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Odour from animal production facilities: its relationship to diet

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Though bad odour has always been associated with animal production, it did not attract much research attention until in many countries the odour production and emission from intensified animal production caused serious nuisance and was implicated in the health problems of individuals living near animal farms. Odour from pig production facilities is generated by the microbial conversion of feed in the large intestine of pigs and by the microbial conversion of pig excreta under anaerobic conditions and in manure stores. Assuming that primary odour-causing compounds arise from an excess of degradable protein and a lack of specific fermentable carbohydrates during microbial fermentation, the main dietary components that can be altered to reduce odour are protein and fermentable carbohydrates. In the present paper we aim to give an up-to-date review of studies on the relationship between diet composition and odour production, with the emphasis on protein and fermentable carbohydrates. We hypothesise how odour might be changed and/or reduced by altering the diet of pigs. Research so far has mainly focused on the single effects of different levels of crude protein and fermentable carbohydrates on odour production. However, also important for odour formation are the sources of protein and fermentable carbohydrates. In addition, it is not only the amount and source of these compounds that is important, but also the balance between them. On the basis of our review of the literature, we hypothesise that odour nuisance from pig production facilities might be reduced significantly if there is an optimum balance between protein and fermentable carbohydrates in the diet of pigs.

Odour nuisance: Pig diets: Animal production

Introduction

Although bad odour has always been associated with animal production, only within recent decades has it attracted increased attention. This is mainly because of the increase in human population and in intensification of animal production in many countries throughout the world. The odour produced and emitted from such intensive animal production can cause serious nuisance to individuals living in the vicinity of livestock farms and was related by some authors to health problems, for example, accelerated decline in pulmonary function, bronchitis, sinusitis, inflamed nasal mucosa, throat irritation and headaches (Schenker *et al.* 1991, 1998; Donham, 2000; Iverson *et al.* 2000).

The odour generated in animal production facilities comes from feed, animal bodies, urine, faeces and manure. Odour production is influenced by many factors, such as dietary composition and environmental factors (Fig. 1). Odour is mainly generated by microbial conversions of non-utilised dietary nutrients and endogenous products secreted in the gastrointestinal tract under anaerobic conditions. There are four main groups of odour: sulfurous compounds; phenols and indoles; volatile fatty acids (VFA); ammonia and volatile amines.

Various means of reducing odour production and emission have been invented and applied, such as bio-scrubbers (Schirz, 1986), bio-filters (Noren, 1986), chemical and biological additives, masking agents, treatment of wastes, and manure-spreading machinery (Phillips *et al.* 1990). These remedies have so far mainly focused on preventing odour from being emitted. These end-of-pipeline interventions are generally costly and/or prone to malfunction. Very few studies so far have focused on reducing the formation of odorous compounds at source, for example, in the large intestine of the animal or in manure storage. The fermentation and hydrolysis of apparently undigested

Abbreviations: AA, amino acid; CEN, European Committee for Standardization; CP, crude protein; DOPA, 3,4-dihydroxyphenylalanine; EROM, European reference odour mass; GC, gas chromatography; ou, odour unit; ou_E, European odour unit; ppm, parts per million; VFA, volatile fatty acid

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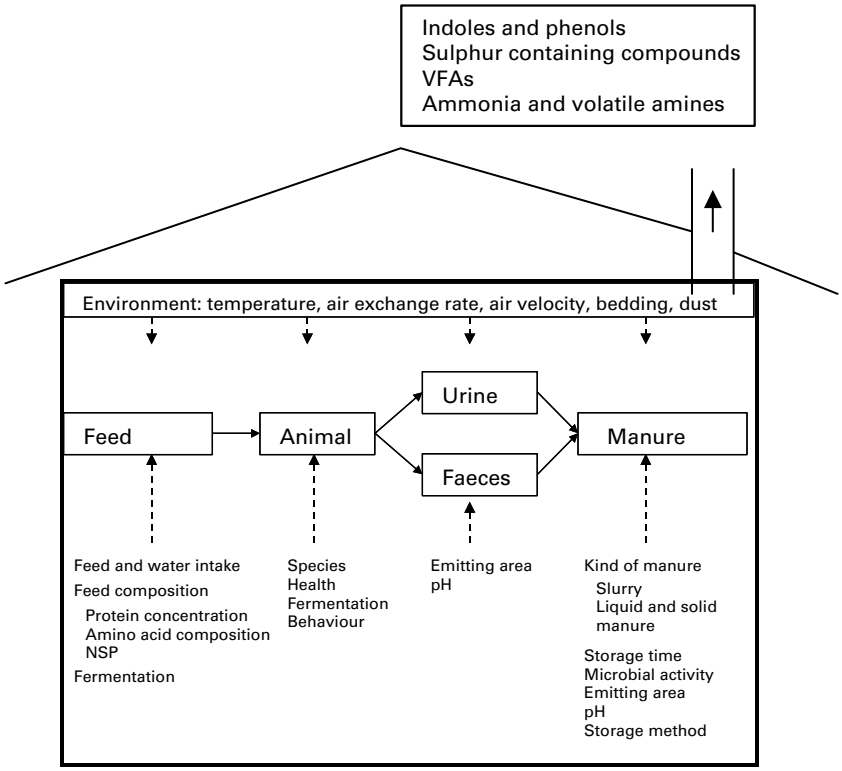

Fig. 1. Sources of odour and the factors influencing odour.

nutrients in the large intestine produces odour directly or provides precursors for odour formation in the manure.

Measurements of odour emission in different farm locations with similar housing systems have shown large variations, with CV ranging from 7 to 83 % (Ogink & Groot Koerkamp, 2001). Diet probably contributes greatly to the variation of odour, because its composition is directly related to odour production. Therefore, odour can be altered by changing the amount and source of each component in the diet. Based on the principle that the primary odour-causing compounds evolve from an excess of degradable proteins and a lack of specific fermentable carbohydrates during microbial fermentation (Sutton *et al.* 1999), the main nutrients in the diet that can be altered to reduce odour production and emission are probably proteins and fermentable carbohydrates. In addition, feed additives can be used to improve the digestibility of specific complexes within feed ingredients and/or to alter the pH of manure to a pH less favourable for odour production.

We suspect that odour production and emission from animal production facilities can be altered by dietary composition. However, research still has to be done before it is possible to manage this process. The present review describes the current state of the art of the science of livestock odour in relation to diet. It examines odour compounds from animal production facilities, especially from pig production facilities with most emphasis on within the large intestine, and within manure. We have attempted to pinpoint the nature of smell, the detection threshold and concentration of important odorous compounds. Later, we address the principles of odour formation and the roles of different bacteria in odour formation and describe the standard methods used to characterise the sensory and chemical values of odour. We discuss the relationships between the diet and odour composition and production and describe different dietary approaches to reduce odour. From this, we are able to identify gaps in the knowledge on reducing odour by altering diets, from which research strategies can be derived.

Odorous compounds from animal production facilities

Sources of odour and the principal groups of odours

Odour generated in animal production facilities comes from: (i) feed; (ii) animal bodies; (iii) urine and faeces or the mixture of both, the manure. The most significant source of odour is from the excreta; urine, faeces and manure, especially their decomposition during collection, handling, storage, and spreading. Odour is emitted into the air from buildings or external manure storage sites or from manure application in the field. There are a great number of odorous compounds present in animal production facilities. O'Neill & Phillips (1992) summarised 168 odorous compounds identified in various studies in animal production facilities. As already mentioned, they can be classified into sulfurous compounds, VFA, phenols and indoles, and ammonia and volatile amines. Thirty of these 168 compounds have an odour detection threshold of 1 $\mu g/m^3$ or less (Table 1). Recently, Susan *et al.* (2001) identified a total of 331 different compounds from pig production facilities in North Carolina.

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Table 1. Compounds with low odour detection threshold in animal manure (O'Neill and Phillips, 1992)

Range of detection threshold (C_{od}; $\mu g/m^3$)	Compound	Lowest detection threshold (C_{od}; $\mu g/m^3$)*
$C_{od} \leq 0{\cdot}01$	Methanethiol	0·0003
	2-Propanethiol	0·0025
	2-Propene-1-thiol	0·005
	2,3-Butanedione	0·007
$0{\cdot}01 \leq C_{od} \leq 0{\cdot}05$	Phenylethanoic acid (phenyl acetic acid)	0·03
	Ethanethiol	0·043
	4-Methylphenol (*p*-cresol)	0·05
$0{\cdot}05 \leq C_{od} \leq 0{\cdot}1$	Hydrogen sulfide	0·1
	1-Octene-3-one	0·1
$0{\cdot}1 \leq C_{od} \leq 0{\cdot}25$	Benzenethiol	0·14
	2,4-Decadienal	0·18
	3-Methylbutanoic acid	0·2
	2,6-Dimethylphenol	0·2
	3-Methylphenol	0·22
	2,4-Nonadienal	0·25
	Dacanal	0·25
$0{\cdot}25 \leq C_{od} \leq 0{\cdot}5$	Trimethylamine	0·26
	Octanoic acid	0·3
	Nonanal	0·3
	Methylthiomethane	0·3
	Ethyldithioethan	0·3
	2-Phenylethanol	0·35
	3-Methylindole (skatole)	0·35
	Butanoic acid	0·4
	2-Methylphenol	0·4
	2-Butene-1-thiol	0·43
	2-Nonenal	0·5
$0{\cdot}5 \leq C_{od} \leq 1{\cdot}0$	Indole	0·6
	Petanoic acid	0·8
	Butanal	0·84

* Lowest odour detection threshold; the lowest concentration that has a 0·5 probability of being detected under the conditions of the test (CEN standard 13 725; European Committee for Standardization, 2003).

Although a huge number of odorous compounds have been identified from animal production facilities, the sources from which they originate are poorly described. Geypens *et al.* (1997) isolated a total of 120 different volatile organic compounds from human faeces, of which twenty-five remained unidentified. Schaefer *et al.* (1974) detected more than seventy compounds, which they assumed to have originated from particles of feed rather than from animal manure. Drasar & Hill (1974) found indole, 3-methyl indole (skatole), phenol, 4-methylphenol (*p*-cresol) and 4-ethylphenol in the urine of pigs. These compounds originate from the putrefactive decomposition of bacteria in the large intestine of the animal. They are then detoxified by the liver and excreted via the urine. According to Spoelstra (1976), phenol, *p*-cresol, and 4-ethylphenol are mainly present in urine as glucuronides. Glucuronides are rapidly and easily converted by glucuronidase in faeces to the compounds mentioned. Odour from the animal body, such as the cutaneous and oral odour, has not been well described. The main sweat compounds from the animal are thought to be propionic and butyric acid (Jackman, 1982). Volatile S compounds, methylamine, dimethylamine, propanonic acid, butyric acid, indole, skatole, and cadaverine are reported to cause oral malodour (Goldberg *et al.* 1994, 1997; Nakano *et al.* 2002). Previous studies have not described clearly the contribution of different sources to the odour production and concentration in animal production facilities. Further studies are required.

Many authors have attempted to elucidate relationships between different odorous compounds or chemical odour groups and odour strength and offensiveness or have tried to find odour markers. Spoelstra (1980) recommended using *p*-cresol and VFA as indicators of odour offensiveness from animal production facilities; Williams & Evans (1981) suggested VFA, phenol, *p*-cresol and skatole as the main odour markers, while Barth *et al.* (1974) reported VFA, NH_3 and hydrogen sulfide as the main odour markers from animal production facilities. According to Schaefer (1977), the primary malodour compounds from animal production facilities are associated with VFA, phenol, *p*-cresol, indole, and skatole. Williams (1984) and Hobbs *et al.* (1997) produced a list of four major groups of odorants; VFA, indoles, phenols and sulfides. According to Curtis (1993), the odour groups are ammonia and volatile amines, sulfurous compounds, VFA, indoles and phenols, alcohols and carbonyls. It would be very efficient in terms of odour reduction if a single compound or a group of compounds could be identified as an odour marker in a specific animal production system. However, the above-mentioned studies did not show very consistent results for odour markers. This inconsistency can be explained, because there are a great number of odorous compounds that are produced in different amounts under different circumstances. In addition, not only the individual odour concentration is important, but the way they interact with each other as well. Furthermore, different diets in different areas of the world might play an important

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role in the production of the different odorous compounds. Although the marker of odour differed between the above-mentioned studies, and one single odour marker can not be expected for all animal production systems, we can see that there are four general odour groups in animal production facilities: VFA; sulfurous compounds; indoles and phenols; ammonia and volatile amines.

Volatile fatty acids

VFA are commonly reported as being major constituents of odour from animal production facilities. About 60 % of the total VFA in manure (w/w) are present as acetic acid. The next most dominant acids are propionic, butyric (*n*-butyric), 2-methylpropionic (isobutyric), 3-methylbutyric (isovaleric), pentanoic (*n*-valeric), and capric acids (McGill & Jackson, 1977; Cooper & Cornforth, 1978; Spoelstra, 1980). The odorous nature of VFA progresses from the pungent smell of acetic acid to the distinctly unpleasant and offensive smell of valeric and caproic acids (Morrison & Boyd, 1987; Zhu, 2000). VFA with high C numbers have a lower odour-detection threshold (Mackie, 1994). A high concentration of VFA in pig manure may not cause very offensive malodour because a large proportion of VFA could be composed of short-chain VFA that are potentially less offensive.

The detection threshold, concentration and odour nature of some important VFA compounds are listed in Table 2; their chemical structures and their potential precursors are listed in Table 3. Although all the researchers used the technique of gas chromatography (GC), it is surprising that concentrations of odorous compounds in general, and VFA in particular, vary so widely among different studies and among different kinds of samples. The variation is probably created by different sampling and measuring methods, different sources of samples, etc. The exact source of samples of odorous air compounds is very important, but in many reports it is unclear. In addition, the studies cited in Table 2 were published from 1975 to 1997 and therefore an important reason for the variation of the concentration of odorous compounds could be the changes that have taken place in the last 30 years in animal production systems (for example, in diet, animal breeds, and housing systems). Furthermore, the detection thresholds of odorous compounds also vary widely. This is probably due to the fact that in the past the measuring of odour concentration was not standardised. So, different protocols were used to determine odour-detection thresholds. The variation of the odour-detection threshold can be reduced by standardising measuring methods.

Sulfurous compounds

S is present in numerous compounds at various states of oxidation. For example, S has a +6 charge as a sulfate anion, a +4 charge as gaseous sulfur dioxide and a sulfite anion, no charge as elemental S, and a −2 charge as a sulfide anion. Several authors have reported that sulfurous compounds are important constituents of odour from livestock manure (Schaefer, 1980; Odam *et al.* 1986; Ohta & Kuwada, 1998). The S excreted in fresh manure is about 76 and 51 g/1000 kg animal mass per d for pig and dairy cattle, respectively (American Society of Agricultural Engineers, 1998). S excretion is quantitatively similar in faeces and urine. When diets contain higher S levels, the excretion ratio is shifted in favour of urine (Bouchard & Conrad, 1973). According to O'Neill & Phillips (1992), six of the ten compounds with the lowest odour-detection threshold contain S. In addition, Table 1 shows that the three compounds with the lowest odour-detection threshold all contain S. Furthermore, it has been shown that sulfurous compounds are the most offensive compounds. Table 2 shows that the odorous nature of sulfurous compounds progresses from the putrid smell of dimethyl disulfide and methanethiol to the rotten eggs smell of hydrogen sulfide.

Hydrogen sulfide is considered one of the most dangerous gases; it has been reported to be responsible for many animal and human deaths (Donham *et al.* 1982; Ji-Qin *et al.* 2000). However, its concentration is usually low, unless the manure is agitated (Patni & Clarke, 1990). Schaefer *et al.* (1974) have reported that hydrogen sulfide in ventilation air has a concentration of about 4 $\mu g/m^3$. Hobbs *et al.* (1999) observed that the rate of hydrogen sulfide emission decreased from 100 to 28 g/m^2 per d during a 112 d study of stored pig manure. They also reported that there was no correlation between hydrogen sulfide concentration and odour concentration. Clanton & Schmidt (2001), however, found that the Pearson correlation coefficient between odour concentration and hydrogen sulfide concentration in the air from pig production facilities was 0·731; this is higher than that of 0·20 determined by Jacobson *et al.* (1997), also in air from pig production facilities. There are several possible reasons for this inconsistency. Sampling and measuring methods, on the basis of which odour and hydrogen sulfide concentration were measured, might differ between these studies. The air sample might be taken from different animal types, from different days, from different farms and the animal might be fed different diets. In addition, hydrogen sulfide production and emission seems to be very much influenced by housing system and manure management; for example, the regular flushing of manure or storing the manure for a long time in a manure pit might give larger differences in hydrogen sulfide production and emission.

Hydrogen sulfide and methanethiol (methylmercaptan) are the most commonly reported sulfurous compounds causing odour offensiveness in pig manure (Spoelstra, 1980). According to Banwart & Bremmer (1975), hydrogen sulfide and methanethiol represented 70 to 97 % of the total S volatilised in manure. They also reported that for pigs and poultry, the amount of methanethiol produced exceeded the amount of hydrogen sulfide produced. Beard & Guenzi (1983) stated that most of the S emanated in the form of hydrogen sulfide (39 %), methanethiol (34 %) and dimethyl sulfide (21 %). According to Hobbs *et al.* (1997), the methanethiol concentration in the headspace air is about 36 000 $\mu g/m^3$. It is from 947 to 120×10^6 times higher than the detection threshold (Table 2). Therefore, methanethiol may be a very important compound causing odour nuisance.

Apart from hydrogen sulfide and methanethiol, the other sulfurous compounds identified in air from pig production facilities include carbon disulfide, 2-propanethiol, dimethyl-disulfide, dimethyltrisulfide, 2-methylthiopropane,

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Table 2. Nature of smell; odour detection threshold and concentration of important odorous compounds from pig production facilities

Group	Odorous compound	Nature of smell	Detection threshold ($\mu g/m^{-3}$)	Reference	Concentration ($\mu g/m^3$)	Source	Reference
Volatile fatty acids	Acetic (ethanoic) acid	Pungent or vinegar	25–10 000	Schaefer *et al.* (1974), Miner *et al.* (1975), Lunn & van de Vyver (1977), Schaefer (1977), Phillips *et al.* (1979), Kowalewsky *et al.* (1980), Spoelstra (1980), Klarenbeek *et al.* (1982), Williams (1984), Yasuhara *et al.* (1984), van Geelen & van der Hoek (1985), Hammond *et al.* (1989), Zahn *et al.* (1997)	0·0015–6700	Ventilation air	Schaefer *et al.* (1974), Miner *et al.* (1975), Kowalewsky *et al.* (1980), van Geelen & van der Hoek (1985)
					1800–4700	Headspace air	Hobbs *et al.* (1997)
					1120–2690	Wet slurry	Hobbs *et al.* (1996)
					2–15·7*	Stored manure	Spoelstra (1979)
					270	Air at 1·5 m above manure basin	Zahn *et al.* (1997)
	Propionic (propanoic) acid	Faecal	2·5–890	Schaefer *et al.* (1974), Miner *et al.* (1975), Lunn & van de Vyver (1977), Schaefer (1977), Phillips *et al.* (1979), Kowalewsky *et al.* (1980), Spoelstra (1980), Klarenbeek *et al.* (1982), Williams (1984), Yasuhara *et al.* (1984), van Geelen & van der Hoek (1985), Hammond *et al.* (1989), Zahn *et al.* (1997)	0·002–1100	Ventilation air	Schaefer *et al.* (1974), Miner *et al.* (1975), Kowalewsky *et al.* (1980), van Geelen & van der Hoek (1985)
					20–2500	Headspace air	Hobbs *et al.* (1997)
					148–400	Wet slurry	Hobbs *et al.* (1996)
					1·2–6·6*	Stored manure	Spoelstra (1979)
					130	Air at 1·5 m above manure basin	Zahn *et al.* (1997)
	Butyric (butanoic) acid	Faecal or stench	0·25–42 000	Schaefer *et al.* (1974), Miner *et al.* (1975), Lunn & van de Vyver (1977), Schaefer (1977), Phillips *et al.* (1979), Kowalewsky *et al.* (1980), Spoelstra (1980), Klarenbeek *et al.* (1982), Williams (1984), Yasuhara *et al.* (1984), van Geelen & van der Hoek (1985), Hammond *et al.* (1989)	0·001–617	Ventilation air	Schaefer *et al.* (1974), Miner *et al.* (1975), Kowalewsky *et al.* (1980), van Geelen & van der Hoek (1985)
					1100–4000	Headspace air	Hobbs *et al.* (1997)
					250–350	Wet slurry	Hobbs *et al.* (1996)
					0·4–3·1*	Stored manure	Spoelstra (1979)
					590	Air at 1·5 m above manure basin	Zahn *et al.* (1997)
	3-Methyl-butyric acid	Faecal	0·017–6·9	Schaefer *et al.* (1974), Miner *et al.* (1975), Lunn & van de Vyver (1977), Spoelstra (1980), Williams & Evans (1981), Williams (1984), Yasuhara *et al.* (1984), van Geelen & van der Hoek (1985), Zahn *et al.* (2001)	0·0012–210	Ventilation air	Schaefer *et al.* (1974), Kowalewsky *et al.* (1980), van Geelen & van der Hoek (1985)
					800–1100	Headspace air	Hobbs *et al.* (1997)
					50–200	Wet slurry	Hobbs *et al.* (1996)
					0·2–1*	Stored manure	Spoelstra (1979)
					98	Air at 1·5 m above manure basin	Zahn *et al.* (2001)
	Pentanoic (*n*-valeric) acid	Faecal	0·26–120	Schaefer *et al.* (1974), Miner *et al.* (1975), Lunn & van de Vyver (1977), Spoelstra (1980), Williams & Evans (1981), Williams (1984), Yasuhara *et al.* (1984), van Geelen & van der Hoek (1985)	0·0012–80	Ventilation air	Kowalewsky *et al.* (1980), Schaefer *et al.* (1974), van Geelen & van der Hoek (1985)
					200	Headspace air	Hobbs *et al.* (1997)
					70–90	Wet slurry	Hobbs *et al.* (1996)
					0·1–1*	Stored manure	Spoelstra (1979)
					360	Air at 1·5 m above manure basin	Zahn *et al.* (2001)
	4-Methyl pentanoic acid	–	37	Schaefer *et al.* (1974), Lunn & van de Vyver (1977), Spoelstra (1980), Yasuhara *et al.* (1984)	0·001–160	Ventilation air	Schaefer *et al.* (1974), Miner *et al.* (1975), Kowalewsky *et al.* (1980), van Geelen & van der Hoek (1985)
					0·2–1*	Stored manure	Spoelstra (1979)

Continued

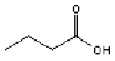
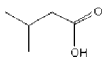
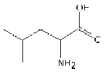
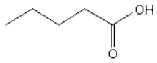
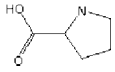
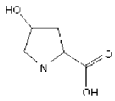
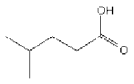
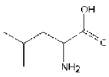
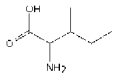
Table 2. *Continued*

Group	Odorous compound	Nature of smell	Detection threshold ($\mu g/m^{-3}$)	Reference	Concentration ($\mu g/m^3$)	Source	Reference
	Hexanoic (*n*-caproic) acid	Pungent	20–520	Schaefer *et al.* (1974), Lunn & van de Vyver (1977), Spoelstra (1980), Yasuhara *et al.* (1984), Zahn *et al.* (2001)	10 110	Ventilation air Air at 1·5 m above manure basin	Schaefer *et al.* (1974) Zahn *et al.* (2001)
	Heptanoic (oenanthic) acid	Pungent	2·8–33	Schaefer *et al.* (1974), Miner *et al.* (1975), Lunn & van de Vyver (1977), Spoelstra (1980), Hammond *et al.* (1989), Zahn *et al.* (2001)	3 8	Ventilation air Air at 1·5 m above manure basin	Schaefer *et al.* (1974) Zahn *et al.* (2001)
Ammonia and volatile amines	Ammonia	Sharp or pungent	27–37 800	Schaefer *et al.* (1974), Miner *et al.* (1975), Lunn & van de Vyver (1977), Schaefer (1977), Kowalewsky *et al.* (1980), Spoelstra (1980), Klarenbeek *et al.* (1982), Williams (1984), Zahn *et al.* (2001)	100–18 000 3700	Ventilation air Air at 1·5 m above manure basin	Klarenbeek *et al.* (1982), Schaefer *et al.* (1974) Zahn *et al.* (2001)
S compounds	Hydrogen sulfide	Rotten eggs	0·1–270	Schaefer *et al.* (1974), Banwart & Bremmer (1975), Lunn & van de Vyver (1977), Schaefer (1977), Phillips *et al.* (1979), Kowalewsky *et al.* (1980), Spoelstra (1980), Hammond *et al.* (1989), Zahn *et al.* (2001)	4 90	Ventilation air Air at 1·5 m above manure basin	Schaefer *et al.* (1974) Zahn *et al.* (2001)
	Carbonyl sulfide	–	250	Banwart & Bremmer (1975), Spoelstra (1980)	–		
	Carbon disulfide	–	–		–		
	Methanethiol (methyl mercaptan)	Garlic/Putrid	0·0003–38	Banwart & Bremmer (1975), Lunn & van de Vyver (1977), Schaefer (1977), Spoelstra (1980)	36 000	Headspace air	Hobbs *et al.* (1997)
	Dimethyl sulfide	Stench	0·3–160	Banwart & Bremmer (1975), Lunn & van de Vyver (1977), Schaefer (1977), Spoelstra (1980)	0·0022 14 000	Ventilation air Headspace air	Miner *et al.* (1975) Hobbs *et al.* (1997)
	Dimethyl disulfide	Putrid, decayed vegetable	1·1–610	Banwart & Bremmer (1975), Miner *et al.* (1975), Lunn & van de Vyver (1977), Spoelstra (1980), Zahn *et al.* (2001)	12 000 17	Headspace air Air at 1·5 m above manure basin	Hobbs *et al.* (1997) Zahn *et al.* (2001)
	Dimethyl trisulfide	Nauseating	7·3	Miner *et al.* (1975), Lunn & van de Vyver (1977), Spoelstra (1980), Yasuhara *et al.* (1984)	5000	Headspace air	Hobbs *et al.* (1997)
	Ethanethiol (ethyl mercaptan)	–	0·043–0·33	Schaefer (1977), Spoelstra (1980), Hammond *et al.* (1989)	–		
Indoles and phenols	Phenol	Aromatic	22–4000	Schaefer *et al.* (1974), Miner *et al.* (1975), Lunn & van de Vyver (1977), Schaefer (1977), Phillips *et al.* (1979), Klarenbeek *et al.* (1982), Williams (1984), Yasuhara *et al.* (1984), Hammond *et al.* (1989), Zahn *et al.* (2001)	0·0025–5 3700–4800 16–47 0·007–0·055* 10–55 25	Ventilation air Headspace air Wet slurry Stored manure Stored manure Air at 1·5 m above manure basin Ventilation air	Miner *et al.* (1975), Schaefer *et al.* (1974) Hobbs *et al.* (1997) Hobbs *et al.* (1996) Spoelstra (1979) Hobbs *et al.* (1999) Zahn *et al.* (2001)

3-Methyl-phenol (*m*-cresol)	–	0·22–35	Spoelstra (1980)	4		Kowalewsky *et al.* (1980)
4-Methyl-phenol (*p*-cresol)	Faecal	0·05–24	Schaefer *et al.* (1974), Miner *et al.* (1975), Lunn & van de Vyver (1977), Schaefer (1977), Phillips *et al.* (1979), Klarenbeek *et al.* (1982), Williams (1984), Yasuhara *et al.* (1984), Hammond *et al.* (1989), Zahn *et al.* (2001)	4600–7000 30–60 0·14–0·34* 10–55 90	Headspace air Wet slurry Stored manure Stored manure Air at 1·5 m above manure basin	Hobbs *et al.* (1997) Hobbs *et al.* (1996) Spoelstra (1979) Hobbs *et al.* (1999) Zahn *et al.* (2001)
4-Ethylphenol	Pungent	3·5–10	Zahn *et al.* (1997)	500–4900 0·3–6·4 0·006–0·072* 4	Headspace air Wet slurry Stored manure Air at 1·5 m above manure basin	Hobbs *et al.* (1997) Hobbs *et al.* (1996) Spoelstra (1979) Zahn *et al.* (1997)
Indole	Faecal or stench	0·6–7·1	Schaefer *et al.* (1974), Spoelstra (1976), Lunn & van de Vyver (1977), Schaefer (1977), Spoelstra (1980), Williams & Evans (1981), Williams (1984), Yasuhara *et al.* (1984), Zahn *et al.* (2001)	3 100–500 4–9·8 0–0·001* 2	Ventilation air Headspace air Wet slurry Stored manure Air at 1·5 m above manure basin	Schaefer *et al.* (1974) Hobbs *et al.* (1997) Hobbs *et al.* (1996) Spoelstra (1979) Zahn *et al.* (1997)
3-Methyl indole (skatole)	Faecal or nauseating	0·0005–6·4	Schaefer *et al.* (1974), Lunn & van de Vyver (1977), Schaefer (1977), Spoelstra (1976), Spoelstra (1980), Williams & Evans (1981), Williams (1984), Yasuhara *et al.* (1984), Zahn *et al.* (1997)	3 100–400 1·7–3·6 0·009–0·054* 2	Ventilation air Headspace air Wet slurry Stored manure Air at 1·5 m above manure basin	Schaefer *et al.* (1974) Hobbs *et al.* (1997) Hobbs *et al.* (1996) Spoelstra (1979) Zahn *et al.* (1997)

* Concentration given in g/kg wet weight.

Table 3. Origin of odorous compounds

Groups	Odorous compounds	Main origin	Reference
Volatile fatty acids	Acetic (ethanoic) acid 	Dietary fibre, L-glycine, L-alanine, L-cysteine, L-lysine, L-serine, L-threonine, L-hydroxyproline, L-aspartate, L-glutamate, L-histidine	Nisman (1954), Stadtman (1963), Loesche & Gibbons (1968), Elsden & Hilton (1978), Turton *et al.* (1983), Mortensen *et al.* (1987), Rasmussen *et al.* (1988), Stryer (1995), Sutton *et al.* (1999)
	Propionic (propanoic) acid 	Dietary fibre Lactate  L-Alanine, L-threonine, L-alanine + L-threonine, L-aspartate, L-methionine	Nisman (1954), Loesche & Gibbons (1968), Elsden & Hilton (1978), Schlegel (1986), Rasmussen *et al.* (1988), Sutton *et al.* (1999)
	Butyric (butanoic) acid 	Dietary fibre, L-cysteine, L-hydroxyproline, L-lysine, L-serine, L-threonine, L-aspartate, L-glutamate, L-histidine	Loesche & Gibbons (1968), Elsden & Hilton (1978), Turton *et al.* (1983), Mortensen *et al.* (1987), Rasmussen *et al.* (1988), Hammond *et al.* (1989), Sutton *et al.* (1999)
	3-Methylbutyric acid 	Fibre L-valine  L-Leucine 	Elsden & Hilton (1978), Britz & Wilkinson (1983), Rasmussen *et al.* (1988), Sutton *et al.* (1999)
	Pentanoic (*n*-valeric) acid 	Fibre L-Proline  L-Hydroxyproline 	Rasmussen *et al.* (1988), Sutton *et al.* (1999)
	4-Methyl pentanoic acid 	L-Leucine  L-Isoleucine 	Nisman (1954), Elsden & Hilton (1978), Rasmussen *et al.* (1988)
	Hexanoic (*n*-caproic) acid 	Ethanol, acetate, CO_2	Smith *et al.* (1985), Kenealy *et al.* (1995)

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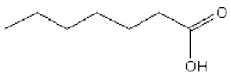
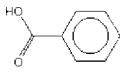
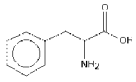
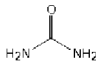
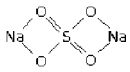
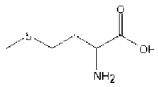
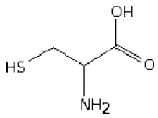
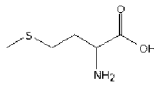
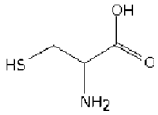
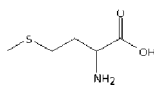
	Heptanoic (enanthic) acid 	Benzoic acid  L-Phenylalanine 	Bisaillon *et al.* (1994), Schneider *et al.* (1997), Gummalla & Broadbent (2001)
Ammonia and volatile amines	Ammonia 	Urea 	Wozny *et al.* (1977), Suzuki *et al.* (1979), Aarnink *et al.* (1996), Canh *et al.* (1998*b*)
S compounds	Hydrogen sulfide 	Deamination of amino acids Sulfate  L-Methionine  L-Cysteine 	Ohkishi *et al.* (1981), Schlegel (1986), Claesson *et al.* (1990), Sutton *et al.* (1999)
	Carbonyl sulfide 	Hydrogen sulfide 	Ren (1999)
	Carbon disulfide	Carbonyl sulfide 	Banwart & Bremmer (1975), Ren (1999)
	Methanethiol (methyl mercaptan) 	L-Methionine  L-Cysteine 	Segal & Starkey (1969), Kreis & Hession (1973), Ferchichi *et al.* (1985), Inoue *et al.* (1995), Hori *et al.* (1996), Mackie *et al.* (1998), Sutton *et al.* (1999), Yoshimura *et al.* (2000)
	Dimethyl sulfide 	L-Methionine 	Kadota & Ishida (1972), Kelly *et al.* (1994), Sutton *et al.* (1999)

Continued

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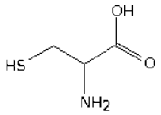
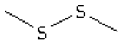
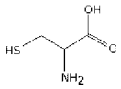
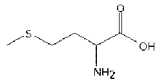
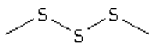
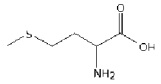
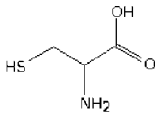
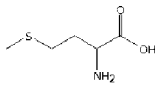
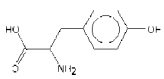
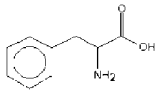
Table 3. *Continued*

Groups	Odorous compounds	Main origin	Reference
		L-Cysteine 	
	Dimethyl disulfide 	Methanethiol 	Segal & Starkey (1969), Chin & Lindsay (1994), Sutton *et al.* (1999), Bonnarme *et al.* (2001)
		L-Cysteine 	
		L-Methionine 	
	Dimethyl trisulfide 	Methanethiol 	Segal & Starkey (1969), Chin & Lindsay (1994), Bonnarme *et al.* (2001)
		L-Methionine 	
		L-Cysteine 	
	Ethanethiol (ethyl mercaptan) 	L-Methionine 	Akobe (1936)
Indoles and phenols	Phenol 	L-Tyrosine 	Ichihara *et al.* (1956), Brot *et al.* (1965), Bakke (1969), Hammond *et al.* (1989), Sutton *et al.* (1999)
		L-Phenylalanine 	

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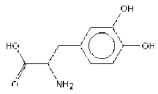
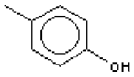
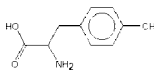
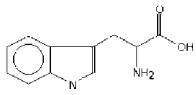
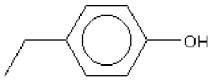
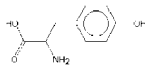
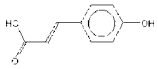
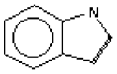
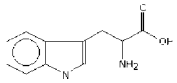
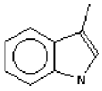
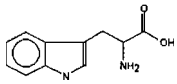
3-Methylphenol (*m*-cresol) 	3,4-Hydroxyphenylalanine 	Drasar & Hill (1974)
4-Methylphenol (*p*-cresol) 	L-Tyrosine 	Bakke (1969), Hammond *et al.* (1989), Hengemuehle & Yokoyama (1990), Sutton *et al.* (1999)
	L-Trptophan 	
4-Ethylphenol 	L-Tyrosine 	Drasar & Hill (1974), Spoelstra (1976), Hammond *et al.* (1989), Hengemuehle & Yokoyama (1990)
	p-Coumaric acid 	
Indole 	L-Tryptophan 	DeMoss & Moser (1969), Drasar & Hill (1974), Elsden *et al.* (1976), Hammond *et al.* (1989), Sutton *et al.* (1999)
3-Methyl indole (skatole) 	L-Tryptophan 	Drasar & Hill (1974), Yokoyama & Carlson (1974), Chung *et al.* (1975), Elsden *et al.* (1976), Hammond *et al.* (1989), Hengemuehle & Yokoyama (1990), Honeyfield & Carlson (1990), Jensen & Jørgensen (1994), Sutton *et al.* (1999)

methaethiocyclopentane, 1-methylthiopentane, dimethyltetrasulfide and dimethylhexasulfide (Odam *et al.* 1986).

The detection threshold, concentration and odour nature of some important sulfurous compounds are listed in Table 2; their chemical structures and their precursors are listed in Table 3. Like VFA, they vary widely among studies and kinds of samples. In general, the concentrations of sulfurous compounds in the air are higher than the concentrations of VFA. In addition, their detection thresholds are lower than VFA. Furthermore, the nature of the smell of sulfurous compounds seems to be more offensive. As a result, sulfurous compounds may cause much more odour nuisance than VFA.

Phenoles and indoles

Phenol, *p*-cresol, 3-methyl phenol (*m*-cresol), and 4-ethylphenol are important representatives of phenolic compounds, whereas indole and skatole are indolic compounds. These two kinds of compounds are considered as the main compounds responsible for the smell in the ventilation air of pig houses (Schaefer, 1977; Williams & Evans, 1981; O'Neill & Phillips, 1992). The nature of the smell of indole and phenol compounds progresses from the aromatic smell of phenol to the stench of indole and the nauseating smell of skatole. Schaefer *et al.* (1974), quoted by O'Neill & Phillips (1992), synthesised the smell of pig manure, in which phenolic compounds were represented in high concentrations (v/v): *p*-cresol (64 %); phenol (26 %). Other compounds, for example, *n*-butyric acid, skatole, and indole were present in lower concentrations. Williams & Evans (1981) reported an increase in concentrations of phenol, *p*-cresol and skatole, and a decrease in the concentration of indole during the accumulation of pig manure in a store. Spoelstra (1980) indicated that the phenol concentration increased during the 150 d measuring period, while indole, *p*-cresol and skatole concentrations increased initially but decreased after 40, 65 and 70 d, respectively.

Despite the great variation among studies, it can be seen from Table 2 that the concentration of *p*-cresol in headspace air ranges from 4600 to 7000 $\mu g/m^3$. The concentration of *p*-cresol in ventilation air, wet slurry and stored manure is

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higher than that of the other phenol and indole compounds listed in Table 2. In addition, it also has a lower odour detection threshold than the other compounds. Therefore, it seems safe to conclude that *p*-cresol is an important compound in terms of odour nuisance compared with other indole and phenol compounds. The next most important compounds might be indole and skatole. Although phenol has a rather high concentration in headspace air (3700–4800 $\mu g/m^3$) it has a high detection threshold (22–4000 $\mu g/m^3$). In addition, the smell of phenol is aromatic; thus phenol may not contribute to odour nuisance in contrast to other indolic and phenolic compounds.

Ammonia and volatile amines

Ammonia has a sharp and pungent smell. The main source of ammonia is urea (Spoelstra, 1980). The ammonia concentration in air samples taken from animal houses, manure tanks and fields spread with manure has been found to correlate well with odour intensity (r^2 0·72) as measured by olfactometry (Kowalewsky *et al.* 1980). Schulte *et al.* (1985) and Miner (1995) found a high correlation between ammonia and odour emission from livestock facilities. However, Liu *et al.* (1993), Oldenburg (1989), Verdoes & Ogink (1997), and Williams (1984) found only a low correlation between ammonia and odour emission from pig houses. According to Oldenburg (1989), ammonia does not seem to be an important odorous compound. He also reported that mean ammonia concentrations were below 8 parts per million (ppm) in cattle barns, between 5 and 18 ppm in pig houses and between 5 and 30 ppm in poultry houses. Studies in the USA suggest that if ammonia levels exceed 7 ppm, workers may suffer clinical effects (Donham *et al.* 1989). Wathes *et al.* (2002) reported that weaner pigs, broiler chickens and adult laying hens were significantly averse to ammonia at concentrations of 20 ppm and higher.

The volatile amines from animal production facilities may include methylamine (putrid smell), ethylamine (fishy smell), trimethylamine (ammoniac-like smell), cadaverine (foul smell), and putrescine (smell of putrefaction). Volatile amines make up a very small part of the volatile nitrogenous compounds. Concentrations of volatile amines from animal production facilities were rarely found in the literature.

Résumé

A great number of odorous compounds have been identified in animal production facilities. However, the relative contribution of the different sources (for example, animals, feed, faeces, urine, and manure) to the formation of odorous compounds has not yet been determined. In order to be able to propose solutions for odour abatement, it is important to clearly identify the different sources of odorous compounds. Sulfurous compounds, indoles and phenols, and VFA are probably the most important groups of odorous compounds from animal production facilities. The huge variation among studies in the odour concentration and odour-detection threshold of odour compounds largely responsible for odour nuisance (see Table 2) might be attributable to the fact that the determined odour concentration is related to many factors (for example, dietary composition, environmental factors, measuring methods and standards, sources of sample). In addition, the relative importance of different compounds causing odour nuisance has seldom been described. In order to propose feasible and efficient solutions for odour reduction it is important to accurately identify the concentration, detection threshold and main source of each odorous compound, and the relative importance of different odorous compounds from animal production facilities. This requires further studies.

Production of odorous compounds from animal production facilities, and the bacterial reactions involved

When feed passes through the digestive tract, food nutrients are hydrolysed and fermented into smaller molecular structures that can be absorbed and used for the growth and development of the animal. The non-utilised nutrients and endogenous compounds in the gastrointestinal tract are excreted via the urine and faeces. The biological degradation process performed by micro-organisms, that starts in the intestine under anaerobic conditions, continues after excretion. This anaerobic microbial degradation process is represented in Fig. 2. Different groups of odorous compounds are produced during anaerobic degradation. Most groups are produced from different precursors in different ways, which may in turn interact with the production of others.

Volatile fatty acids

VFA are mainly formed by microbial conversions of plant fibre and protein residues in the large intestine and in manure under anaerobic conditions. During fermentation, energy is obtained from organic compounds that serve as electron donors and acceptors, replacing oxygen in the latter function.

Dietary fibre residues may include cellulose, hemicellulose and lignin. Lignin is very difficult to degrade under anaerobic conditions. Cellulose and hemicellulose are first hydrolysed by microbial enzymes into oligomers and/or monomers. The latter are subsequently converted by the microbes into VFA such as acetic, propionic and butyric acids. The proportion of acids produced can vary, depending on the type of substrate available, the composition of the anaerobic flora and the prevailing pH. Van Soest (1983) described different pathways of carbohydrate metabolism in general and of dietary fibre in particular in the rumen of cattle (Fig. 3). The same pathways of carbohydrate metabolism are assumed in the large intestine of single-stomached animals, although the amount and ratio of endproducts may differ.

Apart from being formed from carbohydrates, acetic, propionic and butyric acids are also produced by the deamination of amino acids (AA) such as L-glutamate, L-lysine, and L-alanine (Tables 4 and 5). Ammonia, CO_2 and [H] are additional endproducts of this deamination–decarboxylation. The general mechanism of deamination–decarboxylation is presented in equation 1.

$$\mathrm{R{-}\underset{\displaystyle NH_2}{\underset{|}{CH}}{-}COOH + 2H_2O \rightarrow R{-}COOH + NH_3 + 4[H] + CO_2} \qquad (1)$$

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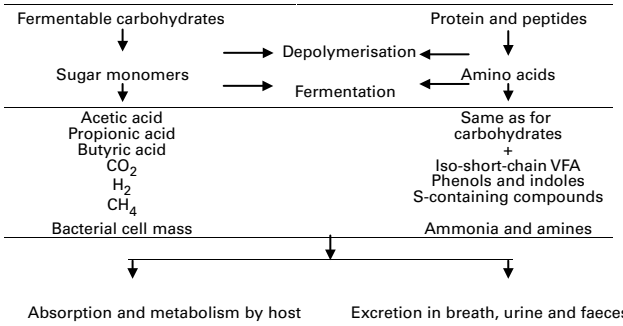

Fig. 2. Major fermentation products formed by the microbiota in the gastrointestinal tract of pigs. VFA, volatile fatty acids (adapted from Jensen & Jørgensen, 1994).

According to Mortensen *et al.* (1987) and Rasmussen *et al.* (1988), carbohydrates are easily converted into acetic acid, propionic acid, and butyric acid in faecal incubation systems, but this has never resulted in the production of branched-chain VFA such as isovaleric acid and isobutyric acid. The latter VFA originate from the breakdown of peptides. Peptolytic bacteria hydrolyse proteins into AA. The latter are then deaminated and decarboxylated to branched-chain VFA. Examples are given in equations 2, 3 and 4.

$$\text{Valine} + 2H_2O \rightarrow \text{isobutyric acid} + NH_3 + CO_2 \quad (2)$$

$$\text{Leucine} + 2H_2O \rightarrow \text{isovaleric acid} + NH_3 + CO_2 \quad (3)$$

$$\text{Isoleucine} + 2H_2O \rightarrow 2-\text{methylbutyric acid} + NH_3 + CO_2 \quad (4)$$

In the gastrointestinal tract of pigs, micro-organisms can synthesise short-chain VFA (fatty acids with chain lengths of two to six C atoms) from unabsorbed nutrients (Giusi-Perier *et al.* 1989). According to Müller & Kirchgessner (1985) and Engehard (1995), 66 to 99 % of the short-chain VFA produced in the large intestine can be absorbed and used as an energy source for the host animal. In addition, short-chain VFA have a high odour-detection threshold. Therefore, short-chain VFA produced in the large intestine of animals are probably not a major concern in terms of odour nuisance.

Briefly, VFA are produced from proteins and carbohydrates under anaerobic conditions in the large intestine of animals and in manure storage. Carbohydrates are transformed to straight-chain VFA only. Proteins are transformed to both straight-chain VFA and branched-chain VFA. Short-chain VFA in the large intestine can be used as an energy source for the host animal and thus are probably not a big problem in terms of odour nuisance. However, when they are in manure storages, VFA may be volatilised and cause malodour.

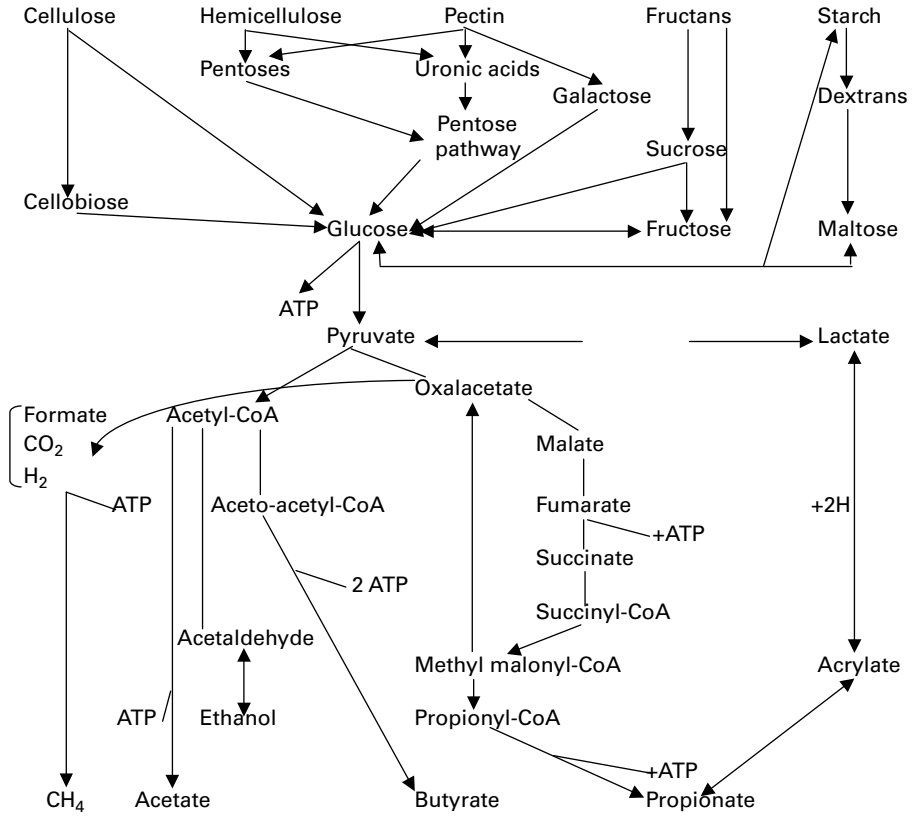

Fig. 3. Pathways of carbohydrate metabolism in the rumen (van Soest, 1983).

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Table 4. Deamination reactions by anaerobic bacteria in the gastrointestinal tract and manure (Mackie *et al.* 1998)

Amino acid	Corresponding VFA produced
Alanine, glycine, serine	Acetic acid
Threonine	Propionic acid
Glutamate, aspartate	Acetic, propionic acid
Valine	Isobutyric acid
Leucine	Isopentanoic acid
Isoleucine	2-Methylbutyric acid
Phenylalanine	Phenylacetic acid
Tyrosine	*p*-Hydroxylphenylacetic acid
Tryptophan	Indoleacetic acid → skatole
Tyrosine	Phenylacetic acid, phenylpropionic acid

VFA, volatile fatty acid.

Sulfurous compounds

There are two main ways of sulfide production; sulfate reduction and the metabolism of sulfurous AA.

Metabolism of sulfurous amino acids. When manure is stored anaerobically, organic sulfurous compounds such as the AA methionine, cysteine and cystine are broken down to release sulfidic compounds. Various anaerobic bacteria perform this process, in which sulfurous AA are used as C and energy sources by the microbes. Some intermediates are produced that can volatilise and create odour. An example is the hydrolysis of methionine, from which methanethiol (methyl mercaptan) is formed, which can be further degraded to sulfide (American Society of Agricultural Engineers, 1989) (equations 5 and 6).

$$CH_3S(CH_2)_2CHNH_2COOH + H_2O \rightarrow CH_3SH$$

$$(\text{methanethiol}) + NH_3 + CH_3CH_2COCOOH \quad (5)$$

$$CH_3SH + H_2O \rightarrow CH_3OH + H_2S \quad (6)$$

Methanethiol as a product of L-methionine degradation can be chemically converted to dimethyl disulfide and dimethyl trisulfide in the presence of Cu(II) or ascorbate plus Fe(III), for example (Parliment *et al.* 1982; Chin & Lindsay, 1994; Bonnarme *et al.* 2001).

Sulfate reduction. The other main source of sulfide formation is sulfate. In urine, sulfate is the primary form of S excreted. Spoelstra (1980) stated that the primary origin of sulfide in manure is the reduction of sulfate into sulfide. Sulfate reduction proceeds via assimilatory or dissimilatory pathways. In the assimilatory process, bacteria produce enough reduced S for the biosynthesis of cysteine and methionine. This is in contrast to the dissimilatory process, in which sulfate is used as an electron acceptor for an anaerobic respiration comparable with the aerobic respiration with oxygen. During respiration with sulfate, copious amounts of malodour are generated. This process has been characterised by Clanton & Schmidt (2001) and Sawyer & McCarty (1978) (equation 7). The bacteria that are sulfate-reducers belong to the genera *Desulfovibrio*, *Desulfotomaculum*, *Desulfobacter*, *Desulfococcus*, and *Desulfonema* (Schlegel, 1986).

$$SO_4^{2-} + \text{organic matter} \xrightarrow[\text{bacteria}]{\text{Anaerobic}} S^{2-} + H_2O + CO_2 \quad (7)$$

Hydrogen sulfide might be transformed to carbonyl sulfide and carbon disulfide (Ren, 1999), although these respective reactions have not been described for gut bacteria.

$$H_2S + CO_2 \rightarrow COS + H_2O \quad (8)$$

$$COS + H_2S \rightarrow CS_2 + H_2O \quad (9)$$

According to Spoelstra (1980), sulfate-reducing bacteria also produce trace amounts of COS, CS_2, and methyl, ethyl and propyl mercaptans.

Briefly, sulfurous compounds are produced under anaerobic conditions from two main sources: sulfate in the urine; proteins or AA containing S in manure. Various bacteria are involved in the production process.

Table 5. Decarboxylation reactions by anaerobic bacteria in the gastrointestinal tract and manure (Mackie *et al.* 1998)

Amino acid	Corresponding amine produced
Glycine	Methylamine
Alanine	Ethylamine
α-Aminobutyrate	Propylamine
Orithine	Putrescine → pyrolidine
Arginine	Putrescine → pyrolidine
Norvaline	Butylamine
Lysine	Cadaverine → pyrolidine
Histidine	Histamine
Tyrosine	Tyramine
Tryptophan	Tryptamine
Phenylamine	Phenylethylamine

Indoles and phenols. Phenolic compounds, for example, phenol itself, *p*-cresol and 4-ethylphenol originate from the microbial degradation of L-tyrosine in the intestinal tract of animals and in manure storage (Fig. 4).

L-Tyrosine can be deaminated to 4-hydroxyphenylpropionic acid, which is either decarboxylated to 4-ethylphenol, or oxidised to 4-hydroxyphenylacetic acid. 4-Hydroxyphenylacetic acid is then either decarboxylated to *p*-cresol or further oxidised to 4-hydroxybenzoic acid. The latter is decarboxylated to phenol (Drasar & Hill, 1974). L-Tyrosine can also be split directly to release ammonia, phenol, and pyruvic acid by *Clostridium tetanomorphum* (Brot *et al.* 1965) and *Escherichia coli* ('*B. coli* phenologenes'; Ichihara *et al.* 1956).

Hammond *et al.* (1989) observed that *p*-cresol was formed from L-tyrosine and L-tryptophan when bacteria from pig manure were incubated with these AA in a synthetic medium. Hengemuehle & Yokoyama (1990)

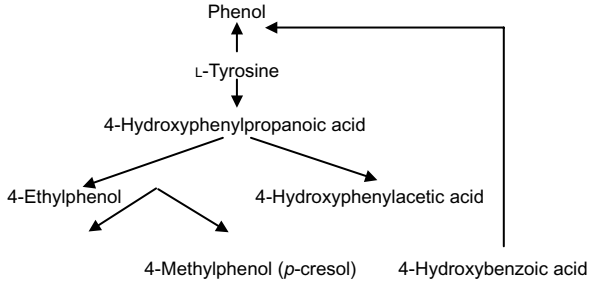

Fig. 4. Breakdown of L-tyrosine in manure stored anaerobically.

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isolated an anaerobic Gram-positive bacterium from the caecal contents of weaning pigs, which produced *p*-cresol by the decarboxylation of 4-hydroxyphenylacetic acid as described in Fig. 4.

Drasar & Hill (1974) reported that 3-methylphenol (*m*-cresol) is one of the metabolites of the degradation of 3,4-dihydroxyphenylalanine (DOPA). DOPA is the precursor of neurotransmitters such as dopamine, noradrenaline, and adrenaline; it is produced by the oxidation of L-tyrosine by the oxygen-dependent enzyme monophenol mono-oxygenase (Dorland, 2003). DOPA is an AA, but is not in the group of twenty AA that are the building blocks of protein. Because only very small amounts of DOPA are expected to be available to intestinal bacteria, the reaction mentioned cannot generate much 3-methylcresol.

Phenolic compounds are absorbed in the large intestine by the host animal and detoxified in the liver by conjugation with glucuronic acid, resulting in glucuronides, or sulfuric acid, resulting in sulfates (Smith & Williams, 1966). However, the sulfate conjugation is of minor importance in pigs (Capel *et al.* 1974). In manure, urinary glucuronides are hydrolysed by faecal β-glucuronidase to release phenolic compounds, again as given in Fig. 4.

Indole production is shown in Fig. 5. Indole and skatole are produced in the large intestine of animals and in manure by microbial fermentation of L-tryptophan. Indoles are partly absorbed and detoxified by the liver to glucuronides, for example, 3-hydroxyindole, hydroxyskatoles and indole-3-carboxylic acid. Then, indolic detoxification products are excreted via the urine. The unabsorbed part of indole and skatole is excreted via the faeces. Therefore, indole and skatole can be found in fresh faeces. Faeces contain a high level of β-glucuronidase of bacterial origin. This enzyme hydrolyses glucuronides. Therefore, it is expected that mixing faeces with urine causes the amounts of free indolic compounds to rise.

The ability to form indole from tryptophan is a taxonomic feature to distinguish between different enterobacteria. The following bacteria are able to form indole from tryptophan: *E. coli* and *Proteus* (except *Proteus mirabilis*); some *Shigella*; *Aeromonas liquefaciens*; some *Fusobacterium* species; *Bacteroides melaninogenicus*; some *Bacteroides fragilis* subspecies; *Bacteroides coagulans*; *Paracolobactrum coliforme*; *Photobacterium harveyi*; *Bacillus alvei*; some clostridia; *Propionibacterium acnes*; *Micrococcus aerogenes*.

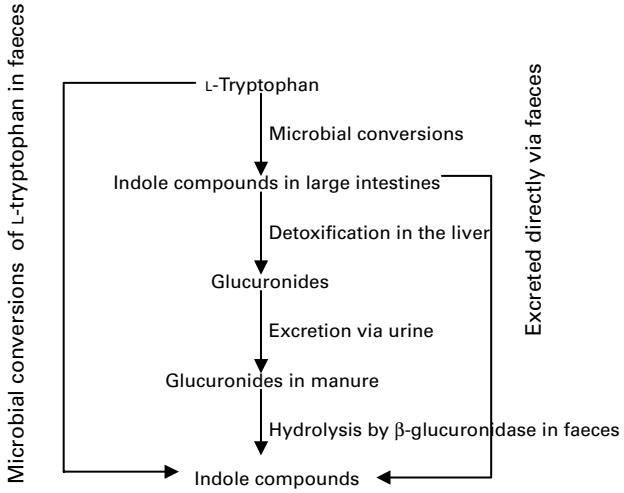

Fig. 5. The production of indole compounds from L-tryptophan.

Tryptophan is converted to indole-3-acetic acid by *E. coli*, *Citrobacter* sp., *Bacteroides fragilis* subsp. *thetaiotamicron*, and *Clostridium* (Chung *et al.* 1975; Elsden *et al.* 1976). This conversion occurs by the transamination of tryptophan to indolepyruvic acid and subsequent decarboxylation (Chung *et al.* 1975). *Lactobacillus* strain 11 201 and three unidentified isolates from the pig intestine have been shown to be able to degrade indole-3-acetic acid to skatole (Yokoyama & Carlson, 1974; Yokoyama *et al.* 1977; Hengemuehle & Yokoyama, 1990; Honeyfield & Carlson, 1990). *Clostridium scatologenes* DSM 757 is capable of generating skatole directly from L-tryptophan (Mikkelsen & Jensen, 1996).

From *in vitro* experiments, Mogens *et al.* (1995) found that the production of indole and skatole is a pH-dependent process; the highest rate of production was observed between pH 6·0 and 7·0, and less than one half of the maximum activity was observed at pH 5·0 or 8·0. The pH had dramatic effects on the relative production of indole and skatole from tryptophan. High pH values favoured the production of indole, while low pH values favoured the production of skatole.

Briefly, phenol and *p*-cresol are produced from L-tyrosine; indole and skatole are produced from L-tryptophan. There are three sources of indole and phenol compounds in manure:

degradation of the AA L-tryptophan and L-tyrosine in manure;
direct excretion from the large intestine of animals via faeces after being formed from tryptophan and tyrosine;
release from glucuronides in urine when placed in contact via faeces.

Ammonia and volatile amines

Ammonia and volatile amines are the main nitrogenous compounds produced during manure storage. When proteins and AA are used as an energy source, their deamination releases ammonia. In manure, Lehninger (1975), cited by Hobbs *et al.* (1999), found an enzymic gateway used by bacteria to convert AA to L-glutamate and then oxidatively deaminate them into ammonia and the respective fatty acids or residual structures. However, the main source of ammonia is urea (Spoelstra, 1980; Aarnink *et al.* 1993). Ammonia present in manure largely arises from the breakdown of urea. Urea is formed in the liver as the endproduct of the protein-destroying metabolism of the animal and is excreted by the kidneys. Urea is quickly hydrolysed by urease present in faeces and fouled floors and converted into ammonium ions. Urease activity is ubiquitous among intestinal bacteria; it has been observed in strains of many species such as *Bacteroides multiacidus*, *Bacteroides ruminicola*, *Bifidobacterium bifidum*, etc (Varel *et al.* 1974; Wozny *et al.* 1977; Suzuki *et al.* 1979). Some of the ammonium ions will dissociate to form free ammonia.

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Ammonia emission into the air is a slow process, controlled by factors such as ammonia concentration, pH and temperature (Aarnink, 1997).

$$CO(NH_2)_2 + 3H_2O \xrightarrow{\text{Urease}} 2NH_4^+ + 2OH + CO_2 \leftrightarrow 2NH_3^{\uparrow} + 2H_2O + CO_2 \quad (10)$$

In manure, ammonia is in equilibrium with ammonium. The rate of ammonia emission depends on this equilibrium. The pH is one of the most important factors influencing ammonia emission. Ammonia volatilisation increases with increasing manure pH (Stevens *et al.* 1989; Sommer & Husted, 1995; Aarnink, 1997). At a solution pH of 9·24, ammonia occurs equally in the form of NH_4^+ and NH_3(aq). Below a pH of 7, ammonia is almost exclusively present as NH_4^+, thereby reducing volatilisation as ammonia gas.

Under anaerobic conditions, volatile amines are often produced from protein-containing products. There are three possible mechanisms of microbial formation of volatile amines.

First, under certain conditions in the gastrointestinal tract and most likely during the storage of fresh manure, AA undergo decarboxylation (Table 5). This mechanism was proposed by Bast *et al.* (1971), cited by Spoelstra (1980). Bacterial genera with decarboxylase activity include *Bacteroides*, *Bifidobacterium*, *Selenomonas*, *Streptococcus* and the enterobacteria.

Second, Bast (1971), cited by Spoelstra (1980), obtained experimental indication that the formation of hexylamine and ethylamine by *Sarcina lutea*, hexylamine by *E. coli*, and isobutylamine by *Aerobacter aerogenes* came about by the amination of the corresponding aldehydes.

Third, another source of amines in manure is urine. For example, the daily excretion of dimethylamine is estimated at 20 mg in man, of which around 50 % originates from choline by the activity of gut flora. Choline is degraded to either ethylamine plus ethanolamine or to trimethylamine which is easily de-methylated (Drasar & Hill, 1974).

Briefly, ammonia is produced from the deamination of AA when they are used as energy sources by bacteria, and by the hydrolysis of urea in urine when it comes into contact with urease. Urea is the main source of ammonia from animal production facilities. Volatile amines are produced from AA by decarboxylation. In addition, they can be produced by the amination of aldehydes and by the de-methylation of choline.

Résumé

Microbial activities are responsible for odour generation in the large intestine of the animal and in manure storage. Odorous compounds are the intermediate or endproducts of microbial conversions under anaerobic conditions. The precursors of odorous compounds are non-utilised nutrients from the diet. Proteins and fermentable carbohydrates are the most important precursors of odorous compounds. Table 3 summarises different odorous compounds and their precursors. The odorous compounds included in Table 3 are thought to be the main causes of odour nuisance from pig production facilities.

Measurements of odour

Odour is the property of a chemical compound or mixture of compounds, which, above a certain concentration, activate the sense of smell and thus initiate an odour sensation (Winneke, 1992). A substance can create an odour impression if it meets certain preconditions, for example, volatility, water solubility, fat solubility and polarity.

Odour can be characterised in three different ways:

by sensory evaluation;
by chemical evaluation;
by electronic sensor evaluation.

The sensory perception of odour can be characterised by three major parameters:

concentration;
intensity;
hedonic tone.

Olfactometry

The three sensory parameters of odour are measured by olfactometry. Olfactometry is based on the use of human panels and an olfactometer, which is in essence a dilution device. The principle of olfactometry is to establish an odour's characteristics in relation to its concentration, intensity and hedonic value.

There are two basic types of olfactometer; static and dynamic. The static olfactometer presents a set volume of diluted sample to the panellist for assessment. The dynamic olfactometer is an apparatus that mixes odorous air from the sample bag with a stream of odour-free air. Because the apparatus produces a continuous stream of different air dilution it is called a dynamic olfactometer. As a result, in dynamic olfactometry a series of known dilutions of the odour sample is offered to a human panel.

Depending on the standard of odour measurement, the minimum number of individuals on a panel may vary from four to sixteen. For example, the European standard requires at least four individuals. Each individual of the panel is pre-selected on the basis of their ability to detect odorants of known odour threshold such as hydrogen sulfide or *n*-butanol (C_4H_9OH). The objective of the pre-selection of panel members is to reduce the variability in odour perception between panel members. Individuals who exhibit abnormal responses should be excluded.

Olfactometry is considered to be a standard method for measuring odour concentrations in odour units (ou), because dynamic olfactometry has the best potential for high accuracy and repeatability. The accuracy and repeatability of the measurements are improved by selecting panel members with similar odour sensitivity based on a standard odorous gas, for example, *n*-butanol.

Odour concentration

Odour concentration measured by olfactometry is expressed as ou or ou/m^3. One ou is defined as the amount of odour-causing gases which, when diluted in 1 m^3 air, can just be distinguished from clean air by 50 % of the members of an odour panel. The definition of an ou is rather complex,

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because it tries to quantify a physiological response to an odorous gas in which different components may be present.

Odour concentration is the most commonly used parameter for signifying the strength of odour. As the sense of smell is complex, it is not surprising that measuring odour is a complicated process and individual responses to odour vary greatly. Therefore, standards must be followed to ensure accuracy and consistency. In Europe, odour measurements have been made for more than 20 years based on various methods, different panel selections, a variety of olfactometers and different reference substances. Recently a working group from The European Standardization Organization (CEN; 2003) completed a new standard method (CEN standard 13 725) to measure odour concentration by olfactometry.

The European ou (ou_E) is that amount of odorant(s) which, when evaporated into 1 m^3 neutral gas at standard conditions, elicits a physiological response from a panel equivalent to that elicited by one European reference odour mass (EROM), evaporated in 1 m^3 neutral gas at standard conditions (CEN standard 13 725; European Committee for Standardization, 2003).

According to the European standard (CEN standard 13 725; European Committee for Standardization, 2003, p. 17): 'one EROM, evaporated into one cubic metre of neutral gas at standard conditions, is the mass of substance that will elicit the D_{50} physiology response (detection threshold), assessed by an odour human panel in conformity with this standard, and has, by definition, a concentration of 1 ou_E/m^3. There is one relationship between ou_E for the reference odorant and that for any mixture of odorants. This relationship is defined only at the D_{50} physiological response level, where: 1 EROM = 123 μg *n*-butanol (CAS-Nr. 71-36-3) = 1 ou_E for the mixture of the odorants. This linkage is the basis of tractability of odour units for any mixture of odorants to that of the reference odorant. It effectively expresses odour concentration in terms of *n*-butanol mass equivalent.'

The odour concentration is expressed as a multiple of 1 ou_E/m^3 neutral gas. The odour concentration can only be assessed at a presented concentration of 1 ou_E/m^3. The odour concentration, in ou_E/m^3, can be used in the same manner as mass concentration (kg/m^3).

Odour measurement in compliance with the European standard is described by CEN standard 13 725 (European Committee for Standardization, 2003). The mixed odorous air and the odour-free air are randomly assigned to the two air tubes. The panellist has to choose from which tube the odorous air is flowing, and has to indicate his or her certainty (certain, fairly sure, doubtful). In general, the first mixture has a very large volume of the diluent (odourless gas). As a result, the human panel cannot detect odour. In subsequent presentations, the volume of the diluent is reduced by a predetermined factor. The series is ended at the dilution step at which all panel members have with certainty pointed out the correct tube in which the mixture of odorous air is flowing. Odour concentration can be calculated based on the volume of diluent at certain stage and the volume of diluent from the preceding step. The odour concentration in terms of ou/m^3 of air is calculated as the geometric mean of the measured individual odour thresholds of the panel members.

It is important to know that not all odours have the same ability to cause annoyance at a given concentration. It is not easy to account for differences in annoyance potential in quantifiable terms. Therefore, most calculations used to predict the impact of odour use odour concentration only, ignoring different characteristics of odour. The odour concentration reduces the question 'how strong and unpleasant is this odour?' to a detection threshold. However, measurements of odour concentration alone are insufficient to assess human perception of odour (Misselbrook *et al.* 1993). The pleasant smell of one odour and the annoying smell of another odour may have the same odour concentration but certainly differ in offensiveness. Some odours judged acceptable or even pleasant at low concentrations could become annoying at higher concentrations (Punter *et al.* 1986). Thus, odour can be more thoroughly characterised by also assessing the intensity and hedonic tone, as well as the odour concentration.

Odour intensity

Odour intensity is the second parameter of the sensory perception of odorants. It refers to the magnitude of the odour sensation. The relationship between odour intensity and the logarithm of odour concentration is expected to be linear.

There are two main methods of measuring odour intensity; the odour intensity referencing scale and the category estimation technique. A common odour intensity referencing scale method uses *n*-butanol as a standard reference odorant. The principle of this method is to compare the intensity of an odour to the intensities of different but known concentrations of *n*-butanol. As described in the previous section, there are two standard procedures for measuring odour intensity using *n*-butanol as the reference. These include dynamic-scale and static-scale procedures.

The category estimation technique method can be derived from the standard document of VDI (1997*a*) guideline 3882; 'Determination of Odour Intensity'. The principle of its measurement is to vary the odour concentration and thus vary perceived intensity. At each concentration presented, human panellists are asked to indicate a value of perceived odour intensity from a seven-point scale that ranges from no odour to overwhelming odour. Odour intensity is then determined from the geometric mean of the different levels (intervals) of the category scales as perceived by a number of panellists. The values of odour intensity are then plotted against the logarithm of odour concentration. The regression line characterises the relationship between perceived intensity and odour concentration. By comparing the intercept and slope of the regression lines, different odours can be characterised.

Hedonic tone

Hedonic tone is used to evaluate odour offensiveness. The odour offensiveness is a measurement of the unpleasantness or pleasantness of a perceived odour. The perception of hedonic tone varies widely among individuals and is strongly influenced by individual odour experience, personal odour preference, and the emotional context in which the odour is perceived. A method for measuring hedonic value is

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based on the standard document of VDI (1997*b*) guideline 3882; 'Determination of Hedonic Tone'. The principle of measurement is to vary the odour concentration and thus vary hedonic value. At each presentation, human panellists are asked to indicate perceived hedonic value, using a nine-point hedonic scale ranging from very pleasant to offensive. Pain *et al.* (1990) described a six-point scale only. The hedonic value of all panel members at each concentration level is calculated, and plotted against the odour concentration in ou_E/m^3. There should be a linear relationship between the logarithm of the odour concentration and the hedonic value at that concentration.

Chemical evaluation of odour

Odour from animal production facilities is usually comprised of a complex mixture of individual compounds. The mixture can be chemically characterised by determining which compounds are in the mixture of odour and at which concentrations. To analyse the mixture, three successive steps are essential; sampling and pre-concentration of the odour separation of components, and identification of the separated components. The basic technique for separating odorous compounds is GC. This technique separates mixtures of gaseous compounds into individual compounds by injecting them onto specific columns that partition these compounds according to vapour pressure and solubility. Because the various compounds of the sample interact with the absorbent to different degrees, compounds will be released from the tube at different and specific times. These elution times are compared with those of known compounds, for identification. In addition, peak areas and heights can be used to quantify the concentration of each odour compound. The use of specific detectors, such as MS, greatly improves the certainty with which compounds may be identified on the basis of their ionised molecular fragment patterns (Zahn *et al.* 1997). The most sensitive technique for identifying volatile odorous compounds in combination with GC is MS (Mellon, 1994). This combination of separation and identification is called GC–MS. With this method, volatile compounds can be quantified as well as identified.

Electronic sensor evaluation

Although olfactometry is considered the most precise method for quantifying odour at present, using a human nose as a sensor to measure odour concentration is labour intensive, time consuming and presents difficulty if on-site measurements are desired. In addition, sensory evaluation methods have a number of limitations. These include rapid saturation of olfactometry senses by some odour compounds, individual variation in sensitivity to different odours, fatigue as a result of adaptation, etc. Currently, researchers are investigating the feasibility of an alternative to olfactometry; using an electronic nose to measure odour concentration. An electronic nose is defined as an instrument consisting of an array of electronic chemical sensors with partial specificity and an appropriate pattern-recognition system capable of recognising odour. When presented with an odour, the electronic nose would initially classify the odour type. Then, using programmed knowledge about the relationship between sensor response and odour concentration for that odour type, the electronic nose would give an integrated response or value for odour concentration. The main application area of this device is quality control, especially in the food-processing industry, but it is still far from implementation in measuring livestock odour.

Résumé

Odour is mainly evaluated sensorily, and chemically. Using olfactometry, three parameters of the sensory characterisation of odour, for example, concentration, intensity and hedonic value, can be evaluated. Olfactometry is considered to be a standard method to measure odour concentration in ou. Using GC–MS, mass concentration of different compounds of odour is quantified. Electronic sensor evaluation seems to be attractive; however, it is still far from implementation in quantifying livestock odour. Measuring odour is a complicated process and the measuring results vary greatly. The basis of the problems related to measuring odour is that there is a huge number of odorous compounds at very low concentration and there are complicated relationships between the mixture of odour compounds and human perception. Therefore, standards must be followed and strictly applied. A new and well-recognised standard of odour measurement is the European standard.

Odour from animal production facilities related to diets

The availability, type and level of odour precursors in the digestive tract of animals and in manure determine the production of odorous compounds. To alter odour production, one may reduce the availability of precursors for odour formation and/or alter the pH in the digestive tract of animals, in urine and in manure. Altering the level and source of proteins and fermentable carbohydrates may be used as important means to implement these strategies, because proteins and fermentable carbohydrates are the main precursors of odour formation. Other possible ways of altering odour production that have been considered are feed additives and other feeding strategies, for example, feed processing, phase feeding and liquid and dry feeding.

Odour from pig production facilities related to protein and amino acids in diets

Attempts to reduce odour production and emission by altering diets have focused on protein. Research so far has focused on two areas; reducing ammonia emission and reducing the emission of other odorous compounds. Many studies were done on ammonia emission reduction because of its environmental effect, not because of trying to reduce odour emission. Although the relationship between ammonia and odour is still debatable, there is a relationship with protein intake. An excessive protein intake will increase both ammonia emission and odour emission. An excessive intake of protein or of AA, or both, has a big effect on faecal and urinary N excretion and thus on ammonia

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emission. In addition, excessive protein from the diet is excreted in three forms: (1) urea, glucuronides and sulfate in urine; (2) non-digested proteins in faeces; (3) bacterial proteins in faeces. These excreta are major precursors for odour formation. Blair *et al.* (1999) reported that with traditional dietary practices (14 % crude protein; CP), growing–finishing pigs may retain less than 40 % of the N fed. According to Aarnink (1997), N retention of growing–finishing pigs was 30 % of the N in feed (Fig. 6). Therefore, a good basis for reducing N excretion and odour production is by reducing the amount of protein in the diet.

The principle of reducing N excretion and ammonia emission through protein is to ensure that the amount of protein in a diet matches the protein requirement and to increase the efficiency of the animals' protein utilisation. There is abundant literature on the impact of the reduction of dietary protein supply to pigs on the reduction of N excretion and ammonia emission (Kerr, 1995; Hobbs *et al.* 1998; Zijlstra *et al.* 2001; Zervas & Zijlstra, 2002). N excretion and ammonia emission can be reduced appreciably by reducing the CP content in diets. Diets with a reduced protein content are often supplemented with essential AA. Reduced-CP diets, supplemented with crystalline AA, have been shown to reduce faecal N excretion by 25 to 30 % (Cromwell & Coffey, 1994; Jongbloed & Lenis, 1993). According to Sutton *et al.* (1999) and Shriver *et al.* (2003), reduced-CP diets supplemented with AA decrease not only N excretion but also manure pH and thus ammonia emission. Generally, as a guide, for each 1 % unit reduction in dietary CP combined with AA supplementation, the estimated ammonia losses are reduced by 10 % in pigs and poultry (Aarnink *et al.* 1993; Jacob *et al.* 1994; Kay & Lee, 1997; Sutton *et al.* 1997).

The impact of feeding a reduced-CP and AA-supplemented diet on reducing odorous compounds is, however, inconsistent. Hobbs *et al.* (1996) showed that five out of ten odorous compounds in the manure of growing pigs and nine out of ten odorous compounds in the manure of finishing pigs declined when pigs were fed reduced-CP diets with supplemented AA, compared with pigs fed commercial diets. They also reported reductions of VFA,

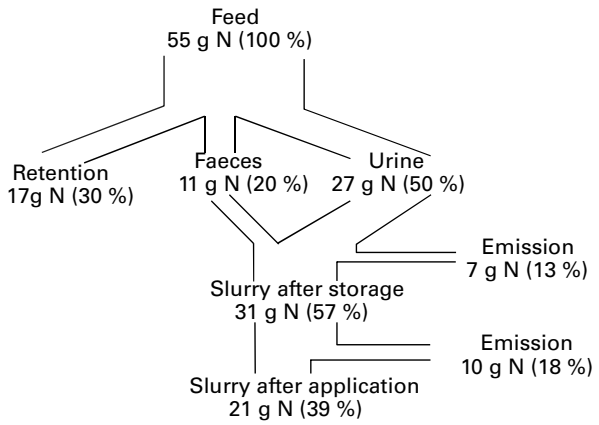

Fig. 6. N flow in growing–finishing pigs (adapted from Aarnink, 1997).

branched-chain VFA, *p*-cresol, indole and skatole in manure from pigs fed low-protein diets (14 and 13 % CP for grower and finisher diets, respectively) compared with pigs fed high-protein diets (21 and 19 % CP for grower and finisher diets, respectively). Sutton *et al.* (1998) reported a 62 % reduction of volatile organic S compounds (dimethyl sulfide, dimethyl disulfide, dimethyl trisulfide, dimethyl sulfoxide and carbon disulfide) in 53 kg gilts when their diet of 13 % CP was compared with an 8 % CP and AA-supplemented diet. According to Stevens *et al.* (1993), increasing the protein content of diets increased the excretion of sulfurous compounds capable of producing sulfide under anaerobic conditions. In addition, in rats, the amounts of phenol, *p*-cresol, and 4-ethylphenol in the caecum was found to be reduced when the amount of dietary protein was reduced (Bakke, 1969).

However, Sutton *et al.* (1999) found that the concentration of volatile organic compounds in the headspace air of manure stored anaerobically did not differ between pigs fed a 10 % CP and AA-supplemented diet and pigs fed a standard 13 % CP diet. They also observed no differences in concentration of phenolic or sulfurous compounds in the faeces from pigs fed 10, 13 or 18 % CP diets. In addition, neither Obrock *et al.* (1997) nor Cromwell *et al.* (1999) found a difference in aerial sulfide concentration after feeding a reduced-CP and AA-supplemented diet compared with a standard one. Furthermore, Obrock *et al.* (1997) reported no difference in odour concentration between pigs fed 13 and 9 % CP with AA-supplemented diets.

Moreover, Otto *et al.* (2003) showed an increase in total VFA concentration in the manure and a tendency to increase odour offensiveness from pigs fed reduced-CP and AA-supplemented diets. In addition, Cromwell *et al.* (1999) reported higher levels of butyric and valeric acids but lower acetic acid in manure when pigs were fed a reduced-CP and AA-supplemented diet, while Shriver *et al.* (2003) reported lower VFA concentrations in manure from pigs fed the reduced-CP but AA-supplemented diet. The effect of dietary protein levels on odour in the above-mentioned studies was inconsistent. There are some possible reasons for this inconsistency. These studies might have used different dietary compositions, for example, different types of protein and fermentable carbohydrates. The type of diets is expected to play a role in odour production. In addition, animal type, housing system and manure storage system where the odour sample was collected might differ between studies. Furthermore, environmental factors, which influence odour production and concentration (PD Le, AJA Aarnink, NWM Ogink and MWA Verstegen, unpublished results), and when and where the studies were done might differ. Moreover, different sampling and measuring methods might partly contribute to the inconsistency of the above-mentioned studies.

Types of protein have effects on odour. According to van Heugten & van Kempen (2002), diets containing fishmeal and a high S content from adding up to 12 % feather meal showed a high odour concentration. They also reported that including feather meal at up to 8 % increased concentrations of butyric, pentanoic, and isovaleric acids in faeces, although concentrations of *m*-cresol, *p*-cresol, indole and

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decane were reduced. Studies on the effect of protein types on odour have had little attention until now. Therefore, further studies in this field are required.

A logical concern arising from reducing the protein level in diets is the possible effect on animal productivity. Oldenburg & Heinrichs (1996) found no negative effects on the performance and leanness of pigs between 50 and 110 kg when protein levels in diets were reduced from 17 % to 13·5 %. According to Canh *et al.* (1998*b*), lowering dietary CP (16·5, 14·5 and 12·5 %) and supplementing AA could reduce ammonia emission by up to 50 % from the manure of growing–finishing pigs while maintaining a normal growth rate. In an experiment in which dietary protein was reduced from 19 % to 15 % in starter diets, from 16 % to 12 % in grower diets and from 14 % to 11 % in finisher diets, with or without AA supplements, Kerr *et al.* (1995) found that a reduction in pig performance and carcass muscle can be prevented by supplementing with the proper AA. According to Lopez *et al.* (1994) and Hahn *et al.* (1995), pigs fed reduced-CP diets (a reduction of 3·5 to 4 %) supplemented with AA had similar carcass characteristics to pigs fed diets with a normal CP.

Briefly, diets generally contain a larger amount of proteins than the animals require. Only a proportion of dietary protein is used for growth or other production activities of the animal. Usually a large part is excreted via the urine and faeces. Proteins and their metabolites in the excreta are precursors for odour formation. Reducing the amount of proteins in the excreta will decrease the available substrates that microbes can metabolise to odour compounds. It is clear from the literature that ammonia from animal production facilities can be decreased considerably by reducing the amount of protein in the diet. However, in the case of other odorous compounds the situation is not so straightforward. Ammonia is a single compound and the techniques and equipment for measuring it have already been standardised. Total odour, however, is a complex mixture of various compounds, which interact with each other. Its measurement techniques and equipment still require standardisation. This may have contributed to the inconsistency in the measured effect of reduced-CP and AA-supplemented diets on odour. However, based on basic knowledge, we believe that feeding animals diets with reduced CP and supplements of AA can decrease odour. To maintain normal growth rate, AA should be supplemented.

Odour from pig production facilities related to fermentable carbohydrates in diets

In common with protein, the type and level of fermentable carbohydrates have received much attention in dietary approaches to reduce odour production and emission. Researchers, however, have mainly focused on ammonia; few have examined odour concentrations as measured by olfactometry. The principle of reducing ammonia production and emission through fermentable carbohydrates is to shift N excretion from the urine to the faeces and to reduce the pH of manure. Increasing the fermentable carbohydrates in diets can result in bacterial proliferation due to an increase in the source of energy for bacteria in both the gastrointestinal tract and in the manure. Bacteria will use ammonia as a source of N for protein synthesis, thus reducing ammonia absorption into the blood and urea excretion via the urine. Fermentable carbohydrates in the gastrointestinal tract shift urinary N excretion to faecal N excretion in the form of bacterial protein (Younes *et al.* 1997), which is less susceptible to rapid hydroxylation. Therefore, the inclusion of fermentable carbohydrates in diets can reduce ammonia emission. Other researchers who have observed this phenomenon include Morgan & Whittemore (1998) and Cromwell *et al.* (1999).

Generally, the inclusion of fermentable carbohydrates in pig diets will increase VFA concentration in faeces and manure storage and thereby will reduce pH and thus ammonia emission (Sutton *et al.* 1997; Canh *et al.* 1998*d*; Kendall *et al.* 1999). Sources of fermentable carbohydrates have an impact on N excretion and ammonia emission, because of the different components in these carbohydrates (Bakker, 1996; Canh *et al.* 1997, 1998*d* (Fig. 7); Mroz *et al.* 2000; Zijlstra *et al.* 2001; Zervas & Zijlstra, 2002).

Although increasing fermentable carbohydrates in diets has a reducing impact on ammonia loss, it clearly increases manure VFA concentrations (Canh *et al.* 1997, 1998*c*,*d*; Sutton *et al.* 1999; Shriver *et al.* 2003). This increase may impact on manure odour concentration, because VFA are important odorous compounds in manure storage (Schaefer, 1977; Williams, 1984; Chen *et al.* 1994; Zahn *et al.* 1997). However, the relationship between the concentration of each odorous compound and odour concentration measured by olfactometry is still unknown. The increase of VFA concentration may increase and/or reduce the concentration of other compounds and odour concentration. DeCamp *et al.* (2001) reported a 32 % increase of total VFA concentration in 6-week-stored manure of pigs fed 10 % soyabean hulls when compared with no soyabean hulls added. In the headspace gases there was a 20 % reduction in aerial ammonia, a 32 % reduction in hydrogen sulfide and an 11 % reduction in odour concentration when

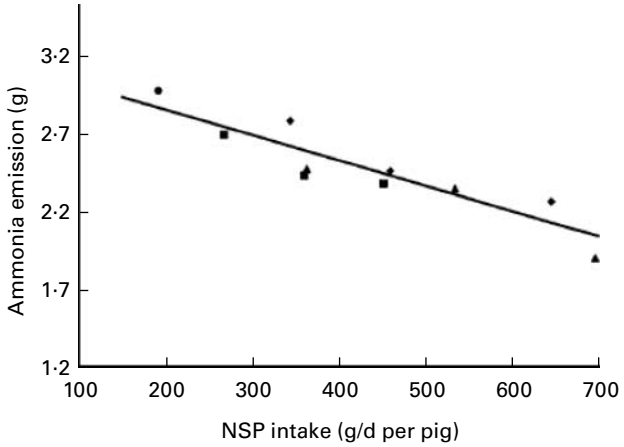

Fig. 7. Ammonia emission from manure during a 16 d storage period related to the daily intake of NSP. (•), Control; (■), coconut; (▲), soyabean; (◆), sugar beet; (—), fitted line (adapted from Canh *et al.* 1998*d*).

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soyabean hulls were added. Goa *et al.* (1999) reported a trend to decrease excretions of *p*-cresol and skatole in fresh faeces (Fig. 8) by adding fibres to the basal diet. Moeser *et al.* (2001) fed soyabean hulls to pigs not adapted to high-fibre diets and noted a decrease in odour. However, Gralapp *et al.* (2002) reported no difference in odour concentration when 10 % distillers dried grain was added to the diets of finishing pigs. Moreover, Hawe *et al.* (1992) reported increased excretions of indole and 3-methyl indole in the faeces of pigs fed diets containing sugar-beet pulp as a fermentable fibre source. Knarreborg *et al.* (2002) observed a significant reduction in the production of indole and skatole in the proximal and distal part of the hindgut in pigs fed a diet rich in sugar-beet pulp. They believed that easily fermentable carbohydrates such as sugar-beet pulp stimulate microbial growth and hence the demand for AA for protein synthesis, leaving less tryptophan for conversion to 3-methyl indole.

The literature contains very little information on the effect of sources of fermentable carbohydrates on the production and emission of odour compounds other than ammonia. Different sources of fermentable carbohydrates are fermented differently by pigs. Thus, different sources of fermentable carbohydrates provide different precursors for odour formation. The effect of fermentable carbohydrate sources depends on the composition of components. Microbial activity in the large intestine is generally increased when diets contain a high concentration of soluble fibre (Jørgensen & Just, 1998). The enhanced microbial activity in the digestive tract means an increase in the excretion of microbial substances, and thus a reduction in the proportion of very volatile compounds such as urea in total excretion.

Apart from their effects on the environment, adding fermentable carbohydrates to pig diets has some controversial disadvantages. They can reduce the apparent ileal and total-tract digestibility of protein (Shi & Noblet, 1993; Bakker, 1996), of fat (Dierick *et al.* 1989), of minerals (Jongbloed, 1987) and of energy. The principles that cause these changes are: a reduced absorption of nutrients, which reduces the true nutrient digestibility; an increased secretion of digestive juices; an increased microbial synthesis of fat and protein, which reduces apparent nutrient digestibility; a reduced retention time of the digesta in the gastrointestinal tract, causing reduced nutrient digestion.

In brief, fermentable carbohydrates have been studied as a means to reduce both ammonia and other odorous compound production and emission from animal production facilities. It is clear from the literature that including fermentable carbohydrates in diets can reduce ammonia emission from animal production facilities considerably. However, the effect on other odorous compounds and odour nuisance is inconsistent and not yet clear. Further studies on the effect of type and level of fermentable carbohydrates on odour production and concentration are required before conclusions can be drawn and the application can be used to reduce odour from animal production facilities.

Odour from pig production facilities related to additives in diets

Feed additives are one of the biochemical and chemical agents that can reduce odour from animal production facilities (Ritter, 1989). The principles of using feed additives to reduce odour formation and emission are to:

alter the microflora in the large intestine of animals and in manure;
change the pH into one less favourable for odour formation;
bind odour.

Microbial activities in the large intestine of the animal both produce odorous compounds and provide precursors for odour formation in manure; thus it is expected that altering the microflora and nutrient supply has the potential to change one or more groups of odorous compounds.

Altering the pH of urine and manure has received the most attention in efforts to use feed additives to reduce ammonia emission. At a low pH, ammonia is protonated to ammonium (NH_4^+), which remains in solution due to its charge. Some kinds of acid salts have been added into diets to reduce ammonia emission based on the principle of pH reduction. According to Canh *et al.* (1998*a*), the addition of Ca salts including $CaSO_4$, $CaCl_2$ and calcium benzoate to diets decreased urinary pH; as a result, ammonia emission was reduced by 30, 33 and 54 %, respectively.

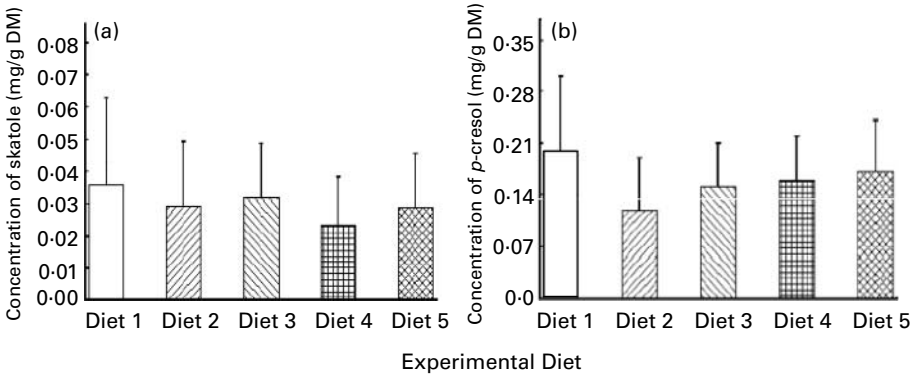

Fig. 8. Adding cellulose and pectin to a maize- and soyabean meal-based diet: the effect on skatole (a) and *p*-cresol (b) in faeces. Diet 1, basal diet; diet 2, basal diet +4·5 % cellulose; diet 3, basal diet +9·0 % cellulose; diet 4, basal diet +4·5 % pectin; diet 5, basal diet +9·0 % pectin (adapted from Goa *et al.* 1999).

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A change in pH may also change the release of other odorous compounds such as hydrogen sulfide. For example, at a high pH, hydrogen sulfide will be reduced but ammonia release will be enhanced. Sutton *et al.* (1999) reported that manure with a higher pH emitted more odour. The literature contains very little further information on the relationship between pH and other odorous compounds from animal production facilities.

Some feed additives are reported to bind ammonia or inhibit urease. Amon *et al.* (1995) reported a 26 % reduction in ammonia emission when fattening pigs were fed De-Odorase (a yucca extract). Some other investigations have also observed reduced ammonia emissions after adding yucca extracts to pig diets (Cromwell *et al.* 1999; Colina *et al.* 2001). However, at present, its inclusion in pig diets to reduce odour is not strongly supported by research. No information on the use of feed additives to bind odour other than ammonia was found in the literature.

In brief, like the two other means of reducing odour (proteins and carbohydrates), the use of feed additives has mainly focused on reducing ammonia emission. Acidifying additives have proved to be effective in reducing ammonia emission. However, their impact on odour has not yet been evaluated.

Other feeding strategies

In addition to using proteins, fermentable carbohydrates and feed additives strategically to curtail odour formation, liquid and dry feeding, phase feeding, and feed processing have also been studied in this context. According to Hobbs *et al.* (1997), the odour concentration from the manure of pigs fed a 4:1 (water–dry feed) diet was significantly less than that of pigs fed dry-feed and 3:1 diets. Hydrogen sulfide was the major odorant in the 3:1 and dry-feed diets. The organic N in manure declined concomitantly with an increase in the water content of the diets, possibly due to an improved digestibility for the diluted diets and hence less substrate for odour formation. Nahm (2002) reported that in growing and finishing pigs, phase feeding can reduce N excretion by 10–13 % and odour from manure by 49–79 %. He also observed that a 27 % reduction of N excretion in finishing pigs and a 22–23 % reduction of N excretion in piglets could be achieved when pigs are fed with proper ground feed. Van der Peet-Schwering *et al.* (1996) reported that moving from a two-phase diet system to a multi-phase programme with optimal housing resulted in a 17 % reduction in ammonia emission. In general, the above-mentioned feeding strategies, especially a phase-feeding regimen, showed promising results to reduce odour production. However, these findings were not confirmed by other studies. Therefore, further studies are still required before conclusions can be finally drawn and the application can be used in practice.

Résumé

Dietary composition and odour production and emission have a cause-and-effect relationship. Altering dietary composition, especially the sources and levels of proteins and fermentable carbohydrates, seems a promising approach to reduce odour nuisance. The attempts made so far to alter diets to reduce ammonia emission have achieved much; the approach can reduce ammonia emission considerably. One shortcoming of most studies to date is that odorous compounds are considered in isolation, i.e. relative changes are measured only in single compounds or in one group of compounds. Only a few studies have used olfactometry to assess the effect of altering dietary composition on odour emission.

Conclusions, gaps in knowledge and further studies required

Odour nuisance from animal production is especially a problem in densely concentrated livestock farming areas, such as those in The Netherlands. It results from the intensification of animal production in the vicinity of a dense population. Such intensive animal production can cause serious nuisance and according to some authors may be even related to health problems as a result of odour production and emission.

Livestock odour does not come from an individual compound but from a complex mix of various compounds. Numerous odorous compounds from animal production facilities have been identified in various studies. However, to date, odorous compounds from different sources, for example, feed, animal bodies, urine, faeces and manure, have not been well described. The main source of odour from animal production facilities is excreta. The odorous compounds that mostly cause nuisance can be classified into four main groups: sulfurous compounds; indoles and phenols; VFA; ammonia and volatile amines.

Odour production is mainly based on microbial conversions involving many bacteria. Odorous compounds are the intermediate or endproducts of microbial conversions of nutrients in the diet that are not utilised. The main precursors of odour formation are proteins and fermentable carbohydrates. The different odorous compounds interact with each other; an increase of one compound may cause others to increase or decrease, or both.

Odour is evaluated sensorily and chemically. Using apparatus, the sensory characteristics of odour strength and offensiveness can be quantified by human noses. This technique is called olfactometry. The chemical characteristics of odour can be evaluated by using GC–MS equipment to determine the concentrations of different odorous compounds. Electronic sensor evaluation appears to be promising, but it is still a long way from being applied in research on livestock odour.

Despite inconsistencies between studies, it has proved possible to compile a list of about twenty important odorous compounds from animal production facilities. The odour concentrations of these compounds from animal production facilities vary widely, depending on diet, climate factors, housing system, pig breed, sampling and measuring methods, etc.

Studies on altering diets to reduce odour production have tended to have two distinct aims; to reduce ammonia emission and to reduce the emission of other odorous compounds. The main reason for reducing ammonia emission was because of its environmental problem, not because of its odour potential. Though there are many

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reports on ammonia emission being successfully altered by adjusting diets, reports of the impact of altering diets on the emission of odorous compounds other than ammonia are inconsistent.

It is clear that many odorous compounds are produced from the breakdown of proteins. Therefore, a promising approach towards reducing odour is to reduce the total protein concentration so that less nitrogenous substrate is available to the microbes inside and outside the animal. Up to now, studies have focused on certain specific odorous compounds and have tended to ignore the effect of protein level on odour production measured by olfactometry. Moreover, there are hardly any published studies on the effects of protein sources on odour production.

The role of fermentable carbohydrates in odour production is not straightforward. Depending on the type and amount of fermentable carbohydrates, different populations of bacteria can be favoured; some of them may reduce odour, while others may increase odour. In common with studies on protein, studies on the effect of fermentable carbohydrates on odour production have tended to focus on certain groups of odorous compounds, though the relationship between each odour group with odour production measured by olfactometry is not yet clear. The literature contains hardly any reports of the effects of fermentable carbohydrates on odour production measured by olfactometry. Nor has the role of specific sources of fermentable carbohydrates on odour production been evaluated.

It is clear that feed additives can reduce ammonia substantially. It remains speculative, however, whether adding these salts will affect microbial fermentation in the large intestine of animals; additives may have no effect on other odorous compounds than ammonia. Generally, the effects of feed additives should always be studied in a wider context. An additive might solve one problem but generate another. This hypothesis remains to be tested, however.

Dietary proteins and fermentable carbohydrates offer the means to reduce odour strength and offensiveness at source, because they are the main precursors of odour production. Research has so far tended to focus on single effects of different levels of CP or fermentable carbohydrates on odour compounds and more or less on odour nuisance. However, it is not only the amount and source of these compounds that are important but also the balance between them, because microflora in the large intestine and manure storage use fermentable carbohydrates as a source of energy and N for protein synthesis. On the basis of our review of the literature, we hypothesise that odour nuisance from pig production facilities can be reduced significantly by achieving an optimum balance between proteins and fermentable carbohydrates in the diet. However, more research must be done in order to arrive at a general principle for reducing odour.

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References

Aarnink AJA (1997) Ammonia emission from houses for growing pigs as affected by pen design, indoor climate and behaviour. PhD thesis, Wageningen Agricultural University, The Netherlands.

Aarnink AJA, Canh TT & Bakker GCM (1996) *Effect of Dietary Fermentable Carbohydrates on the pH and the Ammonia Emission from Slurry of Growing-Finishing Pigs*. Wageningen, The Netherlands: IMAG-DLO.

Aarnink AJA, Hoeksma P & Ouwerkerk ENJ (1993) Factors affecting ammonium concentration in slurry from fattening pigs. In *Nitrogen Flow in Pig Production and Environmental Consequences*, European Association for Animal Production publication no. 69, pp. 413–420 [MWA Verstegen, LA den Hartog and GJM van Kempen, editors]. Wageningen, The Netherlands: EAAP.

Akobe K (1936) Darstellung van D- und L-α-oxy-γ-methiobuttersäure und damit ausgeführte Ernährungsversuche (Description of D- and L-α-oxy-γ-methiobutteracid and their nutrition experiments). *Hoppe-Seyler's Zeitschrift fur Physiologische Chemie* **244**, 14–18.

American Society of Agricultural Engineers (1998) *Manure Production and Characteristics*, Proposal for ASAE D384.1. St Joseph, MI: American Society of Agricultural Engineers.

American Society of Agricultural Engineers (1989) Sulfide: physical, biological, and chemical characteristics. In *Sulfide in Waste Water Collection and Treatment Systems*, ASAE Manual Report of Engineering Practice no. 69, pp. 4–15 [PE Kienow, editor]. New York: American Society of Civil Engineers, Chapter 2.

Amon M, Dobeic M, Sneath RW, Phillips VR, Misselbrook TH & Pain BF (1995) A farm-scale study on the use of clinoptilolite zeolite and De-Odorase for reducing odour and ammonia emissions from intensive fattening piggeries. *Bioresource Technology* **51**, 163–169.

Bakke OM (1969) Urinary simple phenols in rats fed diets containing different amounts of casein and 10% tyrosine. *Journal of Nutrition* **98**, 217–221.

Bakker GCM (1996) Interaction between carbohydrates and fat in pig diets; impact on energy evaluation of feeds. PhD thesis, Wageningen Agricultural University, The Netherlands.

Banwart WL & Bremmer MJ (1975) Identification of sulfur gases evolved from animal manures. *Journal of Environmental Quality* **4**, 363–366.

Barth CL, Hill DT & Polkowski LB (1974) Correlating odour intensity index and odorous components in stored dairy manure. *Transactions of the American Society of Agricultural Engineers* **17**, 742–747.

Beard WL & Guenzi WD (1983) Volatile sulfur compounds from a redox-controlled cattle-manure slurry. *Journal of Environmental Quality* **12**, 113–116.

Bisaillon JG, Beaudet R, Lépine F & Sylvestre M (1994) Microbiological study of the carboxylation of phenols by methanogenic fermentation: a summary. *Water Pollution Research Journal of Canada* **29**, 117–127.

Blair J, de Lange K, Gillis A & Feng C (1999) *Feeding Low Protein Finishing Diets to Reduce Nitrogen Excretion with Pig Manure*, p. 12. Guelph, Canada: University of Guelph, Ontario Swine Research.

Bonnarme P, Lapadatescu C, Yvon M & Spinnler HE (2001) L-Methionine degradation potentialities of cheese-ripening microorganisms. *Journal of Dairy Research* **68**, 663–674.

Bouchard R & Conrad HR (1973) Sulphur requirement of lactating dairy cows II: utilization of sulfates, molasses, and lignin-sulfonate. *Journal of Dairy Science* **56**, 1429–1434.

Britz ML & Wilkinson RG (1983) Partial purification and characterization of two enzymes involved in isovaleric acid synthesis in Clostridium bifermentans. *Journal of General Microbiology* **129**, 3227–3237.

Brot N, Smit Z & Weissbach H (1965) Conversion of L-tyrosine to phenol by Clostridium tetanomorphum. *Archives of Biochemistry and Biophysics* **112**, 1–6.

Canh TT, Aarnink AJA, Mroz Z, Jongbloed AW, Schrama JW & Verstegen MWA (1998*a*) Influences of electrolyte balance and acidifying calcium salts in the diet of growing-finishing pigs on urinary pH, slurry pH and ammonia volatilisation from slurry. *Livestock Production Science* **56**, 1–13.

Canh TT, Aarnink AJA, Schutte JB, Sutton A, Langhout DJ & Verstegen MWA (1998*b*) Dietary protein affects nitrogen excretion and ammonia emission from slurry of growing–finishing pigs. *Livestock Production Science* **56**, 181–191.

Canh TT, Aarnink AJA, Verstegen MWA & Schrama JW (1998*c*) Influences of dietary factors on the pH and ammonia emissions of slurry from growing–finishing pigs. *Journal of Animal Science* **76**, 1123–1130.

Canh TT, Sutton AL, Aarnink AJA, Verstegen MWA, Schrama JW & Bakker GCM (1998*d*) Dietary carbohydrates alter faecal composition and pH and ammonia emission from slurry of growing pigs. *Journal of Animal Science* **76**, 1887–1895.

Canh TT, Verstegen MWA, Aarnink AJA & Schrama JW (1997) Influence of dietary factors on nitrogen portioning and composition of urine and faeces of fattening pigs. *Journal of Animal Science* **75**, 700–706.

Capel ID, Millburn P & Williams RT (1974) The conjugation of 1- and 2-naphthols and other phenols in the cat and pig. *Xenobiotica* **4**, 601–615.

Chen A, Liao PH & Lo KV (1994) Headspace analysis of malodorous compounds from swine waste water under aerobic treatment. *Bioresource Technology* **49**, 83–87.

Chin HW & Lindsay RC (1994) Ascorbate and transition-metal mediation of methanethiol oxidation to dimethyl disulfide and dimethyl trisulfide. *Food Chemistry* **49**, 387–392.

Chung KL, Anderson GM & Fulk GE (1975) Formation of indoleacetic acid by intestinal anaerobes. *Journal of Bacteriology* **124**, 573–575.

Claesson R, Edlund MB, Persson S & Carlsson J (1990) Production of volatile sulfur compounds by various Fusobacterium species. *Oral Microbiology and Immunology* **5**, 137–142.

Clanton CJ & Schmidt DR (2001) Sulfur compounds in gases emitted from stored manure. *Transactions of the American Society of Agricultural Engineers* **43**, 1229–1239.

Colina JJ, Lewis AJ, Miller PS & Fischer RL (2001) Dietary manipulation to reduce aerial ammonia concentrations in nursery pig facilities. *Journal of Animal Science* **79**, 3096–3103.

Cooper P & Cornforth IS (1978) Volatile fatty acids in stored animal slurry. *Journal of the Science of Food and Agriculture* **29**, 19–27.

Cromwell GL & Coffey RD (1994) *Nutritional Technologies to Reduce the Nutrient Content of Swine Manure*. Des Moines, IA: National Park Board.

Cromwell GL, Turner LW, Gates RS, Taraba JL, Lindemann MD, Traylor SL, Dozier WA III & Monegue HJ (1999) Manipulation of swine diets to reduce gaseous emissions from manure that contributes to odour. *Journal of Animal Science* **77**, Suppl. 1, 69 Abstr.

Curtis SE (1993) *Environmental Management in Animal Agriculture*. Ames, IA: Iowa State University Press.

DeCamp SA, Hill BE, Hankins SL, Bundy DC & Powers WJ (2001) Effects of soybean hulls in commercial diet on pig performance, manure composition, and selected air quality parameters in swine facilities. *Journal of Animal Science* **79** Suppl. 1, 252 Abstr.

DeMoss RD & Moser K (1969) Tryptophanase in diverse bacterial species. *Journal of Bacteriology* **98**, 167–171.

Dierick NA, Vervaeke IJ, Demeyer DI & Decuypere JA (1989) Approach to the energetic importance of fibre digestion in pigs. Importance of fermentation in the overall energy supply. *Animal Feed Science and Technology* **23**, 141–167.

Donham KJ (2000) The concentration of swine production. Effects on swine health, productivity, human health and the environment. *Veterinary Clinician of North America. Food Animal Practice* **16**, 559–597.

Donham KJ, Haglind P, Petersen Y, Rylander R & Berlin L (1989) Environmental health studies of farm workers in Swedish confinement buildings. *British Journal of Industrial Medicine* **46**, 31–37.

Donham KJ, Knap LW, Monson R & Gustafson K (1982) Acute toxic exposure to gases from liquid manure. *Journal of Occupation Medicine* **24**, 142–145.

Dorland W (2003) Health Library. *Dorland's Illustrated Medical Dictionary*. W.B. Saunders, Harcourt Health Services. www.mercksource.com/pp/us/cns/cns_home.jsp

Drasar BS & Hill MJ (1974) *Human Intestinal Flora*. London, New York, and San Francisco: Academic Press.

Elsden SR & Hilton MG (1978) Volatile acid production from threonine, valine, leucine and iso-leucine by clostridia. *Archives of Microbiology* **117**, 165–172.

Elsden SR, Hilton MG & Waller JM (1976) The end products of the metabolism of aromatic amino acids by clostridia. *Archives of Microbiology* **107**, 283–288.

Engehard WV (1995) Absorption of short chain fatty acids from the large intestine. In *Physiological and Clinical Aspects of Short Chain Fatty Acid Metabolism*, pp. 149–170 [JH Cummings, JL Rombeau and T Sakata, editors]. Cambridge, UK: Cambridge University Press.

European Committee for Standardization (2003) *CEN Standard 13725. Air Quality – Determination of Odour Concentration by Dynamic Olfactometry*. Brussels, Belgium: European Committee for Standardization.

Ferchichi M, Hemme D & Nardi M (1985) Production of methanethiol from methionine by Brevibacterium linens CNRZ 918. *Journal of General Microbiology* **131**, 715–723.

Geypens B, Claus D, Evenepoel P, Hiele M, Maes B, Peeters M, Rutgeerts P & Ghoos Y (1997) Influence of dietary protein supplements on the formation of bacterial metabolites in the colon. *Gut* **41**, 70–76.

Giusi-Perier A, Fiszlelewicz M & Rerat A (1989) Influence of diet composition on intestinal volatile fatty acids and nutrient absorption in unanesthetized pigs. *Journal of Animal Science* **67**, 386–402.

Goa Y, Rideout T, Lackeyram D, Archbold T, Fan MZ, Squires EJ, Duns G, de Lange CFM & Smith TK (1999) Manipulation of hindgut fermentation to reduce the excretion of selected odor-causing compounds in pigs. In *Symposium of the Hog Environmental Management Strategy (HEMS)*. Agriculture and Agri-food Canada, Ottawa, Ontario. http://www.cpc-ccp.com/HEMS/proceedings.PDF

Goldberg S, Cardash H, Browning HI, Sahly H & Rosenberg M (1997) Isolation of Enterobacteriaceae from the mouth and potential association with malodor. *Journal of Dental Research* **76**, 1770–1775.

Goldberg S, Kozlovsky A, Gordon D, Gelernter I, Sintov A & Rosenberg M (1994) Cadaverine as a putative component of oral malodour. *Journal of Dental Research* **73**, 1168–1172.

Gralapp AK, Powers WJ, Faust MA & Bundy DS (2002) Effects of dietary ingredients on manure characteristics and odorous emissions from swine. *Journal of Animal Science* **80**, 1512–1519.

Gummalla S & Broadbent JR (2001) Tyrosine and phenylalanine catabolism by Lactobacillus cheese flavor adjuncts. *Journal of Dairy Science* **84**, 1011–1019.

Hahn JD, Biehl RR & Baker DH (1995) Ideal digestible lysine level for early- and late-finishing swine. *Journal of Animal Science* **73**, 773–784.

Hammond EG, Heppner C & Smith R (1989) Odors of swine waste lagoons. *Agriculture, Ecosystems and Environment* **25**, 103–110.

Hawe SM, Walker N & Moss BW (1992) The effects of dietary fibre, lactose and antibiotic on the levels of skatole and indole in faeces and subcutaneous fat in growing pigs. *Animal Production* **54**, 413–419.

Hengemuehle SM & Yokoyama MT (1990) Isolation and characterization of an anaerobe from swine cecal contents which produces 3-methylindole and 4-methylphenol. *Journal of Animal Science* **68**, 408A.

Hobbs JP, Brian FP, Roger MK & Lee PA (1996) Reduction of odorous compounds in fresh pig slurry by dietary control of crude protein. *Journal of the Science of Food and Agriculture* **74**, 508–514.

Hobbs PJ, Misselbrook TH & Cumby TR (1999) Production and emission of odours and gases from aging pig waste. *Journal of Agricultural Engineering Research* **72**, 291–298.

Hobbs PJ, Misselbrook TH & Pain BF (1997) Characterisation of odorous compounds and emissions from slurries produced from weaner pigs fed dry feed and liquid diets. *Journal of the Science of Food and Agriculture* **73**, 437–445.

Hobbs PJ, Misselbrook TH & Pain BF (1998) Emission rates of odorous compounds from pig slurries. *Journal of the Science of Food and Agriculture* **77**, 341–348.

Honeyfield DC & Carlson JR (1990) Assay for the enzymatic conversion of indoleacetic acid to 3-methylindole in a ruminal Lactobacillus species. *Applied and Environmental Microbiology* **56**, 724–729.

Hori H, Takabayashi K, Orvis L, Carson DA & Nobori T (1996) Gene cloning and characterization of Pseudomonas putida L-methionine-α-deamino-gamma-mercaptomethane-lyase. *Cancer Research* **56**, 2116–2122.

Ichihara K, Yoshimatsu H & Sakamoto Y (1956) Studies on phenol formation. III. Ammonium and potassium ions as the activator of beta-tyrosinase. *Journal of Biochemistry* **43**, 803.

Inoue H, Inagaki K, Sugimoto M, Esaki N, Soda K & Tanaka H (1995) Structural analysis of the L-methionine gamma-lyase gene from Pseudomonas putida. *Journal of Biochemistry* **117**, 1120–1125.

Iverson M, Kirychuk S, Drost IL & Jacobson (2000) Human health effects of dust exposure in animal confinement buildings. *Journal of Agricultural Safety and Health* **6**, 283–286.

Jackman PJH (1982) Body odour – the role of skin bacteria. *Seminars in Dermatology* **1**, 143–148.

Jacob JP, Blair R, Benett DC, Scott T & Newbery R (1994) The effects of dietary protein and amino acid levels during the grower phase on nitrogen excretion of broiler chickens. In *Proceedings of the 29th Pacific Norhwest Animal Nutrition Conference*, p. 137. Vancouver, B.C., Canada.

Jacobson LD, Clanton CJ, Schmidt DR, Radman C, Nicolai RE & Janni KA (1997) Comparison of hydrogen sulfide and odor emissions from animal manure storages. In *International Symposium on Ammonia and Odour Control from Animal Production Facilities*, 6–10 October 1997, Winkeloord, The Netherlands. pp. 405–412 [JAM Voermans and GJ Monteny, editors]. Rosmalen, The Netherlands: NVTL.

Jensen BB & Jørgensen H (1994) Effect of dietary fibre on microbial activity and microbial gas production in various regions of the gastrointestinal tract of pigs. *Applied and Environmental Microbiology* **60**, 1897–1904.

Ji-Qin N, Albert JH, Claude AD & Teng TL (2000) Ammonia, hydrogen sulphide and carbon dioxide release from pig manure in under-floor deep pits. *Journal of Agricultural Engineering Research* **77**, 53–66.

Jongbloed AW (1987) Phosphorus in the feeding of pigs; effect of diet on the absorption and retention of phosphorous by growing pigs. PhD thesis, Wageningen Agricultural University, Lelystad, The Netherlands.

Jongbloed AW & Lenis NP (1993) Excretion of nitrogen and some minerals by livestock. In *Nitrogen Flow in Pig Production and Environmental Consequences*, European Association for Animal Production publication no. 69, pp. 22–36 [MWA Verstegen, LA den Hartog and GJM van Kempen, editors]. Wageningen, The Netherlands: EAAP.

Jørgensen H & Just A (1998) Effect of different dietary components on site of absorption/site of disappearance of nutrients. In *Fourth International Seminar at the Institute of Animal Physiology and Nutrition*, pp. 230–239 [L Buraczewska, S Buraczewski, B Pastuszewska and T Zebrowska, editors]. Warsaw: Polish Academy of Sciences.

Kadota H & Ishida Y (1972) Production of volatile sulfur compounds by microorganims. *Annual Review of Microbiology* **26**, 127–138.

Kay RM & Lee PA (1997) Ammonia emission from pig buildings and characteristics of slurry produced by pigs offered low crude protein diets. In *International Symposium on Ammonia and Odour Control from Animal Production Facilities*, pp. 253–259 [JAM Voermans and GJ Monteny, editors]. Rosmalen, The Netherlands: NVTL.

Kelly DP, Wood AP, Jordan SL, Padden AN, Gorlenko VM & Dubinina GA (1994) Biological production and consumption of gaseous organic sulphur compounds. *Biochemical Society Transactions* **22**, 1011–1015.

Kendall DC, Richert BT, Sutton AL, Frank JW, DeCamp SA, Bowers KA, Kelly DT & Cobb M (1999) Effects of fibre addition (10 % soybean hulls) to a reduced crude protein diet supplemented with synthetic amino acids versus a standard commercial diet on the performance, pit composition, odour and ammonia levels in swine buildings. *Journal of Animal Science* **77**, Suppl., 176 Abstr.

Kenealy WR, Cao Y & Weimer PJ (1995) Production of caproic acid by cocultures of ruminal cellulolytic bacteria and Clostridium kluyveri grown on cellulose and ethanol. *Applied Microbiology and Biotechnology* **44**, 507–513.

Kerr BJ (1995) *Proceedings of New Horizons in Animal Nutrition and Health*, p. 47. Raleigh, NC: North Carolina State University.

Kerr BJ, McKeith FK & Easter RA (1995) Effect on performance and carcass characteristics of nursery to finisher pigs fed reduced crude protein, amino acid-supplemented diets. *Journal of Animal Science* **73**, 433–440.

Klarenbeek JV, Jongebreur AA & Beumer SCC (1982) *Odour Emission in Pig Fattening Sheds*. Wageningen, The Netherlands: IMAG.

Knarreborg A, Beck J, Jensen MT, Laue A, Agergaard N & Jensen BB (2002) Effect of non-starch polysaccharides on production and absorption of indolic compounds in entire male pigs. *Animal Science* **74**, 445–453.

Kowalewsky HH, Scheu R & Vetter H (1980) Measurement of odour emissions and emissions. In *Effluent from Livestock*, pp. 609–626 [LKE Gasser, editor]. London: Applied Science Publishers.

Kreis W & Hession C (1973) Isolation and purification of L-methionine-alpha-deamino-gamma-mercaptomethane-lyase (L-methioninase) from Clostridium sporogenes. *Cancer Research* **33**, 1862–1865.

Liu QDSB, Bundy DS & Hoff SJ (1993) Utilizing ammonia concentrations as an odour threshold indicator for swine

facilities. In *IVth International Symposium on Livestock Environment*, pp. 678–685 [C Collins and C Boon, editors]. St Joseph, MI: American Society of Agricultural Engineers.

Loesche WJ & Gibbons RJ (1968) Amino acid fermentation by Fusobacterium nucleatum. *Archives of Oral Biology* **13**, 191–201.

Lopez J, Goodband RD, Allee GL, Jesse GW, Nelssen JL, Tokach MD, Spiers D & Becker BA (1994) The effects of diets formulated on an ideal protein basis on growth performance, carcass characteristics, and thermal balance of finishing gilts housed in a hot, diurnal environment. *Journal of Animal Science* **72**, 367–379.

Lunn F & van de Vyver J (1977) Sampling and analysis of air in pig houses. *Agriculture and Environment* **3**, 159–170.

McGill AEJ & Jackson N (1977) Changes in short chain carboxylic acid content and chemical oxygen demand of stored pig slurry. *Journal of the Science of Food and Agriculture* **28**, 424–430.

Mackie RI (1994) Microbial production of odor components. In *International Round Table on Swine Odor Control*, pp. 18–19. Ames, IA: Iowa State University.

Mackie RI, Stroot PG & Varel VH (1998) Biochemical identification and biological origin of key odour components in livestock waste. *Journal of Animal Science* **76**, 1331–1342.

Mellon FA (1994) Mass spectroscopy. In *Spectroscopic Techniques for Food Analysis*, pp. 181–219 [RH Wilson, editor]. New York: VCH Publishers.

Mikkelsen LL & Jensen BB (1996) Growth and skatole (3-methylindole) production by Clostridium scatologenes grown in batch and continuous cultures. *Journal of Applied Bacteriology* **81**, XVIII.

Miner JR (1995) *A Review of the Literature on the Nature and Control of Odors from Pork Production Facilities*, pp. 118. Corvallis, OR: Bioresource Engineering Department, Oregon State University.

Miner JR, Kelly MD & Anderson AW (1975) Identification and measurement of volatile compounds within a swine building and measurement of ammonia evolution rates from manure-covered surfaces. In *Managing Livestock Wastes, Proceedings of the 3rd International Symposium on Livestock Wastes*, ASAE Proc-275, pp. 351–353. St Joseph, MI: American Society of Agricultural Engineers.

Misselbrook TH, Clarkson CR & Pain BF (1993) Relationship between concentration and intensity of odours for pig slurry and broiler houses. *Journal of Agricultural Engineering Research* **55**, 163–169.

Moeser AJ, van Heugten T & van Kempen T (2001) Diet composition affects odor characteristics from swine manure. In *NCSU Annual Swine Report* [E van Heugten, K Rozeboom & T See, editors]. http://mark.asci.ncsu.edu/SwineReports/2001/01manadam.htp

Mogens TJ, Raymond PC & Bent BJ (1995) 3-Methylindole (skatole) and indole production by mixed populations of pigs fecal bacteria. *Applied and Environmental Microbiology* **61**, 3180–3184.

Morgan CA & Whittemore CT (1998) Dietary fibre and nitrogen excretion and retention by pigs. *Animal Feed Science and Technology* **19**, 185–189.

Morrison RT & Boyd RN (1987) *Organic Chemistry*, 5th ed. Boston, MA: Allyn & Bacon.

Mortensen PB, Holtug K & Rasmussen HS (1987) Short-chain fatty acid production from mono and disaccharides in a fecal incubating system: implications for colonic fermentation of dietary fiber in humans. *Nutrition Journal* **118**, 321–325.

Mroz Z, Jongbloed AW, Partanen KH, Vreman K, Kemme PA & Kogut J (2000) The effect of calcium benzoate in diets with or without organic acids on dietary buffering capacity, apparent digestibility, retention of nutrients, and manure characteristics in swine. *Journal of Animal Science* **78**, 2622–2632.

Müller HL & Kirchgessner M (1995) Energetische verwertung von pektin bei sauen. *Zeitschrift für Tierphysiologie, Tierenährung und Futtermittelkde* **54**, 14–20.

Nahm KH (2002) Efficient feed nutrient utilization to reduce pollutants in poultry and swine manure. *Animal Science* **32**, 1–16 Abstr.

Nakano Y, Yoshimura M & Koga T (2002) Correlation between oral malodor and periodontal bacteria. *Microbes and Infection* **4**, 679–683.

Nisman B (1954) The Stickland reaction. *Bacteriological Reviews* **18**, 16–42.

Noren O (1986) Design and use of bio filter for livestock buildings. In *Odour Prevention and Control of Organic Sludge and Livestock Farming*, pp. 234–237 [VC Neilsen, JH Voorburg and P L'Hermite, editors]. London: Elsevier Applied Science Publishers.

Obrock HC, Miller PS & Lewis AJ (1997) *The Effect of Reducing Dietary Crude Protein Concentration on Odour in Swine Facilities*, Nebraska Swine Report, pp. 14–16. Lincoln, NB: University of Nebraska-Lincoln.

Odam EM, Page JMJ, Townsend MG & Wilkins JPG (1986) Identification of volatile components in headspace from animal slurries. In *Odour Prevention and Control of Organic Sludge and Livestock Farming*, pp. 284–295 [VC Nielsen, JH Voorburg and P L'Hermite, editors]. London: Elsevier Applied Science Publishers.

Ogink NWM & Groot Koerkamp PWG (2001) Comparison of odour emissions from animal housing systems with low ammonia emission. *Water Science and Technology* **43**, 245–252.

Ohkishi H, Nishikawa D, Kumagai H & Yamada H (1981) Distribution of cysteine desulfhydrase in microorganisms. *Agricultural and Biological Chemistry* **45**, 253–257.

Ohta Y & Kuwada Y (1998) Rapid deodorization of cattle faeces by microorganisms. *Biological Wastes* **24**, 227–240.

Oldenburg J (1989) Geruchs- und Ammoniak- Emissionen aus der Tierhaltung. In *Munster-Hiltrup*, Herausgegebe vom, Kuratorium für Technik und Bauwensen in der Landwirtschaft e.v. 6100 Darmstadt-Kranichstein.

Oldenburg J & Heinrichs P (1996) Quantitative Aspecte einer proteinreduzierten Schweinemast (Quantitative aspects of a protein-reduced pig fattening). *Lohamann Information* **1**, 13–16.

O'Neill DH & Phillips VRA (1992) Review of the control of odour nuisance from livestock buildings. Part 3: properties of the odorous substances which have been identified in livestock wastes or in the air around them. *Journal of Agricultural Engineering Research* **53**, 23–50.

Otto ER, Yokoyama M, Von Bermuth RD, van Kempen T & Trottier NL (2003) Ammonia, volatile fatty acids, phenolics and odour offensiveness in manure from growing pigs fed diets reduced in protein concentration. *Journal of Animal Science* **81**, 1754–1763.

Pain BF, Misselbrook TH, Clarkson CR & Rees YJ (1990) Odour and ammonia emission following the spreading of anaerobically-digested pig slurry on grassland. *Biological Wastes* **34**, 149–160.

Parliment TH, Kolor MG & Rizzo DJ (1982) Volatile components of Limburger cheese. *Journal of Agricultural and Food Chemistry* **30**, 1006–1008.

Patni NK & Clarke SP (1990) Transient hazardous conditions in animal buildings due to manure gas released during slurry mixing. In *Sixth International Symposium on Agricultural and Food Processing Wastes*, pp. 449–459. [ASOA Engineers, editors]. St Joseph, MI: American Society of Agriculture Engineers.

Phillips D, Fattori M & Bulley R (1979) Swine manure odours: sensory and physico-chemical analysis. In *Joint Meeting of ASAE and CSAE*. Winnipeg.

Phillips VR, Pain BF, Clarkson CR & Klarenbeek JV (1990) Studies on reducing the odour and ammonia emissions during and after the land spreading of animal slurries. *Farm Building Engineering* **7**, 17–23.

Punter PH, Koster EP, Schaefer J & Maiwald KD (1986) Odour concentration and odour annoyance. In *Odour Prevention and Control of Organic Sludge and Livestock Farming*, pp. 146–152 [VC Nielsen, JH Voorburg and P L'Hermite, editors]. London: Elsevier Applied Science Publishers.

Rasmussen HS, Holtug K & Mortensen PB (1988) Degradation of amino acids to short-chain fatty acids in humans. An *in vitro* study. *Scandinavian Journal of Gastroenterology* **23**, 178–182.

Ren Y (1999) Is carbonyl sulfide a precursor for carbon disulfide in vegetation and soil? Interconversion of carbonyl sulfide and carbon disulfide in fresh grain tissues *in vitro*. *Journal of Agricultural and Food Chemistry* **47**, 2141–2144.

Ritter WF (1989) Odour control of livestock wastes: state-of-the-art in North America. *Journal of Agricultural Engineering Research* **42**, 51–62.

Sawyer CH & McCarty PL (1978) Sulfate. In *Chemistry for Environmental Engineering*, pp. 476–481. New York: McGraw-Hill Book Co., chapter 28.

Schaefer J (1977) Sampling, characterization and analysis of malodours. *Agriculture and Environment* **3**, 121–127.

Schaefer J (1980) Development of instrumental methods for measuring odour levels in intensive livestock building. In *Effluents from Livestock*, pp. 513–534 [LKE Gasser, editor]. London: Applied Science Publishers.

Schaefer J, Bemelnans JMH & ten Noever de Brauw MC (1974) Research into the components responsible for the smell of piggeries. *Landbouwkundig Tijdschrift* **86**, 228–232.

Schenker M, Christiani D & Cormier Y (1998) Respiratory health hazards in agriculture. *American Journal of Respiratory Critical Care Medicine* **158**, Suppl., S1–S76.

Schenker M, Ferguson T & Gamsky T (1991) Respiratory risks associated with agriculture. *Occupational Medicine: State of the Art Reviews* **6**, 415–428.

Schirz S (1986) Design and experience obtained with bio-scrubbers. In *Odour Prevention and Control of Organic Sludge and Livestock Farming*, pp. 241–250 [VC Neilsen, JH Voorburg and P L'Hermite, editors]. London: Elsevier Applied Science Publishers.

Schlegel HG (1986) *General Microbiology*. Cambridge, UK: Cambridge University Press.

Schneider S, Mohamed ME & Fuchs G (1997) Anaerobic metabolism of L-phenylalanine via benzoyl-CoA in the denitrifying bacterium Thauera aromatica. *Archives of Microbiology* **168**, 310–320.

Schulte DD, Kottwitz DA & Gilbertson CB (1985) Nitrogen content of scraped swine manure. In *Vth International Symposium on Agricultural Waste*, Chicago, pp. 321–328 [JC Converse, editor]. St Joseph, MI: American Society of Agricultural Engineers.

Segal W & Starkey RL (1969) Microbial decomposition of methionine and identity of the resulting sulfur products. *Journal of Bacteriology* **98**, 908–913.

Shi XS & Noblet J (1993) Contribution of the hindgut to digestion of diets in growing pigs and adult sows: effect of diet composition. *Livestock Production Science* **34**, 237–252.

Shriver JA, Carter SD, Sutton AL, Richert BT, Senne BW & Pettey LA (2003) Effects of adding fiber sources to reduced-crude protein, amino acid-supplemented diets on nitrogen excretion, growth performance, and carcass traits of finishing pigs. *Journal of Animal Science* **81**, 492–502.

Smith GM, Kim BW, Franke AA & Roberts JD (1985) ^{13}C NMR studies of butyric fermentation in Clostridium kluyveri. *Biology and Chemistry* **260**, 13509–13512.

Smith RL & Williams RT (1966) *Glucuronic Acid. Free and Combined*. New York and London: Academic Press.

Sommer SG & Husted S (1995) The chemical buffer system in raw and digested animal slurry. *Journal of Agricultural Science* **124**, 45–53.

Spoelstra SF (1976) Simple phenols and indoles in anaerobically stored piggery wastes. *Journal of the Science of Food and Agriculture* **28**, 415–423.

Spoelstra SF (1979) Microbial aspect of the formation of malodorous compounds in anaerobically stored piggery wastes. PhD thesis, Wageningen Agricultural University, The Netherlands.

Spoelstra SF (1980) Origin of objectionable odorous components in piggery wastes and the possibility of applying indicator components for studying odour development. *Agriculture and Environment* **5**, 241–260.

Stadtman TC (1963) Anaerobic degradation of lysine. II. Cofactor requirements and properties of the soluble enzyme system. *Biology and Chemistry* **238**, 2766–2773.

Stevens RJ, Laughlin RJ & Frost JP (1989) Effect of acidification with sulphuric acid on the volatilization of ammonia from cow and pig slurries. *Journal of Agricultural Science* **113**, 389–395.

Stevens RJ, Laughlin RJ & Frost JP (1993) Effects of diet and storage time on the concentration of sulphides on dairy cow slurry. *Bioresource Technology* **45**, 13–16.

Stryer L (1995) *Biochemistry*, 4th ed.. New York: W.H. Freeman.

Susan SS, Jeanette LB & James HR (2001) Quantification of odors and odorants from swine operations in North Carolina. *Agricultural and Forest Meteorology* **108**, 213–240.

Sutton AL, Kephart KB, Patterson JA, Mumma R, Kelly DT, Bous E, Don BS, Jones DD & Heber AJ (1997) Dietary manipulation to reduce ammonia and odorous compounds in excreta and anaerobic manure storage. In *International Symposium on Ammonia and Odour Control from Animal Production Facilities*, pp. 245–252 [JAM Voermans and GJ Monteny, editors]. Rosmalen, The Netherlands: NVTL.

Sutton AL, Kephart KB, Verstegen MWA, Canh TT & Hobbs PJ (1999) Potential for reduction of odorous compounds in swine manure through diet modification. *Journal of Animal Science* **77**, 430–439.

Sutton AL, Patterson JA, Adeola OL, Richert BA, Kelly DT, Heber AJ, Kephart KB, Mumma R & Bogus E (1998) Reducing sulfur-containing odours through diet manipulation. In *Animal Production Systems and the Environment*, pp. 125–130. Des Moines, IA: Iowa State University.

Suzuki K, Benno Y, Mitsuoka T, Takebe S, Kobashi K & Hase J (1979) Urease-producing species of intestinal anaerobes and their activities. *Applied and Environmental Microbiology* **37**, 379–382.

Turton LJ, Drucker DB & Ganguli LA (1983) Effect of glucose concentration in the growth medium upon neutral and acidic fermentation end-products of Clostridium bifermentans, Clostridium sporogenes and Peptostreptococcus anaerobius. *Journal of Medical Microbiology* **16**, 61–67.

van der Peet-Schwering CMC, Verdoes CMC, Voermans MP & Beelen GM (1996) *Effect of Feeding and Housing on the Ammonia Emission of Growing and Finishing Pig Facilities*, report no. P1.145. Rosemalen, The Netherlands: Research Institute for Pig Husbandry.

van Geelen M & van der Hoek KW (1985) *Odour Abatement Techniques for Intensive Livestock Units. AFRC Engineering Translation* no. 535. Silsoe, Bedford, UK: AFRG Institute of Engineering Research.

van Heugten E & van Kempen TA (2002) Growth performance, carcass characteristics, nutrient digestibility and fecal odorous compounds in growing-finishing pigs fed diets containing hydrolyzed feather meal. *Journal of Animal Science* **80**, 171–178.

van Soest P (1983) *Nutrition Ecology of the Ruminant*. Corvallis, OR: O&B Books, Inc..

Varel VH, Bryant MP, Holdeman LV & Moore WEC (1974) Isolation of ureolytic Peptostreptococcus productus from feces using defined medium; failure of common urease test. *Journal of Applied Microbiology* **28**, 594–599.

VDI (1997*a*) *Guideline 3882,* part 1*, Determination of Odour Intensity.* Düsseldorf, Germany: VDI.

VDI (1997*b*) *Guideline 3882,* part 2*, Determination of Hedonic Tone*. Düsseldorf, Germany: VDI.

Verdoes N & Ogink NWM (1997) Odour emission from pig houses with low ammonia emission. In *International Symposium on Ammonia and Odour Control from Pig Production Facilities,* Winkeloord, The Netherlands, pp. 252–317 [JAM Voermans and GJ Monteny, editors]. Rosmalen, The Netherlands: NVTL.

Wathes CM, Jones JB, Kristensen HH, Jones EKM & Webster AJF (2002) Aversion of pigs and domestic fowl to atmospheric ammonia. *Transactions of the American Society of Agricultural Engineers* **45**, 1605–1610.

Williams AG (1984) Indicators of piggery slurry odour offensiveness. *Agricultural Waste* **10**, 15–36.

Williams AG & Evans MR (1981) Storage of piggery slurry. *Agricultural Waste* **3**, 311–321.

Winneke G (1992) Structure and determinants of psychological response to odorant/irritation air pollution. *Annals of the New York Academy of Sciences* **641**, 261–276.

Wozny MA, Bryant MP, Holdeman LV & Moore WEC (1977) Urease assay and urease-producing species of anaerobes in the bovine rumen and human feces. *Journal of Applied Microbiology* **33**, 1097–1104.

Yasuhara A, Fuwa K & Jimbu M (1984) Identification of odorous compounds in fresh and rotten swine manure. *Agricultural and Biological Chemistry* **48**, 3001–3010.

Yokoyama MT & Carlson JR (1974) Dissimilation of tryptophan and related compounds by ruminal microorganisms in vivo. *Journal of Applied Microbiology* **27**, 540–548.

Yokoyama MT, Carlson JR & Holdeman LV (1977) Isolation and characteristics of a skatole-producing Lactobacillus sp. from the bovine rumen. *Applied and Environmental Microbiology* **6**, 837–842.

Yoshimura M, Nakano Y, Yamashita Y, Oho T, Saito T & Koga T (2000) Formation of methyl mercaptan from L-methionine by Porphyromonas gingivalis. *Infection and Immunity* **68**, 6912–6916.

Younes H, Remesy C, Behr S & Demigne C (1997) Fermentable carbohydrate exerts a urea-lowering effect in normal and nephrectomized rat. *American Journal of Physiology* **272**, 515–521.

Zahn JA, DiSpirito AA, Do YS, Brooks BE, Cooper EE & Hatfield JL (2001) Correlation of human olfactory responses to airborne concentrations of malodorous volatile organic compounds emitted from swine effluent. *Journal of Environmental Quality* **30**, 624–634.

Zahn JA, Hatfield JL, Do YS, DiSpirito AA, Laird DA & Pfeiffer RL (1997) Characterisation of volatile organic emissions and wastes from a swine production facility. *Journal of Environmental Quality* **26**, 1687–1696.

Zervas S & Zijlstra RT (2002) Effects of dietary protein and oat hull fibre on nitrogen excretion patterns and plasma urea in grower pigs. *Journal of Animal Science* **80**, 3238–3246.

Zhu J (2000) A review of microbiology in swine manure odor control. *Agriculture, Ecosystems and Environment* **78**, 93–106.

Zijlstra RT, Oryschak MA, Zervas S & Ekpe DE (2001) Diet manipulation to reduce nutrient content in swine manure. In *Focus on the Future Conference*, Red Deer, Alberta, Canada. http://triumph.usask.ca/psc/pdf/psc/69.pdf