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Review Article

Dietary free fatty acids complex with amylose creating another form of resistant starch: Gastrointestinal formation with fowl and swine

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ABSTRACT

Fat added to poultry and swine feeds often contains abundant free fatty acids (FFA) that can impair digestible energy (DE). Placement of the fatty acid (FA) hydrocarbon chain in the helix core reformed from amylose creates a complex of both nutrients. Resulting modifications create a new structure termed the V-helix that becomes resistant to α-amylase. Granules in grain naturally contain minimal amounts of these complexes with more being generated during food manufacturing when moisture and heat release amylose in the presence of FFA. A paucity of FFA usually exists in complete feeds without sources of poor-quality fat. Animal fats and by-product meals from rendering are prominent in their saturated FFA content which favorably complex within the helix. V-helix-FA complexes may arise during their concurrent encounter of FFA together with amylose during feed manufacture, particularly pelleting. FFA in the gastrointestinal tract (GIT) are speculated to further form complexes when present together with amylose. Although amylose may be dissolved in the gastric and small intestinal milieu, FFA separately coalesce into hydrophobic fat droplets along with other dietary lipids. Formation of complexes is likely restricted until FFA are released into the aqueous phase during fat digestion. Although α-amylase may be prominent, V-helix-FA complexes being resistant to enzymic attack pass into the large intestine. Subsequent microbial catabolism of V-helices may generate volatile fatty acids that are absorbed by the mucosa; however, an inability to use FFA once released leads to their excretion and basis for decreased DE. Immature microbial populations with young animals usually lack the capacity to fully catabolize the V-helix, further extending the loss in DE.

1. Introduction

Fat and starch are dominant sources of dietary energy for poultry and swine. Triglycerides usually represent the greatest proportion of dietary fat with the presence of free fatty acids (FFA) potentially being extensive. High levels of dietary FFA have been shown to impair digestible energy (DE) with poultry (Wiseman and Salvador, 1991) as well as swine (Jøgensen and Fernández, 2000). Increasing unsaturated fatty acids as a proportion of total dietary fat fosters an exponential improvement in feed DE, whereas progressive amounts of FFA cause a linear decrease (Powles et al., 1993). Both fowl and swine respond to unsaturation and FFA in a similar manner (Wiseman et al., 1998).

Poultry and swine also fail to fully recover the DE provided by starch. Such loss is due to a variety of reasons, but usually occurs in the small intestine because of impaired access to the granule and/or altered crystallizations of amylose that resist α-amylase (Manners, 1985; Muir et al., 1995). Several forms of resistant starch (RS) presently exist with all structures being based on the original amylose helix. Each of these common RS's have similar repercussion on DE with fowl (Moran, 2018) as well as swine (Li et al., 2015). Resistance to α-amylase may also occur when amylose becomes complexed with FFA to create a structurally modified V-helix. These complexes were originally found to occur in starch granules during grain development. Fatty acids (FA) associated with these complexes were all saturated and either in free form or esterified as *sn*-2-monoglycerides, as well as *sn*-3- lysophospholipids (Morrison

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and Gadan, 1987; Morrison, 1995). Once these V-helixes were freed from the granule during in vitro amolysis, their resistance to α-amylase allowed them to remain intact, whereas accompanying amylose and amylopectin succumbed (Kitahara and suganuma 1996; 1997; Shu et al., 2009). Various commercial procedures using heat with moisture not only free amylose but may expose the non-reducing end of helixes associated with amylopectin lending to additional complexes if FFA are available (Kweon et al., 1994; Kaneda et al., 1996).

Dietary inclusion of RS has generally been credited with relieving several human health hazards. In this respect, RS may reduce the rate of glucose absorption from the small intestine to moderate insulin release and propensity for obesity. RS eventually enters the large intestine to encounter microbial fermentation creating volatile fatty acids (VFA), particularly butyric acid that is thought to relieve mucosal threats (Topping et al., 2003; Lockyer and Nugent, 2017). To increase the presence of RS in food, a purposeful conversion of various food starches has been approached during food manufacture (Asp et al., 2007). Forming V-helix-FA complexes has also been investigated as a means of increasing RS, but these are structurally separate from those based on amylose crystallization. Early studies on the feeding of synthetic V-helix-FA complexes to rats and dogs impaired live performance and apparent digestibility (Holm et al., 1983; Murray et al., 1998); however, any advantage to health was not mentioned. More recently, feed supplemented with V-helix-FA complexes for rats was observed to enhance *Bifidobacteria* in fecal excreta which could produce butyric acid and favorable terms for large intestinal mucosa (Zheng et al., 2020).

The inclusion of V-helix-FA complexes into the diet has only been attained by direct supplementation and/or synthesis during food manufacture in the presence of FFA. The potential formation of these complexes within the GIT using feeds containing starch together with FFA has not been investigated. Such formation in vivo seems possible given that aqueous mixtures of amylose and FFA readily create corresponding complexes in vitro (Crowe et al., 2000). Further support for V-helix-FA complex formation in the GIT is inferred from many observations where extensive amounts of FFA in feed reduce DE with both fowl and swine.

The following first provides known information surrounding the V-helix-FA complex then rationalizes terms within the GIT for their synthesis and digestion. Once consumed, FFA are initially obligated to coalesce with other dietary lipids that separate them from dissolved amylose. Digestion of coalesced fat in the small intestine is finalized by a transient solubilization of FFA before absorption and a likely occasion for complex formation. Probable digestion of resulting complexes subsequently ensues by the large intestine's microbial population to recover each helix glucose member as VFA while loss in DE results from excreted FA.

2. Amylose-FA complex

2.1. Formation

Generation of the amylose helix represents the basis of each granule's structure and subsequent means to complex FFA. Amylose is a polymer having successive α-1,4- glucose molecules that self-associate into a helix once more than 10 units are connected. Lengthening beyond the minimum number extends the helix; however, polymers having undue length do not self-associate but remain amorphous (Fig. 1). Several helices of varying length may be generated by the plant enabling their strategic assembly into amylopectin once interconnected by α-1,6-bonds (Hizikuri, 1986; Gidley and Bulpin, 1989). Amylose as a single entity exists as a parallel double stranded right-hand helix of fixed diameter.

RS is defined as such when α-amylase is delayed in fulfilling helix digestion and occurs to varying extents with the nature of its modification. Such delay results when the granule is either inaccessible because of cell wall containment (RS-1) or if α-amylase action is obstructed by any of several reorganized crystallizations. As amylose collects and amylopectin is formed, associated helixes are placed adjacent to one another during granule formation. Crystallization accrues in a lateral manner with associated lattices appearing as progressive layers in the granule. The crystal structure occurs as either of 2 polymorphic patterns (Sarko and Zugenmaier, 1980). A-amylose presents an orthorhombic collection which dominates among the seed starches whereas B-amylose exists as a hexagonal unit preferentially found within tubers. Generally, B-units have associated helices mutually held together by H-bonding which reduces their ease of hydrolysis by α-amylase (RS-2). Common grains have “A” type crystallinity while being composed of 75% amylopectin to define the granule's internal structure with 25% amylose being “conveniently” distributed to enhance crystallinity. As the proportion of amylose increases among genotypes so also does granule stability (RS-3). When granules are partially gelatinized to swell then dry, the internal network may partially reform from A to B crystallinity (annealing) to interfere with α-amylase digestion, whereas complete solubilization followed by drying of free polymers involves retrogradation and substantial stabilization of amylose crystallites (RS-4). Enzymic alteration of α-1,6-bonding to distort amylopectin has also been considered as RS-4. Heating with moisture temporarily releases amylose from starch. While soluble, the amylose helix is most susceptible to complex formation; however, drying to create amylose crystallites now prevents FFA access beyond the surface (Roman et al., 2020). V-helix-FA complexes generally retain solubility once formed with the resulting structure itself being directly responsible for resistance to enzymic digestion (RS-5 or V).

The amylose helix as a separate entity in solution presents its outside as a hydrophilic surface while the inside core is hydrophobic. Essentially, the hydroxyl groups protrude externally while hydrogens are presented inward as each glucose member ascends the helix. Having a water compatible surface permits the helix to exist as such in solution, whereas the hydrophobic core provides a haven for those solutes having marginal solubility. Core inclusion by appropriate lipids fosters reformation of a polymer structure that is dictated by the nature of entrants. Saturated fatty acids have a hydrophilic carboxyl group at one end that is followed by a particularly “slender” hydrocarbon chain (Fig. 2). V-helix-FA complexes formed in vitro at room temperature now exhibit resistance to α-amylase that differs with the nature of the core lipid. Such complexes readily occur when free amylose is dissolved together at room temperature with lauric, myristic, palmitic, and oleic acids, whereas stearic acid and cholesterol do not (Crowe et al., 2000).

In response to the core lipid, intra-atomic modifications are initiated that alter the structure from the original amylose helix. These “new” V-helices do not exhibit the original right-hand double stranded polymer but employ a single strand of glucose with a left-hand twist. The double strand apparently “unravels” into single polymers that subsequently “surround” the FA at-hand. Resulting modifications accommodate the FA being encapsulated while improving stability beyond that of the original amylose (Rappenecker and Zugenmaier, 1981; Jane and Robyt, 1984; Hinrichs et al., 1987). Self-association that originally created the double stranded helix with amylose must have been energetically more favorable than remaining amorphous. Similarly, rearrangements provoked with each V-helix must be of further advantage than the “original” amylose helix by employing the single strand. During the “transformation” process, a single strand apparently “wraps around” the existing FFA. V-helices are not as uniformly

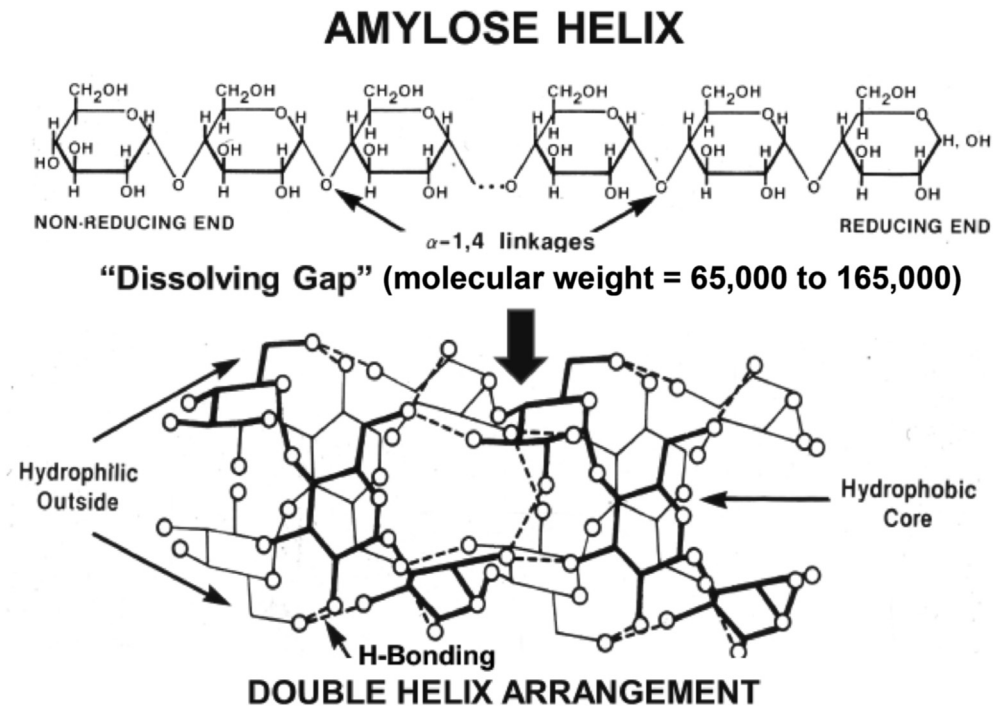

Fig. 1. Amylose is an α-1,4- sequential assembly of glucose units. Self-association of the glucose polymer into a double helix requires a minimum 10 units. Polymerization of glucose beyond ability to form a helix leads to a return of the amorphous state. Polymerization enabling helix formation corresponds to the molecular weight interval referred to as the "dissolving gap." Orientation of glucose hydrogens inward favors a hydrophobic core while external hydroxyls foster a hydrophilic surface.

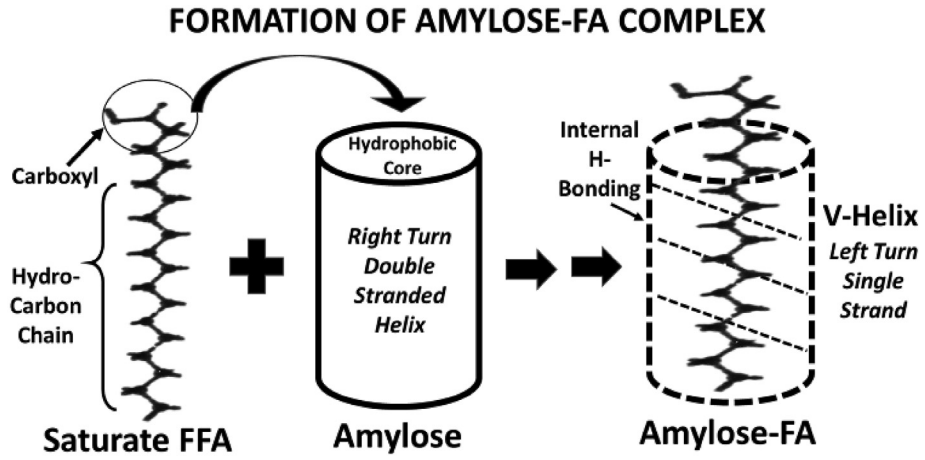

Fig. 2. Access of the hydrocarbon chain of saturated free fatty acids (FFA) into the helix of amylose leads to a complex of both nutrients. Subsequent structural modifications of the amylose helix involve rearrangements of the polymer together with internal hydrogen bonding. Change from amylose helix to V-helix creates resistance to digestion by α-amylase.

shaped as the original amylose but express varying diameters and pitches to suggest that alterations in structure evolve commensurate with "characteristics" of the FA being complexed. Le Bail et al. (2013) noted that V_6 and V_8 helices when formed, represent 6 and 8 glucose units per turn with increasing width and pitch to indicate alterations to core dimension. When crystalized, these complexes not only retain the associated lipid within the existing core but may further entrap lipids between the V-helices.

Changes to the V-helix are central in determining solubility characteristics and resistance to α-amylase. Presentation of the FA carboxyl at the terminus of the new helix acts to favor a continuing aqueous compatibility; however, FA of increasing length have decreased solubility and propensity to complex. Saturated fatty acids are linear and particularly accommodating to limitations in forming the ultimate core. "Disfigurations" created by *-cis* double bonding of the chain not only encounter "difficulty" in arranging helix molecules that surround the "new" core but also increase susceptibility to α-amylase (Marinopoulou et al., 2016a). Exceedingly "large" triglycerides, sterols, and phospholipids cannot be assimilated into a suitable form (Cervantez-Ramirez et al., 2020, Fig. 3). Synthetic V-helix-FA complexes have been shown to be more readily formed as the length of the FA decreases and solubility improves (Karealas and Raphaelides, 1986; Biliaderis and Galloway, 1989). From another perspective, increasing polymerization of the original amylose helix progressively accommodates FFA having increasing length. Approximately, 20 to 30 glucose residues are favorable for lauric and caprylic acids whereas helices having 30 to 40 units enjoy palmitic acid (Godet et al., 1995). Complexes having

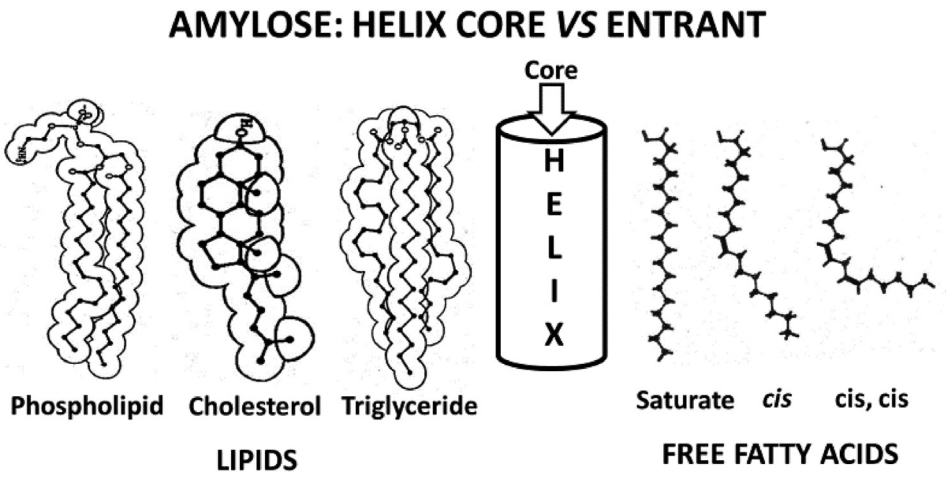

Fig. 3. Amylose is a glucose polymer structured as a helix having a hydrophobic core. Access of co-solubilized lipids as a refuge from their aqueous environment and/or inability to reform the helix and its configuration. Deviating from the linearity of saturated fatty acids by *cis*-double bonding makes reformation into a V-helix progressively more difficult while structurally interfering with resistance to α-amylase.

FA of extended length do not remain soluble, but preferably precipitate into crystallites that become further resistant to α-amylase (Gelders et al., 2004).

2.2. Generating complexes

Formation of V-helix-FA complexes necessitates that amylose co-exist with FFA in an aqueous medium. Although starch may be abundant, free amylose does not readily occur without moisture and heat to drive its release from the granule. Free amylose seems to be of limited amount and duration once solubilized. Amylose located in the granule's lamina can vary with genotype while being particularly extensive at the surface (Sevenou et al., 2002). Heating facilitates entry of moisture into the granule to create a swelling that distorts structure and partial leaching of amylose (Jacobs and Declour, 1998; Exarchopoulos and Raphaelides, 2012). Once externalized, amylose remains soluble until drying leads to crystallites that become resistant to α-amylase (RS-4). Drying of the swollen granule and shrinkage creates localized improvements in crystallization that discourages helix accessibility by FFA in solution while complexes may favorably form at the surface (Chang et al., 2013).

Extended heating with moisture eventually destroys granule integrity. Internally located amylopectin and amylose are freed into solution, whereas surface remnants containing exceptional amylose appear as micro-particulates (Atkins et al., 1998). Solubilized amylopectin becomes susceptible to α-amylase together with increasing ability to form complexes as helix access improves (Zhang et al., 2012; Liu et al., 2020). Amylose when solubilized is easily cleaved by α-amylase as a potential use in formation of a V−helix complex. The existence of crystallite collections of amyloses is not only resistant to digestion but defy ready access to FFA (Myllärinen et al., 2002; Marinopoulou et al., 2016a).

Dietary fat represents a composite of lipids from all feed ingredients. Although grain is usually the most extensive feed ingredient, FFA content is minimal. Heating to remove excess moisture by commercial drying is expected to anneal granules and free amylose within the kernel's endosperm (Brown et al., 1979; Mbuvi and Eckhoff, 2002); however, hydrolytic rancidity of triglycerides in the endosperm (Hargin et al., 1980) and germ is minimal (Purkrtova et al., 2008). Although low, such rancidity eventually contributes to “soapstocks” upon commercial cleaning of extracted oil. Milling of wheat destroys kernel integrity to initiate formation of amylose−lipid complexes during baking if FFA are included in the dough (Schweizer et al., 1986; Bauer et al., 2005). Added FFA are credited with forming complexes that relieve the occurrence of amylose crystallites and the sensory perception of staling. Extrusion is a treatment often used in food manufacture that employs heat and moisture together with pressure (Galloway et al., 1989; Batnagar and Hanna, 1994a,b; Fanta et al., 1999). Such conditions enable FA having extended length and marginal solubility to foster complex formation while helices that have been formed using unsaturated FA subsequently protect the entrant from oxidative threats (Marinopoulou et al., 2013b,c). Feed pelleting employs heat, moisture and pressure which are favorable for complex formation when FFA are present. Menge et al. (2014) added palmitic acid to defatted corn then applied high pressure homogenization and readily formed V-helix complexes. Adding fat of differing qualities during steam pelleting may occur at the time of mixing, after extrusion, and during subsequent drying of feeds (Croston, 1989).

Fats rendered from animals and remaining in resultant meals can provide substantial amounts of FFA to feeds. Although FFA are a secondary contributor to any source triglyceride, the amount is highly variable and represents a significant determinant of economic value (Rouse, 1994). FFA content of animal by-product meals have long been of paramount concern for live production (Schroeder et al., 1936). As mentioned previously, soapstocks result from the cleaning of seed oils. Cleaning involves alkaline water washing to solubilize FFA followed by acidification that permits the decanting of soapstocks. These soapstocks are overwhelmingly FFA and usually blended with animal fats to reduce associated FFA content before feed inclusion. The FFA profile arising from hydrolytic rancidity with each source fat exhibits similar proportions as are present in the triglyceride of origin. Mammalian fats typically have extensive stearic and palmitic acids while fowl favor oleic and linoleic acids (Spencer and HebGormisky, 1976). Seed oils predominately have linoleic and linolenic acids, whereas palm along with coconut kernels provide abundant palmitic acid and lesser medium chain FA.

Varying amounts of dietary medium chain, long chain saturated, and unsaturated FFA lead to differing effects on live performance when substituted for intact triglycerides. Vegetable source soapstocks are typically blended into animal fat to reduce their overall content of FFA, but in so doing also increase the extent of unsaturation. Adverse effects on live production from these blends have generally been minimal to non-existent with poultry (Menge and

Beal, 1973; Lon-Wo and Rodriguez, 1983; Waldroup et al., 1995; Pardio et al., 2001; Vieira et al., 2002). Conversely, the inclusion of long chain saturated FFA as well as medium chain fatty acids adversely affect digestible fat and DE when blended in swine feed (Carlson and Bayley, 1968; Wiseman and Blanch, 1994). Using fowl, Vila and Esteve-Garcia (1996) noted that the substitution of saturated FFA for an equal proportion of fat from either tallow or sunflower oil depressed digestibility of both composites; however, such impairments were not apparent when unsaturated FFA were employed. For the most part, adverse effects on fat digestibility and DE by the inclusion of FFA in feed correspond to a predominance of the saturated FA with palmitic and stearic acids being prominent in this respect.

3. Gastrointestinal system and V-helix-FA complexes

Again, as a short recapitulation of earlier comments, formation of complexes based on amylose and FFA in the GIT is expected to depend on their mutual access in an aqueous system. However, FFA initially join with other dietary lipids to form hydrophobic fat droplets apart from dissolved amylose. These FFA eventually become accessible for complex formation in the small intestinal lumen as droplets are digested. Resulting complexes being resistant to α-amylase likely proceed to the large intestine where helix glucose succumbs to microflora yielding VFA for absorption, whereas FFA would be excreted.

3.1. Gastric digestion

Initial moistening of ingesta occurs either in the crop of fowl or after mastication and entry into the stomach with swine. Both the crop and esophageal area of the stomach have an array of organisms, particularly lactobacilli, that continually "seed" the lumen (Fuller, 1977; McGillivery, 1992). Once microbial source α-amylase avails amylose for resident microbes, FFA complexation seems possible as well. Anaerobic terms lead to lactic acid and reduced pH that would ordinarily impair pancreatic α-amylase but is generally permissive with bacterial amylases (Ishikawa et al., 1991, 1995; Lee et al., 2006). Commercial sources of supplemental amylase are largely of microbial origin and well positioned to operate during ingesta storage (Pande et al., 1991; Valetudie et al., 1993; Najafi et al., 2005).

Although amylose would seem to be continually available in the gastric system, conditions seem less than favorable for FFA to exist in this aqueous medium. FFA have a pK approximating 4 to 5 that leads to a substantial reduction in ionization and solubility as the chain lengthens. This complication is further accentuated upon encountering the very low pH of 2 to 3 during formal gastric digestion. As a result, all lipid amphiphiles coalesce whereas short chain FFA remain soluble as would the lesser medium chain FFA. On the other hand, non-dissociated short chained FFA may pass though cell membranes and gastric mucosa to inflict lethality on susceptible microbes and use them as a source of energy (Argenzio and Southworth 1974).

Although medium chain FFA are solubilized at reduced pH their likelihood of complexing with amylose under gastric terms seems questionable. Although organic acids are normally minimal in the gastric system, their commercial supplementation for microbial control can be substantial (De Smet et al., 2016). Uniquely, medium chain FFA appear with post-parturient mammals consuming milk fat. Piglet lingual and gastric lipases are known to specifically hydrolyze FA from the sn-3 position of milk triglycerides (Armand et al., 1992; Lauridsen, 2020). Mammary alveoli can synthesize an array of medium chain FA that are placed at the *sn*-3-position of triglycerides. Once released, these medium chain FA are likely intended to be microbiocidal and protect the immature mammal. The presence of lactose as the sole carbohydrate in milk avoids potential formation of amylose-FA complexes.

3.2. Small intestine

3.2.1. Emulsification

Coalesced fat upon entering the duodenum is buffered to near neutrality while being introduced to bile and pancreatic enzymes. Such drastic change in pH from gastric digestion initiates the expansion of the droplet's surface area by return of ionization with most constituent amphiphilic lipids. As FFA content in the feed increases, so also will its location at the droplet surface to facilitate emulsification while complementing bile released from the liver. Bile acids are large flat bifacial amphiphiles with their hydrophobic side "sitting" on core neutral lipids whereas the opposite aspect provides aqueous exposure. Phospholipids having 2 hydrophobic chains penetrate the neutral lipid core paralleling FFA. Cholesterol esters being neutral enter the droplet core.

Addition of pancreatic enzymes initiates fat digestion concurrent with emulsification and maximization of droplet surface area. Fowl are anatomically and operationally different from swine at initiating digestion. Fowl have 3 pancreatic ducts that enter together with 2 bile ducts to convey considerable alkaline fluid into the distal duodenum. Peristaltic refluxing with gastric digesta acts to mix and initiate formal digestion. As a direct opposite, Swine have one bile duct immediate to release of gastric digesta from the stomach that is shortly followed by a single "secondary" pancreatic duct (Moran, 1982). Brunner's Glands in the duodenal mucosa release alkaline fluid during segmenting motility that concurrently moves and mixes gastric digesta with bile and pancreatic enzymes. Essentially, neutralization, emulsification, and small intestinal digestion of the coalesced lipid occurs in a similar manner with fowl and swine; however, FFA would not be released into the water phase.

3.2.2. Digestion

Pancreatic enzymes that act on the emulsified fat droplet are represented by lipase, co-lipase, phospholipase A_2, and lipid esterase. Lipase works in conjunction with co-lipase using the bile acids as a "platform" to "operate" at the surface while accessing core triglycerides. Two FFA arise from the *sn*-1-, and *sn*-3-positions along with a *sn*-2-monoglyceride that move to the surface. Phopholipase A_2 releases a FFA from the sn-2-position of phospholipids together with a *sn*-3- lysophospholipid which also move to the surface. Phospholipids originating from bile micelles yield a polyunsaturated FA from the *sn*-2-position leaving a saturated FA at the *sn*-3-position of the lysophospholipid with both complementing all others at the surface. Lipid esterase also operates on the bile acid platform cleaving esters from a multitude of other diverse lipids. FFA contributed by feed are positioned at the surface and shared with digestion products from other lipids.

All products of fat digestion are amphiphiles and thought to progressively "crowd" the droplet surface then "slough off" into the aqueous phase. In a simulation, Hanczyc et al. (2007) described actions at the oil-water interface using oleic acid anhydride as the core lipid. Once hydrolyzed, oleic acid forms at the surface where H^+ is created to reduce the pH of adjacent water. This change in surface pH causes a "rush" of water to "push" accumulating oleic acid "down" the droplet to the opposite end where individual "clusters" are ejected. Anhydrides rising from the core in a repetitive fashion replace surface losses create a "self-propelling" of the droplet. This movement when combined with lumen motility would be of distinct advantage to the dispersal of FFA and products from fat digestion into the aqueous phase.

3.2.3. Absorption versus complex formation

Amphiphiles, after they separate from fat droplets, temporarily appear as independent entities in an aqueous "world." Although FFA are now in the aqueous system, it is expected to be a transient occurrence because they would rapidly be reassembled into micelles (Moran, 1989). The *sn*-3-lysophospholipids having a saturated FA, provide exceptional detergency that rapidly initiates micelle assembly, whereas *sn*-2-monoglycerides are a lesser detergent by carrying alcohol groups at the *sn*-1,3 positions. The weakest of detergents that can be assembled into micelles are long chain FFA, whereas the lesser FFA, if they occur during digestion, enter the water phase and are directly absorbed once convectively conveyed to the mucosa (Ingle et al., 1989).

Although FFA entering the aqueous phase are now available for amylose inclusion to form complexes, competition for these FFA concurrently exists for their collection into micelles. Micelles are an array of amphiphiles largely originating from dietary fat that move once formed from the small intestine to mucosa (Fig. 4). Although saturated FA would be preferentially used to form V-helix-FA complexes, their inclusion into micelles is expected to be competitive. Micelles having extensive stearic acid are thought to create an extended diameter, thereby impairing transit through the unstirred water layer, thereby decreasing apparent digestibility. Extending the proportion of FFA entering the aqueous milieu, particularly the saturated ones, is expected to augment complex formation. Concurrently amylose must also be "at-hand" if complexes are to form. Although starch granules are being eroded by pancreatic α-amylase to avail the amylose helix, any "abundance" in this respect is questionable given their concurrent digestion to yield maltose and maltotriose.

Both *sn*-3-lysophospholipids and *sn*-2-monoglycerides would be additional candidates for complex formation; however, their overriding favorability for micelle inclusion limits helix formation. In one respect, *sn*-3-lysophospholipids have a very low concentration needed to form micelles. Garcia et al. (2016) formed V-helix complexes using glycerol monostearate with various sources of corn and noted that at a low concentration this monoglyceride would preferentially form micelles rather than complex with amylose. In addition, *sn*-2-monoglycerides from all triglyceride sources have a preponderance of polyunsaturated FA at the *sn*-2-position that would "complicate" ready V-helix formation. However, lard is an exception with a large proportion of palmitic acid being placed at the *sn*-2-position during synthesis in swine depots (Brockerhoff et al., 1966; Weber et al., 1971). Separately, triglycerides assembled at the sow's udder using palmitic acid recovered from their depots is again preferential placed at the *sn*-2-position of milk fat (Lauridsen, 2020). Accentuated detergency with the *sn*-2-monoglyceride having palmitic acid is envisaged to substantially foster micelle formation during digestion with the piglet while the preceding *sn*-1,2-diglyceride derived from gastric lipase is positioned to further enhance fat digestion (Frobish et al., 1971). In the absence of dietary starch during nursing, amylose-FA complexes are not expected to form.

In total, palmitic, and stearic acids when free are especially favorable to complex amylose in the small intestine. Their existence in substantial amounts conveyed by feed favors a corresponding presence in the lumen and access to amylose. Unlike the gastric system, the lesser medium chain FFA would be largely dissociated at neutral pH to become readily available for complex formation; however, primary sources being palm and coconut triglycerides would ordinarily make their dietary presence in any amount unusual (Opute, 1979; Valencia et al., 1993). Ca^{++} is also available in the digestive "mix" that may associate with the V-helix-FA carboxyl leading to insoluble soaps. V-helix-FA soaps are expected to further defy digestive efforts by α-amylase. Atteh and Leeson (1984) suggested that formation of insoluble soaps was the basis for their appearance in the excreta and loss in DE (Table 1). In turn, these

Table 1
Effect of dietary calcium on fatty acid absorption and appearance of fatty acid soaps in the fowl's excreta.[1]

Predominant fatty acid	Fatty acid absorption, %		Total excreta soap, %	
	0.8% Ca	1.6% Ca	0.8% Ca	1.6% Ca
Nil	77	75	13	21
Oleic acid	90	78	7	9
Palmitic acid	32	18	56	84
Oleic/Palmitic	56	39	35	51

[1] Selected data from Atteh and Leeson (1984).

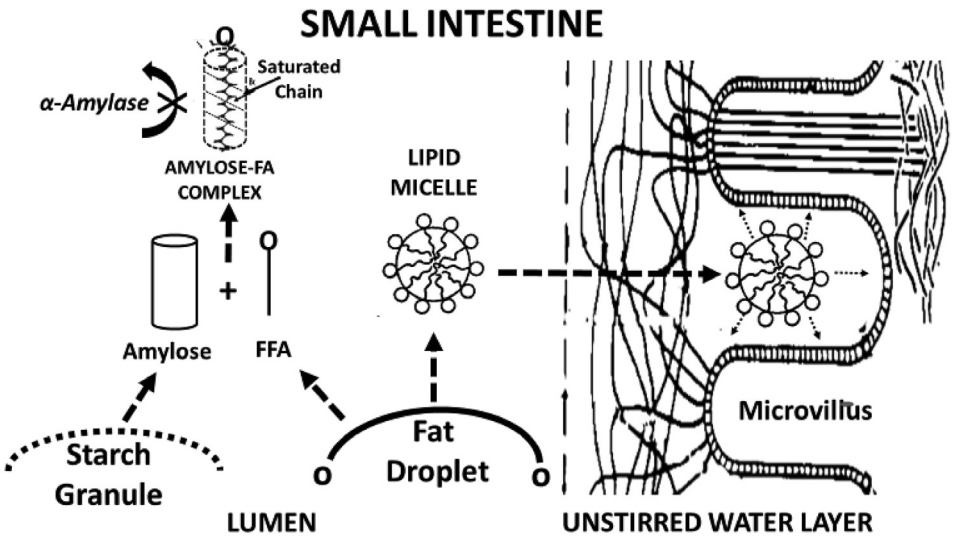

Fig. 4. Illustration comparing the complexing of amylose with fatty acids in the small intestinal lumen with lipid micelle absorption. Released free fatty acids (FFA) from the fat droplet during its digestion permits access to amylose from starch. Resistance to α-amylase by the resulting V-helix enables its continuation to the large intestine; alternatively, micelle formation involves a mixture of FFA, *sn*-2-monoglycerides, lysolecithin, and cholesterol. Micelles are sufficiently small to pass through the unstirred water-layer then absorbed at the mucosal surface.

complexes formed in the small intestine as well as those preformed during feed manufacture are believed to readily enter the large intestine.

3.3. Large intestine

The large intestine's microbial population largely depends on strict anaerobes to effect digestion. Essentially, this microbial population is initiated during early development with a consistent array of members being in place after food intake has been established (Lu et al., 2003; Rehman et al., 2007). Montoro-Dasi et al. (2020) examined the cecal microbiota of broilers raised under 2 separate management systems that created a difference in live performance. In both situations, the members of each population stabilized after 21 days of age. The most prominent members associated with better producing broilers were the *Ruminococcus* spp., *Lactobacillus* spp., and *Bacteroides* spp. Swine have microflora particularly concentrated at haustra, the pouches of the colon. Pigs exhibit a distinct advantage in digesting complex carbohydrates to increase DE with many feedstuffs compared to fowl, whereas CP digestibility is usually unaffected (Rostagno, 2005). This advantage in DE has been attributed to a continuous microbial exposure to all indigesta the indigestible or an extended period within the colon, whereas large particulates would be excluded from the fowl's ceca then rapidly excreted (Moran, 2021).

V-helix-FA complexes (RS-5) differ from all other RS (RS-1,2,3,4) by virtue of the V-helix being the sole basis of resistance. V-helix-FA complexes resemble sucrose-FA esters by having a carbohydrate component associated with FA. Similarly, sucrose-FA esters being resistant to digestion in the small intestine would enter the large intestine where microflora ferment the sugar then excrete resulting FFA (Damron et al., 2001). Using sucrose-FA esters as a dietary fat for animal production has been shown to loose calorific value unless the FA had been hydrolyzed prior to feed inclusion (Rouse, 1994; Kersey and Waldroup, 2000). Anaerobic terms within the large intestine prevent the use of FFA; however, potential hydrogenation of unsaturated members may form saturated FA to alter apparent availability (Just et al., 1980; Droshner and Meyer, 1991). The preceding results with sucrose FA esters infer that the V-helix is being fermented otherwise resulting FFA would be excreted. Fermentation of the carbohydrate component is supported using rats fed a V-helix: oleic acid complex (Zheng et al., 2020). In addition to a reduced live performance, an enhanced presence of *Bifidobacteria* occurred in the large intestine which is known to produce butyric acid from amylose-based RS. Although VFA recovery may occur from the carbohydrate component, the difference in energy from original monosaccharides still represents a decrease in net energy that contributes to loss in DE.

Gain in DE arising from all forms of RS once entering the large intestine depends on having a microbial population competent at fermenting diverse carbohydrates. Microbial exposure immediate to parturition with the pig and in the nest after hatch by fowl normally initiates an “operational” population in the young. However, an initial population would be unlikely with commercial chicks due to the sterile environment in the hatchery followed by placement in a “clean” environment, which would be expected to “delay” its maturity (Campeotto et al., 2007; Moran, 2018). Swine are different because of continuous early exposure to the sow and her excreta, which would augment the piglet's population. Absence of such an advantaged population may adversely influence early digestibility of tallow relative to unsaturated oils. Presumably, the proportional difference in palmitic and stearic acid predisposes differences in the presence of the V-helix and fermentation by an immature microbial population. Experimentation employing conventionally reared chickens consistently indicated that fats having significant amounts of saturated FA were less digestible for chicks than developed fowl (Lessire and Leclercq, 1982; Leeson and Summers, 1991). Presumably, differences in DE attributed to FA saturation were not as extensive with piglets because of their advanced microbial population (Wiseman et al., 1998). Presence of an operational microbial population in the GIT *versus* germ-free terms had an entirely different effect on fatty acid digestion. In germ-free chicks, fats having saturated FA were more favorably digested than if unsaturated, whereas a converse response occurred if a conventional population existed (Table 2). Perhaps, bacteria in the GIT are continually “consuming” unsaturated fatty acids in support of a thriving population only to be excreted, whereas germ-free conditions avoid this loss. The influence of intestinal microflora on modulating V-helix: FA digestion would seem to be underestimated.

Table 2
Effect of differing turkey poult ages and presence of germ-free versus conventional terms with chicks on digestibility of corn oil and tallow.

Variable	Fat type	Fat digestible, %	Fatty acid, % absorbed			
			16:0	18:0	18:1	18:2
Weeks of age (conventional microbes)[1]						
2	Corn oil	96.0	90.0	–	95.0	95.0
8		98.0	98.0	–	100.0	97.0
2	Tallow	57.0	51.0	51.0	49.0	94.0
8		74.0	74.0	84.0	84.0	98.0
Gastrointestinal microbes (2 weeks of age)[2]						
Conventional	Corn oil	85.6	78.1	67.1	87.0	88.8
Germ free		87.6	83.8	78.8	87.0	89.4
Conventional	Tallow	75.0	68.2	55.8	69.9	79.3
Germ free		85.1	73.9	69.1	68.1	75.9

[1] Selected data from Whitehead and Fisher (1975).
[2] Selected data from Boyd et al. (1967). Germ-free chicks measured from 13 to 15 days of age, versus those hatched germ-free and given hen excreta in water from 3 to 15 days.

4. Conclusions

Extensive amounts of FFA in poultry and swine feeds frequently lead to a decrease in DE. Such occurrences apparently involve the formation of complexes formed by association of the FFA hydrocarbon chain with amylose to create the V-helix. The saturated FA are adept at forming these complexes while concurrently creating a resistance to α-amylase. An array of these complexes may occur during feed manufacture, particularly pelleting. Further complex formation hypothetically occurs during fat digestion in the small intestine when FFA are released into the aqueous phase to access amylose. Resistance of these complexes to α-amylase may be furthered in the presence of Ca^{++} to create insoluble soaps. These soaps pass into the large intestine where microbial action on the V-helices results in the partial recovery of DE as VFA; however, FFA would be excreted to cause a loss in DE. Fulfilling helix fermentation depends on a functional microbial population; thus, young animals lacking a favorable membership may falter at generating VFA thereby extending loss in DE.

Author contributions

The sole author is **Edwin T. Moran, Jr.** He is a professor emeritus and assembled the manuscript during his retirement without the benefit of other people.

Conflicts of interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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