Tellus (1986), *38B*, 271–284

Methane production by domestic animals, wild ruminants, other herbivorous fauna, and humans

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(Manuscript received October 22, 1985; in final form May 30, 1986)

ABSTRACT

A detailed assessment of global methane production through enteric fermentation by domestic animals and humans is presented. Measured relations between feed intake and methane yields for animal species are combined with population statistics to deduce a current yearly input of methane to the atmosphere of 74 Tg (1 Tg = 10^{12} g), with an uncertainty of about 15%. Of this, cattle contribute about 74%. Buffalos and sheep each account for 8–9%, and the remainder stems from camels, mules and asses, pigs, and horses. Human CH_4 production is probably less than 1 Tg per year. The mean annual increase in CH_4 emission from domestic animals and humans over the past 20 years has been 0.6 Tg, or 0.75% per year. Population figures on wild ruminants are so uncertain that calculated CH_4 emissions from this source may range between 2 Tg and 6 Tg per year. Current CH_4 emission by domestic and wild animals is estimated to be about 78 Tg, representing 15–25% of the total CH_4 released to the atmosphere from all sources. The likely CH_4 production from domestic animals in 1890 was about 17 Tg, so that this source has increased by a factor of 4.4.

A brief tentative discussion is also given on the potential CH_4 production by other herbivorous fauna, especially insects. Their total CH_4 production probably does not exceed 30 Tg annually.

1. Introduction

Methane plays a large rôle in the photochemistry of the background atmosphere. It is produced and released by various biological processes and is mainly decomposed in the troposphere by reaction with hydroxyl radicals (OH). This reaction initiates complicated reaction pathways leading to the formation of various intermediates that influence the atmospheric concentrations of ozone and hydroxyl (McConnell et al., 1971; Levy, 1971; Crutzen, 1973). The hydroxyl radical, which is present in the atmosphere at an average volume mixing ratio of only 2×10^{-14}, is primarily responsible for the breakdown of natural and anthropogenic trace gases in the atmosphere. As atmospheric methane has been increasing by over 1% per year over the past decade (Rasmussen and Khalil, 1984; Blake, 1984; Seiler, 1984), changes in the background photochemistry of the atmosphere can be expected. Crutzen (1986) has postulated that on the whole, global OH concentrations are decreasing (especially outside the northern mid-latitude zone) and ozone concentrations increasing (especially in northern mid-latitudes and in the upper troposphere).

Methane production by ruminants has been estimated in the past by several authors. The earliest figures on world-wide production rates were published by Hutchinson (1949), who estimated the CH_4 emission by large herbivores to be 45 Tg/year for the 1940's. Ehhalt (1974) calculated a global CH_4 production of 100 Tg CH_4 for 1970 from domestic ruminants. This would constitute 20–35% of the total input of methane to the atmosphere, which is now estimated by various authors to be in the range 300–500 Tg/year (Khalil and Rasmussen, 1983;

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Crutzen and Gidel, 1983; Seiler, 1984). Crutzen (1983) and Seiler (1984) estimated the global CH_4 production from ruminants in 1975 to have been about 60 Tg and 70–100 Tg, respectively. Similar values have also been reported by Khalil and Rasmussen (1983) and Sheppard et al. (1982). None of these papers, however, present a thorough analysis of the derivation of these estimates. In this paper, we will give a detailed account of the worldwide methane production by domestic livestock and wild ruminants, and by humans, using the extensive information which has now become available on methane production by animal species.

2. Energy utilization and methane production in animals

The energy content in food is transformed in the process of digestion and partly lost as chemical compounds in faeces, urine and fermentation gases. The rest is used to produce heat, to perform body work or to build new body tissue (Fig. 1). The magnitude of the various losses of energy depends on the animal species and on the kind and quality of the feedstuff. Measures of feed quality are *digestibility* and *metabolizability*, which are the fractions of the gross energy intake that are converted to digestible energy and metabolizable energy, respectively.

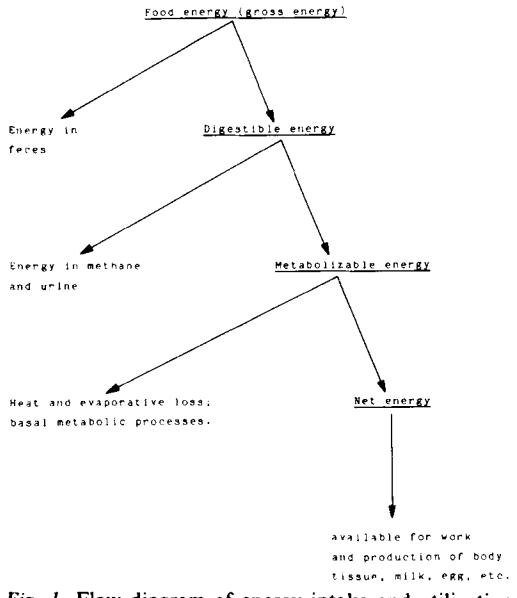

Fig. 1. Flow diagram of energy intake and utilization by animals. The magnitude of the various losses of energy depends on the animal species and utilization, and on the kind and quality of the feed stuff. Based on Kleiber (1961) and Maynard and Loosli (1962).

In adult homeotherms, *basal metabolism* defines the minimum energy demand under conditions of thermoneutrality and total rest. The daily basal metabolism, expressed in megajoules (MJ), is roughly proportional to the $\frac{3}{4}$ power of the body weight W (kg) and is given by the formula:

$$\text{basal metabolism} = 0.293 W^{0.75}, \quad (1)$$

with an uncertainty of about 14% (Menke and Huss, 1975, p. 91). In practice, the energy demand to prevent breakdown of body tissue is higher than the basal metabolism and the actual gross energy uptake is often expressed in terms of units of *maintenance*, that is, the minimum of food needed to prevent any loss of body tissue (Maynard and Loosli, 1962). This quantity varies, depending on utilization and kind of livestock.

Both quality and quantity of the feed, together with the individual performance of the animals, have been found to determine the amount of energy that is lost by methane production. Methane is a byproduct of microbial breakdown of carbohydrates (mainly cellulose) in the digestive tracts of herbivores. Highest CH_4 losses are reported for ruminants, which host large populations of bacteria and protozoans in their rumens (e.g., Blaxter and Czerkawski, 1966; Wolin, 1981).

In the following, the loss of energy through methane generation will be expressed as a fraction of the gross energy intake. For this, we will use the term *methane yield*. Food quantities, often given in weight units, were converted to gross energy intake by using an average conversion factor of 17.5 MJ/kg dry matter (Leith, 1975). The energy content of 1 kg methane is equal to 55.65 MJ.

Early data on methane yields by cows, sheep, goats, horses, and one elephant were published by Ritzman and Benedict (1938) who found CH_4 yields ranging between 4.4% and 7% for ruminants (cows, sheep, goats) fed on maintenance level. The methane release rates by ruminants were lower when fed with protein-rich diets and higher when fed with crude fiber. The

horses and the elephant showed CH_4 yields in the range of 1.5%–3%.

Blaxter and Clapperton (1965), in analysing numerous data on methane production by cows and sheep have shown that at maintenance, methane yields increased from 7.5% to 9% when the digestibility of the feed was raised from 65% to 95%. The methane yields (6.5–7%) were independent of the digestibility at a feeding level of 2 × maintenance and decreased from 6% to 5% at 3 × maintenance when the feed digestibility changed from 60% to 90%. Similar results were reported by Van der Honing et al. (1981) who observed methane yields on 5–6.5% for dairy cows fed on 3.1–3.5 × maintenance. Wainman et al. (1978) measured CH_4 yields of 7.9% from steers fed on 1.5 × maintenance and a 77% digestible diet. Krishna et al. (1978) estimated higher CH_4 yields of 9% in Indian cattle fed on a slightly above maintenance diet and low quality feed.

Published methane yields from sheep show a somewhat larger range of values. Murray et al. (1978) found CH_4 yields to rise from 3.5% to 5.6% with increasing feed intake in Merino ewes fed on protein-rich lucerne chaff with a digestibility of 63%. Kempton and Leng (1979) observed methane yields of 5.4–6.4% in growing lambs, being highest on low protein diets, while Seeley et al. (1969) measured 8.2–9.7% in adult sheep fed on ryegrass hay at maintenance level.

Non-ruminating, well-nourished pigs have much lower methane yields (0.4–0.9%) which seem to be independent of feed mixture (Schneider and Menke, 1982), but pigs given low quality feeds may be expected to show CH_4 yields between 1% and 2% (H. Steingass, personal communication).

From these data, it becomes apparent that the calculation of the global methane release from domestic animals requires consideration of different animal management and feeding schemes. Published information is scarce. We have therefore also made considerable use of information which was kindly provided to us by experts through personal communications.

3. Methane production by cattle

In the US, there are 3 types of cattle: dairy cows, beef cattle on feed, and cattle on range. In Europe and in the USSR, range cattle are rare, and the rearing of dual-purpose cattle for dairy and beef production is common practice. In other countries like Australia or Argentina, cattle are kept primarily on range and dairy cows are relatively less numerous.

Because cattle are fed at different levels of energy intake and quality of food in different parts of the world, we will next present some detailed analyses for the US, West Germany and India. From these data, we will extrapolate to other parts of the world to arrive at global estimates of methane production.

The average number of feed units (1 *feed unit* is the digestible energy contained in 1 pound of corn) consumed in the US by milk cows (including heifers), cattle on feed, and cattle on range are 10150, 6650 and 4800 per animal per year, respectively (G. Allen, personal communication). With an energy content of 6.57 MJ per feed unit, this converts to 230 MJ, 150 MJ and 110 MJ of daily gross energy intake, which corresponds to about 2–3, 1.75 and 1.3 × maintenance. Using Blaxter and Clapperton's (1965) methane yields of 5.5%, 6.5% and 7.5% of gross energy intake for these categories, and an energy content of 55.65 MJ/kg CH_4, the annual methane production per individual in the aforementioned categories are 84 kg, 65 kg and 54 kg, respectively. The US cattle population is made up of 10% dairy cows, 12.5% beef cattle on feed and 77.5% cattle on range (Food and Agricultural Organization of the United Nations (FAO), 1984). The mean methane production by cattle in the US is therefore equal to 58 kg per animal per year.

In West German statistics (Statistisches Bundesamt, 1984), cattle are grouped in age classes: younger than 6 months (2.7 million), 6 to 24 months (6.2 million) and older than 24 months (6.5 million). The latter are subdivided into dairy cows (5.4 million), and heifers or steers (1.1 million).

The feeding level for dairy cows in highly productive stages is 3 to 3.5 × maintenance, equivalent to 300–320 MJ per day (e.g., Van der Honing et al., 1981, Kirchgessner, 1985), but mean gross energy intake over a year's period, is around 260 MJ per day (H. Steingass, personal communication). With a methane yield of 5.5%, we calculate a yearly CH_4 production of 95 kg per dairy cow.

For heifers and steers with body weights of 450 kg and 600 kg, mean gross energy intakes are 125 MJ and 165 MJ per animal per day (Kirchgessner, 1985), respectively, of which 7% is lost as methane (e.g., Wainman et al., 1978). This converts to a yearly methane production of 65 kg per animal as a weighted mean for heifers and steers.

Within the age class younger than 24 months, about 10% of the animal population is kept for veal production. These animals are fed liquid, milky food which strongly limits CH_4 production. Calves younger than 6 months are also fed primarily on milk and other highly digestible feed which do not promote methane production.

Adopting a mean body weight of 340 kg in the age class 6–24 months, the gross energy intake is about 120 MJ per animal per day (Kirchgessner, 1985). As the quality of the feed changes during animal growth from highly digestible to mixtures including more roughage, we adopt a mean CH_4 yield of 6.5%. Consequently, we estimate a production of 51 kg of methane per animal per year in this age class.

Combining the derived methane yields with the cattle populations in the given age classes in West Germany, an average, annual methane production of 57 kg per head is calculated. As other European countries have relatively more beef than dairy cattle and thus slightly lower feed intakes (H. Steingass, personal communication), we will adopt a mean annual CH_4 production of 55 kg per bovin for the developed world by extrapolation of the data derived for the US and West Germany. This figure may have an uncertainty factor of about 15%, mainly due to remaining uncertainties in the methane yields.

Similar methane production rates apply for S. Africa, Australia, Argentina and Brazil. These countries have cattle which are kept mainly on range and fed on roughage (D. E. Johnson, personal communication). For these countries, we assume the CH_4 production rate to be equivalent to that of US cattle on range, i.e., 54 kg per animal per year.

Despite higher methane yields, individual methane production rates from cattle in the developing world are lower, because feed intake is near to, or only slightly above, maintenance, consisting mostly of roughage or kitchen refuse. Pandey (1981) determined the average daily gross energy intake for grazing cattle in Varanasi (India) to be equal to 52.5 MJ for cows, 19 MJ for calves and 73.5 MJ for bullocks. Odend'hal (1972) estimated the mean daily gross energy intake in a cattle population of 3800 individuals in a West Bengal district to be 60.3 MJ per animal. In this population, 14% of the cattle were dairy cows. This is close to the mean for all of Asia (15.6%) and Africa (12.6%) according to the FAO (1984). Adopting an average feed consumption of 60.3 MJ for cattle in the developing world and a CH_4 yield of 9% for low quality feed (Krishna et al., 1978, H. F. Tyrrell, personal communication), we calculate a mean annual CH_4 production rate of 35 kg per animal in the developing world.

According to the FAO (1984), the world cattle population in 1983 was 1.2×10^9. Of this, 53% was kept in the developing and 47% in the developed world, Brazil, and Argentina. Adopting the annual methane production rates of 35 kg and 55 kg, respectively, for these regions, we calculate a global mean annual CH_4 production of about 45 kg per head of cattle, which is considerably less than the 73 kg adopted by Ehhalt (1974). The global methane release to the atmosphere from cattle totals 54 Tg annually (Table 1). Of this about 40% is produced in the developing world.

4. Methane production by other domestic ruminants

Buffalos are kept in some Third World countries for milk production and for farm work. Body weight and feed demand are higher than for cattle, so that buffalos require a gross energy intake of 85 MJ per animal per day (Pandey, 1981). We again assume a CH_4 yield of 9% and therefore estimate a production of 50 kg CH_4 per animal per year. Given a total population of 124 million, the production of CH_4 from buffalos equals about 6.2 Tg per year.

Adult sheep, which weigh 60–70 kg, have a gross energy diet of 30–40 MJ per day in Germany and the US, while immatures are fed 20–25 MJ daily (Kirchgessner, 1985; National Academy of Science, 1975). In West Germany, more than 40% of the sheep population is less than 1-year-old, so that a gross energy intake of

Table 1. *Methane production by domestic animals and humans in 1983* (1 Tg = 10^{12} g)

Animal type and regions	Population [× 10^6]	CH_4 production per individual [kg/year]	CH_4 production by total population [Tg/year]	Production grand total [Tg/year]
Cattle				
Developed countries, Brazil and Argentina	572.6	55	31.5	
Developing countries	652.8	35	22.8	
Total	1225.4			54.3
Buffalos	124.1	50		6.2
Sheep				
Developed countries	399.7	8	3.2	
Developing countries and Australia	737.6	5	3.7	
Total	1137.3			6.9
Goats	476.1	5	2.4	2.4
Camels	17.0	58	1.0	1.0
Pigs				
Developed countries	328.8	1.5	0.5	
Developing countries	444.8	1.0	0.4	
Total	773.6			0.9
Horses	64.2	18	1.2	1.2
Mules, Asses	53.9	10	0.5	0.5
Humans	4669.7	0.05	0.2	0.3
Total				73.7

25 MJ per day be taken as an average. Murray et al. (1978) give smaller values of 15–19 MJ per day for adult Merino ewes in Australia, which may be partly due to a smaller body weight of about 40 kg. Similar values are given by Mathers and Walters (1982) for England. Adopting a mean daily energy intake of 20 MJ in the developed countries and 13 MJ in Australia and in the developing world and applying a mean CH_4 yield of 6% (Kempton and Leng, 1979; Murray et al., 1978), we calculate production rates of 8 and 5 kg CH_4 per animal per year for the developed and less developed world, respectively. The world sheep population in 1983 was estimated by the FAO (1984) to be 1.1×10^9, about equally divided between the developed countries and the developing world, including Australia. Sheep therefore produce about 6.9 Tg of CH_4 annually, worldwide.

The individual, average gross energy intake of goats in India was measured by Pandey (1981) to be 14 MJ per day. This leads to a methane production of about 5 kg per goat per year, similar to that for sheep. The world goat population of about 476 million produces a total of 2.4 Tg methane per year.

Data on feed intake by camels were not available but may be estimated from their average

body weight of 570 kg (Nowak and Paradiso, 1983). Applying the general formula (1) for basal metabolism, we calculate a mean minimum energy demand of 34 MJ per day. The ratio of the mean basal metabolism of cattle in India with a mean body weight between 200–350 kg (H. Steingass, personal communication) to the reported gross energy intake is about 1 : 3. Applying this ratio to camels, we calculate a mean gross energy intake of 100 MJ per animal per day. Camels live essentially on roughage. With 9% methane yield as in the case of Indian cattle, we calculate the methane production from camels to be 58 kg per individual per year, which results in a global yearly CH_4 emission of 1 Tg from a total of 17 million camels. Other camelids (Llamas, Alpaca, etc.) have populations too small (McDowell, 1976) to produce globally significant amounts of CH_4.

5. Methane production by non-ruminant, domestic animals

The methane yield from pigs on highly digestible fattening feeds is less than 1% of the gross energy intake (e.g., Schneider and Menke, 1982). Taking data from Europe, gross energy intake is between 12.5 MJ per day for young pigs and about 90 MJ per day for lactating sows. Based on age and weight-class population statistics from West Germany, we calculate a mean individual gross energy intake of 38 MJ per day. Of this, about 0.6% is released as methane (Schneider and Menke, 1982), yielding 1.5 kg CH_4 per year. We assume that this number applies to developed countries. In developing countries, the animals are smaller and less well nourished, with diets consisting commonly of kitchen refuse or green fodder. With these foods, methane yields might reach 2% (H. Steingass, personal communication). Assuming the gross energy intake to be $\frac{1}{3}$ of that in the developed world and adopting a methane yield of 1.3%, we calculate a yearly CH_4 production rate of 1.0 kg in the developing world. Multiplied with the pig populations in the developed and developing world, this yields about 1 Tg CH_4 per year from pigs.

Methane yields for horses are between those for pigs and ruminants. They equal 3–4% of the digestible energy or 2–3% of the gross energy intake (Kirchgessner, 1985). The energy demand for horses with a mean body weight of 550 kg, executing medium work loads for 2 h a day, is about 78 MJ of digestible energy or 110 MJ of gross energy (National Academy of Sciences, 1973). Similar values are given by Kirchgessner (1985). If 2.5% of the gross energy intake is released as methane, we calculate a mean yearly CH_4 production of 18 kg per animal. The world population of 64 million horses therefore produces a total of 1.2 Tg CH_4 per year. Similarly, we deduce a mean production rate of 10 kg per animal per year for the global mule and donkey population of 54 million, leading to a total emission of 0.5 Tg of CH_4 per year.

6. Methane production by humans

Methanogenic bacteria in the large intestine of humans produce amounts of methane which vary greatly between individuals. The percentage of healthy humans who produce methane ranges from about 30% to more than 50% (Bond et al., 1971; Bjørneklett and Jensen, 1982; McKay et al., 1985). The methane produced in the large intestine is partly absorbed by the blood within the colon wall and exhaled through the lungs, and partly excreted in flatus gas.

Measured CH_4 mixing ratios in exhaled air from methane-producing individuals vary widely, from only a few ppm above ambient air ratios to more than 70 ppm, with an average of 14.8 ppm from 280 healthy individuals (Bond et al., 1971). Levitt and Bond (1970) reported a mean value of 21 ppm CH_4. In a series of experiments on 120 healthy humans, Bjørneklett and Jensen (1982) observed a medium methane mixing ratio in exhaled air of 16.3 ppm. This leads to mean individual CH_4 exhalation rates of 40–50 g per year, assuming a mean breathing volume of 7 l/min (Schulz, 1972). The methane exhalation by the human population of 4.7×10^9 is therefore, equal to about 0.2 Tg per year. This surprisingly small quantity is totally negligible in the global CH_4 budget.

Kirk (1949) measured 2–8% methane in the flatus gases from a group of 20 individuals. The average production of flatus gas from this group was 1.5 ml/min. Extrapolating this information to

the global human population, the release of methane in flatus gas is estimated to be about 0.1 Tg/year. These small methane production numbers are in agreement with other studies (Steggerda, 1968; Marthinsen and Fleming, 1982).

7. Methane release from wild ruminants and other large herbivores

The global production of CH_4 from wild ruminants is difficult to estimate due to lack of sufficient data on animal populations and feed intake. Some population assessments exist, however, for certain regions of the world and can be extrapolated to global conditions. McDowell (1976) gives a population figure of 27 million for wild ruminants in the northern temperate regions (except China). These ruminants are comprised mostly of deer and moose. In Table 2, we have listed their mean body size (Nowack and Paradiso, 1983) and feed intake (e.g. Nyström, 1980; Sadleir, 1982). As wild ruminants live entirely on roughage and herbs near maintenance levels, we assume a CH_4 yield of 9%. Using these figures, we obtain a total release of 0.4 Tg of methane by wild ruminants in the temperate regions, mostly from deer.

Information on populations and mean body weights of wild ruminants in the Serengeti is summarized in Table 3 (Houston, 1979; Western, 1979). The total population of about 2 million mainly consists of gazelle and wildebeest. Data on gross energy intake in Table 3 have been calculated from formula (1) for the basal metabolic rate, multiplied by a factor of 2 to give the likely gross energy requirement of free living ungulates (Moen, 1973; Eltringham, 1974). Again, 9% of the gross energy intake is assumed to be released as methane. With this information, the CH_4 production in the Serengeti from ruminants is estimated to be about 0.02 Tg per year. Assuming the CH_4 production in the Serengeti to be representative of global conditions, the total CH_4 production by the wild ruminant population of 100–500 million in the subtropical and tropical regions (McDowell, 1976) may be estimated to be of 1–5 Tg per year. Together with the contribution from ruminants in the northern temperate regions, the annual CH_4 production from wild ruminants in the world may, therefore, be equal to 2–6 Tg per year which is small compared to the CH_4 production by domestic animals.

Statistics on methane production by other large, non-ruminating herbivores in the Serengeti are likewise listed in Table 4. The most important contributions come from zebras and elephants. The total methane production is less than 10% of that by the ruminants. Altogether, non-ruminating large herbivores are a negligible source of atmospheric methane.

8. Methane emission by other fauna

The consumption of plant matter by the large, wild herbivores considered so far, sums up to 50–200 Tg dry matter. The average consumption of plant matter by herbivorous fauna is estimated to be 7% of the net primary productivity (NPP) of natural ecosystems, or about 7000 Tg dry matter (Whittaker, 1975). Consequently, relatively small

Table 2. *CH_4 production by wild ruminants in temperate northern regions*

Species	Populations [$\times 10^5$]	Mean body weight [kg]	Gross energy intake [MJ/day]	CH_4 production per individual [kg/year]	CH_4 production total [Tg/year]
moose, elk	8.5	350	53	31	0.03
white and black-tailed deer, mule deer, red deer, reindeer, caribou	220	90	26	15	0.33
roe deer	40	15	5	3	0.01
Total	268	—	—	—	0.37

Table 3. *CH_4 production by wild animals in the Serengeti*

Species	Population [$\times 10^3$]	Mean body weight [kg]	Gross energy intake [MJ/day]	CH_4 production per individual [kg/year]	CH_4 production total [10^6 kg/year]
wildebeest	72000	123	22	13	9.4
buffalo	10800	450	57	34	3.7
Thompson's gazelle	98100	15	4	2	2.0
giraffe	1700	750	84	50	0.8
eland	2400	340	46	27	0.6
topi	5600	100	19	11	0.6
impala	11900	40	9	5	0.6
kongoni	2100	125	22	13	0.3
waterbuck	300	160	26	15	0.1
Grant's gazelle	600	40	9	5	—
Total ruminants					18.1
zebra	240	200	31	5	1.2
elephant	5	1725	157	26	0.13
warthog	34	45	10	1	0.03
hippopotamus	2	1000	104	17	0.03
rhinoceros	1	820	90	15	0.02
Total non-ruminants					1.4

Table 4. *Trends in domestic animal populations and CH_4 production rates*

	1890	1921–25	1941–45	1961–65	1983
Cattle					
population [10^6]	310	640	740	1016	1225
CH_4 production rate [kg/animal/year]	35	38.3	40.5	42.8	45
CH_4 production total [Tg/year]	11	25	30	43	54
Sheep					
population [10^6]	590	645	755	1007	1137
CH_4 production rate [kg/animal/year]	5	5.4	5.6	5.9	6
CH_4 production total [Tg/year]	3	3	4	6	7
Other domestic animals, humans etc.					
CH_4 production total [Tg/year]	3	6	8	11	13
Total CH_4 production [Tg/year]	17	34	42	60	74

CH_4 yields from other fauna than that considered so far could produce substantial amounts of methane. In the following, we will briefly consider the possibilities.

According to Whittaker (1975), the consumption of plant matter by fauna is 10–15% of the NPP in grasslands and 4–8% in forest and woodlands. However, only a few investigations on the energy transfer through the food webs in these ecosystems have been published so far, which give information on the main herbivorous consumers. Norton-Griffiths (1979) and Sinclair (1975) estimated the consumption of plant matter by small mammals, mainly voles, in the Serengeti to be 1.2% of the above-ground NPP in long-grass savanna and only 0.1% in short-grass savanna. Much more, 7.6% and 4.1%, respectively, is consumed by invertebrates (mainly grasshoppers), in these two grassland sites (Bourlière, 1983).

In the palm savanna at Lamto, Ivory Coast, the main consumers are fungus-growing termites (6% of NPP), followed by grasshoppers (0.4%) and small rodents, mainly voles (0.25%). Large herbivorous ungulates play no major rôle (Lamotte and Bourlière, 1983). Certain ants and caterpillars are also important consumers but quantitative information on their rôle is not available.

In the Fété Olé savanna in Senegal, termites have also been found to be major harvesters of plant tissue, consuming 10% of the NPP (Josens, 1983). Gillon (1983) states that at this site, grasshoppers and caterpillars may consume as much as grazing mammals, but gives no data on their plant consumption.

In undisturbed temperate grassland sites, primary consumption by invertebrate herbivores is 0.5–9% of the above ground NPP, being lowest in poor, unproductive sites and increasing with productivity (Andrzejewska and Gyllenberg, 1980). Wiegert and Evans (1967) determined an upper limit of 12% for plant consumption by herbivores in an old grass field site in South Carolina, mainly by invertebrates. Only 1% was consumed by vertebrates, mainly field mice and savanna sparrows.

In tropical forests, Janzen (1983) considers defoliating animals as the most important plant consumers, mainly moth larvae, caterpillars, beetles and other invertebrates. Jordan (1983) cites data, indicating that usually no more than 3–8% of the leaf biomass is harvested by insects. In nutrient deficient, low-production forests, the consumption may drop to 2%.

Herbivorous vertebrates are not important as primary consumers in tropical forests. Owen (1983) gives a very low figure of only 72 kg/km^2 for the density of herbivorous mammals at the Tano Nimri Forest (Ghana), consisting of 3 ungulates and 7 primates. These low figures are also confirmed for South Eastern tropical rain forests (Whitmor, 1984). In contrast, in some South American forests, larger populations of sloths and tapirs may be found that may consume a considerable fraction of plant production within the forests (Janzen, 1983). Rodents are also present in tropical forests but apart from some population figures, no energy intake data are available.

In temperate forests, primary consumption by insects is at most 10–15% of the above-ground NPP (Remmert, 1980). Franklin (1970) cites some figures for broad-leaved trees, which range from 5–8%. However, these data contradict those from an intensively investigated forest site in the North-east US, in which Gosz et al. (1978) found less than 1% of the total NPP, including roots, to be consumed by herbivores. In approximate order of importance, these are chipmunks, mice, foliage-eating insects, birds, deer and hares.

Consumption figures from boreal forests or tundra sites are not available. Remmert (1980) gives a rough figure of 1–2% for consumption by vertebrates at Spitzbergen (Norway), but gives no estimates for invertebrates.

Summarizing the above widely different data, it appears that major consumers in natural habitats are invertebrates, mainly insects, and to a much lesser degree small herbivores. If we assume that small herbivores (mainly rodents and lagomorphs, i.e., hares, rabbits, etc.) in natural habitats consume less than 1% of the global NPP, with a CH_4 yield of 1.5% (Johnson, personal communication), we calculate for this group of animals an upper limit of methane production of 2–3% Tg per year.

An estimate for methane production by invertebrates is even more speculative. So far, methane production has only been measured in termites (Zimmerman et al., 1982; Rasmussen and Khalil, 1983; Seiler et al., 1984; Fraser et al., 1986) and in wood-boring larvae of beetles (Bayon, 1980) which utilize symbiotic micro-organisms in their digestive tract to break down cellulose. According to Swift et al. (1979), most insects harbour flagellates in their guts for cellulose digestion. Thus it is likely that insects and probably other invertebrate primary consumers also harbour methanogenic micro-organisms.

Measurements from different genera of termites indicate methane yields of less than 0.01% to 1.5% (Zimmerman et al., 1982; Khalil and Rasmussen, 1983; Seiler et al., 1984). If we adopt this range for all invertebrate primary consumers, the consumption of 6% of the global NPP by herbivorous invertebrate probably could produce at most 28 Tg annually. However, this upper limit estimate is speculative as long as no data on possible CH_4 production yields by insects other than termites are available. According to Owen (1983), plant-feeding insects in tropical forests

are much more abundant than commonly assumed, due to inadequate counting methods. Consequently, more work on the potential CH_4 production by invertebrates is certainly justified.

Our upper estimate of 28 Tg for invertebrate primary consumers overlaps to some degree with global production estimates for termites (including herbivorous species, wood- and dung feeders, soil feeders and others), which range from 2–5 Tg (Seiler et al., 1984) up to 150 Tg (Zimmerman et al., 1982). The most recent study by Fraser et al. (1986) suggests an annual production of 6–42 Tg with an average of maybe 14 Tg.

So far we have primarily been concerned with primary consumers. Most of the plant material produced each year by vegetation is lost to the litter layer and subsequently decomposed by a large variety of organisms. A survey through the literature on soil biology has given no hint on methane production in soils apart from anaerobic environments and termite mounds. Swift et al. (1979) report that certain cockroaches and dung beetles rely upon symbiotic bacteria and protozoans for the digestion of structural polysaccharides. This could imply possible methane production as in the case of termites. Generally, methane can most probably only be produced by macrofauna consumers of plant detritus (primary saprotrophs) as these are the only ones with true anaerobic digestive tracts. Organisms belonging to mesafauna are probably too small in size to develop anaerobic conditions in their guts (Grewe, personal communication). The macrofauna plays a major rôle in the tropics and declines in importance towards the poles. In colder climates, major breakdown of organic compounds is accomplished by microfauna and fungi (Swift et al., 1979), which implies a gradient of decreasing methane production potential from soil fauna from the tropics to the poles.

Earthworms have attained special interest in the past for their ameliorating effect on soils. These animals feed on detritus together with mineral particles and attain huge turnover rates of matter within the soil. Their guts produce a favourable environment for a diverse population of micro-organisms. However, cellulose is very badly digested (Brauns, 1968) and methanogenesis is not reported. Measurements on aerobic soils of temperate and tropical grassland sites (Seiler et al., 1984, 1986) all indicate methane decomposition in the soil and no production. If soil-dwelling organisms produce methane, it seems likely that this is readily decomposed within the soil and does not escape to the atmosphere.

9. Current and past CH_4 production from domestic animals

Data on the estimated global methane production by domestic animals and humans in 1983 are summarized in Table 1. Total methane release to the atmosphere is about 74 Tg/year with an estimated uncertainty of about 15%. By far the largest contribution, about 54 Tg, comes from cattle. About 40% of this emission occurs in the developing world. Next in importance come buffalo and sheep, which produce about 6 Tg and 7 Tg CH_4 per year, respectively. Goats and camels produce 2.4 Tg CH_4 and 1 Tg CH_4 annually. Non-ruminant, domestic animals each year emit about 2.6 Tg CH_4 to the atmosphere. The human contribution is only about 0.2 Tg CH_4 per year. In comparison with the estimated, global methane emission of 74 Tg by domestic animals in the year 1983, the input by wild ruminants of 2–6 Tg is relatively small.

Because of the growing world population of humans and its growing food demand, the population of domestic animals has also increased considerably during the last century, leading to an increase in global methane production rates. According to data published by Mulhall (1892) for the end of the last century and data for the first half of this century (US Department of Agriculture, 1936–1970), the world cattle population has increased from 310 million in 1890 to 640 million in 1920–1925, and 740 million in 1940–1945. The corresponding figures for sheep are 590 million, 645 million, and 755 million, respectively (Table 4). According to the available statistics, the sheep and cattle populations show similar trends for the period 1920–1960, but large differences for 1890–1920, which is probably indicative of less reliable statistical information from the early period.

More detailed statistical information is available for the time period after 1940, particularly due to the work by the Food and Agricultural Organization of the United Nations (FAO, 1973,

1982 and 1984). According to these data, during the last two decades, the world's cattle and sheep populations have grown by 0.8% and 0.6% per year, respectively, reaching figures in 1983 of 1225×10^6 for cattle and 1137×10^6 for sheep. Similar annual increases in global population numbers are found for pigs (1.4%), buffalos (1%), goats (1.2%) and camels (0.5%). The population of mules and asses stayed about constant, while that of horses showed a slight decline of 0.25% per year. According to the available statistics, since 1960, the growth rates of the cattle and sheep populations have slightly declined.

The temporal trends of global CH_4 emission by ruminants are not only dependent on their populations but also on quality and quantity of feed intake. In the developed countries, the average, individual feed intake has increased during the last 20 to 30 years, although the corresponding increase in CH_4 emission may have been compensated to some extent by declining CH_4 yields due to higher feed quality. In the developing world, both feed intake and quality may have declined.

To estimate individual methane production rates prior to 1983, we assume that in 1890, average methane yields in the world were about equal to current yields in the developing world, while between 1890 and 1980, we adopt a linear growth in individual CH_4 emission rates. With this assumption, the CH_4 release from cattle has more than quadrupled during the last century from 11 Tg in 1890 to 54 Tg in 1983. CH_4 emission by sheep has grown from 3 Tg to 7 Tg during the same period (Table 4). Information on declining populations of wild ruminants is not available, but they can certainly not have been sufficient to compensate substantially for the growth in methane emissions by domestic animals. Altogether, our analysis indicates that the total annual CH_4 emission from all animals, including wild ruminants, has increased from 21 Tg in 1890 to about 78 Tg in 1983.

10. Conclusions

Methane is produced by the anaerobic fermentation of organic matter in the rumen and lower gut of domestic and wild animals. The CH_4 emission rate per animal is dependent on quality and amount of feed intake. Based on data that are presently available, we estimate that about 5–9% of the gross energy intake by ruminants is lost to methane production. Lower methane yields in the range 0.5–3% are derived for other domestic animals such as pigs, horses, etc.

The current global CH_4 emission by domestic and wild animals is estimated to be 78 Tg/year. From this, almost 80%, or about 60 Tg/year, comes from cattle and buffalos. The rest is produced by sheep (7 Tg/year), wild ruminants (2–6 Tg/year), and others. About 40% of the total CH_4 produced by domestic animals is emitted in the developing countries, mostly in Asia, followed by South America and Africa. The main source region for methane from cattle in the developed world is North America (11 Tg/year) followed by Europe (8 Tg/year) and the USSR (7 Tg/year).

Methane production by domestic and wild animals constitutes about 15–25% of the total tropospheric CH_4 input, recently estimated by various authors to be in the range of 300–500 Tg/year (Khalil and Rasmussen, 1983; Crutzen and Gidel, 1983; Seiler, 1984). Production by animals represents one of the most important individual sources within the tropospheric CH_4 cycle. It is about two times larger than the production from coal mining and natural gas leaks (Seiler, 1984; Crutzen, 1986; Bolle et al., 1986). The only emissions which could be larger are those from the anaerobic decay of organic matter in rice fields and natural wetlands. Methane release from rice paddies may be about 70–130 Tg/year, if information obtained in Italian rice fields can be extrapolated to tropical conditions (Holzapfel-Pschorn and Seiler, 1986).

The total emission of CH_4 by domestic and wild animals has increased from about 21 Tg in 1890 to 46 Tg in 1940 and 78 Tg in 1983, mainly due to growing populations of cattle, buffalos and sheep. According to these figures, the mean rate of increase in CH_4 emission by domestic and wild animals during the last 43 years has been 1.1% per year.

We have estimated a tentative upper limit of about 30 Tg CH_4 emission per year from other fauna, especially insects. However, this topic requires additional research. Finally, the production of CH_4 in humans appears to be negligibly low, much less than 1 Tg/year.

11. Acknowledgements

Dr. G. Allen (US Department of Agriculture, Economic Research Service, Washington DC), Dr. H. F. Tyrrell (US Department of Agriculture, Science and Education Administration, Beltsville Agricultural Research Center, Beltsville), Dr. D. E. Johnson (Michigan State University, Department of Animal Husbandry, East Lansing, Michigan), Dipl. rer. nat. U. Grewe, Institut für Angewandte Bodenbiologie, Hamburg, and especially Dr. H. Steingass (Universität of Hohenheim, Institut für Tierernährung, Stuttgart, F.R.G.) supplied much information through private communications. This work was partly supported by the Ministry for Research and Technology of the Federal Republic of Germany through grant BMFT/KBF 68.

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