CARBOHYDRATES

INTRODUCTION

1. General

A. Carbohydrates make up 75% of dry weight of many plants on which many animals primarily depend on.
B. Carbohydrates make up 70-80% of swine diets (& also poultry diets), :: important from a nutritional standpoint as well as an economical standpoint.

2. Classification

Based on the No. of sugar units and the No. of carbon atoms per sugar unit (Maynard et al., 1979):

I. Monosaccharides (single glucose unit):
   - Trioses (C₃H₆O₃)
     - Glyceraldehyde & 2. Dihydroxyacetone
   - Tetrose (C₄H₈O₄)
     - Erythrose
   - Pentoses (C₅H₁₀O₅)
     - Ribose, Arabinose, Xylose, and Xylulose
   - Hexoses (C₆H₁₂O₆)
     - Glucose, Galactose, Mannose, and Fructose

II. Oligosaccharides (2 to 10 glucose units):
   - Disaccharides (C₁₂H₂₂O₁₁)
     - Sucrose, Maltose, Celllobiose, and Lactose
   - Trisaccharides (C₁₈H₃₂O₁₆)
     - Raffinose
   - Tetrasaccharides (C₂₄H₄₂O₂₁)
     - Stachyose
   - Pentasaccharides (C₃₀H₅₂O₂₆)
     - Verbascose

III. Polysaccharides (> 10 glucose units):
   - Homoglycan ("single glucose" units)
     - Pentosans (C₅H₈O₄)n
     - Hexosans (C₆H₁₀O₅)n
   - Arabans, and Xylans
     - Glucans
     - Starch (α-linked), Dextrins (α-linked), Glycogen (α-linked), and Cellulose (β-linked)
   - Fructans
     - Galactans
     - d. Mannans
     - Inulin, and Levan

   - Heteroglycan (2-6 different kinds of glucose units)
     - Pectins (α-linked), Hemicellulose (β-linked), Gums & Mucilages, and Mucopolysaccharides

Specialized compounds:

- Chitin
- Lignin (not a carbohydrate)
NUTRITIONALLY IMPORTANT SUGARS/CH₂O

1. Monosaccharides

A. Trioses, glyceraldehyde & dihydroxyacetone, are important intermediates in energy metabolism.

B. Pentoses:

1) Majority of pentoses:
   a) Exist as polymers, pentosans, and only a small fraction as a free form.
   b) Associated with cell walls (hemicellulose).
   c) After fermentation by microbes, can contribute to “energy pool.”

2) Ribose:
   a) Occurs in a No. of compounds such as ATP, ADP, DNA, RNA, etc.
   b) Can be synthesized by animals.

C. Hexoses:

   16 stereoisomers (8 + 8 mirror images) are possible, but probably three are nutritionally important (i.e., in terms of a practical nutrition)!

1) Glucose (dextrose):
   a) Found a free form in fresh fruits, plant fluids, etc.
   b) 1° energy source. ∴ probably the most important sugar.
   c) One of the sugar units of sucrose & lactose.
   d) An end product of starch digestion, and produced commercially by hydrolyzing corn starch.

2) Galactose:
   a) One of the sugar units in lactose.
   b) No free form in the nature.
   c) Converted to glucose in the liver:
      (1) “Congenital galactosemia” - Some people lack the enzyme (phospho-galactose uridyl transferase), which results in accumulation of galactose, ∴ must restrict milk intake!
(2) Also, poultry lack this enzyme. (They can tolerate up to 10% galactose, but higher levels can cause convulsion & death.)

2) Fructose:
   a) One of the sugar units of sucrose.
   b) A ketose sugar.
   c) Relative sweetness (sucrose = “1”): (Maynard et al., 1979)

<table>
<thead>
<tr>
<th>Sugar</th>
<th>Relative Sweetness</th>
</tr>
</thead>
<tbody>
<tr>
<td>D-fructose</td>
<td>1.35</td>
</tr>
<tr>
<td>D-glucose</td>
<td>0.74</td>
</tr>
<tr>
<td>Xylose</td>
<td>0.67</td>
</tr>
<tr>
<td>Sorbitol</td>
<td>0.54</td>
</tr>
<tr>
<td>Maltose</td>
<td>0.45</td>
</tr>
<tr>
<td>Galactose</td>
<td>0.32</td>
</tr>
<tr>
<td>Lactose</td>
<td>0.16</td>
</tr>
<tr>
<td>Saccharin</td>
<td>200-700</td>
</tr>
</tbody>
</table>

(1) The sweetest of sugars, and may be important in baby pig diets.
(2) Occurs free along with glucose & sucrose in fruits & honey.
(3) A polymer (inulin) is found in Jerusalem artichoke, dandelion, etc.
(4) Commercially produced by isomerization of glucose - Being used for soft drinks, canned food, etc.

2. **Disaccharides**

   A. Maltose & isomaltose:

      1) Two glucose molecules joined together by “α-1,4” and “α-1,6 linkages.”
      2) “Near-end” products of starch digestion - Hydrolysis (amylase) → maltose + isomaltose (maltase/isomaltase) → glucose (at the brush border).

   B. Sucrose:

      1) Glucose & fructose joined by an α-1,2 linkage.
      2) Found in sugar cane & beets, fruits, tree sap, etc.
      3) Molasses - A crude preparation of sucrose. Contains glucose, fructose, minerals, etc., and not commonly used in nonruminant diets because of its physical nature and a possibility of causing diarrhea at high levels (> 30%).

   C. Lactose:

      1) Galactose & glucose joined together by a β-1,4 linkage.
2) Synthesized by mammary gland.

- Lactase?
  
  a) Abundant in young animals.
  b) Chickens have no lactase, but they can utilize at low levels of lactose via fermentation in the hind gut.
  c) In humans? Tends to be low in people of Chinese and African descent.

3. **Tri-, Tetra- & Pentasaccharides**

A. Raffinose:

  1) A combination of glucose, galactose & fructose.
  2) Most widely distributed oligosaccharide in the nature except sucrose.

B. Stachyose - Raffinose + D-galactose.

C. Verbascose - Raffinose + 2 D-galactose.

D. Raffinose, stachyose & verbascose:

  1) Galactose molecules are linked by an \( \alpha \)-galactosidic linkage.
  2) Found in substantial quantities in leguminous seeds.
  3) No enzyme to split this linkage in animals:

    a) Cannot be digested & too large to be absorbed, \( \therefore \) passed into hind guts.
    b) Subjecto to microbial fermentation (especially, tetra- & pentasaccharides), which can result in production of a large amount of gas (\( 1\° \) \( \text{H}_2 \) & \( \text{CO}_2 \) gases).

E. Soybean meal, which is a major source of supplemental protein for nonruminants:

  1) Contains 1-2% raffinose & 2-3% stachyose.
  2) May depress performance of pigs, especially young pigs.

F. Soy protein products (concentrate or isolate):

  1) Complex carbohydrates are removed.
  2) Primarily used by the food industry, but also being used as feed ingredients for baby pig diets in recent years.

4. **Polysaccharides**

A. Starch:
1) Storage form of energy in seeds, tubers, etc.
2) Quantitatively, 1° source of energy for animals.
3) Structure of starch: (Adapted & redrawn from Davenport, 1982)

   a) Amylose (α-1,4 linkage) - e.g., accounts for ≈ 20% of corn starch.
   b) Amylopectin (α-1,4 & α-1,6 linkages) - e.g.,
      accounts for ≈ 80% of corn starch.
   ~ Both forms are utilized well by pigs!

B. Dextrins:

1) “α-limit dextrins:” (Adapted & redrawn from Kidder & Manners, 1978)
2) Called “α-limit” dextrins because of the inability of
   α-amylase to break α-1,6 bonds.
3) These intermediates are produced from hydrolysis
   of starch by enzymes (& also by heat).
4) Hydrolyzed at the brush boarder by α-dextranase.

C. Beta glucan:

1) Polymers of D-glucose with mixed linkages (β-1,3 & β-1,4).
2) Commonly found in barley (= 5-8%) - starch & protein are enclosed within endosperm cell walls, which consist 1° of β-glucans & arabinoxylans.
3) Forms a viscous solution in the GI tract, ∴ may interfere digestion process?
4) Dietary β-glucanase supplementation?
   a) Has been shown to be beneficial in barley-based poultry diets.
   b) For swine? - The results have been very inconsistent!

One example - Beta-glucanase supplementation (%) and apparent digestibilities (% in pigs weighing 6.2 to 11.2 kg (Li et al., 1996. Anim. Feed Sci. Technol. 59:223-231):

<table>
<thead>
<tr>
<th>Grain (+ SBM)</th>
<th>Response</th>
<th>0.00</th>
<th>0.05</th>
<th>0.10</th>
<th>0.20</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barley</td>
<td>DM*</td>
<td>84.7</td>
<td>87.1</td>
<td>86.0</td>
<td>88.3</td>
</tr>
<tr>
<td></td>
<td>CP*</td>
<td>81.6</td>
<td>86.0</td>
<td>83.4</td>
<td>88.5</td>
</tr>
<tr>
<td></td>
<td>Energy*</td>
<td>85.2</td>
<td>87.8</td>
<td>86.4</td>
<td>89.5</td>
</tr>
<tr>
<td>Corn</td>
<td>DM</td>
<td>85.6</td>
<td>84.1</td>
<td>83.7</td>
<td>85.2</td>
</tr>
<tr>
<td></td>
<td>CP</td>
<td>84.4</td>
<td>82.5</td>
<td>81.3</td>
<td>82.7</td>
</tr>
<tr>
<td></td>
<td>Energy</td>
<td>85.8</td>
<td>84.4</td>
<td>83.8</td>
<td>85.7</td>
</tr>
</tbody>
</table>

* Linear, $P < 0.05$. (Presented partial data.)
D. Glycogen:

1) Resembles starch in properties (& functions), and often called “animal starch.”
2) Small amounts are found in animals as a reserve (1° in the liver & muscles - < .1% of the body wt).

E. Cellulose:

1) The most abundant carbohydrate in nature.
2) A structural component of cell walls.
3) A polymer of β-1,4-linked D-glucose, and 6 carbon atoms in the trans position.
4) Has an extensive H-bonding, which results in a tightly bound, crystalline structure.
5) Hydrolyzed only by microorganisms, and limited usage by nonruminant species.

F. Hemicellulose:

1) A complex, heterogenous mixture of different polymers of monosaccharides.
2) Found in cell walls.
3) Contains primarily xyloglucans, but also contains xylans, glucomannans & galactoglucomannans.
4) Less resistant to hydrolysis vs others, but more easily utilized than cellulose because of less H-bonding.

DIGESTION

1. Introduction

A. Carbohydrates - Major sources of energy for the pig and poultry:

1) Lipids and protein contribute some energy, but starch & sugars are primarily sources.
2) Fermentation of fibers (largely hemicellulose) - In general, limited contributions to pigs & poultry.

B. Three basic factors that affect the “availability;”

1) Digestibility.
2) Absorption of end products of digestion.
3) Metabolism of absorbed products.

- Digestibility is probably the most important factor in the efficiency of feed utilization, and it is an inherent feature of feedstuffs to a large extent.
2. Digestion in General

A. The sites of carbohydrate digestion:
   (Adapted & redrawn from Kidder & Manners, 1978)

B. Salivary digestion:

1) Fowl - Lacking amylase in saliva.
2) Swine - Pigs have “ptyalin:”
   a) A weak α-amylase in saliva, which is similar to pancreatic amylase.
   b) Can breakdown starch to a mixture of maltose, maltotriose & various dextrans.
   c) Active over the pH range of 3.8 to 9.4 with an optimum pH of 6.9.

C. The GI tract digestion:


3. Digestion (Example in Pigs)

A newly hatched chick has a full complement of enzymes to utilize complex CH₂O, which is different from a newborn pig!


<table>
<thead>
<tr>
<th>Enzyme</th>
<th>Newborn</th>
<th>Adult</th>
</tr>
</thead>
<tbody>
<tr>
<td>Invertase (sucrase)</td>
<td>0</td>
<td>78</td>
</tr>
<tr>
<td>Maltase I</td>
<td>0</td>
<td>55</td>
</tr>
<tr>
<td>Maltase II</td>
<td>1</td>
<td>248</td>
</tr>
<tr>
<td>Maltase III</td>
<td>7</td>
<td>66</td>
</tr>
<tr>
<td>Isoamylase</td>
<td>0</td>
<td>30</td>
</tr>
<tr>
<td>Amylase</td>
<td>26</td>
<td>1800</td>
</tr>
<tr>
<td>Lactase</td>
<td>104</td>
<td>42</td>
</tr>
</tbody>
</table>

*Maltase I is active against maltose, sucrose & maltaose, whereas maltase II & III are active against maltose & isomaltose.
B. Development of enzymes in young pigs:

1) Enzymes for carbohydrate digestion (except lactase) are very low until 4-5 wk of age.
2) Lactase - Concentrations/activities decrease over time regardless of a substrate (lactose) level in the diet, but older animals contain sufficient amounts to utilize whey (dried whey contains ≈ 65-70% lactose).

In certain areas of Europe, feeding a “liquid” whey to pigs is a common practice:

1) “Remains” of cheese production contain ≈ 7% of DM, 90% of lactose, 20% of protein, 40% of Ca & 43% of P originally present in milk.
2) A free-choice of liquid whey + grain fortified with vitamins & minerals can replace ≈ 1/2 of dry feed and(or) protein supplements in growing-finishing pigs and gestating sows.

C. Baby pigs & utilization of various sugars:

1) Blood reducing sugar (glucose & galactose) concentrations after an oral dose of sugars (. . . fasted 3-7 h first). Dollar et al., 1957. Proc Nutr. Soc. 16:xii.”
The bottom line (newborn pigs):

1. Can utilize lactose and glucose, but not maltose or sucrose.
2. Can utilize some maltose and sucrose by 10 days of age & their ability to utilize those sugars continues to increase with age, but not completely ready for diets containing only “complex” carbohydrates at “normal” weaning time!

2) Pre- & starter diets may have to contain some milk products (i.e., dried skim milk, dried whey, etc.) to maximize performance!

e.g., Effect of lactose (14.4%) on baby pig performance: (Tokach et al., 1989. J. Anim. Sci. 67:1307)

<table>
<thead>
<tr>
<th>Criteria</th>
<th>Control</th>
<th>Lactose</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-2 wk postweaning:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gain, g/d</td>
<td>229</td>
<td>289</td>
</tr>
<tr>
<td>Feed, g/d</td>
<td>287</td>
<td>335</td>
</tr>
<tr>
<td>F:G</td>
<td>1.241</td>
<td>1.521</td>
</tr>
<tr>
<td>0-5 wk postweaning:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gain, g/d</td>
<td>369</td>
<td>405</td>
</tr>
<tr>
<td>Feed, g/d</td>
<td>565</td>
<td>605</td>
</tr>
<tr>
<td>F:G</td>
<td>1.512</td>
<td>1.521</td>
</tr>
</tbody>
</table>

Can expect similar response to dried whey!

D. Digestion coefficients (%) in swine fed diets based on various grainsa: (Keys & DeBarthe, 1974. J. Anim. Sci. 39:57)

<table>
<thead>
<tr>
<th>Itemb</th>
<th>Wheat</th>
<th>Milo</th>
<th>Corn</th>
<th>Barley</th>
<th>CV, %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Starch</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duodenum</td>
<td>75.72</td>
<td>63.27</td>
<td>71.83</td>
<td>45.11</td>
<td>15.2</td>
</tr>
<tr>
<td>Ileum</td>
<td>94.97</td>
<td>86.90</td>
<td>93.36</td>
<td>79.14</td>
<td>11.5</td>
</tr>
<tr>
<td>Feces</td>
<td>98.46</td>
<td>94.66</td>
<td>98.65</td>
<td>93.57</td>
<td>1.7</td>
</tr>
<tr>
<td>Amylose</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duodenum</td>
<td>95.95</td>
<td>90.05</td>
<td>94.30</td>
<td>69.37</td>
<td>9.3</td>
</tr>
<tr>
<td>Ileum</td>
<td>97.53</td>
<td>91.43</td>
<td>96.61</td>
<td>85.28</td>
<td>9.5</td>
</tr>
<tr>
<td>Feces</td>
<td>98.62</td>
<td>94.49</td>
<td>98.44</td>
<td>93.59</td>
<td>1.8</td>
</tr>
<tr>
<td>Amylopectin</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duodenum</td>
<td>70.45</td>
<td>52.20</td>
<td>66.52</td>
<td>40.24</td>
<td>26.7</td>
</tr>
<tr>
<td>Ileum</td>
<td>94.30</td>
<td>86.06</td>
<td>92.68</td>
<td>77.74</td>
<td>12.2</td>
</tr>
<tr>
<td>Feces</td>
<td>98.41</td>
<td>94.70</td>
<td>98.67</td>
<td>93.57</td>
<td>1.7</td>
</tr>
<tr>
<td>Sugar</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Duodenum</td>
<td>-86.04</td>
<td>-43.42</td>
<td>-405.79</td>
<td>41.14</td>
<td>167.2</td>
</tr>
<tr>
<td>Ileum</td>
<td>98.58</td>
<td>99.34</td>
<td>91.53</td>
<td>97.87</td>
<td>2.6</td>
</tr>
<tr>
<td>Feces</td>
<td>99.77</td>
<td>99.79</td>
<td>99.35</td>
<td>99.89</td>
<td>.2</td>
</tr>
</tbody>
</table>

aMean of four values.
bDigestibility at duodenum or ileum was determined by the indicator method (Cr2O3), whereas fecal digestibility was determined by total collection method.
1. **General**

A. The process of the absorption of sugars at the SI mucosa is similar for a wide range of species.

B. Although small amounts of disaccharides may be absorbed from gut lumen, a bulk of dietary CH₂O is absorbed as monosaccharides.

2. **Absorption Rate of Some Monosaccharides** (Source, unknown)

<table>
<thead>
<tr>
<th>Sugar</th>
<th>Rat</th>
<th>Chick</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glucose</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>Galactose</td>
<td>110</td>
<td>108</td>
</tr>
<tr>
<td>Fructose</td>
<td>43</td>
<td>67</td>
</tr>
<tr>
<td>Mannose</td>
<td>15</td>
<td>42</td>
</tr>
<tr>
<td>Xylose</td>
<td>15</td>
<td>46</td>
</tr>
<tr>
<td>Arabinose</td>
<td>9</td>
<td>47</td>
</tr>
</tbody>
</table>

3. **Absorption Processes**

A. Can be absorbed either by:

1) Simple diffusion or active transport (absorbed against concentration gradient).
2) The process is specific for an individual sugar or group of sugars.

B. The important process is the one that involves Na: “Transport of glucose (& galactose) - Adapted & redrawn from Martin et al., 1983.

Also transport others such as xylose, arabinose & mannose to some extent.

C. A minimum structure required for “active transport?”

1) Important to have “OH” on carbon 2 (the same configuration as glucose).
2) Has a pyranose ring:
3) Both glucose & galactose meet these requirements, ∴ absorbed rapidly.

But, fructose does not, ∴ suggesting a separate mechanism for fructose!
D. Fructose is generally absorbed slowly:

2) In some species such as hamster, guinea pig & dog, fructose can be partly converted to glucose within the mucosa.
3) But in pigs, not likely or not efficient vs other species.

METABOLISM

1. General

A. Absorbed CH₂O (sugar) is metabolized in three fundamental ways:

1) To be used as an immediate source of energy.
2) To serve as a precursor of liver & muscle glycogen.
3) To serve as a precursor of tissue triglycerides.

B. The metabolic pathways are similar for most animals.

2. As a Source of Energy [See, e.g., Maynard et al. (1979)]

A. Glucose:

1) Glycolysis occurs in the cytoplasm.
2) Phosphorylation to Glu-6-P in the liver and other cells (catalyzed by *hexokinase*).
3) Isomerization (*isomerase*), and the second ATP to form Fru-1,6-diP (PFK).
4) Form 2 pyruvate (or 2 lactate in the anaerobic pathway).
5) Pyruvate can enter "mitochondria," then → acetyl-CoA → citric acid cycle.
6) Net results? - Generation of high-energy bonds (~P) during the catabolism of glucose; (Martin et al., 1983)

<table>
<thead>
<tr>
<th>Catalyzed by</th>
<th>~P production</th>
<th>No. of ~P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Glycolysis</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Glyceraldehyde-3-phosphate dehydrogenase</td>
<td>Resp. chain oxidation</td>
<td>6^a</td>
</tr>
<tr>
<td>Phosphoglycerate kinase</td>
<td>Oxidation at substrate level;</td>
<td>2</td>
</tr>
<tr>
<td>Pyruvate kinase</td>
<td>Oxidation at substrate level</td>
<td>2</td>
</tr>
<tr>
<td>ATP consumption by hexokinase &amp; phosphofructokinase</td>
<td></td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-2</td>
</tr>
<tr>
<td></td>
<td>Net</td>
<td>8</td>
</tr>
</tbody>
</table>
Citric acid cycle

<table>
<thead>
<tr>
<th>Reaction</th>
<th>Formation</th>
<th>NADH oxidation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pyruvate dehydrogenase</td>
<td>Resp. chain oxidation</td>
<td>6 NADH</td>
</tr>
<tr>
<td>Isocitrate dehydrogenase</td>
<td>Resp. chain oxidation</td>
<td>6 NADH</td>
</tr>
<tr>
<td>( \alpha )-ketoglutarate</td>
<td>Resp. chain oxidation</td>
<td>6 NADH</td>
</tr>
<tr>
<td>dehydrogenase</td>
<td></td>
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</tr>
<tr>
<td>Succinate thiokinase</td>
<td>Oxidation at substrate level;</td>
<td>2 FADH₂</td>
</tr>
<tr>
<td>Succinate dehydrogenase</td>
<td>Resp. chain oxidation</td>
<td>4 FADH₂</td>
</tr>
<tr>
<td>Malate dehydrogenase</td>
<td>Resp. chain oxidation</td>
<td>6 NADH</td>
</tr>
</tbody>
</table>

Total per mol of glucose under aerobic conditions: 38
Total per mol of glucose under anaerobic conditions: 2

*Assuming that NADH formed in glycolysis is transported to mitochondria via the malate shuttle. If the glycerophosphate shuttle is used, only 2 \( \text{acetate} \) would be formed per mol of NADH, and a total net production being 36 instead of 38.

B. Galactose:

- Can be converted to glucose readily in the liver. (This ability may be used as a criterion for assessing the “hepatic function” in the galactose tolerance test.)

1) Phosphorylated to Gal-1-P (by \textit{galactokinase}) in the liver.
2) Converted to Glu-1-P in the liver, which is catalyzed by \textit{galactose-1-P uridyl transferase}.

a) Chicks and people with congenital galactosemia lack this enzyme (also, other enzymes?).

b) Galactosemia:

1. Accumulation of Gal-1-P → deplete liver inorganic P.
2. Can result in the liver failure & mental retardation.
3. Only treatment is a galactose-free diet!

3) Converted to Glu-6-P.
4) Follows oxidative pathways or converted to glucose (by \textit{Glu-6-P-tase}) in the liver.

C. Fructose:

1) May be phosphorylated to Fru-6-P by \textit{hexokinase}, but the affinity of this enzyme for fructose is very low vs glucose, so not a major pathway.
2) Phosphorylated to Fru-1-P by \textit{fructokinase}.
3) Split into triose sugars, and metabolized accordingly.
3. **Conversion of Glucose to Glycogen**

   A. Most animals consume food in excess of their immediate needs for energy, and an excess is stored as liver or muscle (... also others ... but not much!) glycogen.

   1) Liver - Maintain blood glucose between meals?
   2) Muscle - Readily available source of glucose for glycolysis within the muscle.

   B. But, the energy stored as carbohydrates or glycogen is very small - e.g., in 70-kg man:

   1) Stored carbohydrates = \( \approx 1,900 \text{ Kcal} \) (350 g muscle glycogen, 85 g liver glycogen, and 20 g glucose in ECF).
   2) vs fat = 140,000 Kcal (... 80-85% of body fuel supplies stored as fat & the remainder in protein).

   B. Glycogenesis & glycogenolysis: (Adapted & redrawn from Ganong, 1983)

   "Need glucose?"

   “Cascade sequence” (i.e., epinephrine \( \rightarrow \) adenylate cyclase ... conversion of phosphorylase b to phosphorylase a) can result in the cleavage of \( \alpha-1,4 \) linkage!

4. **Conversion of Glucose to Fat**

   A. Again, the storage of sugars as glycogen is rather limited, thus the excess is transformed into fats!

   B. Synthesis of fatty acids from glucose:
   (Adapted & redrawn from Martin et al., 1983)

   C. Factors that can influence fatty acid synthesis:

   1) Insulin:

   a) Can ↑ transport of glucose into cells.
   b) Can activate pyruvate dehydrogenase & acetyl-CoA carboxylase.
   c) Can inhibit lipolysis.

   2) Glucagon - Can inhibit acetyl-CoA carboxylase and lipogenesis in general.
D. Limiting step? - Acetyl-CoA carboxylase, which can be inhibited by acetyl-CoA, perhaps via negative feedback?!  
E. Factors affecting acetyl-CoA?  

1) Nutritional status - Inverse relationship between hepatic lipogenesis and serum fatty acids.  
2) Dietary lipids can ↓ lipogenesis. With > 10% dietary lipids, a little conversion of carbohydrates to fatty acids.

5. Fermentation

A. General:

1) Fermentation of starch can yield mostly lactate and propionate & not much acetate.  
2) Fermentation that favors propionate production tends to be more efficient because propionate is “glucose former.”  
3) A reduction in acetate production can lead to ↓ in the milk fat content. (Precursors in blood? - Acetate, triglycerides, and β-hydroxybutyrate.)

B. Fowl:

1) Crop - Some microbial fermentation (1° product being lactic acid).  
2) Colon - Likely to convey digesta rather than active fermentation & absorption.  
3) Ceca - Produces most VFA (acetic, propionic and butyric acids), but only small contributions to the overall needs.

C. Swine:

1) Stomach - Some fermentation in the upper part (1° product being lactic acid).  
2) The LI has more mixed flora, and produces acetic, propionic & butyric acids.  

<table>
<thead>
<tr>
<th>Mucosa</th>
<th>Loss from lumen side</th>
<th>Gain blood side</th>
<th>Tissue content</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gastric stratified squamous</td>
<td>15.2</td>
<td>1.0</td>
<td>2.8</td>
</tr>
<tr>
<td>Cardiac</td>
<td>20.8</td>
<td>2.8</td>
<td>2.0</td>
</tr>
<tr>
<td>Proper gastric</td>
<td>12.6</td>
<td>0.8</td>
<td>2.2</td>
</tr>
<tr>
<td>Pylorus</td>
<td>14.6</td>
<td>1.3</td>
<td>5.6</td>
</tr>
<tr>
<td>Cecum</td>
<td>25.8</td>
<td>10.7</td>
<td>2.8</td>
</tr>
<tr>
<td>Centripetal colon</td>
<td>20.1</td>
<td>9.3</td>
<td>2.8</td>
</tr>
<tr>
<td>Centrifugal colon</td>
<td>24.4</td>
<td>7.7</td>
<td>3.2</td>
</tr>
</tbody>
</table>

5) Once absorbed, VFA are metabolized accordingly:

a) Acetate/butylate → as a source of energy via acetyl CoA.
b) Propionate → as a source of energy via succinyl CoA.

**DIETARY FIBER**


1. **Definition of Fiber**

A. A widely accepted definition: “A sum of lignin and the polysaccharides that are not digested by the endogenous secretions of the digestive tract.” (Trowell et al., 1976. Lancet 1:967)

B. A practical definition (considers some attributes of fibers that can be analyzed easily by existing method): “Non-starch polysaccharides and lignin.” (Low, 1985)

2. **Analytical Methods** (Low, 1985; Fernández & Jørgensen, 1986)

A. Crude fiber:

1) Treat sequentially with petroleum ether, hot sulfuric acid, boiling water & alkali.
2) Insoluble residue contains mainly cellulose & lignin. (But the recovery is not always complete!)

B. Neutral detergent fiber:

1) Digestion by boiling in a neutral detergent solution.
2) Cellulose & lignin are completely recovered, but may lose some hemicellulose. [Water soluble CH₂O (e.g., gum & pectin) are completely lost.]

C. Acid detergent fiber:

1) Digestion by boiling in an acid detergent solution.
2) The residue contains cellulose & lignin. (Almost all other components are lost/excluded.)

D. Non-starch polysaccharides:

1) The removal of starch by enzymic hydrolysis.
2) The residue is separated into cellulose, non-cellulosic polysaccharides and lignin.
3) Acid hydrolysis & colorimetric or gas-liquid chromatographic measurement of component of sugars.

* The word “fiber” is a very generic term, and considerable variations/differences exist in terms of variety/complexity in the chemical component of plant cell walls, physical composition, and their metabolic effects on animals!

3. **Fiber Utilization by Ruminants & Nonruminant Species**

A. Composition of cell walls?

1) e.g., Cellulose, 20-40%; hemicellulose, 10-40%; lignin, 5-10%; pectin, 1-10%.
2) Pectin - Highly fermentable non-starch polysaccharide found in the space between cell walls, but also infiltrate the cell wall itself.

B. Relative efficiency of fiber utilization (left) & fermentation curves for various species (right; Van Soest, 1985):

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4. **Additional Benefits?**

   A. Laxative effect.
   B. Stimulate the colonic growth.
   C. Maintain “normal” microflora.
   D. Buffering effects.
   E. Reduction of energy intake, ∴ leaner carcass (pigs)?
   . . . , etc.

5. **Dietary Fiber (e.g, Swine)**

   A. General:

   1) Nonruminant species (pigs & poultry) compete directly with humans for “high quality” feed ingredients (1° energy/CH₂O sources).
   2) For a successful animal production in the future, must † efficiency of feed utilization to ensure a continuous availability of quality sources of nutrients, and also † the use of alternative ingredients:

      a) Alternative ingredients (by-products and forages) tend to be high in the fiber content.
      b) Unfortunately, the information on fibers, the nutritive value of various types of fibers & their relationships with other nutrients, is inadequate at this time.

   3) Negative aspects of using dietary fiber:

      a) The level of dietary fiber & digestibility (%): (Kass et al., 1980. J. Anim. Sci. 50:175)

      | % Alfalfa: | 0   | 20  | 40  | 60  |
      |-----------|-----|-----|-----|-----|
      | Dry matter| 77  | 61  | 52  | 28  |
      | Cell wall | 62  | 34  | 27  | 8   |
      | ADF       | 56  | 10  | 11  | 1   |
      | Hemicellulose| 67  | 54  | 49  | 22  |
      | Cellulose | 58  | 20  | 9   | 7   |
      | Nitrogen  | 70  | 52  | 41  | 41  |

      b) Also, there is an indication that the digestibility of minerals may be reduced with an increase in dietary fiber . . . Cations can be bound to fibers!

   4) Fiber as a source of energy:

      a) The age of pigs influences the efficiency of utilization:
(1) Cellulose may not be utilized by pigs weighing < 40-50 kg.
(2) Gestating sows can be fed up to 96-98% alfalfa & perform normally.
(3) There might be genotype differences in the ability to utilize fiber - e.g., Chinese pigs can thrive on high-fiber diets.
(4) According to some French data, growing pigs may be able to obtain ≈ 30% of DE from VFA (vs commonly quoted value of 30% of maintenance energy).

PROCESSING OF GRAINS & DIETS

1. Purpose of Processing?

To increase a surface area, obtain a uniform mixture of various ingredients, avoid sorting by animals, and increase digestibility by subjecting to pre-digestion (e.g., heat processing)

2. Common Processing Methods

A. Cold processing:
   1) Grinding (hammer mill) - “Fine (1/8- to 3/16-in screen or smaller), “medium” (¼- to ¾-in screen) or “coarse.”
   2) Rolling/crushing.
   3) Crimping/cracking.

B. Hot processing - Flaking, micronizing & popping.

C. Pelleting or cubing - A combination of cold & hot processing.

3. Effect of Processing on the Performance (e.g., in Pigs)

A. Ground cereal grains & pig performance: [Modified the data compiled by Lawrence, 1985. In: Cole & Haresign (Ed.) Recent Developments in Pig Nutrition]

<table>
<thead>
<tr>
<th>Grain</th>
<th>Whole grain</th>
<th>Coarse ground</th>
<th>Medium ground</th>
<th>Fine ground</th>
<th>Rolled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barley:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight gain, kg/d</td>
<td>0.52</td>
<td>0.64</td>
<td>0.65</td>
<td>0.66</td>
<td>0.66</td>
</tr>
<tr>
<td>Feed:gain</td>
<td>3.98</td>
<td>3.19</td>
<td>3.17</td>
<td>3.14</td>
<td>3.10</td>
</tr>
<tr>
<td>Oats:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight gain, kg/d</td>
<td>0.48</td>
<td>0.48</td>
<td>0.57</td>
<td>0.73</td>
<td></td>
</tr>
<tr>
<td>Feed:gain</td>
<td>4.60</td>
<td>4.60</td>
<td>4.10</td>
<td>3.60</td>
<td></td>
</tr>
<tr>
<td>Maize:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight gain, kg/d</td>
<td>0.56</td>
<td>0.60</td>
<td>0.63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed (DM):gain</td>
<td>2.94</td>
<td>2.63</td>
<td>2.63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sorghum:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight gain, kg/d</td>
<td>0.81</td>
<td>0.85</td>
<td>0.85</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feed:gain</td>
<td>4.01</td>
<td>3.72</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Processing</th>
<th>Barley</th>
<th>Milo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Untreated</td>
<td>22.7</td>
<td>16.0</td>
</tr>
<tr>
<td>Steamed, not flaked</td>
<td>18.4</td>
<td>11.7</td>
</tr>
<tr>
<td>Poorly flaked</td>
<td>26.5</td>
<td>14.4</td>
</tr>
<tr>
<td>Intermediately flaked</td>
<td>36.8</td>
<td>31.3</td>
</tr>
<tr>
<td>Flat flaked</td>
<td>51.2</td>
<td>41.0</td>
</tr>
</tbody>
</table>


<table>
<thead>
<tr>
<th>Item</th>
<th>Corn</th>
<th>Barley</th>
<th>Wheat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry matter, %</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>86</td>
<td>78</td>
<td></td>
</tr>
<tr>
<td>Popped</td>
<td>88</td>
<td>79</td>
<td></td>
</tr>
<tr>
<td>Dry matter, %</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ground</td>
<td>86.9</td>
<td>79.7</td>
<td></td>
</tr>
<tr>
<td>Micronized</td>
<td>86.5</td>
<td>80.9</td>
<td></td>
</tr>
<tr>
<td>Gain to 90 kg, kg/d</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ground</td>
<td>0.76</td>
<td>0.73</td>
<td>0.75</td>
</tr>
<tr>
<td>Micronized</td>
<td>0.83</td>
<td>0.77</td>
<td>0.78</td>
</tr>
<tr>
<td>Efficiency, kg DM/kg gain</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ground</td>
<td>2.17</td>
<td>2.36</td>
<td>2.17</td>
</tr>
<tr>
<td>Micronized</td>
<td>2.04</td>
<td>2.25</td>
<td>2.23</td>
</tr>
</tbody>
</table>

D. Effects of pelleting: (% improvement or the No. of papers reported a positive response)

<table>
<thead>
<tr>
<th>Reference/ criterion</th>
<th>% improvement or No. of papers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth rate</td>
<td>+ 7.9%</td>
</tr>
<tr>
<td>Efficiency</td>
<td>- 2.1%</td>
</tr>
<tr>
<td>Feed intake</td>
<td>- 2.1%</td>
</tr>
<tr>
<td>Braude, 1972. [57 published papers; In: Cole (Ed.) Pig Production]:</td>
<td>38 papers</td>
</tr>
<tr>
<td>Improved growth rate</td>
<td>48 papers</td>
</tr>
<tr>
<td>Improved efficiency</td>
<td>- 2.1%</td>
</tr>
</tbody>
</table>

**PALATABILITY**

1. Palatability of CH$_2$O is important because CH$_2$O make up high percentages of diets.
2. Fortunately, most of high-CH$_2$O ingredients (e.g., corn & milo) are quite palatable.
3. Young pigs may prefer feed with a sweetener - e.g., % of total diet consumed in the diet preference test: (Jensen et al., 1955. Cited by Cunha, 1977)

<table>
<thead>
<tr>
<th>Percentage of Total Diet Consumed</th>
<th>Palatability Score</th>
</tr>
</thead>
<tbody>
<tr>
<td>20% cane sugar . 38%</td>
<td>Dried skim milk . 17%</td>
</tr>
<tr>
<td>10% cane sugar . 13%</td>
<td>15% cane sugar . 20%</td>
</tr>
<tr>
<td>0% cane sugar . 2%</td>
<td>5% cane sugar . . . 5%</td>
</tr>
<tr>
<td>0.05% saccharin . 4%</td>
<td>0% cane sugar . . .</td>
</tr>
</tbody>
</table>