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Significance of grasslands in emission and absorption of greenhouse gases K. MINAMI, J. GOUDRIAAN, E.A. LANTINGA and T. KIMURA

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Significance of grasslands in emission and absorption of greenhouse gases

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ABSTRACT

Grasslands account for about 20% of the terrestrial CO₂ fluxes of the global carbon cycle. They have a similar share in global soil organic carbon. Grasslands are likely to contribute to a global biotic carbon sequestration, reducing the rate of increase of atmospheric CO₂. Methane (CH₄) uptake rates and nitrous oxide (N₂O) emissions are given for established grassland and neighbouring forest-floor soils in Japan. Under aerobic conditions grassland and forest soils act as a sink for atmospheric CH₄. The global terrestrial uptake rate for CH₄ is estimated to range between 7 and 78 Tg CH₄ per year. The sink strength of grasslands is about 8.5% at most of total terrestrial CH₄ consumption. Methane absorption of grassland soils is less than about one tenth of the emission of the cattle. Improving fodder quality can reduce ruminant methane emission. Even when fertilised, grasslands emit probably less nitrous oxide than forest soils.

KEYWORDS: carbon cycle, carbon dioxide, fertilisation, methane, nitrous oxide, sink strength

INTRODUCTION

Grasslands participate in the cycling of greenhouse gases such as CO₂, CH₄ and N₂O. Grassland management may influence the rates of production and absorption of these greenhouse gases.

The rise of atmospheric CO_2 is responsible for more than 50% of the total expected global warming, and CH_4 and N_2O for about 20% (Rodhe 1990). The concentrations of these gases have increased dramatically over the past few decades. CO_2 continues to rise at a rate of about 1.5 ppm per year, and has now passed the 350 ppm level.

The concentrations of CH_4 and N_2O continue to increase at a rate of about 1.1 and 0.25 % per year, respectively (Cicerone & Oremland 1988; Prinn et al. 1990), although the rate of increase of CH_4 is slowing down (Steele et al. 1992),. The total source size is estimated to be equal to 500 Tg for CH_4 and 5.2-16.1 Tg N for N_2O per year (Watson et al. 1992). Reduced sink size may be equally responsible for the increase in these atmospheric concentrations.

Whereas studies have been conducted throughout in the world to assess the sink strength for CH₄ of forest, savannah, tundra, desert and taiga (Keller et al. 1983; Seiler et al. 1984; Whalen & Reeburgh 1990; Whalen et al. 1991; Steudler et al. 1989; Striegl et al. 1992; Crill 1991; Keller et al. 1990; Born et al. 1990; Delmas et al. 1991), little attention has been paid to grasslands. Nitrogen fertilisation of grassland as well as conversion to arable land can both decrease CH₄ uptake and increase N₂O production, thereby contributing to the increasing atmospheric concentrations of these gases (Mosier et al. 1991). The same applies to tropical soils (Keller et al. 1990). Rice paddy fields can both emit CH₄ and consume N₂O when an anaerobic layer becomes developed under flooded conditions (Minami & Fukushi 1984; Yagi & Minami 1990).

Little information exists on $\mathrm{CH_4}$ uptake in grasslands, or its relation to $\mathrm{N_2O}$ production, and the effect of land management or cultivation (Mosier et al. 1991; Schutz et al. 1990; Seiler & Conrad 1987). Here we present measurements of $\mathrm{CH_4}$ uptake by, and $\mathrm{N_2O}$ emissions from, fertilised grassland and forest soils. These studies were carried out from spring to late autumn, 1991 in Japan (Kimura et al. 1992). Also we summarise $\mathrm{CH_4}$ uptake rates by soil for different land uses, and estimate the global $\mathrm{CH_4}$ sink and the part played by grasslands for this atmospheric $\mathrm{CH_4}$ sink.

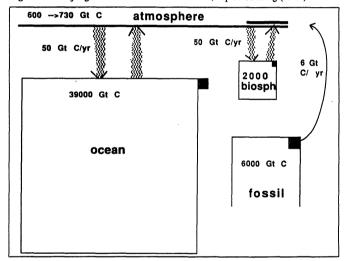
GRASSLANDS AND THE GLOBAL CARBON CYCLE

By far the larger part of carbon (C) on earth occurs in oxidised forms, mainly as carbonates, on one hand in rocks (60 million Pg of carbon; $1 \text{ Pg} = 1 \text{ Gt} = 10^{15} \text{ g}$), and on the other hand as dissolved ions in the sea (39 000 Pg). In comparison, the amount of gaseous CO₂ in the atmosphere is a mere 700 Pg of C. The amount of C in atmospheric methane is even 200 times less and only 3.5 Pg. Most reduced C occurs in the form of coal and oil, formed by photosynthesis in a

remote past. The explorable quantity is probably of the order of 10 000 Pg. The terrestrial biosphere contains an amount of reduced carbon of the order of 2000 Pg, of which about 500 Pg is in vegetation itself and about 1500 Pg is in soil organic matter.

The small size of the atmospheric C reservoir renders it vulnerable to disturbance, whether by man or by natural forces. The huge pool of rock carbonate (Berner & Lasaga 1989) is involved with exchange rates of the order of 0.1 Pg of C per year or less, and can be ignored on the human time scale. The exchange rates of C between atmosphere and ocean and terrestrial biosphere (Fig. 1) are of the order of 50 Pg of C per year each, so that the residence time of a molecule of CO₂ in the atmosphere is about 7 years. Once in the ocean, the residence time of C there is much longer: 800 years. In the biosphere, the C residence time is 40 years as an average, but there is a strong diversification between C in leaves, stemwood and soil C.

Figure 1 Major global reservoirs and fluxes of C, expressed in Pg (or Gt).



The annual rates of production and oxidation of methane are about 0.35 Pg of C (one tenth of the atmospheric stock), and therefore negligible as part of the C cycle. Amounts and fluxes of methane are normally not expressed as C, but as weight of the whole $\mathrm{CH_4}$ molecule, in units of 10^{12} g or Tg. Table 1 summarises the sources and sinks of atmospheric methane. There is an excess of the combined sources over the sinks, reflecting the annual accumulation rate of $\mathrm{CH_4}$ in the atmosphere.

Table 1 Most important global methane emissions in Tg of CH₄/yr (After Bouwman 1990)

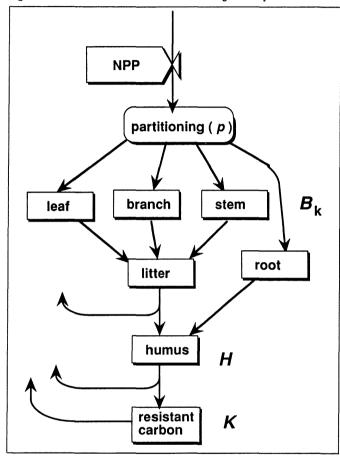
Rice fields	100	<u>-</u>	40
Natural wetlands	100	Ŀ	60
Landfills	50	ŧ	20
Ruminants	75 :	Ė	15
Fossil fuel mining	60 :	£	20
Biomass burning	75 :	£	25
Others (termites etc)	40 :	Ŀ	20
Total sources	500 :	Ŀ	100
Total sinks	450 :	Ŀ	100

Role of vegetation in the global carbon cycle

Net Primary Productivity (NPP) is defined as dry matter growth that remains after subtraction of the plant's own respiration. This flux of plant material, estimated to be 40-60 Pg C/year worldwide, is largely consumed by grazers, insects or large mammals, or left over to be decomposed by fungi and microbes. Live biomass is about 500 Pg in

the form of wood mainly, and after death it turns to litter and soil organic C (about 1500 Pg). The magnitudes of the pools of organic matter in various forms and of the fluxes of formation and consumption are related by residence times and partitioning coefficients. Their basic relationship is given in Fig. 2 as a scheme driven by NPP. The outflow of each state variable in this scheme is calculated as content divided by a longevity, so that its equilibrium content is simply the product of longevity and inflow. The outflows cascade down to litter, humus, and resistant soil C. From biomass to humus a considerable fraction of C is lost by respiratory processes, and also from humus to resistent soil C. The complement of this fraction returns to the atmosphere as respiratory CO₂.

Figure 2 Basic scheme for the flow of carbon through an ecosystem



Above-ground biomass consists of leaves, stemwood, roots, branches and litter. Combination of the driving forces and residence times leads to a steady state distribution of surface densities of C for a biosphere model consisting of six different ecosystem types as presented in Fig. 3 (Goudriaan 1990). The high areal density of soil carbon in temperate forest and in grasslands as compared with agricultural land and tropical forests is noteworthy.

Many ecosystems in the world, however, are not in a steady state, but they accumulate dry matter during a number of years and are then disrupted by fire, so that they go through a saw tooth-like life cycle. Fire is often a natural process, and necessary for rejuvenation of ecosystems. Locally, disruption by fire is a discontinuous event, but summed over the entire globe there is a continuous release of CO, by fire, which is practically compensated by regrowth at the other places. The total C release flux owing to fire is of the order of 4-7 Pg C/year. The largest portion in this flux is on account of periodic burning of tropical grasslands (Hall & Scurlock 1991). Although this flux is almost as large as the rate of fossil fuel consumption, grassland burning does not contribute to the increase of atmospheric CO2. Within a time span of one year most of the material turns to CO₂ anyway, if not by fire then by decomposition. Moreover, fire residues such as charcoal are added to resistant soil C. The relative effects on the production of CH₄ are larger, since biomass burning is estimated to be responsible for about 75 Tg of CH₄ annually (Table 1).

Figure 3 Areas (width of bars) of major ecosystems and their simulated equilibrium C density per unit area (height of the bars)

forest	tempe- rate forest	grass land	agric. land	urban area	desert, tundra	leaf
				[]	**************************************	wood
	nanana	panana.		-		litter
						root humus resistant carbon
I 1 kg C m²			ŀ	100	00 Mh a	

Role of grasslands

On a global scale, grasslands occupy about 20% of the well-vegetated land area, contributing about 23% to both annual C flux and total C storage. The surprisingly large share in terms of C storage is entirely due to the large amount of organic matter that is maintained in grassland soils, owing to a combination of large partitioning of dry matter to belowground parts and to a relatively slow rate of decay of soil organic matter. When a forest is turned into land used for agriculture, the standing biomass is removed (often partly burned), and the disturbance of the soil will give rise to enhanced decomposition of soil organic matter and so to a strong efflux of CO₂. In arable land, the disturbance is repeated annually by ploughing, and after a few decades the soil C content has declined to a much lower level than originally present in the virgin soil. In grassland, however, the situation is different. The soil is much less disturbed, the crop is perennial, and the remnants of leaves, stolons, roots, stubble and of cattle manure accumulate and give rise to a soil organic matter level as high as in the original forest soil. At present grasslands are extended far beyond their natural range. In the Holdridge diagram the term "cool temperate steppe" is used to indicate the climatic zone where grasslands naturally occur. This zone happens to be a rather dry one, with annual potential evapotranspiration exceeding annual precipitation. These truly natural grasslands occur in the prairie zone of North America, the chernozem zone of the Ukraine and in the pampas of Argentina. Their combined area is about 900 Mha, containing a total amount of soil C of 120 Pg (Post et al. 1985) In the actual man-made situation, the most productive grasslands are found in the zone with a larger moisture supply, indicated by the term "moist temperate forests". These natural forests have long ago been replaced by agricultural land, and indeed also by pasture land. The area of these man-made grasslands is also about 900 Mha, but their soil C content is higher than that of natural grasslands, probably around 200 Pg.

Grazing enhances the addition of organic material to the soil. Under intensive grazing about 20% less herbage is removed from the field than by mowing, and a similar fraction of the dry matter production is returned to the soil as undigested components in the dung. Irrespective of level of N fertilisation, young perennial ryegrass swards contained about 10 t/ha more soil organic C after 4 years of grazing than after mowing (Hassink & Neeteson 1991).

Hatch et al. (1991) observed that the accumulation rate of soil organic matter was greater under a fertilised perennial ryegrass sward

than under an unfertilised ryegrass-white clover sward. Both swards were grazed rotationally by young beef cattle. Total C content of the soil under the ryegrass sward rose from 34 t/ha in 1976 (sowing) to 68 t/ha in 1988, and to only 50 t/ha under the grass-clover mixture. This large difference in accumulation rate may have been caused by a lower dry matter production of the grass-clover mixture, and also to a faster decomposition rate of clover residues.

Biotic sequestration of C

Large-scale deforestation has been known for decades as a source of CO_2 but the role of the biosphere as a whole in absorbing CO_2 was still uncertain. More recently it has been estimated that the increase of atmospheric CO_2 itself induces an increase in global plant productivity to the extent that the biosphere can absorb something like 20% of global emission of CO_2 . This CO_2 -induced absorption happens to be of the same order of magnitude (about 1 Pg of C/year) as the amounts released in large scale deforestation.

This role of the biosphere as a sink is suggested from circumstantial evidence. First, the actual rate of increase of CO2 in the atmosphere is so much smaller than the total rate of emission (a gap of more than 50%) that the ocean alone cannot absorb this enormous amount of disappearing CO₂ (Tans et al,1990). Second, there is more and more evidence for the existence of a strong stimulation of plant growth by increased atmospheric CO2, not only in agricultural crops but also in natural vegetation. According to a summary of Kimball (1983), there is a mean 40% increase of dry matter in C₃ crops upon doubling of CO₂, and a 15% increase for C₄ crops. This effect of CO₂ not only occurs in crop plants, but is also a general phenomenon (Lemon 1984). The primary physiological effect of increased CO₂ concentration is a stimulation of the rate of CO₂ assimilation, and also the respiration rate might be reduced (Amthor 1991). The CO, enrichment effect is maintained when growth is limited by water (Gifford 1979), which can be explained by control of both water loss and CO, assimilation by stomatal resistance. Any increase in ambient CO₂ will then stimulate CO₂ uptake without raising water loss. Nutrient shortage, especially of phosphorus and of potassium, tends to impose a more absolute limitation to crop growth without leaving much room for stimulation by CO₂. Nitrogen, however, differs from other nutrients in that it permits a small positive CO₂ effect, even under rather severe nitrogen shortage. Adaptation to higher ambient CO2 does occur to a certain extent. Recently, Ryle et al. (1992) showed that doubling CO2 resulted in only 10% increase of total dry weight of perennial ryegrass, in spite of a stimulation of photosynthesis by about 50%. They hypothesised that the effect of CO, must have been restricted by a lack of response in tiller formation. Indeed, tiller number was doubled at each leaf appearance interval, which is a morphological maximum (Neuteboom & Lantinga 1989).

Arp (1991) showed that part of the conflicting evidence in literature on adaptation of plants during growth can be explained by differences in pot size used in the reported experiments, the disappearance of the $\rm CO_2$ effect on growth being associated with small pot size. In the field, a primary $\rm CO_2$ stimulus can lead to better exploration of the soil (Rosenberg 1981; Idso 1989), so that nutrient uptake may go up even under nutrient limited circumstances. Indeed, in an experimental study during 4 years of continued exposure of a natural salt marsh vegetation to high $\rm CO_2$, Arp et al.(1991) found no decline in increased photosynthesis and no decline in water use efficiency.

One implication of a global $\rm CO_2$ enrichment effect is most likely a further accumulation of soil organic matter, estimated at an annual rate of the order of 1 Pg of C/year (Goudriaan 1992). The role of grassland in this process will increase, because of enhancement of $\rm CO_2$ enrichment effects by increased nitrogen supply (Thornley et al. 1991).

THE GLOBAL METHANE FLUXES

Soil and land-use related processes represent the most important sinks of atmospheric CH_4 (Table 1). According to Bouwman (1990) and Schutz et al. (1990), the land area of the globe can be subdivided into 14 ecosystem types. These are listed, with their total land areas, in Table 3 which also shows the soil and land-use related CH_4 sinks (following Schutz et al. 1990).

The uptake of CH_4 by soils was first demonstrated by Seiler et al. (1984) via measurements in a subtropical broad-leaf savannah type in South Africa. Their measurements showed a consumption rate of CH_4 at the soil surface of 52 μ g/(m²h) during the rainy season. Thereafter,

Table 2 CH₄ uptake rates in grassland and other types of vegetation

Sinks	CH ₄ μg/(m² h)	Reference
Semi-arid grassland	6 - 61	Mosier et al. (1991)
Tropical forest	6 - 24	Keller et al. (1983)
Subtropical savannah	52	Seiler et al. (1984)
Floodplain taiga soils	10	Whalen et al. (1991)
Temperate forest	10 - 160	Steudler et al. (1989)
Desert soils	10 - 38	Striegl et al. (1992)
Temperate woodland soil	- 200	Crill (1991)
Central Panama forest soil	33	Keller et al. (1990)
Central Panama agricultural soil	8	Keller et al. (1990)
Temperate zone aerated soils	10 - 148	Born et al. (1990)
Temperate grassland	0 - 41	Kimura et al. (1992)
Temperate forest	41 - 112	Kimura et al. (1992)
Landfill cover soils	1875	Whalen et al. (1990)
Dry savanna soils	19	Delmas et al. (1991)

 ${\rm CH_4}$ uptake has also been observed in forest, grassland, tundra, taiga, desert, agricultural soils and landfill cover soils, as is shown in Table 2. From these data the combined ${\rm CH_4}$ uptake by the 14 ecosystem types was estimated to range between 7 and 78 Tg ${\rm CH_4}$ per year, or about 2-16% of the total turnover of atmospheric ${\rm CH_4}$ of approximately 500 Tg per year. The sink strength of grassland is about 8.5% at most of the total terrestrial ${\rm CH_4}$ consumption. The grassland-related ${\rm CH_4}$ sources together, fire and cattle, produce about 120 Tg of ${\rm CH_4/year}$, or 25% of the total global emission. In contrast the sink strength is only 10 Tg/year at most (Table 3).

Table 3 Global soil and land use related CH₄ sinks

Eco	system/type	Area	CH₄sink rates	Annual duration	CH₄ deposition
		(Mha)	(µg/(m² h))	(days)	(Tg/yr)
1.	Trop. rain forest	711	6-24ª	365 ^b	0.43-17.1 ^b
2.	Trop. seas. forest	710	10-21 ^{a,b} , 6-24 ^c	365	0.71-1.7
3,	Temp. evergr. forest	731	10-160 ^{b,c,d} , 41-112° 33 ^f , 10-148 ^g	200 ^b	0.35-5.6 ^b
4.	Temp. decid. forest	683	10-160 ^{b,c,d} , 41-112° 33 ¹ , 10-148°	200 ^b	0.33-5.3 ^b
5.	Boreal (taiga)	701	10-160 ^b , 10 ^h	120 ^b	0.34-5.4 ^b
6.	Woodland/shrubl.	717	52 ¹ , 200 ¹ , 10-148 ⁹	365 ^b	0.71-14.2
7.	Savannah	1069	52 ⁱ , 19 ^k	365 ^b	2.00-5.6
8.	Tropical grassland	211	0-41°, 6-61	365	0-1.1
9.	Temp. grassland	1047	0-41°, 6-61 ¹ , 0-23 ⁹	365	0-5.6
10.	Desert/semi-	1200	52 ⁱ , 10-38 ^m	365 ^b	1.20-6.2
11.	Extreme desert	1257	52 ^l , 10-38 ^m	365 ^b	1.30-6.5
12.	Cultivated land	1578	8 ⁿ , 0-23 ^g	365	0-3.2
13.	Swamp/marsh/flood	210			
14.	Tundra/alpine	695			
15.	Miscellaneous	152			*
Tota	al of sinks	7.4-77.5			

Keller et al. 1986; ^b Schutz et al. 1990; ^c Keller et al. 1983; ^d Harriss et al. 1982;
 Kimura et al. 1992; ¹ Keller et al. 1990; ⁹ Born et al. 1990; ^h Whalen et al. 1991;
 Seiler et al. 1984; ¹ Crill 1991; ^k Delmas et al. 1992; ¹ Mosier et al. 1991; ^m Striegl et al. 1992; ⁿ Keller et al. 1990.

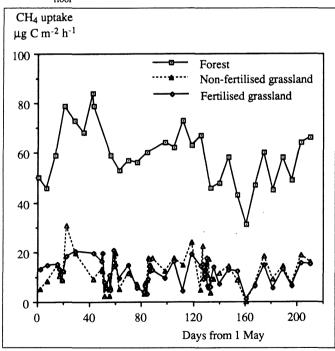
On a global scale, biomass burning causes an annual release of methane of about 75 \pm 25 Tg/year (Table 1). A large portion of this burning occurs in tropical grasslands and savanna's, probably more than about 40 Tg/year. Cattle releases another 75 \pm 25 Tg of CH₄/year (Crutzen et al. 1986). Although considerable research has focused on measuring CH₄ emissions from major biological sources, much less is known about the magnitude of, and the factors controlling biological sinks of CH₄. The largest biological sink for CH₄ are micro-organisms in aerobic soils (Seiler & Conrad 1987), which consume about 30 Tg CH₄/year (Cicerone & Oremland 1988; Born et al. 1990). Spatial and temporal variability in the rate of CH₄ consumption by soil are not yet completely understood (Born et al. 1990; Keller et al. 1983; Seiler et al. 1984; Megraw & Knowles 1987; Steudler et al. 1989; Whalen & Reeburgh 1988; Crill 1991; Delmas et al. 1992; Mosier et al. 1991; Whalen et al. 1991). Also there is a lack of understanding of the apparent inhibitory (Steudler et al. 1989; Keller et al. 1983; Mosier et al. 1991) or enhancing (Whalen & Reeburgh 1990) effects of changes in land use.

Steudler et al. (1989) reported a study of $\mathrm{CH_4}$ uptake by aerobic temperate-forest soils. They measured $\mathrm{CH_4}$ daily consumption rates of up to 3.17 mg $\mathrm{CH_4}$ - $\mathrm{C/m^2}$ which is higher than previously reported. Globally, soils of temperate and boreal forests may consume up to 9.3 Tg $\mathrm{CH_4}$ - $\mathrm{C/year}$. These researchers also found that the $\mathrm{CH_4}$ uptake rates by these soils were decreased significantly by elevated soil moisture and nitrogen additions. This implies that nitrogen fertilisation may reduce the $\mathrm{CH_4}$ sink.

Grassland and other land use types

Using a closed-chamber technique, Kimura et al. (1992) measured CH₄ and N₂O fluxes above an established grassland (orchardgrasswhite clover) sward and above a neighbouring red pine forest soil, both situated on brown lowland soil with volcanic ash. Both the grassland and the forest soil were a sink for CH₄ and a source for N₂O. Methane uptake rate in grassland ranged from 0 to 41 µg CH₄/m² per hour between May and November 1991, and averaged 15 µg CH, irrespective of either fertilisation or vegetation. The methane uptake rate by the forest-floor was 5 to 6 times higher (41 to 112 µg CH₄/m² per hour) than the uptake by grassland (Fig. 4). Nitrous oxide emission from unfertilised grassland and forest-floor ranged from 1 to 15 µg of N/m² per hour, and averaged 5 µg of N/m² per hour between May and November, 1991. Fertilised grassland showed a higher rate of N₂O emission than the unfertilised grassland did (Fig. 5). Fig. 6 shows the results of the total N₂O and CH₄ efflux between the different vegetation and/or fertilisation from May 1 to June 12, 1991. Much of the N₂O, 0.2 to 1.0 % of applied nitrogen, evolved through nitrification during the cultivation period after the application of nitrogen fertiliser (urea) (Fig. 5). These values are almost the same as the data obtained for an upland field in Japan (Minami 1987). There was no relationship between the CH₄ uptake and N₂O emission rates (Fig. 7). Fresh faeces and cattle slurry applied to the grassland surface released both CH, and N₂O to the atmosphere during 15 days after their application and may be considerable sources of both CH₄ and N₂O in grassland (Kimura et al. 1992).

Figure 4 Methane uptake from non-fertilised and fertilised grassland and forestfloor



Mosier et al. (1991) reported that semi-arid grasslands represent a significant global sink for atmospheric CH_4 . Methane uptake by grasslands ranged from 6 to 61 μ g CH_4 , compared with uptake rates of 6-24 (Keller et al. 1983), 52 (Seiler et al. 1984), and 10-160 (Steudler et al. 1989; Schutz et al. 1990) μ g CH_4 in tropical forest, subtropical broad-leaf savannah, tundra and temperate forest soils, respectively. From these data, they suggested that 0.5-5.6 Tg of CH_4 are removed from the atmosphere by these grasslands each year. They found that

Figure 5 Nitrous oxide emission from non-fertilised and fertilised grassland, and forest land

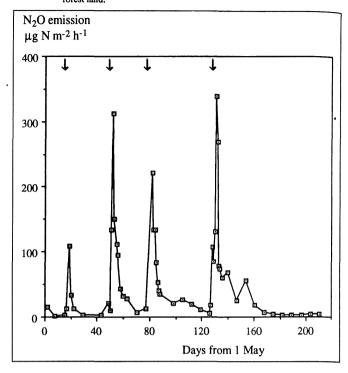
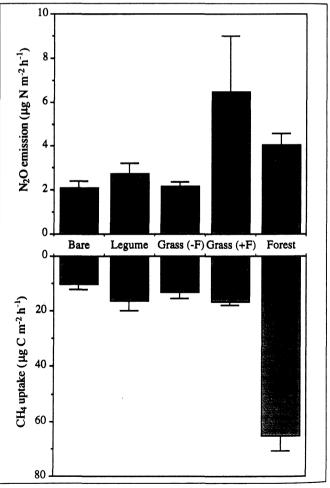
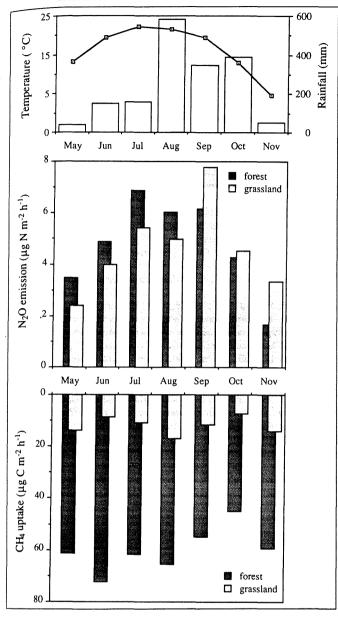


Figure 6 Nitrous oxide and methane fluxes from various types of vegetated land during 1 May - 12 June 1991



nitrogen fertilisation decreased CH_4 uptake by an average of 41%, and increased N_2O emission by a factor of 2-3. However, Kimura et al. (1992) found that nitrogen fertilisation had no influence on CH_4 uptake across various types of grassland vegetation.

Figure 7 Seasonal progression of N₂O emission and CH₄ absorption of grassland and forest soil



Laboratory and in situ measurement of soil methane consumption in the humid forests of central Panama indicated that the conversion of forests to agricultural lands would diminish the soil sink for atmospheric CH₄ (Keller et al. 1990). They found the rates of microbial CH₄ consumption in agricultural soils to be one fourth of those of undisturbed forest soils. This reduction in soil CH₄ consumption may partially account for the present increase in atmospheric methane concentration. Field measurements using flux chambers have confirmed the results of in vitro experiments, and indicate that fluxes into agricultural soils are about one fourth of those into forest soils.

Born et al. (1990) calculated the flux of methane into the soil from the concentration gradient at the soil surface. In this study, depending on the permeability of $\mathrm{CH_4}$ in the air-phase of soil at an individual site, yearly mean uptake rates between 0.09 and 1.3 g $\mathrm{CH_4/m^2}$ have been observed in temperate forest soils. The $\mathrm{CH_4}$ flux from the atmosphere into the soil shows only a weak seasonality, with about a 50% higher uptake rate in summer than during winter. They indicated that the $\mathrm{CH_4}$ flux into the soil is controlled mainly by the transport resistance of the soil, rather than by the potential microbial decomposition rate.

Crill (1991) reported that CH_4 is always taken up by woodland soils after the spring thaw in April. Maximum daily rates of consumption were 4.8 mg CH_4/m^2 in 1989, and 4.9 mg CH_4/m^2 in 1990. Annually, therefore about 600 mg CH_4 could be consumed, whilst approximately 2 kg of CO_2 would be emitted per m^2 .

Striegl et al. (1992) observed daily $\rm CH_4$ uptake by desert soils rates as large as 4.38 mg $\rm CH_4/m^2$. Indeed 50% of the measured rates were between 0.24 and 0.92 mg $\rm CH_4/m^2$. Uptake of $\rm CH_4$ by desert soil is enhanced by rainfall, which is opposite to the response of temperate forest soils (Steudler et al. 1989). Methane can be consumed down to a depth of about 2 m, which allows for deep removal of atmospheric $\rm CH_4$ even if near-surface conditions are unfavourable. On the basis of an annual average daily $\rm CH_4$ consumption rate of 0.66 mg $\rm CH_4/m^2$, they estimated that the global $\rm CH_4$ sink term needs to be increased by about 7 Tg/year to account for the contribution of desert soils.

From a one-year study of CH₄ fluxes in the Bonanza Creek long-term ecological research area, Whalen et al. (1991) showed that soil consumption of atmospheric CH₄ by floodplain and upland taiga sites was significant. Methane emission occurred only sporadically in the earliest successional stages of the floodplain system. All other floodplain and upland sites were net CH₄ consumers. Their results suggest that upland and floodplain taiga soils are an atmospheric CH₄ sink of about 0.8 Tg/year. Point-sources of bogs and fens are, of course, the only important CH₄-emitting sites in taiga. Whalen et al. (1991) pointed out that increased consumption of atmospheric CH₄ by these ecosystems could provide a significant negative feedback to increases in atmospheric CH₄. The same applies to tundra soils (Whalen & Reeburgh 1990).

In CH₄ flux measurements over dry savannah soils, Delmas et al. (1992) reported the average hourly uptake rate to be 19 μ g/m² using static chambers. Seiler et al. (1984) reported that CH₄ is consumed by tropical and subtropical soils with average hourly decomposition rates of 52 μ g/m². Their annual CH₄ consumption is estimated to be 21 Tg, which exceeds the CH₄ emission rate by termites.

The highest reported rate (45 g/m²day) of methane oxidation was observed in a topsoil covering an abandoned landfill (Whalen et al. 1990). This microbial community had the capacity to rapidly oxidise CH_4 at concentrations ranging from <1 ppm to >10⁴ ppm.

Potential role of management

Cattle are closely associated with grassland, and as a first approximation there will be a strong correlation between total grassland production and number of cattle. An increase in grassland productivity will probably be followed by an increase in cattle density, and so of CH₄ emission. However, emission by cattle is also one of the few sources of CH₄ that could be manipulated. Crutzen et al. (1986) estimated that domestic ruminants produce nearly 80% of the total CH₄ emission from animals: beef and draught animals 50%, dairy cows 19% and sheep 9%. Rumen micro-organisms ferment feed constituents to volatile fatty acids (VFA) with CH_A and CO₂ as by products and utilise the energy derived for their growth. The partitioning of the feed digestible energy over VFA and microbial cells and the release of $\mathrm{CH_4}$ and $\mathrm{CO_2}$ depends on a number of factors. Feeds that allow a high efficiency of microbial cell synthesis produce low amounts of CH₄ per unit of feed digested. In poor quality forage a number of essential microbial nutrients are usually deficient (particularly nitrogen), and consequently microbial growth efficiency in the rumen is low. In these conditions CH4 produced may represent 15-18% of the digestible energy. For high quality forage this reduces to about 7% (Leng 1991). With high quality forage also the metabolisable energy content is increased, and so CH₄ production per unit milk or meat may be reduced ultimately by a factor 4-6 (Leng 1991).

GRASSLAND AND NITROUS OXIDE

Bouwman (1990) listed published data for N_2O flux from grassland soils. A great difficulty in the assessment of N_2O emissions is the extrapolation of the measurements to other field conditions. This is due to the complex and time-dependent interactions between temperature, microbial populations, supply of organic C, oxygen diffusion, water content, nitrate concentration and root systems.

The increased use of nitrogen (N) fertilisers has contributed to the increased emissions of N_2O , directly from agricultural land, and indirectly after the transfer of N to other environments (Smith & Arah 1990). However, much release of N_2O from soils has nothing to do with fertilisers or manures, but comes from mineralisation processes, especially in tropical forests.

 N_2O is not released only in the anaerobic process of denitrification, but also in the aerobic process of nitrification. The production of N_2O

during nitrification is enhanced in well-aerated conditions, in the presence of high concentration of ammonium ions and at above neutral pH (Bremner & Blackmer 1978). These conditions prevail in the period after the deposition of urine in grasslands with a low water content in the topsoil. Nitrification in grazed grasslands may therefore be an important source of N_2O .

In non-grazed fertilised grassland the loss of plant-available N through N_2O emission is generally far below 2% of the N input (Ryden 1984). Only after conversion of grassland to arable land may additional N_2O be lost when mineralisation of stored fertiliser-derived N produces elevated concentrations of inorganic N. Several studies have shown that very high rates of N_2O emission are possible when peat soils are drained (Smith & Arah 1990). However, some sink activity for N_2O has also been observed in grassland soils under conditions of moderate to high soil water content, very low nitrate content (below 1 [Picture]g N/g dry soil) and temperatures above 5-8 [Picture]C (Ryden 1981). Unfortunately, estimates of the magnitude of this sink are yet not available.

In grazed grassland, accumulation of non-utilised NO2 from nitrified, excreted N returned to the sward by animals, can provide a substantial supply of substrate to be denitrified. In experiments on a number of soils, average annual denitrification losses in the topsoil of fertilised grazed swards have been measured of 5 and 12% of the fertiliser input (range 0-800 kg N/ha/year) on a well-drained and a poorly drained soil type, respectively (Jarvis et al. 1991). De Klein & van Dijk (unpublished results) measured a N loss of about 15% through denitrification in (artificial) urine patches which contained 400 kg N/ ha. There are only few measurements on the proportion of N2O in the denitrification process, but in grazed swards with a high fertiliser N input it may be as high as 25% (de Klein, pers. comm.). Generally, its proportion is increased when the nitrate content of soil is large, a feature characteristic of grazed swards, particularly the urine-affected areas (Pyden 1984). Therefore, the most immediately strategy to reduce N₂O emission from grazed swards is to restrict the use of fertiliser N and to supplement grazing cattle with good quality concentrates or forages with a relatively high energy and low protein content. Injection of slurry, instead of surface-spreading, minimises ammonia (NH₃) volatilisation, does not increase the risk of leaching and stimulates denitrification through increased anaerobic conditions (Jarvis et al. 1987). However, since apparent recovery of slurry N in herbage increases about two-fold by means of injection, particularly after spring application, this is an acceptable loss. There is also considerable scope for reducing the emissions of N₂O from fertilisers by modification of existing fertiliser use and soil management practices (Smith & Arah 1990).

CONCLUSIONS

Grasslands are almost as important as forests in the cycling of greenhouse gases. Soil organic matter under grasslands is of the same order of magnitude as tree biomass. Carbon storage capacity of grassland soil can be increased by avoidance of soil disruption (tillage), and by increasing net primary productivity. Most likely rising atmospheric CO₂ actually raises the capacity of grassland soils to store carbon, so that grasslands help to reduce the rate of increase of atmospheric CO₂.

With respect to methane, grassland soil has a smaller sink capacity than forest soil. The sink capacity of grasslands (up to about 8 Tg/year) is far too small to compensate for the $\mathrm{CH_4}$ emission of the cattle (about 75 Tg/year), or even of the regular fires (about 40 Tg/year). Improved fodder quality can help to reduce methane emission.

For N₂O, the situation is less clear. No correlation has been found with CH₄ fluxes. Nitrous oxide emission may be particularly patchy, concentrated on urine spots. Forest soils, although generally not fertilised, emit at least as much N₂O as grassland soils (Watson et al. 1990).

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