
Gain, kg/d	0.532	0.519	0.488	0.483	0.029	0.434	0.454	0.503	0.407[b]	0.020
Feed intake, kg/d	1.035	1.024	0.956	1.079	0.057	0.899	0.907	0.991	0.839[c]	0.040
Feed efficiency (gain:feed)	0.515	0.506	0.511	0.448[d]	0.020	0.484	0.502	0.511	0.486	0.014

[1]Superscripts significant least-squares differences within each trial:

[a]B vs SH P<.06; SH vs AM P<.05.
[b]B vs SH, SH vs AM P<.05; OH vs AM P<.10.
[c]SH vs AM P<.05.
[d]AM vs B, OH and SH P<.05.

Appendix table 8. Effect of dietary oat hulls, soybean hulls or alfalfa meal on nitrogen and energy utilization by growing pigs in trials 1 and 2

Criteria	Trial 1					Trial 2				
	B	OH	SH	AM	SEM	B	OH	SH	AM	SEM
Bodyweight, kg	47.0	47.6	44.6	42.9	1.4	26.6	26.5	30.5	25.4	1.3
Bodyweight, $kg^{.75}$	17.9	18.1	17.3	16.8	0.4	11.7	11.7	13.0	11.3	0.4
Daily gain, g	577	522	470	365	49	374	307	300	352	46
Feed intake, % $kg^{.75}$	8.48	8.74	8.69	9.04	0.09	10.25	10.42	10.43	10.29	0.09
Nitrogen[1]										
Intake	2.08	2.18	2.17	2.20	0.02	2.46	2.71	2.58	2.49	0.02
Feces	0.27	0.37	0.49	0.54	0.03	0.40	0.51	0.52	0.56	0.03
Urine	0.65	0.60	0.66	0.60	0.06	0.70	0.75	0.65	0.58	0.06
Absorbed	1.81	1.82	1.67	1.66	0.03	2.06	2.20	2.06	1.93	0.03
Retained	1.16	1.14	1.02	1.06	0.07	1.36	1.45	1.42	1.34	0.06
Digestibility, %	86.9	83.2	77.2	75.6	1.3	83.6	81.2	80.0	77.4	1.2
Retained/absorbed,%	63.9	62.7	60.9	63.7	3.6	66.0	66.0	68.7	69.8	3.3
Retained/intake, %	55.8	52.2	46.8	48.2	3.2	55.1	53.6	55.3	54.0	2.9
Energy[2]										
Intake	340.4	358.6	347.8	368.4	3.9	411.3	423.7	420.3	420.5	3.8
Feces	39.1	78.2	57.9	78.4	4.0	56.3	91.9	78.6	89.8	3.8
Absorbed	301.3	280.4	289.9	290.0	3.9	354.9	331.8	341.7	330.7	3.7
Digestibility, %	88.5	78.2	83.3	78.7	0.9	86.3	78.3	81.3	78.7	0.9

[1]Intake, feces, urine, absorbed and retained expressed as g/($kg^{.75}$ bodyweight · d).

[2]Intake, feces and absorbed expressed as kcal/($kg^{.75}$ bodyweight · d).

Appendix table 8 continued

Levels of significance for comparisons of like diets between trials and between diets within trials 1 and 2

	Between trials				Within trials	
	B	OH	SH	AM	1	2
Bodyweight, kg	.01	.01	.01	.01	1	2
Bodyweight, $kg^{.75}$	.01	.01	.01	.01	3	4
Daily gain, g	.01	.01	.02	NS	5	NS
Feed intake	.01	.01	.01	.01	5	NS
Nitrogen						
Intake	.01	.01	.01	.01	6	7
Feces	.02	.02	NS	NS	6	6
Urine	NS	NS	NS	NS	NS	NS
Absorbed	.01	.01	.01	.01	8	9
Retained	.07	.01	.01	.01	NS	NS
Digestibility,%	.08	NS	NS	NS	10	11
Retain./Absorb.,%	NS	NS	NS	NS	NS	NS
Retained/Intake,%	NS	NS	NS	NS	2	NS
Energy						
Intake	.01	.01	.01	.01	10	12
Feces	.01	.04	.01	.06	13	13
Absorbed	.01	.01	.01	.01	14	15
Digestibility,%	.10	NS	NS	NS	13	13

[1]B vs AM P<.05.
[2]B vs SH P<.10.
[3]B vs AM P<.06.
[4]B vs SH P<.04.
[5]B vs AM P<.01.
[6]B vs OH, SH P<.05; B vs AM P<.01.
[7]B vs OH, SH P<.01.
[8]B vs SH, AM P<.01.
[9]B vs OH, AM P<.01.
[10]B vs OH P<.09; B vs SH, AM P<.01.
[11]B vs AM P<.01; B vs SH P<.06.
[12]B vs OH P<.04.
[13]B vs OH, SH, AM P<.01.
[14]B vs OH P<.01; B vs SH, AM P<.05.
[15]B vs OH, AM P<.01; B vs SH P<.05.

Appendix table 9. Effect of dietary oat hulls, soybean hulls or alfalfa meal on dry matter, neutral-detergent fiber and acid-detergent fiber utilization by growing pigs in trials 1 and 2

Criteria[1]	Trial 1					Trial 2				
	B	OH	SH	AM	SEM	B	OH	SH	AM	SEM
Dry matter										
Intake	78.1	80.7	80.1	83.0	0.9	94.2	96.6	96.6	95.8	0.8
Feces	8.1	17.4	12.1	16.2	0.9	11.5	19.6	16.6	18.2	0.8
Digested	70.0	63.3	68.0	66.8	0.9	82.6	77.1	80.1	77.5	0.8
Digestibility, %	89.6	78.4	84.9	80.5	0.9	87.7	79.8	82.8	81.0	0.9
Neutral-detergent fiber										
Intake	8.34	15.44	15.75	13.24	0.14	8.90	15.36	17.26	14.42	0.13
Feces	2.64	10.30	4.66	6.93	0.45	4.60	10.79	8.54	8.69	0.43
Digested	5.70	5.14	11.08	6.31	0.42	4.30	4.58	8.72	5.73	0.40
Digestibility, %	68.4	33.2	70.4	47.7	4.1	48.3	29.8	50.5	39.8	4.0
Acid-detergent fiber										
Intake	2.54	6.75	8.34	7.47	0.07	3.40	7.46	10.07	8.73	0.07
Feces	0.89	5.29	2.28	4.05	0.21	1.45	5.16	5.18	5.02	0.20
Digested	1.65	1.45	6.07	3.42	0.19	1.95	2.30	4.88	3.72	0.18
Digestibility, %	64.9	21.6	72.8	45.9	3.8	57.3	30.8	48.5	42.6	3.6

[1]Values for intake, feces and digested expressed as g/($kg^{.75}$ bodyweight · d).

Appendix table 9 continued

Levels of significance for comparisons of like diets between trials and between diets within trials 1 and 2

	Between trials				Within trials	
	B	OH	SH	AM	1	2
Dry matter						
Intake	.01	.01	.01	.01	1	2
Feces	.02	NS	.01	NS	3	3
Digested	.01	.01	.01	.01	4	5
Digestibility,%	NS	NS	NS	NS	3	3
Neutral-detergent fiber						
Intake	.01	NS	.01	.01	3	3
Feces	.01	NS	.01	.02	3	3
Digested	.03	NS	.01	NS	6	7
Digestibility,%	.01	NS	.01	NS	8	9
Acid-detergent fiber						
Intake	.01	.01	.01	.01	3	3
Feces	.07	NS	.01	.01	3	3
Digested	NS	.01	.01	NS	10	10
Digestibility,%	NS	NS	.01	NS	8	4

[1]B vs OH P<.08; B vs AM P<.01.
[2]B vs OH, SH P<.06.
[3]B vs OH, SH, AM P<.01.
[4]B vs OH P<.01; B vs AM P<.02.
[5]B vs OH, AM P<.01; B vs SH P<.05.
[6]B vs SH P<.01.
[7]B vs SH P<.01; B vs AM P<.03.
[8]B vs OH, AM P<.01.
[9]B vs OH P<.01.
[10]B vs SH, AM P<.01.

Appendix table 10. Effect of dietary oat hulls, soybean hulls or alfalfa meal on cellulose, hemicellulose and lignin utilization by growing pigs in trials 1 and 2

Criteria[1]	Trial 1					Trial 2				
	B	OH	SH	AM	SEM	B	OH	SH	AM	SEM
Cellulose										
Intake	2.29	5.36	7.24	5.28	0.06	2.54	5.37	8.07	5.81	0.05
Feces	0.69	3.68	1.70	2.61	0.17	1.28	3.90	4.62	3.52	0.16
Digested	1.60	1.67	5.54	2.67	0.16	1.26	1.48	2.45	2.30	0.15
Digestibility, %	69.8	31.2	76.5	50.6	4.1	49.6	27.4	42.8	39.6	3.9
Hemicellulose										
Intake	5.80	8.69	7.40	5.76	0.06	5.50	7.91	7.20	5.69	0.06
Feces	1.74	5.02	2.39	2.88	0.27	3.15	5.63	3.36	3.67	0.26
Digested	4.05	3.68	5.02	2.88	0.26	2.35	2.28	3.84	2.01	0.25
Digestibility, %	69.9	42.3	67.8	50.1	4.5	42.7	28.8	53.3	35.5	4.3
Lignin										
Intake	0.34	1.15	0.93	1.84	0.02	0.82	1.60	1.96	2.73	0.02
Feces	0.14	1.03	0.48	1.14	0.04	0.17	0.80	0.53	1.20	0.04
Digested	0.20	0.12	0.45	0.70	0.03	0.65	0.80	1.43	1.52	0.03
Digestibility, %	57.7	10.5	48.5	38.0	2.4	78.8	49.8	73.1	55.9	2.3

[1]Values for intake, feces and digested expressed as g/(kg$^{.75}$ bodyweight · d).

Appendix table 10 continued

Levels of significance for comparisons of like diets between trials and between diets within trials 1 and 2

	Between trials				Within trials	
	B	OH	SH	AM	1	2
Cellulose						
Intake	.01	.01	.01	.01	1	1
Feces	.03	NS	.01	.01	1	1
Digested	NS	NS	.01	NS	2	2
Digestibility,%	.01	NS	.01	.07	3	4
Hemicellulose						
Intake	.01	.01	.03	NS	5	6
Feces	.01	NS	.02	.05	7	8
Digested	.01	.01	.01	.03	9	10
Digestibility,%	.01	.07	.04	.03	3	11
Lignin						
Intake	.01	.01	.01	.01	1	1
Feces	NS	.01	NS	NS	1	1
Digested	.01	.01	.01	.01	2	1
Digestibility,%	.01	.01	.01	.01	12	7

[1]B vs OH, SH, AM $P<.01$.
[2]B vs SH, AM $P<.01$.
[3]B vs OH, AM $P<.01$.
[4]B vs OH $P<.01$; B vs AM $P<.09$.
[5]B vs OH, SH $P<.01$.
[6]B vs OH, SH $P<.01$; B vs AM $P<.04$.
[7]B vs OH, AM $P<.01$; B vs SH $P<.10$.
[8]B vs OH $P<.01$.
[9]B vs SH $P<.02$; B vs AM $P<.01$.
[10]B vs SH $P<.01$.
[11]B vs OH $P<.05$.
[12]B vs OH, AM $P<.01$; B vs SH $P<.02$.

Appendix table 11. Effect of dietary oat hulls, soybean hulls or alfalfa meal on Ca, P and Mg utilization by growing pigs in trials 1 and 2

Criteria[1]	Trial 1					Trial 2				
	B	OH	SH	AM	SEM	B	OH	SH	AM	SEM
Calcium										
Intake	499.3	512.5	530.1	510.2	5.7	607.4	631.1	620.1	565.1	5.3
Feces	222.5	255.0	241.5	250.7	23.5	405.3	383.7	425.0	354.8	22.1
Urine	15.1	12.4	42.8	69.3	9.1	44.0	40.2	20.7	7.0	8.6
Absorbed	276.8	257.4	288.6	259.5	22.4	202.1	247.1	195.1	210.3	21.2
Retained	261.7	245.1	245.8	190.2	20.2	158.0	207.2	174.4	203.3	19.2
Absorbed, %	55.4	50.2	54.5	50.8	4.2	33.3	39.2	31.4	37.3	3.7
Retained, %	52.4	47.8	46.4	37.3	3.6	26.0	32.8	28.1	36.1	3.4
Phosphorus										
Intake	440.4	443.9	429.3	459.9	4.9	529.0	539.9	533.2	522.8	4.7
Feces	257.5	276.4	262.4	245.4	12.9	255.6	254.4	242.1	230.2	12.2
Urine	3.6	7.1	4.5	1.4	6.0	3.3	7.8	16.5	19.0	5.7
Absorbed	182.9	167.5	167.0	214.5	12.8	273.4	285.5	291.1	292.6	12.1
Retained	179.4	160.4	162.4	213.1	14.0	270.1	277.7	274.7	273.6	13.8
Absorbed, %	41.6	37.7	38.9	46.6	2.6	51.7	52.9	54.6	56.0	2.4
Retained, %	40.8	36.1	37.8	46.3	3.0	51.0	51.4	51.5	52.4	2.8
Magnesium										
Intake	109.0	116.8	128.7	126.7	1.3	115.4	126.1	135.1	135.7	1.2
Feces	74.4	83.9	94.7	91.5	4.9	85.3	99.2	99.2	105.2	4.6
Urine	9.3	14.2	28.6	25.2	4.2	19.9	31.4	35.9	25.8	4.0
Absorbed	34.7	33.0	34.0	35.2	4.5	30.1	27.0	35.9	30.3	4.2
Retained	25.3	18.8	5.4	10.0	3.6	10.3	- 4.4	0.1	4.5	3.4
Absorbed, %	31.8	28.2	26.5	27.8	3.5	26.1	21.4	26.6	22.4	3.3
Retained, %	23.2	16.1	4.2	7.9	2.9	8.8	- 3.5	0.0	3.4	2.7

[1]Values for intake, feces, urine, absorbed and retained expressed as mg/($kg^{.75}$ bodyweight · d).

Appendix table 11 continued

Levels of significance for comparisons of like diets between trials and between diets within trials 1 and 2

	Between trials				Within trials	
	B	OH	SH	AM	1	2
Calcium						
Intake	.01	.01	.01	.01	1	2
Feces	.01	.01	.01	.01	NS	NS
Urine	.04	.06	.09	.01	3	4
Absorbed	.03	NS	.01	NS	NS	NS
Retained	.01	NS	.02	NS	5	6
Absorbed, %	.01	.09	.01	.03	NS	NS
Retained, %	.01	.02	.01	NS	7	8
Phosphorus						
Intake	.01	.01	.01	.01	5	NS
Feces	NS	NS	NS	NS	NS	NS
Urine	NS	NS	NS	.05	NS	8
Absorbed	.01	.01	.01	.01	8	NS
Retained	.01	.01	.01	.01	NS	NS
Absorbed, %	.02	.01	.01	.02	NS	NS
Retained, %	.02	.01	.01	NS	NS	NS
Magnesium						
Intake	.01	.01	.01	.01	11	11
Feces	NS	.06	NS	.06	12	13
Urine	.08	.02	NS	NS	12	14
Absorbed	NS	NS	NS	NS	NS	NS
Retained	.01	.01	NS	NS	15	16
Absorbed, %	NS	NS	NS	NS	NS	NS
Retained, %	.01	.01	NS	NS	15	17

[1]
[2]B vs SH P<.01.
[3]B vs OH, AM P<.01.
[4]B vs SH P<.04; B vs AM P<.01.
[5]B vs SH P<.08; B vs AM P<.01.
[6]B vs AM P<.02.
[7]B vs OH P<.10.
[8]B vs AM P<.01.
[9]B vs AM P<.10.
[10]B vs OH, SH, AM P<.01.
[11]B vs SH P<.01; B vs AM P<.02.
[12]B vs OH,SH P<.06; B vs AM P<.01.
[13]B vs OH P<.06; B vs SH P<.02.
[14]B vs SH, AM P<.01.
[15]B vs OH P<.01; B vs SH P<.06.
[16]B vs OH P<.01; B vs SH P<.04.

Appendix table 12. Effect of dietary oat hulls, soybean hulls or alfalfa meal on Na and K utilization by growing pigs in trials 1 and 2

Criteria[1]	Trial 1					Trial 2				
	B	OH	SH	AM	SEM	B	OH	SH	AM	SEM
Sodium										
Intake	5.69	6.06	5.83	7.25	0.07	7.40	7.11	7.93	8.69	0.07
Feces	0.89	1.96	1.08	1.32	0.25	1.63	2.59	2.22	2.79	0.24
Urine	1.72	1.24	2.56	1.92	0.47	2.62	1.98	2.82	3.43	0.45
Absorbed	4.80	4.10	4.75	5.93	0.26	5.77	4.53	5.71	5.90	0.25
Retained	3.09	2.86	2.19	4.01	0.38	3.15	2.55	2.90	2.47	0.36
Absorbed, %	84.5	67.6	81.5	81.8	3.8	77.9	63.6	72.0	67.9	3.6
Retained, %	54.2	47.3	37.5	55.2	5.8	42.6	35.8	36.6	28.5	5.4
Potassium										
Intake	13.30	14.41	15.47	21.60	0.21	18.21	20.50	21.52	26.42	0.20
Feces	2.73	3.71	3.60	5.07	0.32	3.02	5.25	4.74	5.60	0.30
Urine	5.02	7.52	10.42	11.51	7.01	14.90	32.78	21.35	5.98	6.63
Absorbed	10.57	10.70	11.87	16.53	0.32	14.59	15.25	16.78	20.82	0.30
Retained	5.55	3.18	1.45	5.02	6.97	-0.31	-17.53	-4.58	14.84	6.59
Absorbed, %	79.5	74.3	76.7	76.6	1.7	80.1	74.4	78.0	78.8	1.6

[1]Values for intake, feces, urine, absorbed and retained expressed as mmol/($kg^{.75}$ bodyweight · d).

Appendix table 12 continued

Levels of significance for comparisons of like diets between trials and between diets within trials 1 and 2

	Between trials				Within trials	
	B	OH	SH	AM	1	2
Sodium						
Intake	.01	.01	.01	.01	1	2
Feces	.05	NS	.01	.01	3	4
Urine	NS	NS	NS	.04	NS	NS
Absorbed	.02	NS	.02	NS	5	6
Retained	NS	NS	NS	.01	7	NS
Absorbed, %	NS	NS	.08	.02	6	8
Retained, %	NS	NS	NS	.01	9	10
Potassium						
Intake	.01	.01	.01	.01	11	11
Feces	.06	.01	.02	NS	12	13
Urine	NS	.03	NS	NS	NS	14
Absorbed	.01	.01	.01	.01	15	15
Retained	NS	.07	NS	NS	NS	14
Absorbed	NS	NS	NS	NS	14	3

[1]B vs OH, AM P<.01.
[2]B vs OH P<.02; B vs SH, AM P<.01.
[3]B vs OH P<.04.
[4]B vs OH P<.02; B vs AM P<.01.
[5]B vs OH P<.10; B vs AM P<.01.
[6]B vs OH P<.01.
[7]B vs SH P<.10; B vs AM P<.09.
[8]B vs OH P<.02; B vs AM P<.07.
[9]B vs SH P<.05.
[10]B vs AM P<.09.
[11]B vs OH, SH, AM P<.01.
[12]B vs OH, SH P<.06; B vs AM P<.01.
[13]B vs OH, AM P<.01; B vs SH P<.02.
[14]B vs OH P<.09.
[15]B vs SH, AM P<.01.

Appendix table 13. Effect of dietary oat hulls, soybean hulls or alfalfa meal on Zn, Fe, Cu and Mn utilization by growing pigs in trials 1 and 2

Criteria[1]	Trial 1					Trial 2				
	B	OH	SH	AM	SEM	B	OH	SH	AM	SEM
Zinc										
Intake	4.34	5.03	5.28	4.61	0.06	6.63	6.33	6.48	6.08	0.05
Feces	3.34	3.90	4.57	4.07	0.30	5.31	4.37	4.85	4.18	0.28
Urine	0.065	0.042	0.091	0.073	0.023	0.104	0.116	0.132	0.086	0.022
Absorbed	1.01	1.14	0.71	0.54	0.28	1.33	1.96	1.63	1.90	0.27
Retained	0.94	1.09	0.62	0.47	0.27	1.22	1.85	1.50	1.82	0.27
Absorbed, %	23.2	22.6	13.5	11.7	4.8	20.0	31.1	25.2	31.4	4.6
Iron										
Intake	9.72	11.85	15.63	15.86	0.16	12.02	17.23	20.89	17.90	0.15
Feces	6.72	9.16	11.09	8.91	0.47	8.30	12.92	15.93	13.90	0.45
Urine	0.096	0.043	0.099	0.054	0.069	0.157	0.227	0.338	0.164	0.066
Absorbed	3.00	2.70	4.54	6.94	0.40	3.71	4.31	4.96	4.00	0.38
Retained	2.90	2.65	4.44	6.89	0.40	3.56	4.09	4.62	3.83	0.38
Absorbed, %	30.9	22.7	29.1	43.9	2.8	30.9	25.0	23.7	22.4	2.7
Copper										
Intake	1.57	2.03	1.75	1.83	0.02	1.99	2.20	2.19	2.12	0.02
Feces	0.99	1.25	1.25	1.24	0.04	1.24	1.33	1.36	1.38	0.04
Urine	0.021	0.010	0.018	0.017	0.006	0.021	0.025	0.017	0.020	0.006
Absorbed	0.58	0.78	0.49	0.60	0.04	0.75	0.87	0.83	0.74	0.04
Retained	0.56	0.77	0.47	0.58	0.04	0.73	0.85	0.81	0.72	0.04
Absorbed, %	37.0	38.3	28.2	32.6	2.1	37.8	39.6	37.9	34.9	2.0
Manganese										
Intake	1.73	2.38	2.09	2.70	0.03	2.11	3.05	2.71	3.06	0.02
Feces	1.51	2.14	1.90	2.16	0.08	1.93	2.74	2.44	2.90	0.08
Urine	0.023	0.011	0.020	0.022	0.011	0.029	0.054	0.054	0.034	0.011
Absorbed	0.22	0.25	0.18	0.54	0.08	0.18	0.31	0.27	0.16	0.08
Retained	0.19	0.24	0.16	0.52	0.08	0.16	0.26	0.21	0.12	0.08
Absorbed, %	12.6	10.3	8.7	20.0	3.2	8.8	10.2	9.8	5.2	3.0

[1] Values for intake, feces, urine, absorbed and retained expressed as mg/($kg^{.75}$ bodyweight · d).

Appendix table 13 continued

Levels of significance for comparisons of like diets between trials and between diets within trials 1 and 2

	Between trials				Within trials	
	B	OH	SH	AM	1	2
Zinc						
Intake	.01	.01	.01	.01	1	2
Feces	.01	NS	NS	NS	3	4
Urine	NS	.06	NS	NS	NS	NS
Absorbed	NS	.08	.04	.01	NS	NS
Retained	NS	.10	.04	.01	NS	NS
Absorbed, %	NS	NS	.09	.01	5	5
Iron						
Intake	.01	.01	.01	.01	1	1
Feces	.03	.01	.01	.01	1	1
Urine	NS	NS	.03	NS	NS	NS
Absorbed	NS	.02	NS	.01	6	7
Retained	NS	.04	NS	.01	6	8
Absorbed, %	NS	NS	NS	.01	9	10
Copper						
Intake	.01	.01	.01	.01	1	1
Feces	.01	NS	.09	.03	1	11
Urine	NS	NS	NS	NS	NS	NS
Absorbed	.01	NS	.01	.03	12	8
Retained	.01	NS	.01	.03	12	8
Absorbed, %	NS	NS	.01	NS	13	NS
Manganese						
Intake	.01	.01	.01	.01	1	1
Feces	.01	.01	.01	.01	1	1
Urine	NS	.03	.05	NS	NS	NS
Absorbed	NS	NS	NS	.01	14	NS
Retained	NS	NS	NS	.01	14	NS
Absorbed, %	NS	NS	NS	.01	NS	NS

[1]B vs OH, SH, AM P<.01.
[2]B vs OH, AM P<.01; B vs SH P<.07.
[3]B vs SH P<.01; B vs AM P<.09.
[4]B vs OH P<.04; B vs AM P<.02.
[5]B vs AM P<.10.
[6]B vs SH P<.02; B vs AM P<.01.
[7]B vs SH P<.04.
[8]B vs SH P<.07.
[9]B vs OH P<.08; B vs AM P<.01.
[10]B vs SH P<.09; B vs AM P<.05.
[11]B vs SH P<.05; B vs AM P<.03.
[12]B vs SH P<.01.
[13]B vs OH P<.01.
[14]B vs AM P<.02.

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THE EFFECT OF HIGH-FIBER DIETS ON NUTRIENT UTILIZATION AND INTESTINAL MORPHOLOGY OF GROWING PIGS

by

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Animal Science

(ABSTRACT)

Three balance experiments were conducted to determine the effects of dietary fiber on mineral balance and intestinal morphology of growing pigs. Fiber sources were added to corn-soybean meal diets at levels which increased neutral-detergent fiber levels by 6 to 8%. In experiment 1, 10% oat hulls (OH) decreased Ca ($P<.06$) and Zn ($P<.01$) balances of pigs after a 7 d feeding period. Wheat bran (20%) increased Mg intake and balance ($P<.02$), but did not affect Ca and Zn balances. In experiment 2, pigs were fed diets (with or without supplements of Zn, Fe and Mg) containing 15% OH or soybean hulls (SH) for 5 d or 26 d. SH increased Fe intake and balance ($P<.01$) and Mg absorption ($P<.01$). Compared with balances at 5 d, Zn balance was similar, while Fe and Mg balances were higher at 26 d for pigs fed the basal ($P<.05$) or SH ($P<.01$) diets. However, Zn balance was lower ($P<.05$) at 26 d, but Fe balance did not change over time for pigs fed the OH

diets. At each time period, Zn balance was not different between pigs fed the basal or high-fiber diets. In experiment 3, Ca, Zn and Mg absorption were not affected by 15% OH or SH or 20% alfalfa meal (AM) after 67 d or 39 d, although SH and AM increased Fe balance ($P<.01$). Intestinal surface morphology of 12 pigs fed in experiment 3 was examined by scanning electron microscopy. Villus morphology was variable in jejunum, ileum and colon, although evidence of villus blunting and folding accompanied by erosion of microvilli and loss of epithelial cells was observed in small intestine of some pigs fed the SH and AM diets. Damage was not consistent in all sites examined in individual pigs, and did not occur in all pigs fed any specific diets. Although Ca and Zn balances were decreased by OH in two of the balance trials, the inability of OH to consistently decrease mineral balance suggests that the ability of the pig to adapt to different diets may be sufficient to overcome the mild inhibitory effect on mineral absorption of some fiber sources. When viewed together, the results of the balance trials indicate that moderate amounts of dietary fiber have a minimal negative impact on mineral balance of pigs fed practical corn-soybean meal diets. However, the results also indicate that fiber sources such as SH and AM, are rich sources of some minerals for

the pig, particularly Fe. Evidence of intestinal damage was evident in pigs fed the high-fiber diets. However, not all animals fed a particular diet were affected, which suggests that some pigs within a given population may be susceptible to detrimental effects of dietary fiber on intestinal structure or function.