Biogenic, biomass and biofuel sources of trace gases in southern Africa

L.B. Otter[a*], L. Marufu[b] and M.C. Scholes[c]

Biogenic processes in southern African savannas are estimated to produce 1.0 Tg NO yr^{-1}, 44.2–87.8 Tg C yr^{-1} as non-methane hydrocarbons (NMHCs) and to consume 0.23 Tg CH_4 yr^{-1}. Floodplains and wetlands in southern Africa are estimated to generate between 0.2 and 10 Tg CH_4 yr^{-1} (excluding the effects of aquatic vegetation on emissions). Biogenic emissions from the subcontinent's savannas constituted twice the amount of NO, and significantly exceeded the amount of NMHCs produced from biomass burning (0.55 Tg yr^{-1} for NO and 0.49 Tg yr^{-1} as NMHCs) as well as that of industrial emissions (1.75 Tg NO yr^{-1} and 0.61 Tg yr^{-1} as NMHCs). Methane emissions from floodplains and wetlands could be more important than the combined effect of savanna burning (0.38 Tg yr^{-1}), biofuel burning (0.24 Tg yr^{-1}) and anthropogenic (2.59 Tg yr^{-1}) emissions in the region. Biofuel combustion produces similar amounts of CO and NMHCs, half the amount of CO_2 and CH_4, and a quarter of the NO_x that savanna burning does. Industrial emissions are shown to be important contributors to regional CO (5.6 Tg yr^{-1}) and CO_2 (360.0 Tg yr^{-1}) emissions. These results indicate that biogenic, pyrogenic and anthropogenic sources all need to be considered in regional and national emission budgets, and as bases for the recommendation of policy and mitigation strategies within the region.

Introduction

Anthropogenic and biogenic emissions are of interest to scientists as well as policy makers. Central and southern Africa have undergone and continue to undergo large social, economic and political changes that contribute to large-scale modifications of land use and land cover. Anthropogenic influences, along with a strong source of biogenic emissions and a large natural variability in both regional climate and ecosystem processes, combine to effect changes in the biogeochemical cycling of the region and lead to increased pollution. The mounting burden of air pollution and the deposition of pollutants has serious implications for human health, ecosystem functioning and corrosion of materials. The transboundary movement of aiborne pollutants means that regions that are not even heavily industrialized can be affected by them. The response to climate change in each country will vary according to differences in climate, geography and vegetation. It is therefore important that southern Africa itself assesses the effect of global climate change in this region.

Large-scale air pollution has traditionally been associated with anthropogenic activities in industrialized parts of the world, primarily in the northern hemisphere. However, recent satellite measurements of tropospheric ozone (O_3) have shown that, in addition to distinct plumes emanating from North America, Asia and Europe, large quantities of O_3 originate from tropical Africa.[1–3] This source is reported as being most prominent during September (late dry season). Since the industrial inputs to the atmosphere from this region were believed to be small, it was thought that the ozone was formed by gaseous precursors derived from biomass burning. Biomass burning, both natural and anthropogenic, has been identified as a significant source of radiatively and chemically active atmospheric gases and particulates.[4] These include CO_2, CH_4, CO, O_3, NO_x (NO + NO_2), non-methane hydrocarbons (NMHCs), and particulate matter. Biomass burning is common and widespread in Africa particularly during the dry, winter period (May–October). It is estimated that about 40% of global biomass combustion takes place in Africa, of which about 40% involves savanna burning.[5–7]

A field campaign, called the Southern African Fire–Atmosphere Research Initiative (SAFARI), was undertaken in 1992 to improve our understanding of trace gas emissions on the subcontinent, particularly from biomass burning. This project showed that although bush fires are a large source of aerosols and trace gases (which can contribute to the high ozone levels), they were not the only source

Another source of trace gases and aerosols is the burning of wood for energy. Although bush fires have been investigated, research on the use of domestic fuels is minimal. Each household fire may be small but collectively they provide a continuous supply of by products into the atmosphere throughout the year. Although fossil fuels, hydropower and nuclear power supply most of our direct energy needs, the majority of the developing world's population relies principally on fuelwood, animal dung and crop residues for domestic heating. These traditional fuels are used mainly for cooking and space heating. In view of its widespread occurrence, particularly in the developing world, there is growing concern about the impact that biofuel burning may have on the environment.

Besides emissions from burning, there are also biogenic sources of hydrocarbons, CO, CO_2, NO, N_2O and aerosols. Microbial activity in the soil is the main biological source of NO; soil emissions of NO are equal to or greater than those from lightning, and much larger than any other biological source. The global NO budget was estimated by Logan[8] to be between 25 and 99 Tg NO-N yr^{-1} with the microbial activity in soil contributing in the range of 4–20.2 Tg N yr^{-1}.[8–10] These figures as well as flux rates reported in more recent studies (0.1–13.3 ng NO-N m^{-2} s^{-1})[11,12] indicate that the biogenic component is comparable to the global NO_x emissions from fossil-fuel combustion.[13,14] Non-methane hydrocarbons are emitted from vegetation, which is estimated to be the source of 90% of the global NMHC budget, with tropical savannas producing an estimated 46.4 Tg C yr^{-1} as isoprene, 15.6 Tg C yr^{-1} as monoterpenes and 12% as other reactive volatile organic compounds.[15] The total global emission rate of biogenic volatile organic carbons is 1150 Tg C yr^{-1}, which is more than 10 times that of the estimated annual global anthropogenic emission rate of 100 Tg C yr^{-1}.[16,17] Biogenic emissions of CH_4 contribute approximately 37% (25% from natural wetlands, 12% from rice paddies) to the global CH_4 budget.[18] Other sources are termites,[19–21] oceans, landfills,[22] sewage, manure[23] and rumi-

[a]CSIR, Division of Water, Environment and Forestry Technology, P.O. Box 395, Pretoria, 0001 South Africa.
[b]Climatology Research Group, University of the Witwatersrand, Private Bag 3, WITS, 2050 South Africa.
[c]Department of Animal, Plant and Environmental Sciences, University of the Witwatersrand.
*Author for correspondence. E-mail: lotter@csir.co.za

nants.[24,25] Furthermore, savannas and grasslands are considered to be CH_4 sinks, but the few measured fluxes in such regions differ by more than an order of magnitude because CH_4 is emitted as well as consumed.[21,26–28] The flux of CH_4 (emission and consumption) in tropical savannas and grasslands needs to be more accurately estimated because, owing to the large area covered, these ecosystems could significantly affect the global CH_4 budget.

SAFARI-92 significantly improved our understanding of emissions from biomass burning in southern Africa. However, it indicated that our knowledge of trace gas emissions from sources other than biomass burning needed to be improved. This article summarizes the results of recent studies on the emissions of trace gases from biogenic activities and biofuel burning (burning of wood for domestic purposes) in southern Africa. We update quantitative estimates of biomass burning emissions on the subcontinent for the base year 1989, which was chosen as the base year because of its average weather conditions including rainfall and hence biofuel abundance. Furthermore, this paper compares biofuel and biogenic emissions to those of biomass burning and discusses the implications these emissions may have for regional atmospheric chemistry and climate.

Methods

A variety of laboratory and field techniques, as well as modelling exercises, were used to determine the biogenic emissions of NO, NMHCs and CH_4 from savannas and the biofuel burning emissions in the southern African region over the last few years. These methods have been described elsewhere[29–34] and only a synthesis of the results are presented here. Additional data on biogenic emissions of CO and CO_2 emissions have been obtained from the literature and are referenced accordingly.

Results and discussion

Emissions from biomass burning

Estimates of biomass burned

To estimate biomass burning emissions we have to know the types of biomass combusted, burning activity levels or quantities of material affected, emission factors for the trace species of interest and, in the case of biofuels, efficiencies of the technologies used to burn the fuel.

The vegetation types of southern Africa, their biomass densities, burning frequencies and corresponding emission factors have been relatively well studied.[35–37] The types of biofuel used in the region are also well known (they are wood, charcoal, agricultural residues and dung).[32,33,38–40] In many parts of southern Africa, up to 90% of households burn wood on open fires.[32,33,40] Open-fire emission factors for most trace species (CO_2, CO, NO, CH_4, NMHCs, organic acids and aerosols) have been estimated.[34,41] Recent studies have revealed that for the four most commonly used biofuels (wood, charcoal, agricultural residues and dung), emission factors of the various trace species do not vary significantly in time, geographically or with plant species.[34] The most uncertain parameter in estimating the contribution of biomass burning to atmospheric emissions, relative to other sources, in southern Africa is the quantity of wood burnt. This is mainly because, to date, most of the studies conducted have been localized, and as such have not taken spatial and temporal variations into account. However, modelling attempts are being used to rectify this uncertainty.

Biofuels: in this paper parameters derived by Marufu *et al.*[33] for Zimbabwe are used to calculate annualized biofuel consumption estimates for each of the southern African states. It is assumed that the dependencies observed in Zimbabwe apply to neighbouring countries. This is a useful approach to give an initial estimate for the region. In the case of charcoal and dung, for which consumption rates have not been measured locally, we have relied on average rates derived from country studies to estimate activity levels in user countries.

Estimates of annual consumption by country (Table 1) were calculated by combining the national consumption rates of various fuel types with population data from the United Nations World Urbanization Prospects.[42] Fractional fuel type contributions of about 90% wood, 5% agricultural residues, 3% dung and 2% charcoal were assumed.

Bush fires: in this paper, the term bush fire refers to all biomass burning other than that conducted for purposes of energy generation. It includes both naturally occurring and anthropogenically initiated fires. Most bush fires start as a result of anthropogenic activities, with the only natural cause being lightning. Data on the amounts of biomass consumed annually by these fires in southern Africa are scarce and the few that are available are highly variable. The lack of data is, to a large extent, attributable to problems associated with bush fire documentation. These include fragmented burning patterns due to topographic and fuel discontinuities, and heterogeneity in fuel loads, fuel composition and fuel moisture content. Variations in past and present land-use practices also have important influences on fuel composition and characteristics.[19] Furthermore, relative humidity, fuel moisture content and the ratio of surface area to volume of the predominant fuel have substantial influence on the fraction of the available biomass that is consumed during a burn.

To date, the only detailed studies conducted in the region, which have taken some of the above factors into account, are those by Hao *et al.*[36] and Scholes *et al.*[35] Using a computational method, Hao *et al.*[36] estimated the amount of biomass burned annually in Africa south of the equator to be 1200 Tg dry matter (DM). Their approach involved the classification of the region into vegetation types and estimation of the mean fuel load and area burned per type. This approach is considered to be inaccurate as it does not take into account heterogeneity with respect to fuel load, fuel composition and fire frequency.[35] Scholes *et al.*[35] applied a more comprehensive, modelling, approach in which the fuel load, fire probability and completeness of burn are

Table 1. Annual biofuel consumption estimates per country in Africa south of the equator. The dashes indicate areas where no data are available.

Country	Biofuel consumption (Tg/yr)			
	Wood	Maize residues	Charcoal	Dung
Angola	3.46	0.52	0.18	0.30
Botswana	0.43	0.06	–	0.07
Lesotho	0.62	0.12	–	0.52
Madagascar	6.04	0.69	0.28	0.40
Malawi	6.35	0.11	0.32	0.30
Mauritius	0.002	0.06	0.001	0.03
Mozambique	10.82	1.88	0.10	0.44
Namibia	1.34	0.07	–	0.04
Reunion	0.02	0.03	–	–
South Africa	18.40	1.99	–	1.19
St. Helena	0.002	0.00	0.00	–
Swaziland	0.41	0.02	–	0.01
Tanzania	27.91	0.90	0.56	0.62
Zaire	28.84	–	–	–
Zambia	7.78	0.45	1.11	–
Zimbabwe	9.76	0.45	–	0.31
Total	122.19	7.33	2.55	4.24

calculated separately. The amount of biomass consumed by bush fires in Africa south of the equator was calculated to be 177 Tg DM yr^{-1}, which is substantially less than that reported by Hao *et al.*[36] The lower estimate was attributed to the fact that, by using calibrated satellite data, the estimated area burned was much reduced. Furthermore, their method accounted for aridity, herbivory and biomass decay, which had the effect of reducing the estimated fuel load. The estimate does not include burning associated with land clearing for agriculture and disposal of agricultural waste.[35]

Emission estimates

Estimating emissions from biomass burning requires, in part, knowledge of emission factors for the different trace species involved. The emission factor is defined as the mass of the species released per unit mass of fuel combusted. The few studies that have focused on the estimation of biomass burning emission factors in Africa have all emphasized the importance of the combustion phase (flaming/smoldering) on the relative release of individual trace species. The release of compounds such as CO_2 and NO has been widely reported as being highest during the high temperature, flaming phase of combustion, while that of products of incomplete combustion (CO, CH_4, NMHCs, and particulate matter) is highest in the low-temperature, smoldering phase.[34,43]

Biofuel burning: in spatially and temporally extensive studies in Zimbabwe and Nigeria, Ludwig *et al.*[34] compared integrated $\Delta CO/\Delta CO_2$ (where Δ means the change in CO or CO_2) and $\Delta NO/\Delta CO_2$ emission ratios observed during domestic combustion of different biofuel types at several locations. Despite the observed spatial variations in firing methods, they concluded that emission ratios, and hence emission factors of the trace species emitted from domestic biofuel combustion in Africa, did not vary significantly in time or space.

In this paper, for wood, maize residues and cattle dung, the CO_2, CO, and NO emission factor estimates of Ludwig *et al.*[34] (based on a Zimbabwe study) were used. Emission factors for CH_4, NMHCs, aerosols and for the making and burning of charcoal were taken from similar measurements conducted in West Africa[44] (Table 2). Biomass burning estimates for each country were calculated using these emission factors[32] (Table 3). For the base year, 1989, biofuel burning contributed 59.07 Tg CO_2-C, 6.08 Tg CO-C, 0.118 Tg NO-N, 0.236 Tg CH_4-C, 0.472 Tg NMHC-C, 0.945 Tg organic acid (OA)-C, and 1.89 Tg aerosol-C, to southern African emissions. No emission factor estimates were available for OA emissions from crop residue and cattle-dung fuel. The OA emission estimates presented do not therefore include the contributions of these fuels.

Bushfires: bushfire emission estimates by country according to Scholes *et al.*[45] are shown in Table 4. Emissions of 87.49 Tg CO_2-C, 6.41 Tg CO-C, 0.38 Tg CH_4-C, 0.49 Tg NO_x-N, 0.28 Tg N_2O-N and 1.083 Tg aerosol-C for the base year 1989 were estimated.

Biogenic emissions

The SAFARI-92 programme highlighted the importance of biogenic emissions, and results reported in this section were obtained since 1992. It should be noted that the biogenic fluxes are not related to the 1989 baseline emissions of the biomass burning section.

Vegetation and litter emissions

NMHCs are important because of their influence on regional photochemical oxidant formation and acid deposition. The oxidation of hydrocarbons can lead to the production of compounds such as CO, CO_2, hydrogen (H_2), PAN, oxygenated secondary compounds and secondary organic aerosols.[46–51] Hydrocarbons also affect the regional distribution of ozone as, in the presence of high levels of NO_x, the oxidation of hydrocarbons leads to the production of ozone.[52–56]

Isoprene and monoterpenes are the main hydrocarbons emitted by vegetation. Isoprene emissions are influenced by light intensity, leaf temperature and nutrient availability,[57–61] while monoterpene emissions are affected by leaf temperature, vapour pressure and relative humidity.[62–66] The high temperatures and radiation fluxes associated with tropical and subtropical regions make them a potentially large source of biogenic NMHC emissions, as predicted by global models.[15,67]

In South African savanna landscapes, average emission capacities vary from 0.6 to 0.9 mg C m^{-2} h^{-1} for isoprene and from 0.05 to 3 mg C m^{-2} h^{-1} for monoterpenes.[29] Isoprene and monoterpene emissions show a high seasonal variation, with emissions of less than 5 mg C m^{-2} d^{-1} during the winter months (June–September), increasing to the highest levels (115.8 and 29.9 mg C m^{-2} d^{-1} for isoprene and monoterpenes, respectively) during mid-summer. This seasonal pattern is strongly dependent on foliar density, but is also enhanced by the seasonal variation in light intensity and temperature. Southern African savannas are estimated to emit between 44.2 and 87.8 Tg C y^{-1} as isoprene and monoterpenes.

Carbon monoxide is an important trace gas species as it affects the concentration of OH radicals in the atmosphere, and it can also lead to the production or consumption of tropospheric ozone. In remote, unpolluted areas natural CO emissions are estimated to account for more than 50% of total emissions. CO is emitted from green plants as well as dead vegetation and litter,[68–71] with wet litter producing more CO than dry.[68] CO can be produced photochemically and thermally from plant matter, the former being the dominant source during the day. Schade *et al.*[68] measured emissions from litter in South African savannas and found emission rates of 0.4 to 1.4 μg CO per gram of dry weight per day (μg CO dw^{-1} d^{-1}) for grass litter and 1.0 to 3.21 μg CO dw^{-1} d^{-1} for tree leaf litter. These emission rates are similar to those measured in West Africa and South America. Emissions of CO from dead plant material are positively related to light intensity and temperature. Globally, photochemical CO production from standing dead plant material and litter in grasslands and deciduous forests is estimated to be 20–65 Tg CO yr^{-1}.[68] Schade *et al.*[68] further estimated that by including other potential CO sources, 60 Tg CO yr^{-1} is emitted by photochemical degradation of decaying plants, and a further 40 Tg CO yr^{-1} from the global topsoil non-woody litter pool. This brings the total global source of CO to within the range of 50–170 Tg CO yr^{-1}.

Soil fluxes

The majority of trace gas exchanges between soils and the atmosphere are due to microbial activity. Emissions from soils are controlled by two microbial processes, namely production and consumption (or oxidation). Although production and consumption may occur simultaneously in the soil, the relative magnitudes of these processes differ under varying environmental conditions.[18,72–74] It is important that we understand the effects of the environment on fluxes, to make extrapolation to landscape, regional and global scales more accurate.

Nitric oxide emissions from soils are low during the dry, winter season and increase over the wet, summer months.[30,71,75–77] This is because soil temperature and moisture are the major controlling factors, alongside nitrogen fertilization, of NO production and emission.[72,73,78–82] Otter *et al.*[30] investigated the effects of soil temperature and moisture on NO emissions from South African

142

Table 2. Average emission factors calculated for combustion of different biofuels in Africa. For wood, maize residues and cattle dung, CO_2, CO, and NO emission factors are based on on-line emission measurements conducted in Zimbabwe,[94] while those of CH_4, NMHC, and aerosols are from similar measurements conducted in West Africa.[44] All emission factors for charcoal-making and combustion are from Brocard and Lacaux.[44] Emission factors are given as g C or N per kg of dry fuel.

Fuel type	Moisture correction factor[a]	Emission factors						
		CO_2	CO	NO	CH_4	NMHC	OA[b]	Aerosols[c]
Wood	0.85	450	43	0.52	1.5	2.5	0.36	5.5
Charcoal making	0.85	120	30	0.02	8	2	0.2	4
Charcoal burning	1	170	25	0.29	0.5	0.1	0	2
Maize residues	0.95	469	27	1.7	4.49	7.5	–	5
Cattle dung	0.95	439	36	4.41	4.49	7.48	–	5

[a]The moisture correction factor is the ratio of fuel dry weight to fuel moist weight. Moist refers to the state in which the fuel is normally used, i.e. air dry.
[b]Organic acids (acetic + formic acids).
[c]Units: g C per kg of dry fuel.

savannas under controlled conditions in the laboratory. They showed that NO production was at its maximum when soil moisture is near field capacity and that emissions increase exponentially with temperature. NO emissions show a sharp pulse after the first rains of the season. Although this pulse is short lived and does not contribute significantly to the annual NO budget,[30,77] the period of high concentration coincides with that of high ozone levels off the coast of west Africa. The NO pulse after the first rain is therefore suggested to contribute significantly to the production of ozone during this period.

Soil microorganisms also significantly influence the atmospheric carbon budget. Soil respiration has been estimated to produce 68 ± 4 Pg C yr^{-1} globally,[83] with tropical and subtropical savannas and grasslands in Africa producing an estimated 0.4–0.8 g C m^{-2} d^{-1}.[71,84,85] Carbon dioxide is taken up during the process of photosynthesis, therefore there is a net release of CO_2 only when respiration exceeds photosynthesis. Soil moisture is a more important controlling factor of soil CO_2 fluxes than temperature.[71,85] Thus, as with NO, CO_2 fluxes are low during dry, winter months and increase by a factor of 20 during the wet summer period. Soil CO_2 fluxes are not significantly influenced by burning but, after a fire, CO_2 is released through soil respiration and decomposition of non-living organic matter.

Soils are considered to be a sink of CO. However, the flux data from savannas are conflicting, with some sites showing net emission.[71,86,87] Fluxes range between 0.12 and 12 mg CO m^{-2} d^{-1}. The flux of CO between the soil and the atmosphere is mostly dependent on soil temperature, but is also influenced by soil moisture, soil management and burning.[27,88,89] Burning increases these fluxes for a few days, and if there is rain on the burnt site then fluxes increase even more.[71]

Savannas are also considered to be an important sink for CH_4. Potter *et al.*[90] indicated that 40% of the global CH_4 consumption occurs in relatively dry, warm ecosystems. Upland soils are estimated to consume 17–23 Tg CH_4 yr^{-1} globally,[90] but the variability in CH_4 fluxes from savannas has been shown to be high, with some studies indicating consumption[26,71,91] and others production.[26–28,92] Most of these studies were short-term. A two-year study by Otter and Scholes,[31] however, showed that CH_4 consumption occurs during winter, and emission in summer. Not much is known about CH_4 emissions from aerobic soils, but it has been suggested to be due to upward diffusion from natural gas reservoirs,[26] and termites in the soil.[26,91] The latter was initially thought to be the case in South Africa. Otter and Scholes,[31] however, suggest otherwise. In their study emissions were measured from two areas, one of which had a large termite population (68% being soil feeders; 32% litter feeders) and one a relatively small population.[85] Both sites demonstrated emissions in summer. Scholes and Andreae[14] reported also that there is no net CH_4 emission from soil surfaces of savannas. Further investigations of CH_4 production in aerobic soils are required to understand the processes involved.

Soil moisture is an extremely important regulator of CH_4 fluxes in the savanna. Emissions occur when soils have a high moisture content and a low effective diffusivity.[93,94] In very dry soils (<3% water-filled-pore-space (WFPS) in this study), CH_4 emission and consumption are almost zero. An increase in moisture of between 5 and 20% WFPS leads to a decline in CH_4 consump-

Table 3. Biofuel burning emission estimates by country in Africa south of the equator. Organic acid emission estimates do not include the contribution of cattle dung and crop residues.

Country	Emission estimates						
	CO_2 (Tg C yr^{-1})	CO (Tg C yr^{-1})	NO (Gg N yr^{-1})	CH_4 (Gg C yr^{-1})	NMHC (Gg C yr^{-1})	OA (Gg C yr^{-1})	Aerosols (GgC yr^{-1})
Angola	1.77	0.17	3.68	12.22	14.23	1.16	22.51
Botswana	0.22	0.02	0.58	1.11	1.85	0.13	2.65
Lesotho	0.51	0.04	2.65	3.52	5.86	0.19	5.94
Madagascar	2.94	0.28	5.58	19.23	22.35	2.02	37.36
Malawi	2.78	0.28	4.37	17.84	18.42	2.14	36.19
Mauritius	0.04	0.00	0.22	0.41	0.63	0.00	0.44
Mozambique	5.21	0.47	9.70	26.13	40.10	3.37	62.97
Namibia	0.56	0.05	0.89	2.20	3.66	0.41	6.82
Réunion	0.02	0.00	0.06	0.17	0.28	0.01	0.26
South Africa	8.42	0.76	16.33	37.01	61.72	5.63	101.12
Seychelles	0.01	0.00	0.02	0.07	0.08	0.00	0.09
Swaziland	0.17	0.02	0.25	0.64	1.06	0.13	2.05
Tanzania	11.63	1.13	16.57	55.89	73.54	8.88	145.58
Zaire	16.97	2.04	22.34	241.67	138.35	13.39	261.75
Zambia	3.77	0.42	4.55	39.16	26.52	3.05	54.11
Zimbabwe	4.06	0.38	6.34	15.68	26.14	2.98	49.22
Total	59.08	6.08	65.16	236.30	472.59	945.18	1890.37

Table 4. Pyrogenic emissions of trace gases per country in Africa south of the equator. Derived from Scholes *et al.*[45] and converted from per compound to per C/N basis.

Country	CO_2 (Tg C yr^{-1})	CO (Tg C yr^{-1})	CH4 (Tg C yr^{-1})	NO_x (Tg N yr^{-1})	N_2O (Gg N yr^{-1})
Angola	17.15	0.958	0.051	0.075	43.52
Botswana	3.56	0.187	0.010	0.014	4.99
Burundi	0.92	0.075	0.005	0.006	4.93
Lesotho	0.11	0.005	0.000	0.001	0.26
Malawi	1.92	0.107	0.005	0.008	7.49
Mozambique	6.91	0.445	0.025	0.034	25.79
Namibia	1.19	0.059	0.003	0.005	0.19
Rwanda	0.27	0.039	0.003	0.003	0.77
South Africa	3.08	0.193	0.011	0.015	3.71
Swaziland	0.03	0.000	0.000	0.000	0.00
Tanzania	11.07	0.698	0.038	0.054	31.68
Zambia	14.47	1.076	0.063	0.082	47.17
Zimbabwe	1.94	0.114	0.006	0.009	4.29
Others (partly included)	24.87	2.457	0.155	0.187	109.82
Total	87.49	6.413	0.375	0.493	284.61

tion.[31,95–98] In the South African savanna, CH_4 emissions occurred as the soil moisture increased above 20% WFPS.

The period (during a year) in which consumption occurs is longer than that for emissions, therefore the savannas on an annual basis are a weak CH_4 sink, consuming 0.04 g CH_4 m^{-2} yr^{-1}. Savannas in Africa south of the equator are estimated to consume 0.23 Tg CH_4 yr^{-1}, which is much less than was previously estimated.[26]

Fluxes from floodplains and water surfaces

The highly seasonal rainfall in savannas and surrounding areas can lead to spatial and temporal changes in soil moisture and inundation. These changes all have important implications for CH_4 fluxes in a region. There are a number of small wetlands and floodplains in South Africa, but the more northern countries of southern Africa have a much larger percentage of their land surface covered by floodplains, marshes, pans and dambos (seasonally inundated shallow depressions). Natural wetlands contribute up to 25% to the global CH_4 budget.[18]

Water-table depth is one of the main factors influencing CH_4 emissions in wetlands. As water levels rise to the soil surface, CH_4 consumption declines and when the water level rises above the soil surface emissions occur.[100–102] Methane emissions are highest from regions where the water table is between 0.1 m below the soil surface to 0.4 m above.[31,101–103] Regions of open water with a depth greater than 0.4 m have positive but very low flux rates. This is probably due to the consumption of CH_4 in the aerobic layers, the greater diffusive resistance and less mixing of the strata in the deep waters. CH_4 fluxes from the dry floodplain are minimal and do not differ significantly from the upland savanna fluxes.

CH_4 fluxes from a floodplain in South Africa after flooding were high with a mean of 465.6 mg CH_4 m^{-2} d^{-1}.[31] These high flux rates could be due to the mineralization of the large organic matter layer which had accumulated over an extended dry period. The seasonal mean fluxes vary between 0.48 and 465.6 mg CH_4 m^{-2} d^{-1}, which are higher than those reported for flooded regions in other countries,[97,104–108] but were in the range found for an Australian floodplain.[109] Comparison is, however, difficult owing to differences in the water depth and temperature. The fluxes from flooded regions showed a strong seasonal pattern with high emission rates being observed during the following summer. This is because of the exponential relationship between CH_4 emission from the flooded areas and the sediment temperature. Boon *et al.*[109] also found a strong seasonal variation in the fluxes from a floodplain in Australia, with higher emissions in summer. It is, however, difficult to establish dependencies as high temperatures and precipitation occurred at the same time of the year. These results indicate that the presence of water and temperature is more important for CH_4 emissions than the actual flood event.

Estimating the amount of CH_4 from floodplains in southern Africa is difficult, not only because of the large number of variables involved, but also because the extent of floodplains in the subcontinent is not well known. It is estimated (using information from Cowan and van Riet[110] and Hughes and Hughes[111]) that southern African floodplains can produce between 0.3 and 10 Tg CH_4 yr^{-1}. Other wetland types, such as pans, swamps and marshes, could produce an additional 4 to 5 Tg CH_4 yr^{-1}. It should be noted that these values are underestimates as they do not include CH_4 transported through the vegetation.

Comparison of biogenic, biomass, biofuel and anthropogenic emissions and their effect on regional atmospheric chemistry

The biogenic emission estimates for NO and NMHCs in southern African savannas given in this paper are within the range of previous calculations.[29,77] The recent CH_4 flux results of Otter and Scholes[31] indicate that savannas are a smaller sink than previously suggested by Seiler *et al.*[21] This is mainly because of the production of CH_4 in the savanna during the wet season. Otter and Scholes[31] have produced the only CH_4 emission estimates for floodplains and wetlands in southern Africa. This study shows that wetland systems can contribute significantly to CH_4 budgets in the region. The small uptake of CH_4 by savannas and the additional sources of methane from floodplains and wetlands, as well as termites and ruminants, indicates that the sources of CH_4 are much greater than the sinks. This has implications not only for regional carbon budgets but also global budgets.

Southern Africa experiences highly seasonal rainfall and has the potential to produce a large pulse of NO during September/October. It was suggested that NO emissions may combine with high NMHC emissions from vegetation to produce the peak in the tropospheric ozone seen off the coast of Africa during spring.[1,3] Non-methane hydrocarbon emissions from southern Africa are, however, not very high in spring, due to the low leaf mass density at this time of the year. It is suggested that the spring-time ozone high results from a combination of biomass burning (at the end of the dry season) and biogenic emissions

Table 5. Comparison of trace gas emissions (Tg yr^{-1}) from biogenic, pyrogenic, biofuel burning and industrial sources in southern Africa. The dashes indicate that there are no known emissions at present, whereas the question marks indicate areas where there are possible emissions but insufficient data for scaling up to the regional level.

Trace gas	Biogenic	Savanna burning[a]	Biofuel burning[b]	Industrial
CH_4 soils	–0.23	–	NA	NA
CH_4 wetlands	0.2–10	NA	NA	NA
CH_4 vegetation	–[c]	0.38	0.24	NA
CH_4 animals	0.32	NA	NA	NA
CH_4 industry	NA[d]	NA	NA	2.59
NMHC	44.2–87.8	0.55	0.47	0.61
NO_x	1.0	0.49	0.12	1.75
N_2O	?	0.28	–	?
CO industry	NA	NA	NA	5.6
CO soil	?	–	NA	NA
CO vegetation	0.5–?	6.04	6.1	NA
CO_2	?	87.5	59.1	360.0

[a]From Table 4.
[b]From Table 3.
[c]CH_4 is not actually emitted by vegetation but is transported from river sediments to the atmosphere via wetland vegetation. There is very little information on this for southern African wetland vegetation and often this value is incorporated into wetland emissions.
[d]NA, not applicable.

(beginning of the rainy season). Biomass burning can produce large amounts of hydrocarbons and these could combine with the pulse of NO from soils after the first rain to produce ozone.

Comparison of biogenic fluxes with those from biomass burning indicates the extreme importance of biogenic fluxes within the southern African region. Biogenic NO emissions from southern African savannas are equal to the amount of NO generated by biomass burning but are slightly less than that from industry (Table 5). Hydrocarbon emissions from industry and fires are significantly less than those from vegetation. The CH_4 generated by animals is greater than the soil sink, leading to a slight net CH_4 production in a year. The net CH_4 is still less than that produced by pyrogenic or industrial emissions. If, however, wetlands fluxes are included in the CH_4 budget, then the biogenic emissions far exceed those from biomass burning and industry, making biogenic fluxes the most important factor contributing to the southern African CH_4 budget. Uncertainty about wetland areas, flooding period and vegetation emissions of CH_4 in the subcontinent all contribute towards a large variation in emission estimates for wetlands. Considering the effect that wetland emissions may have on regional CH_4 budgets, it is critical that these emission estimates are improved in the future.

It is also apparent from this summary that the data for biomass and biofuel emissions are more extensive than those of the biogenic component estimated for each country. Future research should therefore focus on trying to model and estimate the biogenic emissions for the various countries in southern Africa, so that better comparisons can be made.

Future climatic changes will also have important consequence for biogenic emissions from savannas. Global warming will generally lead to an increase in emissions. On the other hand, high temperatures may lead to an increase in evapotranspiration, which may result in a reduction in soil moisture and thus in NO emissions. Conversely, elevated CO_2 could cause a reduction in evapotranspiration and increasd water use efficiency in plants, so that water may not be the limiting factor for vegetation emissions. Rainfall and moisture could affect the annual NMHC emissions through an alteration in the length of the warm, wet season. Most of the savanna vegetation has leaves only during the wet season; a shorter wet season would therefore mean a lower leaf biomass each year. This translates into a reduction in annual NMHC emissions, as hydrocarbons are produced and emitted via the leaves. An alteration in vegetation distribution and composition may occur due to such climatic changes and this will affect NMHC emission patterns. Vegetation distribution and soil characteristics are not only altered by climate but also by a change in land use.

Savannas support most of the human population of Africa and population growth in these areas is rapid. As a result, extensive changes in land use are happening. It is desirable that we know what the biogenic emissions are in a natural landscape before novel land use practices, such as slash and burn agriculture, are introduced. In this way the effect of new uses of land on emissions can be anticipated. Understanding the relationship between biogenic emissions and their environmental controlling factors, as well as the effects that fires have and what trace gases they produce, can aid scientists in predicting the possible effects of climate and land-use change on future emissions.

In conclusion, the results discussed in this review add to our understanding of pyrogenic emissions and significantly improve the biogenic emission estimates for the region. Summary results such as in Table 5 are important for: comparing emissions from the various sources within the region; giving focus to future research and contributing to country studies. More importantly, the information contained in these tables can be used to inform policy makers of the present situation and which industrial emissions far exceed natural levels. This could lead to the development of policy and mitigation strategies within the region for specific trace gases. These summary tables are very seldom, if ever, reported and future research should aim at developing and producing such syntheses at the regional scale. This would, in turn, contribute to the improvement of global budget estimates.

We thank the National Research Foundation and the University of the Witwatersrand Bursaries Office for providing financial support for L.O.'s biogenic flux research. Furthermore, M.C.S.'s position at the University of the Witwatersrand is endowed by SAPPI. Thanks also go to J.G.J. Olivier of R.I.V.M., Bilthoven, The Netherlands, for allowing L.M. the use of extracts from EDGAR version 2.0 Emission Inventories for comparison purposes. The reviewers are thanked for providing comments on this manuscript.

1. Fishman J. and Larsen C.J. (1987). The distribution of total ozone and stratospheric ozone in the tropics. Implications for the distribution of tropospheric ozone. *J. Geophys. Res.* **92**, 6627–6634.
2. Fishman J., Mannis P. and Reichle H.G. (1986). The use of satellite data to study tropospheric ozone in the tropics. *J. Geophys. Res.* **91**, 14451–14465.
3. Fishman J., Watson C.E., Larsen J.C. and Logan J.A. (1990). The distribution of tropospheric ozone determined from satellite data. *J. Geophys. Res.* **95**, 3599–3617.
4. Crutzen P.J., Heidt L.E. and Seiler W. (1979). Biomass burning as a source of

atmospheric trace gases CO, H_2, N_2O, NO, CH_3Cl and COS. *Nature* **282**, 253–256.

5. Andreae M.O. (1991). Biomass burning: its history, use and distribution and its impact on environmental quality and global climate. In *Global Biomass Burning*, ed. J.S. Levine, pp. 3–28. MIT Press, Cambridge, MA.
6. Helas G. (1995). Emissions of atmospheric trace gases from vegetation burning. *Phil. Trans. R. Soc. Lond.* **351**, 297–312.
7. Helas G., Lacaux J.P., Delmas R., Scharffe D., Lobert J., Goldhammer J. and Andreae M.O. (1992). Ozone as biomass burning product over Africa. *Fresenius Environ. Bull.* **1**, 155–160.
8. Logan J.A. (1983). Nitrogen oxides in the troposphere: global and regional budgets. *J. Geophys. Res.* **88**, 10785–10807.
9. Davidson E.A. (1991). Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems. In *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes*, eds J.E. Rogers and W.B. Whitman, pp. 219–235. American Society for Microbiology, Washington, D.C.
10. Potter C.S., Matson P.A., Vitousek P.M. and Davidson E.A. (1996). Process modeling of controls on nitrogen trace gas emissions from soils worldwide. *J. Geophys. Res.* **101**, 1361–1377.
11. Serça D., Delmas R., Jambert C. and Labroue L. (1994). Emissions of nitrogen oxides from equatorial rainforests in central Africa: origin and regulation of NO emissions from soils. *Tellus* **46B**, 143–254.
12. Serça D., Delmas R., Le Roux X., Parsons D.A.B., Scholes M.C., Abbadie L., Lensi R., Ronce O. and Labroue L. (1998). Comparison of nitrogen monoxide emissions from several African tropical ecosystems and influence of season and fire. *Global Biogeochem. Cycles* **12**, 637–651.
13. Levine J.S., Parsons D.A.B., Zepp R.G., Burke R.A., Cahoon D.R., Cofer W.R., Miller W.L., Scholes M.C., Scholes R.J., Sebacher D.I., Sebacher S. and Winstead E.L. (1997). Southern African savannas as a source of atmospheric gases. In *Fire in Southern African Savannas: Ecological and Atmospheric Perspectives*, eds B.W. Van Wilgen, M.O. Andreae, J.G Goldhammer and J.A. Lindesay, pp. 135–160. Witwatersrand University Press, Johannesburg.
14. Scholes M.C. and Andreae M.O. (2000). Biogenic and pyrogenic emissions from Africa and their impact on the global atmosphere. *Ambio* **29**, 23–29.
15. Guenther A., Hewitt C., Erickson D., Fall R., Geron C., Graedel T., Harley P., Klinger L., Lerdau M., McKay W., Pierce T., Scholes R., Steinbrecher R., Tallamraju R., Taylor J. and Zimmerman P. (1995). A global model of natural volatile organic compound emissions. *J. Geophys. Res.* **100**, 8873–8892.
16. Hough A. and Johnson C. (1991). Modelling the role of nitrogen oxides, hydrocarbons and carbon monoxide in the global formation of tropospheric oxidants. *Atmos. Environ.* **25A**, 1819–1835.
17. Muller J-F. (1992). Geographical distribution and seasonal variation of surface emissions and deposition velocities of atmospheric trace gases. *J. Geophys. Res.* **97**, 3787–3804.
18. Conrad R. (1997). Production and consumption of methane in the terrestrial biosphere. In: *Biogenic Volatile Organic Compounds in the Atmosphere*, eds G. Helas, J. Slanina and R. Steinbrecher, pp. 27–44. SPB Academic Publishing, Amsterdam.
19. MacDonald J.A., Eggleton P., Bignell D.E., Forzi F. and Fowler D. (1998). Methane emission by termites and oxidation by soils, across a forest disturbance gradient in the Mbalmayo Forest Reserve, Cameroon. *Global Change Biol.* **4**, 409–418.
20. MacDonald J.A., Jeeva D., Eggleton P., Davies R., Bignell D.E., Fowler D., Lawtons J. and Maryati M. (1999). The effect of termite biomass and anthropogenic disturbance on the CH_4 budgets of tropical forests in Cameroon and Borneo. *Global Change Biol.* **5**, 869–879.
21. Seiler W., Conrad R. and Scharffe D. (1984). Field studies of methane emission from termite nests into the atmosphere and measurements of methane uptake by tropical soils. *J. Atmos. Chem.* **1**, 171–186.
22. Bingemer H.G. and Crutzen P.J. (1987). The production of methane from solid wastes. *J. Geophys. Res.* **92**, 2181–2187.
23. Woodbury J.M. and Hashimoto A. (1993). Methane emissions from livestock manure. In *International Methane Emissions*. Environmental Protection Agency, Washington, D.C.
24. Crutzen P.J., Aselmann I. and Seiler W. (1986). Methane production by domestic animals, wild ruminants, other herbivorous fauna and humans. *Tellus* **38B**, 271–284.
25. Judd M.J., Kellier F.M., Ulyatt M.J., Lassey K.R., Tate K.R., Shelton I.D., Harvey M.J. and Walker C.F. (1999). Net methane emissions from grazing sheep. *Global Change Biol.* **5**, 647–657.
26. Hao W.M., Scharffe D. and Crutzen P.J. (1988). Production of N_2O, CH_4, and CO_2 from soils in the tropical savanna during the dry season. *J. Atmos. Chem.* **7**, 93–105.
27. Sanhueza E., Donoso L., Scharffe D. and Crutzen P.J. (1994). Carbon monoxide fluxes from natural, managed, or cultivated savannah grasslands. *J. Geophys. Res.* **99**, 16421–16427.
28. Scharffe D., Hao W.M., Donoso L., Crutzen P.J. and Sanhueza E. (1990). Soil fluxes and atmospheric concentration of CO and CH_4 in the northern part of the Guayana Shield, Venezuela. *J. Geophys. Res.* **95**, 22475–22480.
29. Guenther A., Otter L., Zimmerman P., Greenberg J., Scholes R. and Scholes M. (1996). Biogenic hydrocarbon emissions from southern African savannas. *J. Geophys. Res.* **101**, 25859–25865.
30. Otter L.B., Yang W.X., Scholes M.C. and Meixner F.X. (1999). Nitric oxide emissions from a southern African savanna. *J. Geophys. Res.* **104**, 18471–18485.
31. Otter L.B. and Scholes M.C. (2000). Methane sources and sinks in a periodically flooded South African savanna. *Global Biogeochem. Cycles* **14**, 97–111.
32. Marufu L., Ludwig J., Andreae M.O., Meixner F.X. and Helas G. (1997). Domestic biomass burning in rural and urban Zimbabwe — Part A. *Biomass and Bioenergy* **12**, 53–68.
33. Marufu L., Ludwig J., Andreae M.O., Lelieveld J. and Helas G. (1999). Spatial and temporal variation in domestic biofuel consumption rates and patterns in Zimbabwe: implications for atmospheric trace gas emissions. *Biomass Bioenergy* **16**, 311–332.
34. Ludwig J., Marufu L., Andreae M.O., Meixner F.X. and Helas G. (in press). Combustion of biomass fuels in developing countries: a major source of atmospheric pollutants.
35. Scholes R.J., Kendall J. and Justice C.O. (1996). The quantity of biomass burned in southern Africa. *J. Geophys. Res.* **101**, 23667–23676.
36. Hao W.M., Liu M.H. and Crutzen P.J. (1990). Estimates of annual and regional releases of CO_2 and other trace gases to the atmosphere from fires in the tropics, based on the FAO statistics for the period 1975–1980. In *Fire in the Tropical Biota*, ed. Goldhammer, pp. 440–462. Springer, Heidelberg.
37. Ward D.E., Hao W.M., Susott R.A., Babbitt R.E., Shea R.W., Kauffman J.B. and Justice C.O. (1996). Effect of fuel composition on combustion efficiency and emission factors for African savanna ecosystems. *J. Geophys. Res.* **101**, 23569–23576.
38. Hemstock S.L. and Hall D.O. (1995). Biomass energy flows in Zimbabwe. *Biomass Bioenergy* **8**, 151–173.
39. Kaul S. and Lui Q. (1992). Rural household energy use in China. *Energy* **17**, 405–411.
40. Kigathi D.L. and Zhou P. (1995). Biofuel use assessment in Africa: implication for greenhouse gas emissions and mitigation strategies. *Environ. Monitor. Assess.* **38**, 253–269.
41. Brocard D., Lacaux C., Lacaux J.P., Kouadio G. and Yoboue V. (1996). Emissions from the contribution of biofuels in Western Africa. In *Biomass Burning and Global Change*, ed. S.J. Levine, pp. 350–360. MIT Press, Cambridge, MA.
42. United Nations (1995). *World Urbanisation Prospects: The 1994 Revision*. Department for Economic and Social Information and Policy Analysis, New York.
43. Lobert J.M. (1989). *Biomass burning as a source of atmospheric trace gases: CN-compounds, CO, CO_2,* and NO_x. Ph.D. thesis, Johannes Gutenberg University, Germany.
44. Brocard D. and Lacaux P.J. (1998). Domestic biomass combustion and associated emissions in West Africa. *Global Biogeochem. Cycles* **12**, 127–139.
45. Scholes R.J., Ward D.E. and Justice C.O. (1996). Emissions of trace gases and aerosol particles due to vegetation burning in southern hemisphere of Africa. *J. Geophys. Res.* **101**, 23667–23676.
46. Hatakeyama S., Izumi K., Fukuyama T., Akimoto H. and Washida N. (1991). Reactions of OH with A-pinene and B-pinene in air: Estimate of global CO production from the atmospheric oxidation of terpenes. *J. Geophys. Res.* **96**, 947–958.
47. Hoffman T., Odum J.R., Bowman F., Collins D., Klockow D., Flagan R.C. and Seinfeld J.H. (1997). Formation of organic aerosols from the oxidation of biogenic hydrocarbons. *J. Atmos. Chem.* **26**, 189–122.
48. Logan J.A., Prather M.J., Wofsy S.C. and McElroy M.B. (1981). Tropospheric chemistry: a global perspective. *J. Geophys. Res.* **86**, 7210–7254.
49. Pandis S.N., Paulson S.E., Seinfeld J.H. and Flagan R.C. (1991). Aerosol formation in the photooxidation of isoprene and A-pinene. *Atmos. Environ.* **25A**, 997–1008.
50. Paulson S.E., and Seinfeld J.H. (1992). Development and evaluation of a photooxidation mechanism for isoprene. *J. Geophys. Res.* **97**, 20703–20715.
51. Zimmerman P.R., Greenberg J.P. and Westberg C.E. (1988). Measurements of atmospheric hydrocarbons and biogenic emission fluxes in the Amazon boundary layer. *J. Geophys. Res.* **93**, 1407–1416.
52. Bowman F.M. and Seinfeld J.H. (1994). Ozone productivity of atmospheric organics. *J. Geophys Res.* **99**, 5309–5324.
53. Calogirou A., Larsen B.R. and Kotzias D. (1999). Gas-phase terpene oxidation products: a review. *Atmos. Environ.* **33**, 1423–1439.
54. Liu S.C., Trainer M. and Fehsenfeld F., *et al.* (1987). Ozone production in the rural troposphere and the implications for regional and global ozone distributions. *J. Geophys. Res.* **92**, 4191–4207.
55. Roselle S.J., Pierce T.E. and Schere K.L. (1991). The sensitivity of regional ozone modelling to biogenic hydrocarbons. *J. Geophys. Res.* **96**, 7371–7394.
56. Vogel B., Fiedler F. and Vogel H. (1995). Influence of topography and biogenic volatile organic compounds emission in the state of Baden-Wuerttemberg on ozone concentrations during episodes of high air temperatures. *J. Geophys. Res.* **100**, 22907–22928.
57. Harley P.C., Litvak M.E., Sharkey T.D. and Monson R.K. (1994). Isoprene emission from velvet bean leaves: interactions among nitrogen availability, growth photon flux density, and leaf development. *Plant Physiol.* **105**, 279–285.
58. Jobson B.T., Wu Z., Niki, H. and Barrie L.A. (1994). Seasonal trends of isoprene, C_2-C_5 alkanes and acetylene at a remote boreal site in Canada. *J. Geophys. Res.* **99**, 1589–1599.
59. Lerdau M. and Keller M. (1997). Controls on isoprene emission from trees in a

subtropical dry forest. *Plant Cell Environ.* **20**, 569–578.

60. Monson R.K., Jaeger C.H., Adams W.W., Driggers E.M., Silver G.M. and Fall, R. (1992). Relationships amongst isoprene emission rate, photosynthesis, and isoprene synthase activity as influenced by temperature. *Plant Physiol.* **98**, 1175–1180.
61. Tingey D.T., Evans R.C., Bates E.H. and Gumpertz M.L. (1987). Isoprene emissions and photosynthesis in three ferns — the influence of light and temperature. *Physiol. Plant.* **69**, 609–616.
62. Lerdau M. (1991). Plant function and biogenic terpene emission. In *Trace Gas Emissions by Plants*, eds T. Sharkey, E. Holland and H. Mooney, pp. 121–134. Academic Press, San Diego.
63. Lerdau M., Dilts S., Westberg H., Lamb B. and Allwine G. (1994). Monoterpene emission from Ponderosa pine. *J. Geophys. Res.* **99**, 16609–16615.
64. Lerdau M., Matson P., Fall R. and Monson R. (1995). Ecological controls over monoterpene emissions from Douglas-fir *(Pseudotsuga menziesii)*. *Ecology* **76**, 2640–2647.
65. Lerdau M., Litvak M., Palmer P. and Monson R. (1997). Controls over monoterpene emissions from boreal forest conifers. *Tree Physiol.* **17**, 563–569.
66. Schade G.W., Goldstein A.H. and Lamanna M.S. (1999). Are monoterpene emissions influenced by humidity?, *Geophys. Res. Lett.* **26**, 2187–2190.
67. Guenther A. (1999). Modeling biogenic volatile organic compound emissions to the atmosphere. In *Reactive Hydrocarbons in the Atmosphere*, ed. C. Hewitt, pp. 97–118. Academic Press, New York.
68. Schade G.W., Hofmann R-M. and Crutzen P.J. (1999). CO emissions from degrading plant matter (I). Measurements. *Tellus* **51B**, 889–908.
69. Schade G.W. and Crutzen P.J. (1999). CO emissions from degrading plant matter (II). Estimate of a global source strength. *Tellus* **51B**, 909–918.
70. Tarr M.A., Miller W.L. and Zepp R.G. (1995). Direct carbon monoxide photoproduction from plant matter. *J. Geophys. Res.* **100**, 11403–11413.
71. Zepp R.G., Miller W.L., Burke R.A., Parsons D.A.B. and Scholes M.C. (1996). Effects of moisture and burning on soil-atmosphere exchange of trace carbon gases in a southern African savanna. *J. Geophys. Res.* **101**, 23699–23706.
72. Conrad R. (1996). Soil microorganisms as controllers of atmospheric trace gases (H_2, CO, CH_4, OCS, N_2O, and NO). *Microbiol. Rev.* **60**, 609 640.
73. Galbally I.E. (1989). Factors controlling NO_x emissions from soils. In *Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere*, eds M.O. Andreae and D.S. Schimel, pp. 23–38. John Wiley, New York.
74. Saad O.A.L.O. and Conrad R. (1993). Temperature dependence of nitrification, denitrification and turn-over of nitric oxide in different soils. *Biol. Fertil. Soils* **15**, 21–27.
75. Levine J.S., Winstead E.L., Parsons D.A.B., Scholes M.C., Scholes R.J., Coffer W.R., Cahoon D.R. and Sebacher D.I. (1996). Biogenic soil emissions of nitric oxide (NO) and nitrous oxide (N_2O) from savannas in South Africa: The impact of wetting and burning. *J. Geophys. Res.* **101**, 23689–23697.
76. Parsons D.A.B., Scholes M.C., Scholes R.J. and Levine J.S. (1996). Biogenic NO emissions from savanna soils as a function of fire regime, soil type, soil nitrogen, and water status. *J. Geophys. Res.* **101**, 23683–23688.
77. Scholes M.C., Martin R., Scholes R.J., Parsons D. and Winstead E. (1997). NO and N_2O emissions from savanna soils following the first simulated rains of the season. *Nutrient Cycling in Agroecosystems* **48**, 115–122.
78. Davidson E.A. (1991). Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems. In *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes*, eds J.E. Rogers and W.B. Whitman, pp. 219–235. American Society for Microbiology, Washington, D.C.
79. Davidson E.A. (1993). Soil water content and the ratio of nitrous oxide to nitric oxide emitted from soil. In *The Biogeochemistry of Global Change: Radiatively Active Trace Gases*, ed. R.S. Ormeland, pp. 369–386. Chapman and Hall, New York.
80. Firestone M.K. and Davidson E.A. (1989). Microbiological basis of NO and N_2O production and consumption in soil. In *Exchange of Trace Gases Between Terrestrial Ecosystems and the Atmosphere*, eds M.O. Andreae and D.S. Schimel, pp. 7–21. Wiley, Chichester.
81. Meixner F.X. (1994). Surface exchange of odd nitrogen oxides. *Nova Acta Leopoldina* **NF 70**, 299–348.
82. Williams E.J., Hutchinson G.L. and Fehsenfeld F.C. (1992). NO_x and N_2O emissions from soil. *Global Biogeochem. Cycles* **6**, 351–388.
83. Raich J.W. and Schlesinger W.H. (1992). The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* **44B**, 81–99.
84. Delmas R.A., Marenco A., Tathy J.P., Cros B. and Baudet J.G.R. (1991). Sources and sinks of methane in the African savanna. CH_4 emissions from biomass burning. *J. Geophys. Res.* **96**, 7287–7299.
85. Scholes R.J. and Walker B.H. (eds) (1993). *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge University Press, Cambridge.
86. Conrad R. and Seiler W. (1982). Arid soils as a source of atmospheric carbon monoxide. *Geophys. Res. Lett.* **9**, 1353–1356.
87. Conrad R. and Seiler W. (1985). Destruction and production rates of carbon monoxide in arid soils under field conditions. In *Ecology*, eds D.E. Caldwell, J.A. Brierley and C.L. Brierley, pp. 112–119. Van Nostrand Reinhold, New York.
88. Moxley J.M. and Smith K.A. (1998). Factors affecting utilization of atmospheric CO by soils. *Atmos. Environ.* **30**, 65–79.
89. Zepp R.G., Miller W.L., Tarr M.A., Burke R.A. and Stoks B.J. (1997). Soil-atmosphere fluxes of carbon monoxide during early stages of post-fire succession in upland Canadian forest. *J. Geophys. Res.* **102**, 29301–29311.
90. Potter C.S., Davidson E.A. and Verchot L.V. (1996). Estimation of global biogeochemical controls and seasonality in soil methane consumption. *Chemosphere* **32**, 2219–2246.
91. Anderson I.C. and Poth M.A. (1998). Controls on fluxes of trace gases from Brazilian cerrado soils. *J. Environ. Qual.* **27**, 1117–1124.
92. Poth M.A., Anderson I.C., Miranda H.S., Miranda A.C. and Riggan P.J. (1995). The magnitude and persistance of soil NO, N_2O, CH_4, and CO_2 fluxes from burned tropical savanna in Brazil. *Biogeochem. Cycles* **9**, 503–513.
93. Keller M. and Reiners W.A. (1994). Soil-atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica. *Global Biogeochem.Cycles* **8**, 399–409.
94. Van den Pol-van Dasselaar A., van Beusichem M.L. and Oenema O. (1997). Effects of grassland management on the emission of methane from intensively managed grasslands on peat soil. *Plant and Soil* **189**, 1–9.
95. Adamsen A.P.S. and King G.M. (1993). Methane consumption in temperate and subarctic forest soils: rates, vertical zonation, and responses to water and nitrogen. *App. Environ. Microbiol.* **59**, 485–490.
96. Castro M.S., Steudler P.A., Melillo J.M., Aber J.D. and Bowden R.D. (1995). Factors controlling atmospheric methane consumption by temperate forest soils. *Global Biogeochem. Cycles* **9**, 1–10.
97. Whalen S.C., Reeburgh W.S. and Kizer K.S. (1991). Methane consumption and emission by taiga. *Global Biogeochem. Cycles* **5**, 261–273.
98. Whalen S.C. and Reeburgh W.S. (1996). Moisture and temperature sensitivity of CH_4 oxidation in boreal soils. *Soil Biol. Biochem.* **28**, 1271–1281.
99. Bubier J.L., Moore T.R., Bellisario L., Comer P.M. and Crill P.M. (1995). Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada. *Global Biogeochem. Cycles* **9**, 455–470.
100. Funk D.W., Pullman E.R., Peterson K.M., Crill P.M. and Billings W.D. (1994). Influence of water table on carbon dioxide, carbon monoxide, and methane fluxes from taiga bog microcosms. *Global Biogeochem. Cycles* **8**, 271–278.
101. Moore T.R. and Roulet N.T. (1993). Methane flux: water table relations in northern wetlands. *Geophys. Res. Lett.* **20**, 587–590.
102. Dise N.B., Gorham E. and Verry E.S. (1993). Environmental factors controlling methane emissions from peatlands in northern Minnesota. *J. Geophys. Res.* **98**, 10583–10594.
103. Klinger L.V., Zimmerman P.R., Greenberg J.P., Heidt L.E. and Guenther A.B. (1994). Carbon trace gas fluxes along a successional gradient in the Hudson Bay lowland. *J. Geophys. Res.* **99**, 1469–1494.
104. Bartlett K.B., Crill P.M., Sebacher D.I., Harriss R.C., Wilson J.O. and Melack J.M. (1988). Methane flux from the central Amazonian floodplain. *J. Geophys. Res.* **93**, 1571–1582.
105. Delmas R.A., Servant J., Tathy J.P., Cros B. and Labat M. (1992). Sources and sinks of methane and carbon dioxide exchanges in mountain forest in equatorial Africa. *J. Geophys. Res.* **97**, 6169–6179.
106. Devol A.H., Richey J.E., Clark W.A., King S.L. and Martinelli L.A. (1988). Methane emissions to the troposphere from the Amazon floodplain. *J. Geophys. Res.* **93**, 1583–1592.
107. Tathy J.P., Cros B., Delmas R.A., Marenco A., Servant J. and Labat M. (1992). Methane emission from flooded forest in Central Africa. *J. Geophys. Res.* **97**, 6159–6168.
108. Wassmann R. and Thein U.G. (1996). Spatial and seasonal variation of methane emission from an Amazon floodplain lake. *Mitt. Internat. Verein. Limnol.* **25**, 179–185.
109. Boon P.I., Mitchell A. and Lee K. (1997). Effects of wetting and drying on methane emissions from ephemeral floodplain wetlands in south-eastern Australia. *Hydrobiologia* **357**, 73–87.
110. Cowan G.I. and van Riet W. (1998). *A Directory of South African Wetlands*. Department of Environmental Affairs and Tourism, Pretoria.
111. Hughes R.H. and Hughes J.S. (1992). *A Directory of African Wetlands*. IUCN, Gland, Cambridge; UNEP, Nairobi, Kenya; WCMC, Cambridge.