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Journal
Chemosphere - Global Change Science, 3(1)

ISSN
1465-9972

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Publication Date
2001

DOI
10.1016/s1465-9972(00)00023-4

PERGAMON

Chemosphere – Global Change Science 3 (2001) 73–91

CHEMOSPHERE– GLOBAL CHANGE SCIENCE

An estimate of natural volatile organic compound emissions from vegetation since the last glacial maximum

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Received 12 May 1999; accepted 1 December 1999

Importance of this paper: Organic chemicals evaporating out of vegetation may affect various aspects of the earth's environment – including the amount of haze in the air, which affects the earth's heat balance by reflecting sunlight back into space, and also the lifetime of methane gas in the atmosphere. Based on reconstructed vegetation zones for the coldest phase of the Last Glacial Period (about 20,000 years ago) and the warmer present interglacial (the last 11,000 years), we estimated the total amount of the substances evaporating from the world's vegetation. In the cooler, drier, less forested world of the Last Glacial, the fluxes of these compounds were probably reduced by about one-third to one-half. The resulting reduction in haze might have tended to keep the earth slightly warmer during the Glacial than it would otherwise have been. In addition, Glacial methane levels may have been lowered because of the lack of volatile organics 'mopping up' reactive free radicals that would otherwise break down methane.

Abstract

The flux of volatile organic chemicals from natural vegetation influences various atmospheric properties including oxidation state of the troposphere via the hydroxyl radical (OH), photochemical haze production and the concentration of greenhouse gases (CH_4, H_2O, CO). Because the Volatile Organic Compound (VOC) flux in the present-day world varies markedly with both vegetation cover and with climate, changes in the emission of VOCs may have damped or amplified past climate changes.

Here we conduct a preliminary study on possible changes in VOC emission resulting from broad scale vegetation and climate change since the Last Glacial Maximum (LGM). During the general period of the LGM (~25–17,000 years before present {BP}), global forest cover was considerably less than in the present potential situation. The change in vegetation would have resulted in a ~30% reduction in VOC emission at 643 Tg y^{-1} relative to the present potential vegetation (912.9 Tg y^{-1}). Uncertainty in global vegetation cover during the LGM bounds the VOC estimate by ±15%. In contrast, during the warmer early-to-mid Holocene (8000 and 5000 BP), with greater forest extent and less desert than during the late Holocene (0 BP), emission rates of VOCs seem likely to have been higher than at present.

Further modifications in VOC emission may have been mediated by a reduction in mean tropical lowland temperatures (by around 5–6°C) decreasing the LGM VOC emission estimate by 38% relative to the warmer LGM scenario.

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PII: S1465-9972(00)00023-4

Increased VOC emissions due to forest expansion and increased tropical temperatures since the LGM may have served as a significant driver of climate change over the last 15 ka y through the influence of VOC oxidation; this can impact tropospheric radiative balance through reductions in the concentration of OH, increasing the concentration of CH_4.

The error limits on past VOC emission estimates are large, given the uncertainties of present-day VOC emission rates, paleoecosystem distribution, tropical paleoclimatic conditions, and physiological assumptions regarding controls over VOC emission. Nevertheless, the potential significance of changes in natural VOC emission over the last 20 ka and their influence on climate are an important unknown that should at least be borne in mind as a limit on the understanding of past atmospheric conditions. Elucidation of the role of VOCs in climate change through paleoclimatic general circulation model simulations may improve understanding of past and future changes in climate.

Abbreviations: Ecosystem class (EC); Leaf area index (LAI, leaf area per unit ground area); Last glacial maximum (LGM); Quaternary environments network (QEN); Volatile organic compounds (VOC)

Keywords: Terpenoids; Vegetation; Glacial; Holocene; Climate change; VOC; Paleoclimate; Paleovegetation; Climate feedbacks

1. Introduction

Volatile Organic Compounds (VOCs) play an important role in atmospheric chemistry by influencing the observed tropospheric concentrations of ozone and methane. Methane is of particular interest as a significant greenhouse gas which has 10 times the global warming potential of CO_2 on a mass basis (Lashof and Ahuja, 1990); it may also be critical in determining the changes in the earth's radiative balance in both the past and the future. At low VOC concentration, methane is a dominant sink for OH and results in low atmospheric CH_4 concentrations ($\sim$ 1 ppm) and a half-life of decades (Prather, 1994). However, at greater concentrations of VOCs that are more reactive towards OH than methane, the concentration and lifetime of CH_4 in the atmosphere might increase (Fehsenfeld, 1992) facilitating warmer global temperatures. From ice cores, methane concentrations are known to have varied by at least 50% during the upper Quaternary climate cycles (Chappellaz et al., 1993), and it is possible that changing VOC emission during that period influenced global temperatures mediated in part by the atmospheric CH_4 concentration. Volatile organic compounds may also decrease regional and global temperatures through the production of atmospheric aerosols that increase atmospheric albedo.

The effect of natural aerosols (terrestrial and oceanic) on the global energy balance in the present-day world is poorly understood, but their cooling effect may well exceed the warming produced by a doubling of the preanthropogenic CO_2 concentration (Charlson et al., 1992; Schwartz, 1996). In spite of the uncertainty regarding the impact of changes in VOC emission on global radiative forcing, it is critical that the process is better understood, in order to predict the drivers of global climate change.

The actual present-day rates of VOC emission from vegetation are still subject to considerable uncertainty, but recently published inventories have been used to make global and continental scale estimates for the present-day world (Geron et al., 1994; Guenther et al., 1995) and projections for future conditions (Constable et al., 1999a). VOCs emitted from vegetation encompass a wide range of compounds originating from the mevalonic acid pathway (including isoprene and monoterpenes) that differ in size, oxygenation and reactivity. The rate at which these compounds are emitted varies according to both the biological properties of the vegetation and the physical environment. Principal biological controls include the ecosystem type, species composition, and canopy structure (Monson et al., 1995). The major physical controls over emission rate are temperature and light intensity.

Simulation of past climates and of past biogeochemical processes is a major challenge for earth system science. The main goal is to better understand why changes in climate have occurred in the past and elucidate the potential driving forces behind future changes. At present, most work in paleoclimatic and biogeochemical modeling is concerned with the global-scale fluctuations in climate which have occurred repeatedly over the last 2.4 million years of the Quaternary period (Crowley and North, 1991). During the last 700,000 years, climate has fluctuated on a roughly 100,000 year timescale between cool, dry interglacial periods and warmer, more moist interglacials. Although the earth's orbital patterns are known to set the timing of these changes (Crowley and North, 1991), the amplifying factors involved are unclear. Important additional factors in these climate fluctuations are thought to include changes in ocean plankton ecology, the spatial distribution of terrestrial ecosystems, dust fluxes from desert surfaces, carbon uptake and release from soil and vegetation, atmospheric water vapor concentration, methane fluxes from wetlands and variation in fluxes of VOC from terrestrial vegetation.

At present, global climate models do not predict certain important features of the glacial world, including the degree of aridity and the apparent magnitude of land surface cooling; a limitation that may be due to the omission of key parameters from these models. It is our intention here to explore how global VOC emissions from vegetation may have varied during part of the current glacial–interglacial cycle as a step towards improving understanding of the drivers of paleoclimatological conditions. The goal of this paper is to estimate from a priori principles variation in the fluxes of three classes of VOCs; isoprene, monoterpenes and other reactive VOCs (ORVOC, reactive VOC with atmospheric lifetimes <1 day) between the extreme of the Last Glacial Maximum (LGM), the early-Holocene ($\sim$ 8 ka {= thousands of years} BP {before present, in radiocarbon years} and the present Holocene interglacial, while accounting for uncertainty in vegetation distribution and temperature patterns.

2. Materials and methods

There are two clearly identifiable factors which may have caused large changes in VOC emission between glacial and interglacial conditions. Firstly, alteration in vegetation distribution and composition are well documented for all parts of the world (Adams et al., 1990; Frenzel, 1992; Crowley, 1995). As different vegetation classes exhibit a wide range of VOC emission rates (e.g., isoprene varies over 200-fold on a land area basis), shifts in the relative area coverage of the different classes likely resulted in an alteration of the potential of vegetation to emit VOCs into the atmosphere (Constable et al., 1991; Turner et al., 1991; Guenther et al., 1993; 1999a,b; Martin and Guenther, 1995). Secondly, changes in temperature greatly influence VOC emission (Guenther et al., 1993). Therefore, shifts in annual temperature conditions over a glacial–interglacial cycle could similarly affect VOC emission.

The importance of these two factors in controling VOC emission are essential for accurate emission estimates, however, reconstructions of late Quaternary environments are always problematical with respect to ‘no analog’ conditions (different in possibly significant ways from present-day conditions) during the LGM: Perhaps importantly, (i) CO2 concentration was about 80 ppm lower during the LGM than during the Holocene (Alley et al., 1993), but the effects of this change on VOC emission is unknown and (ii) there were differences in relative abundance of potentially key VOC emitting species that may modify the rate of VOC emission from certain ecosystems. The possible effects of these factors are not explicitly addressed here in this study, but their potential to modify the estimates of VOC emission presented here may be significant and should be borne in mind as a topic for future investigation.

2.1. Reconstruction of past vegetation–climate zones

The uncertainty regarding fine scale resolution of shifts in vegetation types is considerable for most paleoecological reconstructions, but broad generalizations can be utilized. We have represented global vegetation as a composite of 29 vegetation classes based on those defined by Olson et al. (1983) (Table 1), and previously mapped and published for the late Quaternary period by Adams and Faure (1997) or QEN (1995). The distribution of these ecosystem classes for each time period was reconstructed using digitalized hand-drawn maps based on continual checking and input from a large number of Quaternary scientists as a component of the quaternary

Table 1
Equivalency between QEN ecosystems and those of Olson

Ecosystem type	Olson code equivalents
1. Tropical rainforest	29, 33
2. Monsoon forest	29, 32
3. Tropical woodland	59
4. Tropical thorn scrub	59
5. Tropical semi-desert	51
6. Tropical grassland	40, 41
7. Tropical desert	50
9. Savanna	43
10. Warm temperate forest	26, 27
11. Giant conifer forest	20
12. Tropical montane forest	28
13a. Mediterranean forest	46
13b. Mediterranean scrub	46
14. Cool temperate forest	24, 25, 26, 23
15. South taiga	20, 21, 22
16. Mid Taiga	20, 21, 22
17. Open boreal woodlands	21, 23, 24
18a. Temperate woodland	24, 40, 41
18b. Temperate scrub	24, 40, 41
19a. Montane/dry tundra	53
19b. Lowland tundra	53
20a. Steppic steppe-tundra	53
20b. Tundra-like steppe-tundra	53
21. Polar/montane desert	
22. Temperate desert	50, 51, 52
23. Temperate semi-desert	50, 51, 52
24a. Moist steppe	41, 42
24b. Dry steppe	41, 42
25. Forest steppe	41, 42
26. Forest tundra	53
27. Bog/swamp	44
28. Ice	
29. Lake/river	

environments network (QEN). Vegetation biome distributions and general climate zone distributions are, generally speaking, interchangeable on the broad scale because vegetation is so much a product of the climatic background.

We have assumed that the widely accepted QEN vegetation/ecosystem maps (Adams and Faure, 1997) represent approximately the dominant ecosystem classes that would have occurred, respectively, during the LGM, the early-Holocene (though with 'error limits' to take in most of the range of opinion in the Quaternary community), and the conditions on the globe prior to industrialization and large-scale transformation of natural ecosystems to agricultural ones through anthropogenic activity (present potential vegetation). Furthermore, we have assumed that the analogous ecosystem classes used in this study have broadly similar climatic requirements under both present day and past conditions.

In the QEN (1995) maps, past biome distributions were reconstructed from a combination of indicators: the vegetation conditions indicated by plant fossils (pollen and macrofossils), animals (vertebrates and invertebrates characteristic of particular vegetation or bioclimatic conditions) as well as paleotemperatures of groundwaters from isotopes and noble gas ratios, sediment chemistry and depositional structures indicating a particular bioclimatic regime, etc. (Adams and Faure, 1997). These biome distributions themselves thus implicitly contain climate information (a crucial factor in VOC emission rates), and in this sense are analogous structurally and climatically to the biome distributions in Guenther et al. for present-day world VOC emissions.

For the tropical latitudes, there are various indications (from floras, faunas, groundwater composition, oxygen isotopes in eggshells, and from marine indicators from some tropical shelf sea areas) that lowland mean annual temperatures were 5–6°C lower than present throughout the tropics at the LGM. This possibility, perhaps crucial in affecting VOC emission from the tropics at that time because the evaporation process is so temperature dependent (Guenther et al., 1995) is allowed for in our low-temperature scenario. However, because the scenario of significant tropical temperature lowering at the LGM remains somewhat controversial (due to contradictions with open ocean surface temperature indicators) we have not presented this as our 'most likely scenario' in terms of VOC emissions.

2.1.1. Present potential vegetation

For purposes of comparison with the LGM and the early-Holocene periods, the current state of global vegetation is summarized in a map of the present potential vegetation. The present potential vegetation represents that most likely to have occurred prior to anthropogenic modification of ecosystem class (EC) species composition and spatial distribution. The vegetation distribution represents a compilation of the present actual vegetation distribution maps of Olson et al. (1983) and various regional present potential vegetation maps (e.g. Walter, 1971). On an area basis, the present potential vegetation is dominated by tropical rainforest (EC 1) that covers approximately 9.6% of the total vegetated area, this is followed by tropical deserts, tropical scrub, cool temperate forest and savanna (ECs 7, 4, 14 and 9, respectively) (Table 2).

2.1.2. Early-holocene vegetation

For the early-Holocene (~8000 BP), forest coverage in almost all regions was greater than the present-potential (Frenzel, 1992), with a major forest expansion occurring in Africa (Hamilton and Taylor, 1991) and SE Asia (including China) due to stronger summer monsoons. The areas of the Saharan and central Asian deserts were much smaller due to increased rainfall (Ritchie, 1994) that may have increased the coverage of grassland, and scrub vegetation may have predominated in both these areas at this time (Frenzel, 1992) (Table 2). These changes are incorporated into the maps as increases in the coverage of tropical forests, scrub vegetation and desert (ECs 1–5) in addition to expansions in warm (EC 10) and cool (EC 14) temperate forest, and mid-Taiga (EC 16). The enhancement of coverage by forest vegetation resulted in the decline of coverage for tropical grasslands, tropical deserts, and savanna (EC: 6, 7 and 9, respectively) in addition to reductions in temperate woodland and scrub and desert (EC: 18a, 18b and 22, respectively).

2.1.3. Last glacial maximum vegetation

Maps of global vegetation coverage for the period around the LGM have been produced by several different sources over the past few years. Crowley (1995) performed a series of calculations for LGM carbon storage based on a 220-site pollen database. Peng (1994) produced a set of Northern Hemisphere/global estimates of carbon storage based on the vegetation maps of Grichuk (1992) and the climate reconstruction maps of Frenzel (1992). Published maps also exist of regions or sub-regions of the world for the LGM and Holocene (Frenzel, 1992; Clapperton, 1993). The maps utilized here represent an approximate 'consensus' picture developed by the QEN (Adams, 1995; Adams and Faure, 1997).

Evidence used to support the QEN ecosystem reconstructions include (1) flora and fauna fossil data and (2) sedimentological indicators such as buried soil types, sedimentary structures and sediment chemistry. Plant fossils are the preferred direct indicators of past vegetation, but can produce misleading results for local vegetation if concentrated in sediments by selective transport or preservation. Furthermore, plant fossil data

Table 2
Reconstructed global areas of ecosystem types, from Adams and Faure (1997). Bracketed values are for the low forest and high forest scenarios, respectively. Values are in Mkm^2

Ecosystem code	LGM	8000 ya	5000 ya	Present pot.
1. TrRfr	**5.56** (4–8)	**16.38** (14.38–18.00)	**15.77** (13.8–16.5)	**12.47**
2. MsnFor	**1.9** (1.2–2.5)	**4.5** (3.00–5.00)	**4.5** (3.00–5.00)	**2.96**
3. TrWd	**1.19** (1.19–2.69)	**6.62** (5.00–6.62)	**6.17** (4.50–6.17)	**6.17**
4. TrThnSc	**3.33** (5.33–4.33)	**5.99** (8.99–5.49)	**7.49** (9.49–6.99)	**10.85**
5. TrSDes	**4.64** (4.64–3.15)	**9.43** (9.43–8.43)	**10.97** (10.97–9.97)	**6.98**
6. TrGrs	**10.50** (12–10.50)	**7.64** (7.64–7.64)	**3.89** (4.89–3.89)	**2.79**
7. TrDes	**13.83** (13.83–11.83)	**0.39** (0.39–0.39)	**1.69** (0.39–2.00)	**11.73**
9. Sav	**12.25** (9.25–12.83)	**10.87** (10.00–11.50)	**11.82** (11.82–10.82)	**8.45**
10. WarmTemFor	**0.76** (0.2–1.0)	**4.55** (4.0–4.55)	**4.59** (4.0–5.09)	**3.45**
11. CtGiantConfr	**0**	**0.35** (0.25–0.35)	**0.38** (0.35–0.38)	**0.38**
12. TrMontFor	**0.54** (0.54–0.74)	**1.20** (1.20–1.20)	**1.10** (1.10–1.10)	**0.96**
13a. MdtnForest	**0**	**0.68** (0.50–0.68)	**0.78** (0.50–0.78)	**0.41**
13b. MdtnScrub	**0.17** (0.17–0.27)	**0.66** (0.56–0.66)	**0.20** (0.40–0.20)	**0.2**
14. CoolTempFor	**0.2** (0.1–1.0)	**9.75** 9.20–11.00)	**11.27** (11.00–12.5)	**10.82**
15. SouthTaiga	–	**6.53** (5.53–7.00)	**8.87** (7.87–9.00)	**5.7**
16. Mid Tg	**0.86** (0.86–2.5)	**7.17** (6.17–7.60)	**5.68** (6.68–5.68)	**6.26**
17. OpnBWd	**2.50** (2.5–2.5)	**4.84** (4.84–6.53)	**3.83** (3.83–4.83)	**3.22**
18a. Temp wdld	**4.35** (4.35–4.35)	**2.06** (2.06–2.06)	**2.26** (1.26–2.26)	**2.03**
18b. Temp Scrub	**2.91** (2.91–2.91)	**0.46** (0.46–0.46)	**0.46** (0.46–1.46)	**1.18**
19a. Mtn/dry Tu	**0.73** (0.73–0.73)	**2.57** (2.57–2.57)	**3.01** (3.01–3.33)	**3.33**
19b. Lowl Tu	**0.13** (0.13–0.9)	**1.80** (1.00–2.00)	**2.67** (2.67–2.67)	**4.49**
20a. Steppic St-Tu	**11.82** (11.82–12.82)	**0**	**0**	**0**
20b. Tundric St-Tu	**3.34** (3.34–4.32)	**0**	**0**	**0**
21. Polar/Mtn Des	**15.52** (15.52–8.5)	**1.95** (1.95–1.75)	**2.22** (2.22–2.00)	**2.08**
22. TempDes	**12.50** (12.5–8.5)	**0.20** (0.50–0.10)	**0.20** (0.50–0.10)	**2.42**
23. TempSDes	**7.10** (7.10–6.60)	**8.16** (6.01–5.61)	**8.70** (7.20–6.80)	**7.72**
24a. Moist Steppe	**0.50** (0.2–1.0)	**3.50** (3.00–4.50)	**4.71** (4.81–5.71)	**4.87**
24b. Dry Steppe	**6.50** (7.5–6.50)	**3.93** (4.93–2.93)	**3.03** (5.20–4.03)	**3.39**
25. ForSt	**1.3** (0.7–2.5)	**1.20** (1.20–1.20)	**1.57** (1.57–1.57)	**1.96**
26. ForTu	–	**2.71** (1.50–3.00)	**1.08** (1.08–1.08)	–
27. Bog/Swamp	–	**1.82** (1.82–1.82)	**2.30** (2.35–2.35)	**2.43**
28. Ice	**36.09**	**19.86**	**15.91**	**15.91**
29. Lake/river	**1.3**	**2.4**	**2.7**	**2.65**
Global area	**161.58** (Mkm^2)	**150.17** (Mkm^2)	**149.80** (Mkm^2)	**149.85** (Mkm^2)

is relatively sparse for the period around the LGM due to aridity. The QEN ecosystem reconstructions emphasize 14C-dated evidence, whether palynological, sedimentological or zoological, however, the error bars on the age of each site often span a few thousand years. Nevertheless, it is reasonable to suggest that there was an overlapping period when cool and arid conditions occurred across many different regions of the globe, although not necessarily the LGM *sensu stricto*. This would produce a global vegetation distribution much like that which has been reconstructed in the QEN maps for the LGM. The climatic changes associated with the LGM reduced the coverage of tropical vegetation (43% of the total vegetated area), whereas polar/boreal vegetation expanded (34% of the vegetated area) (Table 2).

As there are still significant uncertainties concerning the actual global vegetation cover over the last 25,000 years, the ecosystem distribution during the LGM was bounded by creating three variations in forest ecosystem distribution that covers the range of forest cover estimates. Our baseline forest cover distribution scenario is thus derived from the QEN ecosystem maps (Adams and Faure, 1997) and is designated the medium forest area (MFA) distribution (Table 2). The general consensus among the Quaternary community, reflecting in the MFA, is that there was a major (>50%) loss of forest cover from the tropics and expansions of desert zones throughout the globe relative to the present potential vegetation distribution. The QEN (Adams and Faure, 1997) maps for the LGM show large reductions in forest vegetation, especially in the higher latitudes where the forests were mostly replaced by ice sheets, polar desert and by the arid, cold-climate steppe tundra vegetation (Adams and Faure, 1997). In the QEN maps and the sources upon which they are based, temperate forest vegetation seems almost to have disappeared from

Europe (Frenzel, 1968, 1992; Turner and Hannon, 1988; Bennett et al., 1991) and boreal forest disappeared from most of Eurasia (Velichko and Spasskaya, 1991; Velichko and Isavea, 1992), leaving only isolated pockets scattered through mountainous areas. In China and Japan temperate forest vegetation was replaced mainly by open woodlands, forest steppe and grasslands (Tong and Shao, 1991; Frenzel, 1992; Ooi, 1992; Wang and Sun, 1994; Liew et al., 1995). Lower latitudes also showed major desert expansions in Australia (Bowler, 1976), north Africa (Schulz, 1986), northwest India (Singh et al., 1974) and parts of South America, and retreat of forests and woodlands in Africa (van Neer, 1984; Lézine and Cassanova, 1989; Hamilton and Taylor, 1991), Australia (Thom et al., 1994), central and South America (Clapperton, 1993; Leyden et al., 1993; Suguio et al., 1993; van der Hammen and Absy, 1994) and southeast Asia (An et al., 1991; Thomas and Thorp 1991).

However, significant uncertainties do remain for the forest distribution during the LGM, and other scenarios are presented to take account of the full range of existing and possible interpretations in the literature. The second forest distribution scenario is the 'high forest area' (HFA) scenario that is more closely in line with the mapping efforts of Peng (1994) and Crowley (1995); in which the LGM has greater coverage of forest and other moist climate vegetation such as woodland and moist steppe than the MFA (Table 2). Data supporting the HFA scenario is principally derived from use of a relatively limited amount of pollen data that require moist depositional conditions for preservation and therefore tend to concentrate at more moist localities favoring interpretation as increased forest distribution. The third forest distribution scenario is a 'low forest area' (LFA) scenario suggesting vegetation distributions in which forest, woodland and moist steppe were restricted in distribution (Frenzel, 1992; Clapperton, 1993) as suggested primarily by sedimentological and geomorphological data in conjunction with limited use of plant fossil evidence (Table 2).

2.2. Global temperature conditions

The temperature conditions experienced by vegetation are as important as its structure and composition in determining VOC emission (see below). We assume here that each EC had broadly similar climate requirements to its closest analogs in the present-day world, even if the detailed mosaic of community composition was different. In this study, the temperature conditions were assumed to be roughly constant for present-day and past biomes, with the biomes having shifted in the past to position themselves along temperature gradients. Thus for most biomes, the emission factors for each biome used in our main source reference on global land VOC emissions (Guenther et al., 1995) automatically include temperature effects.

There are some examples in which temperature relationships of species and biomes during the LGM could have differed from present conditions (e.g. an extinct warm-temperate form of *Picea* along the Gulf coast of North America during the LGM), however, in most areas both vegetation and other independent temperature indicators suggest roughly similar biome temperature requirements in the past.

Only for the tropics (below) is this distinction important; the tropical lowlands represent the extreme upper end of the global temperature scale, and if global temperature everywhere cooled substantially, the tropics themselves would have been existing under lower mean temperatures (other bioclimatic zones could shift latitudinally, but there would be nowhere else for tropical zones to shift to if they all cooled substantially). Thus, one potentially important difference between the present conditions and those of the LGM was the lower tropical lowland temperatures (Broecker, 1985) that could (i) eliminate high VOC emitting vegetation assemblages, by in effect pushing the climatic tropics equatorwards, and even with the tropics reducing the abundance of characteristic 'tropical' forms and replacing them with lower montane and warm temperate forms and (ii) reduce the VOC emission from remaining vegetation. A 5°C lowering of mean annual temperature in most areas of the lowland tropics now seems likely on the basis of floristic, isotopic and other indicators from the tropical landmasses, and also from certain oceanic indicators (Broecker, 1985; Crowley, 1995). A low tropical temperature scenario (LT) was superimposed upon the LGM MFA distribution to assess the potential effects of lower tropical temperatures on total annual VOC emission. The Low Temperature (LT) scenario reduced the mean annual temperature for tropical ecosystem classes (EC: 1–9) by 5°C. The mean annual temperatures of tropical montane forest (EC 12) was not reduced by 5°C as the hypothesized reduction was confined to lowland locations (it is assumed that montane forest would move downslope, keeping a steady emission rate). Furthermore, tropical montane forest contributes only a small fraction to VOC emission both from tropical ecosystems as a whole and to the total annual global VOC emission. The reductions in temperature were achieved by subtracting 5°C from the mean annual temperature value used in calculating emissions rates for total areas which contained tropical ecosystem classes 1–9.

2.2.1. Estimating voc emission from vegetation and paleovegetation

VOC output from vegetation depends on such biological factors as leaf area index (LAI, leaf area per unit ground area), specific VOC emission rate of foliage, and canopy temperatures. The estimates of Guenther et al. (1995) for present-day base VOC emission rates of ecosystem classes can be tentatively applied to the past vegetation, assuming (i) minimal alteration of climatic and structural relationships between past ecosystem classes and those occurring in the present-day world and (ii) limited changes in the types of VOCs emitted by vegetation and the environmental control over their biochemical production and emission. The emission factors assigned to vegetation types in this study are derived from the base VOC emission factors of Guenther et al. (1995) that were developed from a literature survey of current VOC emission studies and are considerably different from those used in most previous studies (Table 3).

Addressing the influences of temperature (see above) are essential for VOC emission simulations of both monoterpenes and isoprene, whereas accurate illumination conditions are critical for isoprene alone (Guenther et al., 1993, 1995). Algorithms for estimating VOC flux from vegetation at the foliar level under standard environmental conditions, utilizing empirical emission coefficients to account for the effects of illumination and temperature, have achieved considerable predictive success (Guenther et al., 1993). Additional work (Guenther et al., 1995) scaled leaf level VOC emission to the canopy on a monthly time frame incorporating information on monthly NPP and leaf area index (LAI) from satellite-derived normalized difference vegetation index (NDVI). Additional modifications incorporated the influence of specific leaf weight (g m-2) and canopy structure that defined either sun or shade leaves to improve emission estimates. The Guenther et al. (1995) methods were applied to the QEN ECs (Table 1) to calculate global fluxes of isoprene; monoterpenes; and ORVOCs during the LGM, early-Holocene and present potential vegetation conditions.

Table 3
Per-unit area emission rates for VOCs (Tg Mha y) (after Guenther et al., 1995)

Ecosystem type	Iso/Mha	MT/Mha	ORVOC/Mha
1. TrRfr	19.49	2.42	9.08
2. MsnFor	13.1	1.41	1.76
3. TrWd	3.87	0.76	1.43
4. TrThnSc	3.83	0.76	1.43
5. TrSDes	0.63	0.09	0.17
6. TrGrs	5.07	1.25	1.57
7. TrDes	0.09	0.09	0.09
9. Sav	7.23	1.44	3.63
10. WarmTemFor	3.28	0.53	0.99
11. CtGiantConfr	0.53	1.24	0.94
12. TrMontFor	6.92	2.73	5.21
13a. MdtnForest	1.64	0.65	0.76
13b. MdtnScrub	1.64	0.65	0.76
14. CoolTempFor	3.28	0.53	0.99
15. SouthTaiga	0.53	1.24	0.94
16. Mid Tg	0.53	1.24	0.94
17. OpnBWd	0.53	1.24	0.94
18a. Temp wdld	3.68	3.68	2.36
18b. Temp Scrub	3.82	0.76	1.43
19a. Mtn/dry Tu	0.13	0.04	0.07
19b. Lowl Tu	0.13	0.04	0.07
20a. Steppic St-Tu	0.13	0.04	0.07
20b. Tundric St-Tu	0.13	0.04	0.07
21. Polar/Mtn Des	0	0	0
22. TempDes	0.09	0.09	0.09
23. TempSDes	0.63	0.09	0.17
24a. Moist Steppe	5.07	1.25	1.57
24b. Dry Steppe	5.07	1.25	1.57
25. ForSt	5.07	1.25	1.57
26. ForTu	0.13	0.04	0.07
27. Bog/Swamp	0.38	0.38	0.38
28. Ice	0	0	0
29. Lake/river	0	0	0

Estimating VOC emission from vegetation and paleovegetation. VOC output from vegetation depends on such biological factors as leaf area index (LAI, leaf area per unit ground area), specific VOC emission rate of foliage and canopy temperatures. The estimates of Guenther et al. (1995) for present-day base VOC emission rates of ecosystem classes can be tentatively applied to the past vegetation, assuming (i) minimal alteration of climatic and structural relationships between past ecosystem classes and those occurring in the present-day world and (ii) limited changes in the types of VOCs emitted by vegetation and the environmental control over their biochemical production and emission. Here we have assigned VOC flux values on a land surface area basis to the QEN classification based on those estimated for current ecosystems by Guenther et al. (1995) (Table 3).

Addressing the influence of temperature (see above) is essential for VOC emission simulations of both monoterpenes and isoprene, whereas accurate illumination conditions are critical for isoprene alone (Guenther et al., 1993, 1995). Algorithms for estimating VOC flux from vegetation at the foliar level are scaled from standard environmental conditions, utilizing empirically determined modifiers account for the effects of illumination and temperature (Guenther et al., 1993). The emission of monoterpenes is calculated as an exponential function from emission rate measured under standard environmental conditions modified by an empirical coefficient defining the temperature dependence of monoterpene emission (Guenther et al., 1993). Isoprene emission is calculated by scaling emissions measured under standard conditions using empirically derived factors accounting for the effects of temperature and illumination. The illumination factor describes an approximately linear increase in isoprene emission up to a saturation point, whereas the temperature factor approximates an inverted parabola simulating the change in enzymatic activity with temperature (Guenther et al., 1993). Additional work (Guenther et al., 1995) scaled leaf level VOC emission to the canopy on a monthly time frame incorporating information on monthly NPP and leaf area index (LAI) from satellite-derived normalized difference vegetation index (NDVI). Additional modifications incorporated the influence of specific leaf weight (g m^{-2}) and canopy structure that defined either sun or shade leaves to improve emission estimates. The Guenther et al. (1995) methods were applied to the QEN ECs (Table 1) to calculate global fluxes of isoprene; monoterpenes; and ORVOCs during the LGM, early-Holocene and present potential vegetation conditions.

3. Results

3.1. Present potential vegetation and VOC emission

The present potential vegetation of the globe (Fig. 1(a)) includes 26 of the 29 QEN ecosystem classes, not present in the distribution maps are both forms of steppe-tundra (EC 20a, b) and forest tundra (EC 26). Both steppe-tundra and forest tundra occur in localized areas in the present-day world, but their extent was considered too small to map. Of the remaining ecosystem classes, 41% of the total vegetated area is covered, in order, by tropical rainforest, tropical desert, tropical scrub, cool temperate forest and savanna (EC: 1, 7, 5, 14 and 9). The combination of present potential vegetation and climatic conditions estimates a global total annual VOC emission of 912.9 Tg y^{-1} (61% isoprene; 13% monoterpenes; 24% ORVOC) (Figs. 2–4). Present potential VOC emissions are dominated by tropical rainforest (EC 1) representing 41% of the total, however, significant contributions are provided by savanna (EC 9), cool temperate forest (EC 14), and monsoon forest (EC 2) that account for 11.4%, 5.7% and 5.3% of the annual total VOC emission, respectively. High rates of VOC emission (>15 Tg Mha^{-1} y^{-1}) are geographically centered within 10° latitude around the equator in Africa, but extends as far as 15° around the equator in the Americas (Fig. 1(a)). In Asia, high VOC emission rates are limited in their southern extension, but approach 30°N latitude in northern India and around the Bay of Bengal (Fig. 1(a)). Regions of low VOC emission (<2 Tg Mha^{-1} y^{-1}) are apparent throughout north Africa, the Arabian peninsula and central Asia, whereas more limited low VOC emission regions are confined to deserts in North and South America, southern Africa, and Australia (Fig. 1(a)).

3.2. Vegetation distribution and VOC emission during the early-Holocene and Mid-Holocene

The total vegetation cover of the earth during the early-Holocene (~8 and ~5 ka BP) (differed relatively little from the vegetation cover of the present-potential. However, there were significant expansions in the areal coverage of tropical rainforests, monsoon forests and tropical grasslands (Table 2) that are all significant emitters of VOCs (Table 3). Additional expansions occurred in savanna and a range of ecosystem classes covering more minor areas (Table 2). The expansion of the above ecosystem classes occurred at the expense of others that were reduced considerably in areal coverage including tropical scrub, tropical desert and lowland tundra, respectively. Our calculation suggest that the alteration in ecosystem distribution and a shift towards the relative balance of ecosystems that emit VOCs at high rates to those at low rates resulted in a 20% increase in total annual VOC emissions over the present potential vegetation to 1095 Tg y^{-1} (Figs. 2–4). The effects of the warmer and more moist environmental conditions on VOC emissions of the globe are the result of large reductions in ecosystem classes emitting VOCs at low rates (<2 Tg Mha^{-1} y^{-1}) (Fig. 1(c) and (d)). During the early-Holocene, desert regions are dramatically reduced in area, while regional deserts in North America and Australia remain those in South America are eliminated, whereas the vast deserts extending from North Africa to Central Asia become confined to Central Asia alone (Fig. 1(c) and (d)). In contrast to the marked reduction in desert ecosystem distribution, those occurring in ecosystem classes emitting VOCs at the greatest rates (>15 Tg Mha^{-1} y^{-1}) are only slightly expanded relative to present potential conditions (Fig. 1(c)).

3.3. Vegetation distribution and VOC emission during the last glacial maximum

The cooler and drier glacial conditions of the LGM produced significant changes in the relative areas covered by different ecosystem classes (Fig. 1(b)), relative to the present potential conditions. Conditions during the LGM favored the development of open herbaceous steppe-tundra across mid and northern latitudes; this vegetation type that does not occur over any significant area in the present potential vegetation. LGM cold and aridity virtually eliminated coastal giant conifer, Mediterranean forest, south taiga and bog/swamp (Table 2).

While the general pattern of increasing aridity during the LGM is supported by data across many continents, reconstruction of vegetational distribution and emissions on a finer scale is confounded by the fact that detailed information on changes in species composition over time are generally only available for the forest regions of North America and Europe. The most problematic case is the 'steppe-tundra' ecosystem (vegetation classes 20a, 20b) which covered much of the northern latitudes during the LGM (9.4% of the global land area), but is absent from the present potential vegetation maps; the nearest analogs occur on isolated south facing slopes

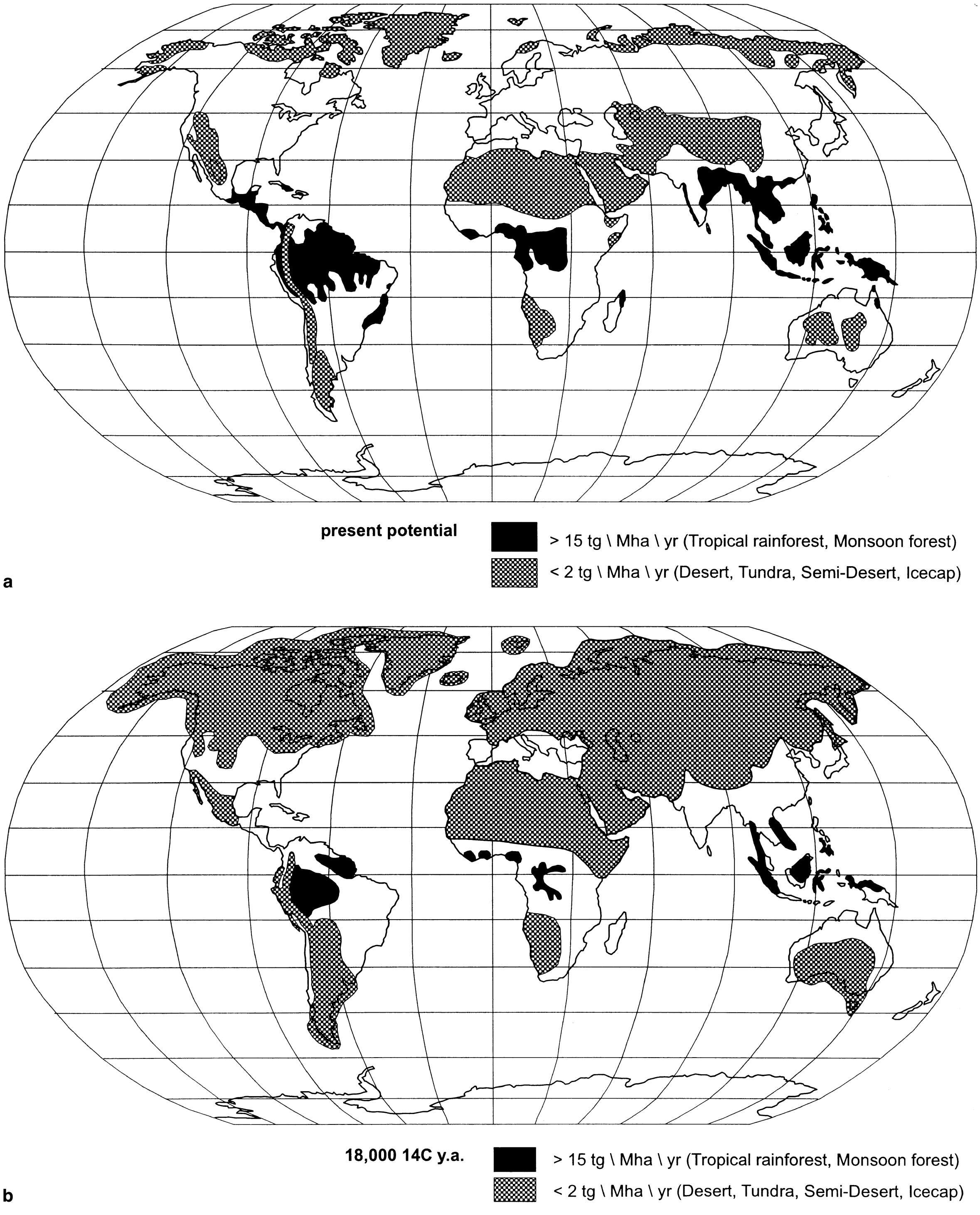
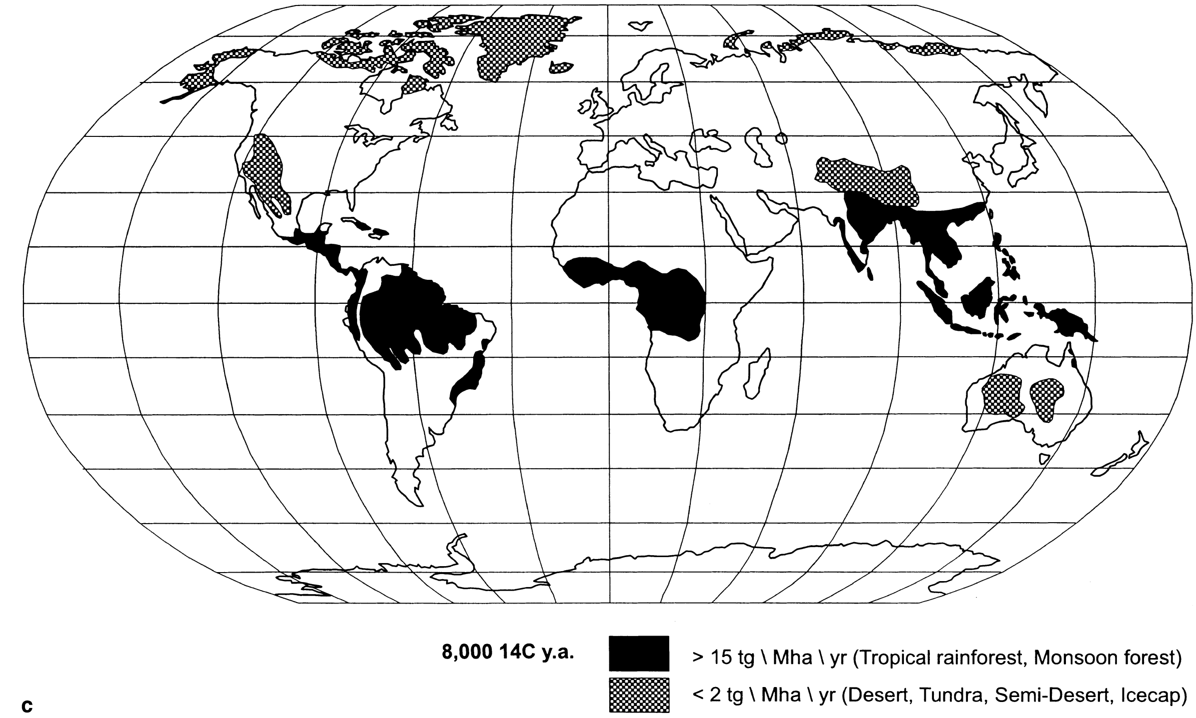


Fig. 1. Global distribution of vegetation emitting total VOCs at rates >15 Tg Mha^{-1} y^{-1} (dark shading) and vegetation emitting total VOCs at rates <2 Tg Mha^{-1} y^{-1} (light shading) for: (a) present potential vegetation distribution; (b) the LGM (~18 ka BP); (c) the early-Holocene (~8 ka BP) and (d) Mid-Holocene (~ 5 ka BP).



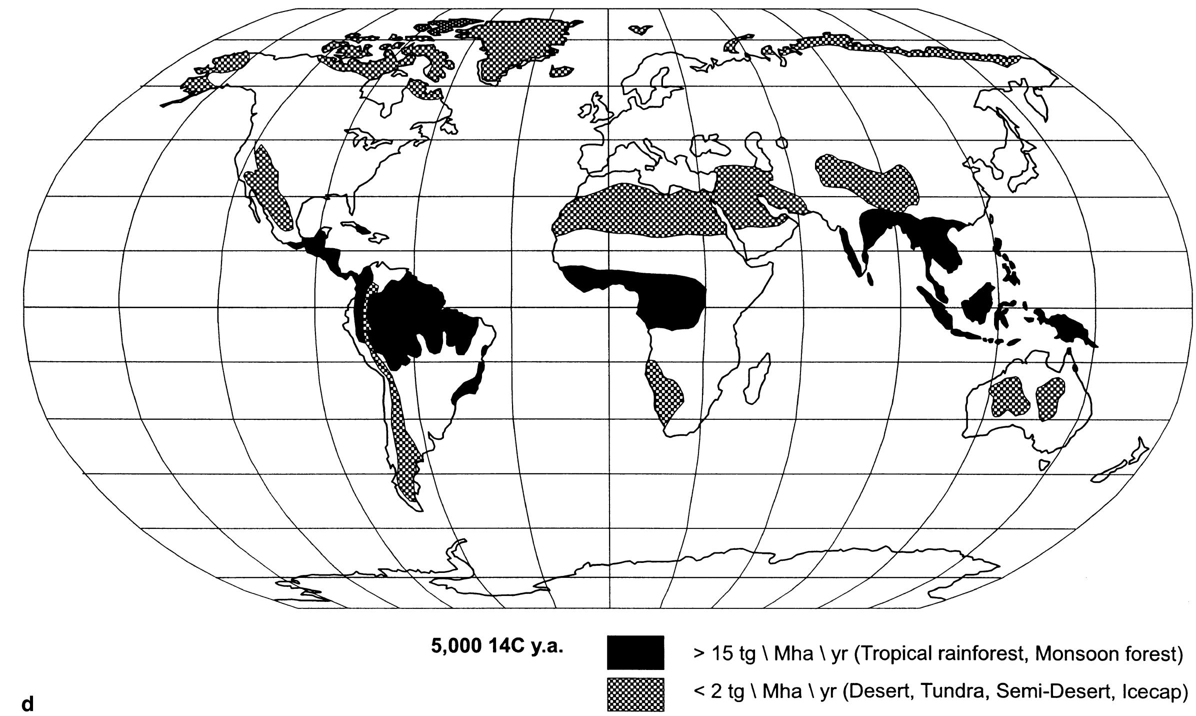


Fig. 1. (Continued).

in north-eastern Siberian mountains, and even here there are important differences in plant assemblages from the LGM 'steppe-tundra'. A range of floristic, zoological and sedimentological indicators suggest that the LGM steppe-tundra ecosystem was a fairly sparse vegetation (at least 50% open ground) resembling semi-desert or

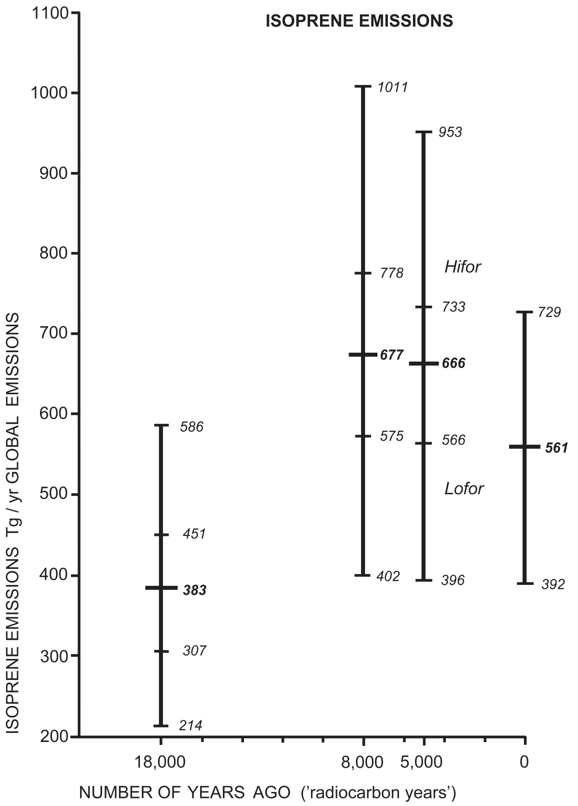


Fig. 2. Total annual global isoprene emission (Tg y^{-1}) for present potential vegetation, early-Holocene ($\sim$ 8 ka BP), and the LGM (LGM, $\sim$ 20 ka BP).

dry steppe in most areas, existing under fairly brief cool dry summers and very cold winters (Velichko and Spasskaya, 1991; Spasskaya, 1992; Kolpakov, 1995; Adams and Faure, 1997). By analogy with present-day ecosystems existing under relatively similar conditions, we have assumed a 'dry tundra' set of VOC emission characteristics for the steppe-tundra. Even if one assumes a 'dry steppe' or 'cold semi-desert' set of emissions characteristics for the steppe-tundra', this would not profoundly affect the global VOC emission.

Relative to the VOC emission from the present potential vegetation, emission from vegetation of the LGM MFA is 29% less at 643 Tg y^{-1} (Figs. 2–4). Although the percentage contribution from ORVOC emission to the total is similar to present potential vegetation, there is a shift towards slightly lower isoprene emission (59% of the total) and slightly higher monoterpene emission (16% of the total) (Figs. 2–4). These shifts reflect the vegetational distribution towards lower coverage of the high isoprene emitting tropical forests and greater coverage of temperate and polar/boreal ecosystems that emit more monoterpenes. An examination of the change in VOC emission of specific ecosystem classes reveals large shifts in the proportion of the total VOC emission originating from each ecosystem class (Figs. 2–4). During the LGM, low VOC emitting vegetation expanded to cover substantial fractions of both North and South America; similarly vegetation of North Africa, the majority of Europe and Asia are all converted to low VOC emitting forms of vegetation (Fig. 1(b)). As the low VOC emitting ecosystem classes expanded during the LGM there was a contraction in the area covered by ecosystem classes emitting VOCs at high rates. During the LGM tropical forests became confined to a region east of the Andes Mountains in South America, isolated populations in central Africa and tropical southeast Asia (Fig. 1(b)). The Low Forest Scenario assumes further large reductions in forest and other moist climate vegetation types, resulting in a further reduced VOC emission relative to the present (Figs. 2–4 and Tables 4–7).

3.4. Effects of reduced tropical temperatures on VOC emission during the last glacial maximum

The incorporation of the possible LGM lowering of tropical lowland temperatures into the estimation of total annual VOC emissions results in a significant alteration in the total annual VOC emissions and the relative proportions of isoprene, monoterpenes and ORVOCs.

The 5°C reduction of tropical temperatures reduced emission of all VOC classes from tropical vegetation by approximately 50% resulting in an annual VOC emission of 241 Tg y^{-1}, as compared to 486 Tg y^{-1} for all tropical ecosystem classes in the LGM MFA scenario. The effects of the lower VOC emission from tropical vegetation lowered total annual global VOC emission during the LGM MFA by 38% to 395 Tg y^{-1} (Figs. 2–4). The trend observed between the LGM and present potential vegetation in terms of the relative proportions of VOCs originating from different VOC classes is repeated when the simulation temperatures for tropical lowland forests are reduced (i.e., the fraction attributed to isoprene) declines (56% of total), whereas the fraction attributable to monoterpenes increases (17% of total); the fraction attributable to ORVOCs increases slightly (Figs. 2–4).

4. Discussion

Our a priori study of possible changes in VOC emission suggests that the change between LGM and Holocene conditions could well have been large. Comparison of the emission estimates for the present potential vegetation simulations serves to validate the general approach. The 561 Tg y^{-1} annual isoprene emission estimates from this study are considerably greater than estimated by Turner et al. (1991),

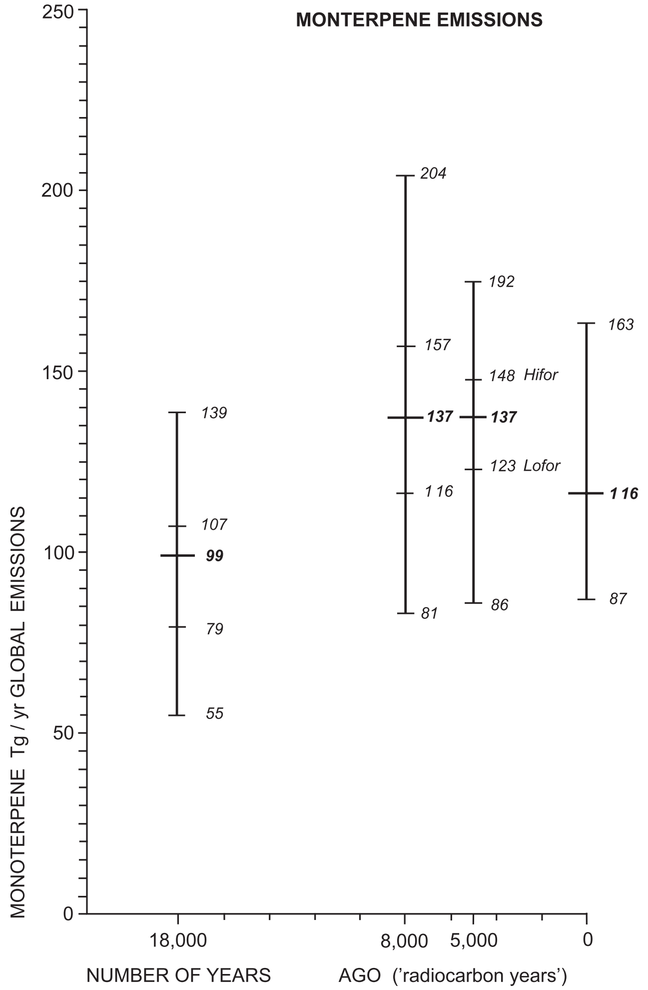


Fig. 3. Total annual global terpenoid emission (Tg y^{-1}) for present potential vegetation, early-Holocene ($\sim$ 8 ka BP), and the LGM (LGM, $\sim$ 20 ka BP).

Zimmerman (1979) or Müller (1992) at 285, 350 and 250 Tg y^{-1}, respectively (though these other estimates were for the present-actual world without agricultural effects on forest cover). But they are of similar magnitude to the ~450 Tg y^{-1} estimated by both Dignon and Logan (1990) and Rasmussen and Khalil (1988); and the 503 Tg y^{-1} estimated by Guenther et al. (1995). Similarly, the published range of annual monoterpene emission varies considerably, but the 125 Tg y^{-1} simulated here are very close to those of Müller (1992) and Guenther et al. (1995), but approximately one-fourth those estimated by Zimmerman (1979). With respect to the total annual VOC emission, those estimated here are 21% lower than the 1150 Tg y^{-1} estimated by Guenther et al. (1995), but almost double the 491 Tg y^{-1} estimated by Müller.

The range of published estimated values for both total VOCs and specific VOC components can be traced to a range of methodological differences between the models including varying estimates of ecosystem class coverage and differing incorporation of temperature and/or illumination influences on VOC emission. However, the greatest cause of the variation lies in the use of the base VOC emission factors of Guenther et al. (1995) that were developed from a literature survey of VOC emission studies and are a factor of 3–5 greater than those previously used.

Our results suggest that the annual global rate of total VOC emission could have been $\sim 30 \pm 10\%$ lower during the LGM than during the Early-Holocene and present potential conditions depending on the particular scenario for forest coverage. The reduction in VOC emission during the LGM could be even greater if there were a substantial (e.g. 5°C) reduction in the mean annual temperatures of the lowland tropics. This would reduce the VOC emission of during the LGM to 56% less than the present potential vegetation. However,

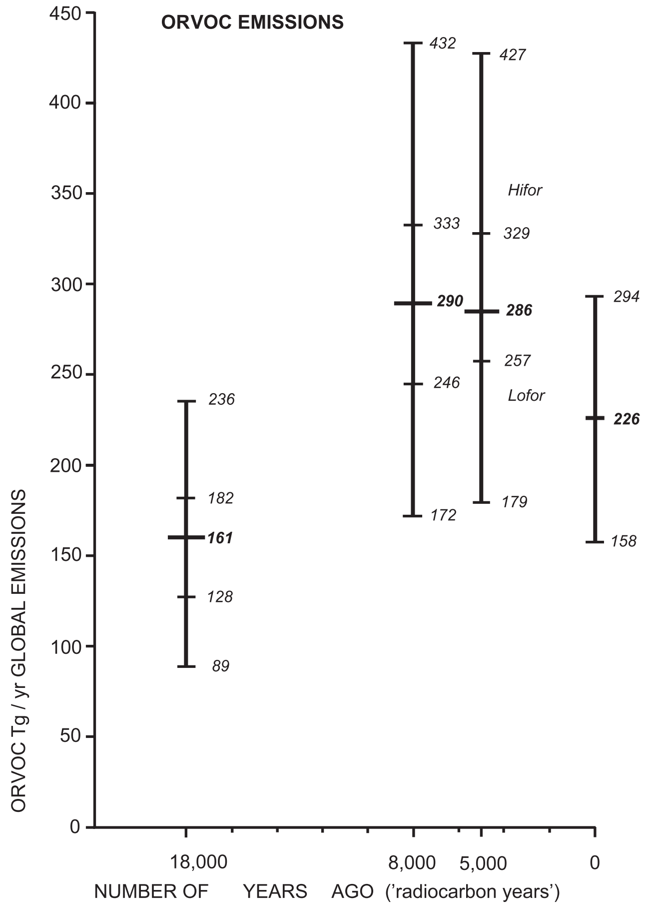


Fig. 4. Total annual global emission of other related volatile organic compound emissions (Tg y^{-1}) for present potential vegetation, early-Holocene ($\sim$ 8 ka BP), and the LGM (LGM, $\sim$ 20 ka BP).

emission of VOC from specific ecosystem classes between the LGM and the present potential vegetation are highly variable, reflecting the differential effects of cooler LGM temperatures on the spatial distribution of different ecosystem classes. For example, during the LGM there would be a reduction on VOC emission from tropical rainforests (EC 1) due to aridity and cooling, but greater emission from steppic-steppe tundra (EC 20a) representative of the changes in areal coverage of these two ecosystem classes. In spite of the combination of uncertainties in areal coverage of ecosystem classes during the LGM, the exact climatic conditions and ecosystem class VOC emission rate, the general changes which occurred between the cool and dry LGM to a warmer more vegetated Holocene resulted in a substantial increase in VOC emission. In temperate latitudes the reduction in total annual VOC emission would have been driven by the replacement of forest ecosystems by either ice sheets or ecosystems (such as tundra and grasslands) that emit VOCs at negligible rates. The expansion of grasslands during the LGM relative to present day is supported by the physiological modeling work of Collatz et al. (1998). The decline in the areal coverage of tropical low latitude forests during the LGM relative to present potential vegetation would have resulted in a decline in VOC emission, because in most cases tropical forest emit VOCs at greater rates than the dry tropical and temperate ecosystems that replaced them (Table 3).

The emission characteristics of the 'steppe-tundra' vegetation of the LGM remain somewhat problematic (Spasskaya, 1992; Velichko and Spasskaya, 1992; Kolpakov, 1995; Adams and Faure, 1997). By analogy with present-day ecosystems existing under what appear to be the most nearly similar conditions (cold winters, fairly cool summers, low vegetation cover), we have assumed a 'dry tundra' set of VOC emission characteristics for the steppe-tundra. However, this matter may require further debate and consideration.

As explained in more detail above, in order to address the uncertainty of vegetational distribution during the LGM, we repeated the VOC emission simulations

Table 4
Suggested global emission totals (Tg y) for each class of compound for the LGM vegetation distribution

Ecosystem type	LGM Iso	LGM Mono	LGM ORVOC
1. TropRainfr	108.3	13.4	50.0
2. MonsoonFr	25.4	3.5	3.4
3. TropWdld	4.6	2.0	1.7
4. TrThnScrb	12.7	3.2	4.7619
5. TrSemiDesert	2.9	0.2	0.7
6. TropGrass	53.2	13.1	16.4
7. TropDesert	1.2	1.0	1.2
9. Savanna	88.5	18.4	44.4
10. WarmTemFor	2.4	0.4	0.7
11. CtGiantConfr	0	0	0
12. TrMontFor	3.7	2.0	2.8
13a. MeditnForest	0	0	0
13b. MeditnScrub	0.2	0.1	0.1
14. CoolTempFor	0.6	0.2	0.1
15. SouthTaiga	0	0	0
16. Mid Taiga	0.6	3.1	1.1
17. OpenBoreal Woodlands	1.3	4.3	2.3
18a. Tempte woodland	16.0	16.0	10.2
18b. Tempte Scrub	11.1	2.2	4.1
19a. Mtn/dry Tundra	0.09	0.02	0.05
19b. Lowland Tundra	0.01	0.03	0.009
20a. Steppic Steppe-Tundra	1.5	0.5	0.8
20b. Tundric Steppe-Tundra	0.4	0.1	0.2
21. Polar/Mtn Desert	0	0	0
22. TemperateDes	1.1	0.7	1.1
23. TempSemi-Desert	4.4	0.7	1.2
24a. Moist Steppe	2.5	1.2	0.7
24b. Dry Steppe	32.9	8.1	10.2
25. ForestSteppe	6.5	1.6	2.0
26. ForstTundra	0	0	0
27. Bog/Swamp	0	0	0
28. Ice	0	0	0
29. Lake/river	0	0	0
Data for Fig. 4. LF/MT	307	79.2	128.8
MF/MT	383.1	99.06	161.6
HF/MT	451.7	107.7	182.3

Table 5
Suggested global emission totals (Tg y) for each class of compound for the early Holocene (~ 8000 ya) vegetation distribution

Ecosystem type	8000 ya Iso	8000 ya Mono	8000 ya ORVOC
1. TropRainfr	319.2	39.6	151.0
2. MonsoonFr	58.9	6.3	7.9
3. TropWdld	25.6	5.03	9.4
4. TrThnScrb	22.9	4.5	8.5
5. TrSDesert	5.9	0.8	1.6
6. TropGrass	38.7	9.5	11.9
7. TropDesert	0.03	0.03	0.03
9. Savanna	78.5	15.6	39.4
10. WarmTemFor	14.9	2.4	4.5
11. CtGiantConfr	0.1	0.4	0.3
12. TrMontFor	8.3	3.2	6.2
13a. MeditnForest	1.1	0.4	0.5
13b. MeditnScrub	1.0	0.4	0.5
14. CoolTempFor	31.9	5.1	9.6
15. SouthTaiga	3.4	8.0	6.1
16. Mid Taiga	3.8	8.8	6.7
17. OpenBoreal Woodlands	2.5652	6.0016	4.5496
18a. Tempte woodland	7.5808	7.5808	4.8616
18b. Tempte Scrub	1.7572	0.3496	0.6578
19a. Mtn/dry Tundra	0.3341	0.1028	0.1799
19b. Lowland Tundra	0.234	0.072	0.126
20a. Steppic Steppe-Tundra	0	0	0
20b. Tundric Steppe-Tundra	0	0	0
21. Polar/Mtn Desert	0	0	0
22. TemperateDes	0.018	0.018	0.018
23. TempSemi-Desert	5.1	0.7	1.3
24a. Moist Steppe	17.7	4.3	5.4
24b. Dry Steppe	19.9	4.9	6.1
25. ForestSteppe	6.08	1.5	1.8
26. ForstTundra	0.3	0.1	0.1
27. Bog/Swamp	0.6	0.6	0.6
28. Ice	0	0	0
29. Lake/river	0	0	0
Data for Fig. 4. 8000 LF	575	116.4	246.5
8000 MF	677.3	137.4	290.9
8000 HF	778.5	157.5	333.5

using estimates of forest area both lower (LFA) and higher (HFA) forest areas than that of the baseline LGM MFA forest distribution (Table 2). The relatively limited effects of the LFA and HFA scenarios on total annual VOC emission (−13% and +15%, respectively) is due to the fact that the change in area of the tropical vegetation (EC: 1–9 and 12) is relatively limited (−3% in the LFA and +5% in the HFA scenarios, respectively) (Table 2). As tropical forests account for a large fraction of total VOC emissions, limited changes in the coverage of these ecosystem classes have a large impact on total annual VOC emissions. The changes in the relative contribution of isoprene, monoterpenes and ORVOCs to the total annual VOC emission are influenced similarly by the LFA and HFA forest distribution scenarios.

Further uncertainty exists regarding the climate of the LGM, specifically the annual temperature regime. Temperature exerts significant leverage on the emission of VOCs on an instantaneous (Guenther et al., 1993), continental (Constable et al., 1999a) and global (Guenther et al., 1995) scales. The paleoclimatic reconstructions noted by Broecker (1985), among others, suggest that not only was the mean annual global temperature cooler during the LGM, but that tropical zones had substantially cooler-than-present lowland tropical temperatures. To simulate the effect of this putative tropical land surface cooling on VOC emission, the simulations were repeated with a 5°C reduction in the mean annual temperature for areas containing ecosystem classes 1–9. The resulting impact on total annual VOC emission was

Table 6
Suggested global emission totals (Tg y) for each class of compound for the Mid-Holocene (~ 5000 ya) vegetation distribution

Ecosystem type	5000 ya Iso	5000 ya Mono	5000 ya ORVOC
1. TropRainfr	307.3	38.1	143.1
2. MonsoonFr	58.9	6.3	7.9
3. TropWdld	23.8	4.6	8.8
4. TrThnScrb	28.6	5.6	10.7
5. TrSDesert	6.9	0.9	1.8
6. TropGrass	19.7	4.8	6.1
7. TropDesert	0.03	0.03	0.03
9. Savanna	78.2	15.5	39.2
10. WarmTemFor	15.0	2.4	4.5
11. CtGiantConfr	0.2	0.4	0.3
12. TrMontFor	14.5	5.7	10.9
13a. MeditnForest	1.2	0.5	0.5
13b. MeditnScrub	0.3	0.1	0.1
14. CoolTempFor	36.9	5.9	11.1
15. SouthTaiga	4.7	10.9	8.3
16. Mid Taiga	3.0	7.0	5.3
17. OpenBoreal Woodlands	2.1	4.9	3.7
18a. Tempte woodland	8.3	8.3	5.3
18b. Tempte Scrub	1.7	0.3	0.6
19a. Mtn/dry Tundra	0.4	0.1	0.2
19b. Lowland Tundra	0.3	0.1	0.1
20a. Steppic Steppe-Tundra	0	0	0
20b. Tundric Steppe-Tundra	0	0	0
21. Polar/Mtn Desert	0	0	0
22. TemperateDes	0.01	0.01	0.01
23. TempSemi-Desert	5.4	0.7	1.4
24a. Moist Steppe	23.8	5.8	7.3
24b. Dry Steppe	15.3	3.7	4.7
25. ForestSteppe	7.9	1.9	2.4
26. ForestTundra	0.1	0.04	0.07
27. Bog/Swamp	0.8	0.8	0.8
28. Ice	0	0	0
29. Lake/river	0	0	0
Data for Fig. 4. 5000 LF	566.5	123.8	257.8
5000 MF	666.5	137.6	286.5
5000 HF	733.1	158.2	329.4

Table 7
Suggested global emission totals (Tg y) for each class of compound for the present potential vegetation distribution

Ecosystem type	PP Iso	PP Mono	PP ORVOC
1. TropRainfr	243.0	30.9	113.7
2. MonsoonFr	38.7	4.1	5.2
3. TropWdld	23.8	4.6	8.8
4. TrThnScrb	41.5	8.2	15.5
5. TrSDesert	4.3	0.6	1.1
6. TropGrass	14.1	3.4	4.3
7. TropDesert	1.0	1.0	1.0
9. Savanna	61.0	12.1	30.6
10. WarmTemFor	11.3	1.8	3.4
11. CtGiantConfr	0.2	0.4	0.3
12. TrMontFor	6.6	2.6	5.0
13a. MeditnForest	0.6	0.2	0.3
13b. MeditnScrub	0.3	0.1	0.1
14. CoolTempFor	35.4	5.7	10.7
15. SouthTaiga	3.0	7.0	5.3
16. Mid Taiga	3.3	7.7	5.8
17. OpenBoreal Woodlands	1.7	3.9	3.0
18a. Tempte woodland	7.4	7.4	4.7
18b. Tempte Scrub	4.5	0.8	1.6
19a. Mtn/dry Tundra	0.4	0.1	0.2
19b. Lowland Tundra	0.5	0.1	0.3
20a. Steppic Steppe-Tundra	0	0	0
20b. Tundric Steppe-Tundra	0	0	0
21. Polar/Mtn Desert	0	0	0
22. TemperateDes	0.2	0.2	0.2
23. TempSemi-Desert	4.8	0.6	1.3
24a. Moist Steppe	24.6	6.0	7.6
24b. Dry Steppe	17.1	4.2	5.3
25. ForestSteppe	9.9	2.4	3.0
26. ForstTundra	0	0	0
27. Bog/Swamp	0.9	0.9	0.9
28. Ice	0	0	0
29. Lake/river	0	0	0
Data for Fig. 4. PP-30%	392.9	87.8	158.4
PP	561.4	116.5	226.3
PP+30%	729.8	163.1	294.2

38% less than simulated for the LGM under baseline climatic conditions. For this reason, variation in total VOC emission during the LGM is influenced to greater magnitude by the reduction in mean annual temperature of the tropical zones (−38%) than by variation in total global forest cover (−13.9% and +15.2% for the LFA and HFA forest cover scenarios, respectively) Figs. 2–4. This conclusion highlights that fact that improved accuracy in estimation of VOC emissions during the LGM requires improved estimates of global temperature distribution patterns rather than improved maps of vegetation distribution.

Distributional and climatic uncertainty may affect the simulations at the global scale, but the biological controls (baseline emission rate, vegetation seasonality, canopy structure) over VOC emission may be similarly influenced as do the existence of 'no analog' species or ecosystem classes under present potential vegetation conditions. The assumption that vegetation during the LGM-emitted VOCs at rates comparable to present conditions is unverifiable, but considerable uncertainty exists around the actual present-day VOC emission rates from the world's vegetation (Guenther et al., 1995). In spite of this uncertainty the simulations presented represent a valid approximation of the total annual VOC emissions from vegetation during the LGM. The influence of 'no analog' conditions under present day conditions for those during the LGM is problematical (e.g., lower concentrations of atmospheric CO_2 or extinction of important VOC emitting species). With respect to the reduced concentration of CO_2 during the LGM (~285 ul l^{-1}) relative to current levels (365 ul l^{-1}) (ref), it is possible that the reduction in carbon supply could alter the production of carbon-rich VOCs. The response of isoprene emission to elevated CO2 is highly variable with oak exhibiting increased emissions, whereas aspen displayed a reduction in isoprene emission (Sharkey et al., 1991). Studies examining the effect of double growth CO2 concentration on monoterpene emission may be less problematic as they demonstrated no change in monoterpene emission rate (Lincoln and Couvet, 1989; Constable et al., 1999b). Assuming these relationships hold for conditions during the LGM, the 80 μmol mol^{-1} decline in atmospheric CO_2 concentration may have had a negligible effect on monoterpene emission from vegetation. The influence of CO_2 concentration on ORVOCs is uncertain as the diversity of ORVOC compounds makes if difficult to assign uniform CO_2 responses to a range of metabolic processes. However, as ORVOCs contribute significantly to the total VOC emission it is necessary to clarify the control that CO_2 supply exerts on emission of these compounds. While the direct effects of CO_2 on VOC emission and production may be limited, CO_2 could indirectly affect VOC emission through an alteration of the leaf area index (LAI, unit area foliar surface/unit area ground surface). In experiments doubling of CO_2 has, at least temporarily, increased the LAI of ponderosa pine (Tingey et al., 1996) and loblolly pine (Tissue et al., 1997). Assuming that broadleaf species respond similarly and that a negative relationship occurs when CO_2 concentration is reduced it is possible that the VOC emissions simulated here overestimate those that may have occurred during the LGM. The potential for now extinct species or subspecies to have emitted VOC at greater or lesser rates than those assumed by analogy with present day vegetation classes is difficult to resolve. For example within the genus *Quercus* there is a phylogenetic separation between those species that emit isoprene and those that emit monoterpenes (Loreto et al., 1998). Should a similar situation exist between extant and extinct genotypes between present potential vegetation and the LGM the VOC emission simulated from a specific ecosystem class simulated here could be erroneous. In the pollen record, it is often difficult to tell closely related tree species apart, and thus shifts in species composition of vegetation that might result in changes in VOC emission cannot be detected and quantified.

What would be the influence of lower global VOC emissions in terms of atmospheric chemistry? There are some clues to this from a modeling experiment by Guenther et al. (1999a,b) they used a global three-dimensional chemistry and transport model (CTM) to characterize the impact of changing isoprene and monoterpene emission on distributions of the chemical compounds responsible for the oxidation capacity of the troposphere. They found that predicted distributions of ozone, CO, NOx, peroxymethacrylyl nitrate (MPAN), OH, H_2O_2, HO_2 and other compounds were sensitive to the magnitude of biogenic VOC emissions. For example factor of 2 increase in biogenic isoprene and monoterpene emissions resulted in a 10–20% decrease in OH, a 15–35% increase in H_2O_2 and a 5–15% increase in O_3 near terrestrial surfaces. The model also predicted that this factor of 2 increase in emission results in a 6–10% increase in CO throughout the southern hemisphere (up to 18 km AGL), and a 5–15% decrease in OH at heights between 7 and 14 km AGL in the tropics. While we recognize that there are other major uncertainties associated with global CTM predictions of trace gas distributions, the analysis of Guenther et al. (1999a,b) suggests that the predicted changes in biogenic isoprene and monoterpene emissions between the present time and the LGM could indeed have resulted in a significant perturbation to the chemistry of the Earth's atmosphere.

Although the uncertainty associated with the simulations is considerable, the lower total annual VOC emission during the LGM could serve to partially explain lower atmospheric CH_4 levels recorded in ice cores. Decreased VOC emission during the LGM could limit the atmospheric concentration of CH_4 by allowing reaction of hydroxyl radicals with CH_4 due to a decreased supply of the more reactive VOCs. If this situation were to prevail, the warming potential of CH_4 in the atmosphere would be minimized and surface temperature would remain cooler relative to current conditions. Without running complex atmospheric chemistry models, and identifying seasonal VOC emission rates calculated from palaeotemperature reconstructions, it is speculative to discuss the actual implications of these changes in emission rates for atmospheric chemistry or climate (which could have been offset by or add to the effects of VOC emissions from the oceans which seem to have changed greatly between glacial and interglacial conditions). However, as the experiments by Guenther et al. (1999a,b) (above) indicate, assuming the basic chemistry of the atmosphere during the LGM is similar to those of the preindustrial atmosphere there is the potential for VOC emission changes to affect the radiative balance of the atmosphere. The results of this study show that there is a clear potential for major changes in VOC emission between glacial and interglacial conditions. Indirectly by affecting atmospheric haze content and methane concentrations, these changes could account for some of the temperature and rainfall distribution differences between the LGM and those of the Holocene.

Also to be considered is that greater VOC fluxes should produce more low-level ozone, perhaps counteracting the cooling effect of haze production through the greenhouse gas properties of ozone (Hansen et al., 1997). This remains a further challenge for atmospheric chemical and climate modeling.

5. Conclusions

The difficulties of reconstructing and considering the implications of long-term changes in VOC emission are considerable, but this does not mean that the factor should be ignored. The indications are, from changes in global vegetation distribution and tropical temperatures since the LGM, there have been quite large changes in VOC emission from vegetation. These were changes in both overall quantity, and in the relative importance of different classes of compounds. Such changes present a potentially very significant 'unknown' in the climate system; something which could have affected both haze production (and thus the global heat balance) and atmospheric methane chemistry. If such an unknown factor exists, even if it cannot be precisely quantified, it must be properly allowed for in defining the error limits and range of scenarios for reconstructing past climates.

Though the scenarios we have compared are the extremes of the system, it is necessary to bear in mind that most of the last 100,000 years has been spent in intermediate vegetation states, cooler and drier than presently, but not as cold and dry as the LGM. Furthermore, there have been many sudden regional (and possibly global) transitions in climate, involving warming by several degrees in mean annual temperature in as little as a few decades (e.g. see review by Adams et al., 1999). Such changes might have been either amplified or damped by changes in vegetation cover, producing rapid changes in the efflux of VOCs. Even a pre-existing vegetation cover, such as tundra or open conifer woodland, could perhaps have responded to a sudden climate warming with a dramatic increase in VOC output, without any shift in species ranges. In at least some areas, such as European Russia, rapid warming events such as the end of the last Glacial phase were followed by a very rapid spread of early successional forest taking only a few hundred years. Many early successional species are known to be strong sources of VOCs.

Following on from our preliminary study, further work is required to explore these potential changes in VOC emissions and their implications in greater detail, using the increasingly detailed knowledge of factors controlling VOC emission rates, and using atmospheric chemical modeling techniques.

Acknowledgements

This work was in part carried out while Jonathan Adams was funded by the Lockheed-Martin Corporation as a Wigner Fellow, in the Environmental Sciences Division of Oak Ridge National Laboratory.

References

Adams, J.M., Faure, H., Faure-Denard, L., McGlade, J.M., Woodward, F.I., 1990. Increases in terrestrial carbon storage from the last glacial maximum to the present. Nature 348, 711–714.

Adams, J.M., Maslin, M., Thomas, E., 1999. Sudden climate transitions during the quaternary. Progress in Physical Geography 23, 1–36.

Adams, J.M., Faure, H., 1997. Paleovegetation maps of the world since the last glacial maximum; an aid to archaeological understanding. J. Archaeological Sci. 24, 623–647.

Alley, R.B., Meese, R.B., Shuman, A.J., 1993. A new Greenland ice-core record from GISP2. Nature 366, 443–445.

An, Z., Wu, X., Lu, Y., Zhang, D., Sun, D. Dong G., Wang, S., 1991. Quaternary palaeovegetation of China. Advances in the Natural Sciences 64, 131–165 (in Chinese).

Bennett, K.D., Tzedakis, P.C., Willis, K.J., 1991. Quaternary refugia of north European trees. J. Biogeography 18, 103–115.

Bowler, J.M., 1976. Aridity in Australia: age, origins and expression in aeolian landforms and sediments. Earth-Sci. Rev. 12, 279–310.

Broecker, W.S., 1985. Cooling the tropics. Nature 376, 212–213.

Chappellaz, J.M., Blunier, T., Ratnaud, D., Barnola, J.M., Schwander, J., Stauffer, B., 1993. Synchronous changes in atmospheric CH_4 and Greenland climate between 40 and 8 kyr BP. Nature 366, 443–445.

Charlson, R.J., Schwartz, S.E., Hales, J.M., Cess, R.D., Coakley Jr., J.A., Hansen, J.E., Hofmann, D.J., 1992. Climate Forcing by anthropogenic aerosols. Science 255, 423–430.

Clapperton, C.M., 1993. Quaternary Geology and Geomorphology of South America. Elsevier, London.

Constable, J.V.H., Guenther, A.B., Schimel, D.S., Monson, R.K., 1999a. Modeling changes in VOC emission in response to climate change in the continental US. Global Change Biology 5, 1–16.

Constable, J.V.H., Litvak, M.E., Greenberg, J.P., Monson, R.K., 1999b. Monoterpene emission from coniferous trees in response to elevated CO_2 concentration and climate warming. Global Change Biology (in press).

Crowley, T.J., 1995. Ice age terrestrial carbon changes revisited. Global Biogeochem. Cycles (in press).

Crowley, T.J., North, G.R., 1991. Palaeoclimatology. Oxford University Press, Oxford.

Dignon, J., Logan, J. 1990. Biogenic emission of isoprene: a global inventory. EOS, Transactions of the American Geophysical Union 71, p. 1260.

Fehsenfeld, F., 1992. Emissions of volatile organic compunds from vegetation and the implications for atmospheric chemistry. Global Biogeochemical Cycles 6, 389–430.

Frenzel, B., 1968. The pleistocene vegetation of northern eurasia. Science 161, 637–639.

Frenzel, B. 1992. Vegetation during the maximum cooling of the last glaciation. In: Frenzel, B., Pecsi, B., Velichko, A.A. (Eds), Atlas of Palaeoclimates and Palaeoenvironments of the Northern Hemisphere. INQUA/Hungarian Academy of Sciences. Budapest.

Geron, C., Guenther, A.B., Pierce, T.E., 1994. An improved model for estimating the emission of volatile organic compounds from forests of the eastern US. J. Geophys. Res. 99, 12773–12791.

Grichuk, V.P., 1992. Main types of vegetation (ecosystems) during the maximum cooling ofthe last glaciation. In: Frenzel, B., Pecsi, B, Velichko, A.A. (Eds), Atlas of Palaeoclimates & Palaeoenvironments of the Northern Hemisphere. INQUA/Hungarian Academy of Sciences. Budapest.

Guenther, A.B., Zimmerman, P.R., Harley, P.C., Monson, R.K., Fall, R., 1993. Isoprene and monoterpene emission rate variability: model evaluations and sensitivity analysis. J. Geophys. Res. 98, 12609–12617.

Guenther, A.B., Hewitt, C.N., Erickson, D., Fall, R., Geron, C., Graedel, T., Harley, P., Klinger, L., Lerdau, M., McKay, W.A., Pierce, T., Scholes, B., Steinbrecher, R., Tallamraju, R., Zimmerman, P., 1995. A global model of natural volatile organic compound emissions. J. Geophys. Res. 100, 8873–8892.

Guenther, A., Archer, S., Greenberg, J., Harley, P., Helmig, D., Klinger, L., Vierling, L., Wildermuth, M., Zimmerman, P., Zitzer, S., 1999a. Biogenic hydrocarbon emissions and landcover/climate change in a subtropical savanna. Physics and Chemistry of the Earth 24, 659–667.

Guenther, A., Baugh, B., Brasseur, G., Greenberg, J., Harley, P., Klinger, L., Serca, D., Vierling, L., 1999. Isoprene emission estimates and uncertainties for the Central African EXPRESSO study domain, J. Geophys. Res. (in press).

Hansen, J., Sato, M., Ruedy, R., 1997. Radiative forcing and climate response. J. Geophys. Res. 102, 6831–6864.

Hammen van der, T, Absy, M.L., 1994. Amazonia during the last Glacial. Palaeogeogr., Palaeoclim., Palaeoecol., 109, 247–261.

Hamilton, A.C., Taylor, D., 1991. History of climate and forests in tropical Africa during the last 8 Million years. Climate Change 19, 65–78.

Kolpakov, V.V., 1995. Ventifacts on the territory of the former USSR. Abstracts, INQUA Congress, Berlin, p. 140.

Lashof, D.A., Ahuja, D.R., 1990. Relative contributions of greenhouse gas emissions to global warming. Nature 344, 529–531.

Leyden, B.W., Brenner, M., Hodell, D.A., Curtis, H., 1993. Late pleistocene climate in the central american lowlands. In: Climate Change in Continental Isotopic Records. Geophysical Monograph 78. American Geophysical Union, pp. 165–178.

Lézine, A.M., Cassanova, J., 1989. Pollen and hydrological evidence for interpretation of past climates in tropical west Africa. Quaternary Sci. Rev. 8, 45–55.

Liew, P-M., Kuo, C-M., Tseng, M.-H., 1995. Vegetation of northern Taiwan during the last glacial maximum as indicated by new pollen records. Abstracts, 14th INQUA Congress, Berlin, p. 161.

Loreto, F.P., Ciccioli, E., Brancaleoni, R., Valentini, M., DeLillis, M., Csiky, C., Seufert, G., 1998. A hypothesis on the evolution of isoprenoid emission by oaks based on the correlation between emission type and Quercus taxonomy. Oecologia 115, 302–305.

Martin, P.H., Guenther, A.B., 1995. Insights into the dynamics of forest succession and non-methane hydrocarbon trace gas emissions. J. Biogeography 22, 493–499.

Monson, R.K., Lerdau, M.T., Sharkey, T.D., Schimel, D.S., Fall, R., 1995. Biological aspects of constructing volatile organic compound emission inventories. Atmospheric Environment 29A, 2989–3002.

Müller, J-F., 1992. Geographical distribution and seasonal variation of surface emissions and deposition velocities of atmospheric trace gases. J. Geophys. Res. 97, 3787–3804.

Ooi, N., 1992. Pollen spectra from around 20,000 years ago during the Last Glacial from the Nara Basin, Japan. The Quaternary Research (Japan) 31, 203–212.

Olson, J.S., Watts, J.A., Allinson, L.J., 1983. Carbon in Live Vegetation in Major World Ecosystems. Environmental Sciences Division Publication No. 1997. Oak Ridge National Laboratory, Tennessee.

Peng, C., 1994. Reconstruction du stock de carbone terrestre du passe a partir de donnees polliniques et de modelels biospheriques depuis le dernier maximum glaciaire. Abstract, PhD thesis. Universite d'Aix-Marseille II.

Prather, M.J., 1994. Lifetimes and eigenstates in atmospheric chemistry. Geophys. Res. Lett. 21, 801–804.

QEN, 1995. Adams, J.M., Faure, H. (Eds). The Quaternary Environments Network Atlas and Review of Palaeovegetation during the last 20,000 years. World Wide Web address; http://www.soton.ac.uk/~tjms/adams1.html.

Rasmussen, R., Khalil, M., 1988. Isoprene over the Amazon basin. J. Geophys. Res. 93, 1417–1421.

Ritchie, J.C., 1994. Holocene pollen spectra from Oyo, northwestern Sahara: problems of interpretation in a hyperarid environment. The Holocene 4, 9–15.

Schulz, E., 1986. Holocene vegetation in central Sahara (eastern Niger and southern Libya). In: Faure, H., Faure, L., Diop, E.S. (Eds), Changements Globaux en Afrique durant le Quaternaire: Passé-présent-futur. X Travaux et documents 197, Editions de l'ORSTOM, Paris, pp. 427–429.

Schwartz, S., 1996. The whitehouse effect – shortwave radiative forcing of climate by anthropogenic aerosols: an overview. J. Aerosol Sci. 27, 359–382.

Sharkey, T.D., Loreto, F., Delwiche, C.F., 1991. High carbon dioxide and sun/shade effects on isoprene emission from oak and aspen tree leaves. Plant Cell and Environment 14, 333–338.

Singh, G., Joshi, R.D., Chopra, S.K., Singh, A.B., 1974. Late Quaternary history of vegetation and climate of the Rajasthan Desert. India. Phil. Trans. Roy. Soc. London 267, 467–501.

Spasskaya, I.I., 1992. Dominant geomorphic processes during the maximum cooling of the last glaciation. Frenzel, B., Pecsi, B., Velichko, A.A.; Atlas of Palaeoclimates and Palaeoenvironments of the Northern Hemisphere. INQUA/Hungarian Academy of Sciences. Budapest.

Suguio, K., Absy, M.L., Flexor, J.M., Ledru, M.P., Martin, L., Sifeddine, A., Soubies, F., Turcq, B., Ybert, J.-P., 1993. Evolution of continental and coastal environments during the last climatic cycle in Brazil (120 ky B.P. to the present). Bol. IG-USP, Ser. Cient. 24, pp. 27–41.

Thom, B., Hesp, B., Bryant, E., 1994. Last glacial coastal dunes in Eastern Australia and implications for landscape stability during the Last Glacial Maximum. Palaeogeogr., Palaeoclim., Palaeoecol. 111, 229–248.

Tingey, D.T., Johnson, M.G., Phillips, D.L., Johnson, D.W., Ball, J.T., 1996. Effects of elevated CO_2 and nitrogen on the synchrony of shoot and root growth in ponderosa pine. Tree Physiology 16, 905–914.

Tissue, D.T., Thomas, R.B., Strain, B.R., 1997. Atmospheric CO_2 enrichment increases growth and photosynthesis of Pinus taeda: a 4 year experiment in the field. Plant Cell and Environment 20, 1123–1134.

Tong, G., Shao, S., 1991. Evolution of quaternary climate in China. In: Zhang, Z. (Ed.), The Quaternary of China. China Ocean Press, pp. 42–76.

Turner, C., Hannon, G.E., 1988. Vegetational evidence for late quaternary climate changes in SW Europe. Phil. Trans. Roy. Soc. 285, 451–485.

Turner, D.P., Baglio, J.V., Wones, A.G., Pross, D., Vong, R., McVeety, B.D., Phillips, D.L., 1991. Climate change and isoprene emissions from vegetation. Chemosphere 23, 37–56.

Van neer, W., 1984. Faunal remains from Matupi cave, an iron age and late stone age site in Northeastern Zaire. Academiae Analecta 46, 58–76.

Velichko, A.A., Isavea, L.L., 1992. Landscape types during the last glacial maximum. In: Frenzel, B., Pecsi, B., Velichko, A.A., Atlas of Palaeoclimates and Palaeoenvironments of the Northern Hemisphere. INQUA/Hungarian Academy of Sciences. Budapest.

Velichko, A.A., Spasskaya, I.I. (Eds), 1991. Legend of Regions of the Land During Maximum Stage of Late Valdai Glaciation. Geogeodezia SSSR.

Walter, H., 1971. Ecology of Tropical and Subtropical Vegetation. Oliver & Boyd, Edinburgh.

Wang, P., Sun, X., 1994. Last glacial maximum in China: comparison between land and sea. Catena 23, 341–353.

Zimmerman, P., 1979. Testing of hydrocarbon emissions from vegetation, leaf litter and aquatic surfaces, and development of a method for compiling biogenic emissions inventories. Report EPA-450-4-70-004. US Environmental Protection Agency, Research Triangle Park, NC, USA, p. 103.

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