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Modelling changes in VOC emission in response to climate change in the continental United States

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Abstract

The alteration of climate is driven not only by anthropogenic activities, but also by biosphere processes that change in conjunction with climate. Emission of volatile organic compounds (VOCs) from vegetation may be particularly sensitive to changes in climate and may play an important role in climate forcing through their influence on the atmospheric oxidative balance, greenhouse gas concentration, and the formation of aerosols. Using the VEMAP vegetation database and associated vegetation responses to climate change, this study examined the independent and combined effects of simulated changes in temperature, CO_2 concentration, and vegetation distribution on annual emissions of isoprene, monoterpenes, and other reactive VOCs (ORVOCs) from potential vegetation of the continental United States. Temperature effects were modelled according to the direct influence of temperature on enzymatic isoprene production and the vapour pressure of monoterpenes and ORVOCs. The effect of elevated CO_2 concentration was modelled according to increases in foliar biomass per unit of emitting surface area. The effects of vegetation distribution reflects simulated changes in species spatial distribution and areal coverage by 21 different vegetation classes. Simulated climate warming associated with a doubled atmospheric CO_2 concentration enhanced total modelled VOC emission by 81.8% (isoprene +82.1%, monoterpenes +81.6%, ORVOC +81.1%), whereas a simulated doubled CO_2 alone enhanced total modelled VOC emission by only +11.8% (isoprene +13.7%, monoterpenes +4.1%, ORVOC +11.7%). A simulated redistribution of vegetation in response to altered temperatures and precipitation patterns caused total modelled VOC emission to decline by 10.4% (isoprene −11.7%, monoterpenes −18.6%, ORVOC 0.0%) driven by a decline in area covered by vegetation classes emitting VOCs at high rates. Thus, the positive effect of leaf-level adjustments to elevated CO_2 (i.e. increases in foliar biomass) is balanced by the negative effect of ecosystem-level adjustments to climate (i.e. decreases in areal coverage of species emitting VOC at high rates).

Keywords: climate change, isoprene, modelling, monoterpenes, VOC emission.

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Introduction

The emission of volatile organic compounds (VOCs, including isoprene, monoterpenes, and others) from terrestrial vegetation plays an important role in the concentrations and lifetimes of atmospheric trace gases including CO (Hatakeyama *et al.* 1991), ozone (Liu *et al.* 1987), aerosols (Andreae & Crutzen 1997), and OH radical (Jacob & Wofsy 1988), affecting the global carbon cycle (Fehsenfeld *et al.* 1992). Changes in the concentrations of these gases are important for issues relating to local and regional ozone pollution and potential influence on climate change. These concerns have prompted the development of national and global inventories of the emission of VOCs into the atmosphere from natural sources which contribute to more than two thirds of the

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global VOC emissions (Müller 1992; Guenther *et al.* 1995). Because of the dominance of biogenic VOC emission in the total emission budget it is crucial to understand the biological controls over these processes (Monson *et al.* 1995).

Volatile organic compounds are of particular concern because of their potential to influence the radiative balance of the atmosphere through their influence on greenhouse gases (Hatakeyama *et al.* 1991; Johnson & Derwent 1996) and aerosol formation upon oxidation (Hatakeyama *et al.* 1989). VOCs may facilitate radiative forcing by reducing concentrations of OH, the major sink for methane, which could allow the atmospheric concentration and lifetime of methane to increase (Wayne 1991; Fehsenfeld *et al.* 1992). In contrast, oxidation of monoterpenes to form aerosols (Zhang *et al.* 1992; Pandis *et al.* 1991) may have a negative effect on radiative forcing by increasing the atmospheric albedo and minimizing surface warming (Andreae & Crutzen 1997). Therefore, understanding changes in concentrations of VOCs and their effects on methane and other greenhouse gases may be important for estimating changes in the forcing of global temperature.

In addition to VOCs playing an important role in climate through atmospheric chemistry, climate also directly affects the rate at which VOCs are emitted to the atmosphere through direct and indirect mechanisms. The principal direct effect involves the influence of temperature on the vapour pressure of VOCs, whereas indirect effects are mediated by the influence of temperature and light intensity on vegetation biochemistry and therefore VOC production. Annual mean temperature and precipitation patterns also indirectly influence VOC emission by determining vegetation species composition and vegetation characteristics including productivity, leaf area index, vegetation phenology, and canopy structure. Advances in our understanding of these direct and indirect drivers of emission have increased VOC emission model complexity and accuracy (Guenther *et al.* 1993; Lamb *et al.* 1993; Geron *et al.* 1994; Guenther *et al.* 1995).

Current annual global VOC emission is estimated to be ≈ 510 Tg isoprene, 130 Tg monoterpenes, and 260 Tg ORVOC (other reactive VOCs with atmospheric lifetimes < 1 d) and 260 Tg other VOC (all VOCs with atmospheric lifetimes > 1 d) (Guenther *et al.* 1995). In North America the VOC contributions of woodlands are particularly important as they often contain isoprene-emitting species and they cover a large portion of the United States. In order to improve VOC emission resolution from eastern North America, Geron *et al.* (1994) incorporated genera-specific emission rates and detailed species distribution information into existing emission models. They determined that VOC emission from this region could be 3–5 times higher than previous estimates and that regional emission estimates are highly influenced by assumptions concerning forest species composition (Geron *et al.* 1994). Using existing estimates of annual VOC emission from the U.S as a comparison, estimates of how VOC emission will change in response to climatic alterations can be generated. Climatic alterations due to anthropogenic activities will likely result in a suite of environmental changes that will affect VOC emission including mean annual temperature, availability of carbon for VOC production, and changes in species distribution patterns. As the emission of VOCs is highly dependent upon both climatic and vegetation characteristics it is critical to estimate how future changes in these factors could alter the VOC emission inventory for the United States.

The goals of the current study were to simulate the effects of different aspects of climate change on annual VOC emission from the United States by: (i) linking measured VOC emission rates and estimates of present potential vegetation patterns of the continental U.S. to estimate present potential VOC emissions; and (ii) independently estimate how annual VOC emission from the continental U.S. is influenced by (a) modelled changes in local annual temperature regimes; (b) a simulated doubling of atmospheric CO_2 concentration; (c) simulated changes in species distribution pattern; and (d) the combined influences of temperature, doubled CO_2 concentration and vegetation redistribution.

Materials and methods

Estimation of how VOC emission may change in response to alteration of environmental conditions was determined by combining models of general circulation (for climate), biogeochemistry and biogeography (for vegetation processes and distribution) and plant physiology (for VOC emission). The estimation of temperature and precipitation changes was generated using a general circulation model (GCM) developed by the United Kingdom Meteorological Office (UKMO) in a doubled CO_2 atmosphere. The effect of a doubled CO_2 atmosphere on plant processes and VOC emission was determined by estimating the change in annual net primary productivity (NPP) using the CENTURY biogeochemistry model (Parton *et al.* 1993). The effects of the potential alteration in vegetation distribution were examined in coupled simulations that linked the CENTURY model to an alteration in the spatial distribution of different vegetation types as predicted by the MAPSS biogeography model (Neilson 1995). The changes in vegetation characteristics (NPP, foliar density, vegetation type) under each of the climate scenarios (increased temperature; doubled CO_2 concentration, altered vegetation distribution; and a combination of all three) were combined with the physiological algorithms developed by Guenther *et al.* (1995) and modified by Guenther (1997) to estimate changes in emission of isoprene, monoterpenes, and ORVOC.

UKMO climate change scenarios

General circulation models have been developed to provide a tool to predict how anthropogenic alterations in the composition of the atmosphere may impact global temperature and precipitation patterns. The VEMAP study (VEMAP Members 1995) examined the effects of three different GCMs on the vegetation of the United States that provide a range of potential changes in annual temperature and precipitation patterns across the country. The UKMO GCM (Wilson & Mitchell 1987) utilized here predicted the greatest annual temperature increase of the three GCMs used in the VEMAP study in addition to a 12% increase in precipitation. The greater temperature predictions of the UKMO GCM are the result of a simplified cloud structure that minimizes the global cooling effect of increased cloud albedo and a penetrative convection scheme as opposed to using a moist convective adjustment. The UKMO model version used here incorporates storage and vertical exchange of heat and moisture with the atmosphere using a 'mixed-layer' ocean representation, however, horizontal ocean currents are not simulated. Global simulation output from the UKMO GCM represents the magnitude of climate warming predicted for the years 2070–2099 for a doubled CO_2 atmosphere. The grid size for the UKMO simulations was $2.5° \times 3.75°$, each of which were decomposed to estimate the temperature increases at the finer-scale VEMAP grid of $0.5° \times 0.5°$ (VEMAP Members 1995).

Vegetation types and distribution

The present potential vegetation of the U.S. is based on the work of the VEMAP study that estimated the distribution and area coverage of 21 vegetation types (Table 1) throughout the United States (VEMAP Members 1995). The $0.5° \times 0.5°$ resolution utilized by the VEMAP study greatly simplifies the complexities of many vegetation types with respect to precise species composition, age and canopy structure in addition to their geographical boundaries. Although the vegetation composition is simplified it serves as an approximation of the vegetation distribution from which the emission of VOCs can be estimated. The present potential U.S. vegetation distribution and the UKMO GCM simulations served as an input to the linked CENTURY and MAPSS models to predict how climatic alterations might affect vegetation productivity and distribution, respectively, due to estimated changes in mean annual temperature and precipitation patterns.

Estimation of VOC emission rates

Emission rates of isoprene, monoterpenes, and ORVOC are highly dependent upon physical conditions (temperature and light intensity) and vegetation characteristics (type, canopy structure, leaf area index, leaf characteristics). Accurate accounting of the changes in emission with climate must address these issues in a realistic manner. Recent sophisticated models incorporate the effects of light attenuation through the canopy on isoprene emission and vegetation characteristics including foliage phenology. Guenther *et al.* (1993) described isoprene and monoterpene emission rate as a function of both temperature and light intensity using semi-mechanistic algorithms with empirically determined parameterization coefficients. The emission of ORVOC as influenced by temperature and light are unknown and likely vary for different compounds, as such, estimates of ORVOC emission are uncertain. In these simulations emission of ORVOC is treated identically to monoterpenes in being influenced only by temperature. Additionally, a common emission rate and temperature coefficient for ORVOCs was applied to all vegetation classes.

The Guenther *et al.* (1993) equations developed for estimating changes in instantaneous VOC emission rate were reformulated by Guenther *et al.* (1995) to estimate global emissions of VOCs by adjusting the emission rates according to variations in vegetation NPP, foliar phenology, specific leaf weight (SLW, g dry mass per m^2 projected leaf area), average annual temperature, and canopy structure effects on light attenuation. The Guenther *et al.* (1995) equations were modified in several respects in order to address the potential effects of climate change on VOC emission. First, the correction factor for the influence of temperature on isoprene emission was adjusted according to the recommendations of Guenther (1997). Second, the Olson vegetation types (Olson 1992) and standard emission rates used in Guenther *et al.* (1995) were condensed to approximate the VEMAP vegetation types and allow estimation of VOC emission for each climate change scenario (Tables 1 and 2). Third, it is documented that an increase in growth CO_2 concentration results in an increase in SLW that could change VOC emissions through an alteration in canopy structure. Although the effects of CO_2 on SLW are variable depending on species, we approximated the effects for each vegetation class based on a literature review (Table 2, Appendix 1). Changes in leaf SLW alter VOC emission by changing light penetration into the

Table 1 Description of VEMAP vegetation classes and equivalency to the vegetation classes used by Guenther *et al.* (1995) and area coverage (10^3 km^2) for each. Vegetation categories are denoted by capitals, vegetation classes are denoted by numbers.

VEMAP Vegetation Class	Description	Guenther *et al.* (1995) Class Equivalent	Area coverage (10^3 km^2)
Tundra			
1	Tundra	53	21
Forests			
2	Boreal Conifer Forest	21	164
3	Maritime Temperate Conifer Forest	22, 62	208
4	Continental Temperate Conifer Forest	22, 27	488
5	Cool Temperate Mixed Forest	24	422
6	Warm Temperate/Subtropical Mixed Forest	24, 26, 27	957
7	Temperate Deciduous Forest	26	882
8	Tropical Deciduous Forest	Not Present	0
9	Tropical Evergreen Forest	Not Present	0
Xeromorphic woodlands and forests			
10	Temperate Mixed Xeromorphic Woodland	59	113
11	Temperate Conifer Xeromorphic Woodland	48	162
12	Tropical Thorn Woodland	Not Present	0
Savannas			
13	Temperate/Subtropical Deciduous Savanna	43	693
14	Warm Temperate/Subtropical Mixed Savanna	41	173
15	Temperate Conifer Savanna	27	18
16	Tropical Deciduous Savanna	Not Present	0
Grasslands			
17	C3 Grassland	Other crop/grass	816
18	C4 Grassland	Other crop/grass	1040
Shrublands			
19	Mediterranean Shrubland	46	38
20	Temperate Arid Shrubland	52	793
21	Subtropical Arid Shrubland	41, 59	423

canopy, thereby influencing the emission of isoprene, but not emission of monoterpenes and ORVOC.

Results

Present climate

Current potential vegetation. The present potential vegetation of the United States contains all of the VEMAP vegetation classes excepting tropical deciduous and evergreen forests (classes 8 and 9), tropical thorn woodland (class 12) and tropical deciduous savanna (class 16) (Table 1). Using the six major vegetation categories identified by the VEMAP study, forests dominate potential vegetation covering ≈41% of the vegetated area (Table 1). Significant fractions of area are also covered by savannas and shrublands that account for 24.7% and 16.7% of the vegetated area, respectively (Table 1). The largest area covered by a single vegetation type is C4 grasslands (species possessing the C4 photosynthetic pathway, class 18) covering $\approx 1 \times 10^6$ km^2, or 13.9% of the total vegetated area of the U.S. (Table 1). Significant areas are also covered by warm temperate/subtropical mixed forest (class 6) and temperate deciduous forest (class 7) (accounting for ≈12.2% each), C3 grassland (species possessing the C3 photosynthetic pathway, class 17, 10.9%) temperate arid shrubland (class 20, 10.6%), and temperate/subtropical deciduous savanna (class 13, 9.2%). The remaining vegetated area is covered by the remaining vegetation classes (Table 1).

Current VOC emissions. The areal extent of vegetation coverage by the different classes is critical for estimating VOC emissions as the base emission rates vary over a 9-fold range for isoprene and a 12-fold range for monoterpenes (Table 2). Isoprene emissions on a gram dry weight basis (Table 2) dominate VOC emissions from temperate deciduous forests (class 7) and temperate conifer xeromorphic woodlands (class 11) that occupy ≈11.7% and 3.5%, respectively, of the vegetation cover of

Table 2 Vegetation base emission rates of isoprene (Isop. Emis.) and monoterpenes (Mono. Emis.) ($\mu gC\ g^{-1} h^{-1}$) and specific leaf weight (SLW, g m^{-2} projected area) for growth under current (350 $\mu L\ L^{-1}$ CO_2) and elevated (700 $\mu L\ L^{-1}$ CO_2) CO_2 conditions for the VEMAP vegetation classes. VOC emission rates were derived from Guenther *et al.* (1995) and SLW from a literature review (see Appendix 1).

Vegetation class		Isop. Emis.	Mono. Emis.	SLW 350	SLW 700
1	Tundra	16.0	0.8	0.06	0.07
2	Boreal Conifer Forest	8.0	2.4	128.5	145.2
3	Maritime Temperate Conifer Forest	8.0	2.4	102.5	116.1
4	Continental Temperate Conifer Forest	12.0	2.4	102.5	116.1
5	Cool Temperate Mixed Forest	24.0	0.8	117.8	133.5
6	Warm Temperate/Subtropical Mixed Forest	28.3	1.3	103.2	119.7
7	Temperate Deciduous Forest	45.0	0.8	88.1	99.8
8	Tropical Deciduous Forest	Not Present			
9	Tropical Evergreen Forest	Not Present			
10	Temperate Mixed Xeromorphic Woodland	16.0	0.8	209.1	236.7
11	Temperate Conifer Xeromorphic Woodland	45.0	2.4	318.8	353.9
12	Tropical Thorn Woodland	Not Present			
13	Temperate/Subtropical Deciduous Savanna	16.0	0.8	49.3	58.2
14	Warm Temperate/Subtropical Mixed Savanna	24.0	1.2	40	47.2
15	Temperate Conifer Savanna	16.0	2.4	318.8	353.9
16	Tropical Deciduous Savanna	Not Present			
17	C3 Grassland	5.0	0.2	40.3	55.6
18	C4 Grassland	5.0	0.2	39.8	54.1
19	Mediterranean Shrubland	16.0	1.2	150.1	177.7
20	Temperate Arid Shrubland	16.0	0.8	180.2	213.3
21	Subtropical Arid Shrubland	20.0	1.0	165.2	195.5

the U.S. (Table 1). Monoterpene emissions occur at a much lower rate on a gram dry weight basis than isoprene (Table 2) and occur principally from coniferous vegetation (vegetation classes 2, 3, 4, and 15) that, when combined, occupy $\approx$11.7% of the U.S. vegetation cover (Table 1). The total modelled annual VOC emission from vegetation of the U.S. is estimated at 24.1 Tg and is composed of 64% isoprene, 16% monoterpenes, and 20% ORVOC (Fig. 1). Using the broad isoprene emission classes defined in Table 3, low isoprene emission vegetation covered 2.2×10^6 km^2 or 29.6% of the vegetated area and an additional 28.8% of the area is covered by vegetation that emits isoprene at a low to medium rate. In contrast, medium-to-high and high isoprene emission vegetation covered 26.3% and 15.2% of the vegetated area, respectively.

The total annual U.S. emission of isoprene is dominated by three vegetation classes, warm temperate/subtropical mixed forest (class 6), temperate deciduous forest (class 7) and temperate/subtropical deciduous savanna (class 13) that together account for over 70% of the estimated annual emissions (Fig. 2). The top three vegetation classes for the emission of monoterpenes and ORVOC account for 63% and 54% of their respective totals (Fig. 2). The only vegetation class that ranks as one of the highest emitters for all three types of VOCs was the warm temperate/subtropical mixed forest (class 6). Although this vegetation class only covers 12.7% of the vegetated area of the U.S., it dominates as a VOC emission source (Fig. 2).

Effects of changes in climate factors

Altered temperature scenarios. The UKMO simulations predict annual temperature increases for the United States between 4.3 °C and 9.1 °C with an average increase of 6.7 °C. Increases of 6.0–7.0 °C are relatively evenly distributed in the western U.S., whereas in the eastern portion of the country increases between 8.0 °C and 9.1 °C are more common. Of the vegetated grid cells; 29% show a temperature elevation greater than 7.0 °C, 57.6% an increase between 6.0 °C and 7.0 °C, and 13.3% an increase < 6.0 °C (Fig. 3). The largest temperature increases occur in the north-east quadrant of the country forming a crescent around the Great Lakes. The large temperature increases in this region affect several vegetation classes including boreal conifer forest (class 2), continental temperate conifer forest (class 4), cool temperate mixed forest (class 5), and temperate deciduous forest (class 7). Additionally, there are smaller areas of temperature elevation above the U.S. average in central western Texas and the Pacific North-west. The largest localized temperature increase

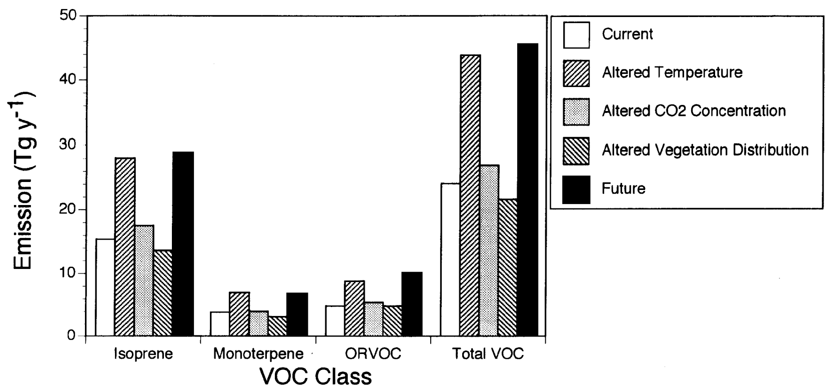

Fig. 1 Change in annual emissions from the United States of isoprene, monoterpenes, other reactive VOCs (ORVOC), and their sum (Total VOC) under current climatic conditions (open bars), elevated temperatures as predicted by the UKMO GCM conditions (forward hatched bars), doubled CO_2 conditions (light shaded bars), altered vegetation distribution as predicted by the MAPSS model conditions (rearward hatched bars), and future climatic conditions with elevated temperatures, doubled CO_2 concentration, and vegetation redistribution (dark shaded bars).

Table 3 Isoprene emission categories and their component vegetation classes.

Isoprene emission category	Isoprene emission rate (μgC g^{-1} h^{-1})	Component vegetation classes
High	>30	7, 11
Medium High	$20 < \times < 30$	5, 6, 14, 21
Medium Low	$10 < \times < 20$	1, 4, 10, 13, 15, 19, 20
Low	<10	2, 3, 17, 18

occurs in southern Alabama spreading west into Mississippi and east into Georgia. Superimposing the UKMO temperature elevations on the vegetation distributions illustrates that different vegetation classes are exposed to widely differing temperature elevations (Table 4). Temperate mixed xeromorphic woodland, Mediterranean shrubland, and subtropical arid shrubland (classes 10, 19, and 21) experience temperature elevations of 5.8 °C. In contrast, boreal conifer forest, cool temperate mixed forest, temperate deciduous forest, and temperate/subtropical deciduous savanna (classes 2, 5, 7, and 13) are exposed to temperature elevations in excess of 7.0 °C (Table 4). Of the 17 vegetation classes within the present potential vegetation of the U.S., five experience increases above the U.S. mean increase of 6.7 °C including cool temperate mixed forest (class 5) and temperate deciduous forest (class 7) (Table 4). The remaining 12 vegetation classes are subject to a temperature elevation below the average predicted for the U.S. (Table 4). Additionally, there is substantial variation in the temperature increase occurring within a single vegetation class. For example, grid cells containing boreal conifer forest (class 2) are subject to a range of temperature increases spanning 2.4 °C (6.2 °C to 8.8 °C), whereas in continental temperate conifer forest (class 4) the range is more extreme at 3.9 °C (Table 4). The least variation occurs in vegetation types covering a limited area including tundra (class 1) and temperate conifer savanna (class 15) (Table 4).

The total U.S. NPP increased 18% under the UKMO temperature elevation scenarios (Table 5). However, the different vegetation categories responded differently; the elevation of NPP in forests and shrublands exceeded those of other vegetation classes (Table 5). An increase of 83% is predicted for the NPP of Mediterranean shrubland (class 19), whereas NPP of forests (classes 2, 3, 4, and 5) and temperate conifer savanna (class 15) all increased ≈ 40%. In contrast, temperate deciduous forests (class 7) and warm temperate/subtropical mixed forests (class 6) are predicted to increase 22.4% and 11.2%, respectively. The increase in NPP in the different vegetation classes result partially from variation in the temperature elevation of the different grid cells containing a specific vegetation class (Table 4).

Effects of altered temperature on VOC emission. The estimated VOC emissions are highly influenced by temperature, typically exhibiting an exponential response. The broad-based increase in temperature across the U.S. as simulated by the UKMO GCM produced a large increase in the simulated emission of all types of VOCs from all vegetation classes. This resulted in an increase of 81.8% in total simulated annual U.S. VOC emission (Fig. 1). Although temperature produced large increases in VOC emissions from all vegetation classes, not all classes were stimulated equally. In the case of isoprene, the largest percentage increase occurred in cool temperate mixed forest (class 5) at 108%, whereas the smallest percentage increase (67.8%) occurred in temperate mixed xeromorphic woodland (class 10). Change in modelled VOC emission within a vegetation class were variable depending upon the grid cell specific temperature increase. Emission of isoprene from warm temperate/subtropical mixed forest (class 6), for example, increased between 90% and almost 200% (Plate 1a),

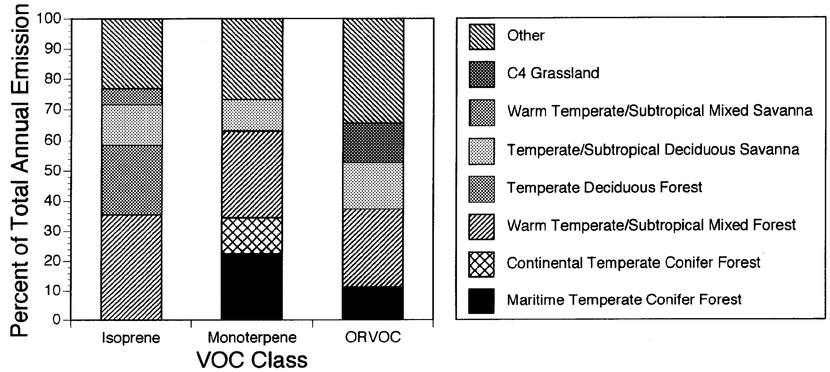

Fig. 2 Percentage contribution of major vegetation classes to the total emission of isoprene, monoterpenes, and ORVOC under present potential vegetation and climate.

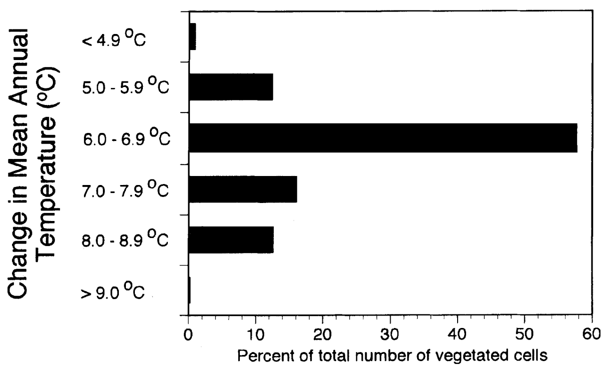

Fig. 3 Magnitude of changes in mean annual temperature as predicted by the UKMO GCM as a percentage of the total number of vegetated 0.5° × 0.5° cells used in the VEMAP study.

whereas monoterpenes increased between 60% and 100% (Plate 2a). Similarly striking were the large emission increases around the Great Lakes for both isoprene (Plate 1a) and monoterpenes (Plate 2a). These enhanced simulated emissions occurred across several vegetation types and largely reflects the large temperature increases predicted by the UKMO GCM in this region. The basic order for the dominance of emission by specific vegetation classes was unchanged from that in present potential conditions (Fig. 2).

Altered CO_2 scenarios. An increase in CO_2 concentration eliminates the carbon limitation on maximum photosynthetic rate imposed by the biochemical characteristics of the primary photosynthetic carboxylation enzyme. Enhanced carbon availability frequently stimulates growth, however, growth may be limited by the availability of other resources, especially nitrogen (McGuire *et al.* 1995). The potential effects of a doubled CO_2 concentration produced an increase in total U.S. NPP of 5.0%, however, variable increases in NPP occurred in specific vegetation categories (e.g. grasslands + 9.8% NPP and forests + 3.3% NPP) (Table 5). A 10.2% increase in NPP occurred in temperate mixed xeromorphic woodlands (class 10) and 8% – 9% increases in C3 and C4 grasslands (classes 17 and 18), temperate conifer savanna (class 15), tundra (class 1), and Mediterranean shrubland (class 19) (Table 5). Additionally, NPP of certain vegetation classes was essentially unaltered by growth at elevated CO_2 experiencing an increase < 2.5% including cool temperate mixed forests (class 5), warm temperate/subtropical mixed forest (class 6), and subtropical arid shrubland (class 21). In conjunction with changes in NPP, growth at elevated CO_2 is also predicted to result in increased SLW (Table 2). On average SLW of all vegetation classes increased ≈ 16.6%, but there were a wide range of responses within the different vegetation categories. Grasslands (classes 17 and 18) exhibited a 37% increase in SLW, in shrublands (classes 19, 20, and 21) SLW increased 18%, whereas in the remaining vegetation classes SLW increased between 4% and 21%.

Effect of altered CO_2 concentration on VOC emission. The effects of increased growth CO_2 on modelled VOC emission are the result of concurrent changes in NPP and foliar density. The emission of isoprene is influenced by both of these factors due to the interaction between isoprene emission and light intensity. However, neither monoterpene or ORVOC emission is affected by variation in light intensity restricting emission changes in these VOC types to changes caused by altered NPP alone. Through the linked effects of changes in foliar density and NPP, growth at elevated CO_2 caused simulated annual U.S. isoprene emission to increase 13.7%, whereas emission of monoterpenes and ORVOC increased 4.1% and 11.7%, respectively (Fig. 1). Growth at elevated CO_2 generally enhanced the emission of isoprene from all vegetation classes between 15% (tundra, class 1) and 165% (Mediterranean shrubland, class 19) with monoterpenes and ORVOCs showing similar trends. Variation in modelled VOC emission response to increased growth CO_2 concentration is due to

Table 4 Mean elevation in temperature (°C) as predicted by the UKMO GCM (see text) for each of the 21 VEMAP vegetation classes.

Vegetation Class		Temp. Elevation Mean ± SD (range)
1	Tundra	6.49 ± 0.18 (6.1–6.7)
2	Boreal Conifer Forest	7.18 ± 0.95 (6.2–8.8)
3	Maritime Temperate Conifer Forest	6.39 ± 0.26 (5.4–6.6)
4	Continental Temperate Conifer Forest	6.83 ± 0.79 (5.2–9.1)
5	Cool Temperate Mixed Forest	8.19 ± 0.48 (6.5–9.1)
6	Warm Temperate/Subtropical Mixed Forest	6.39 ± 0.72 (4.3–7.9)
7	Temperate Deciduous Forest	7.38 ± 0.72 (5.4–8.6)
8	Tropical Deciduous Forest	Not Present
9	Tropical Evergreen Forest	Not Present
10	Temperate Mixed Xeromorphic Woodland	5.83 ± 0.36 (5.2–6.5)
11	Temperate Conifer Xeromorphic Woodland	6.22 ± 0.32 (5.1–6.8)
12	Tropical Thorn Woodland	Not Present
13	Temperate/Subtropical Deciduous Savanna	7.16 ± 0.82 (5.5–8.6)
14	Warm Temperate/Subtropical Mixed Savanna	6.28 ± 0.24 (5.5–6.8)
15	Temperate Conifer Savanna	6.53 ± 0.14 (6.3–6.7)
16	Tropical Deciduous Savanna	Not Present
17	C3 Grassland	6.66 ± 0.41 (5.4–7.6)
18	C4 Grassland	6.52 ± 0.72 (5.1–8.3)
19	Mediterranean Shrubland	5.81 ± 0.22 (5.6–6.4)
20	Temperate Arid Shrubland	6.49 ± 0.15 (5.7–6.8)
21	Subtropical Arid Shrubland	5.87 ± 0.30 (5.0–6.4)

variation in how NPP of the different vegetation classes is controlled by other environmental factors. For example, tundra VOC emission rise only slightly as the temperature limited growth conditions limit the ability to assimilate additional carbon. However, VOC emissions were not always stimulated by growth at elevated CO_2. Emissions of all VOCs were reduced from boreal conifer forest (class 2, –9.3%), maritime temperate conifer forest (class 3, –28%), temperate/subtropical deciduous savanna (class 13, –17.9%) and warm temperate/subtropical mixed savanna (class 14, –36.7%). As observed with the elevated temperature scenarios, considerable spatial variability exists in the magnitude of the changes in VOC emission at elevated CO_2 (Plates 1 and 2). An average decline of 35% in isoprene and monoterpene emission occurs from warm temperate/subtropical savanna (class 14) in central and western Texas, but the reductions range between 0% and –80% depending on specific grid cells (Plates 1b and 2b). More uniform declines occur in maritime temperate conifer forests (class 3) in the states of Washington and Oregon (Plates 1b and 2b).

Altered vegetation distribution scenarios. The alteration of vegetation distribution due to climate change was predicted using the UKMO GCM data in conjunction with the MAPSS biogeography and the CENTURY biogeochemistry models. Although a redistribution of vegetation in the absence of climate change is unlikely, it is possible to link the predicted changes in vegetation distribution to current climatic conditions in order to estimate how vegetation redistribution alone contributes to changes in VOC emissions in the future.

The vegetation of the United States as simulated by the MAPSS biogeography model changes markedly in response to an alteration of climate (Fig. 4). The change in area coverage of specific vegetation types spans the range from elimination to marked expansion (Fig. 4). The MAPSS model predicts that tundra (class 1) will be eliminated from the continental U.S., while shrublands and forests will decline in areal coverage by 67.7% and 8.6%, respectively (Fig. 4). The remaining vegetation categories will expand in areal coverage between 30% and 46% (Fig. 4). The large decline in shrublands occurred principally in temperate arid and subtropical arid shrubland (classes 20 and 21), but Mediterranean shrubland also declined in area by 21% (Fig. 4). Although forest vegetation declined in cover by only 8.6%, there was a reorganization in forest distribution; boreal conifer forest (class 2) was eliminated, whereas maritime temperate conifer forest (class 3), cool temperate mixed forest (class 5), and temperate deciduous forests (class 7) all declined in area between 52% and 80% (Fig. 4). These losses are compensated by a 24% increase in the coverage of continental temperate conifer forest (class 4) and an 88% increase in warm temperate/subtropical mixed forest (class 6) (Fig. 4). Xeromorphic woodlands and forests (classes 10–12) expanded in area as temperate mixed xeromorphic woodland (class 10), increased in area coverage by over 350%; in a similar manner, the

Table 5 Current annual net primary production (NPP, 10^3 g m^{-2} y^{-1}) for the different vegetation categories and classes under current climatic conditions and each of the climate change scenarios.

		Current	Elevated Temp.	Elevated CO_2	Altered Vegetation Distribution	Future
Vegetation Category						
	Tundra	35	40	38	25	0
	Forests	7937	10004	8197	11185	8286
	Xeromorphic Woodlands and Forests	279	339	298	156	471
	Savanna	2591	2552	2754	779	3677
	Grasslands	1893	2042	2079	1041	3551
	Shrublands	571	729	601	128	148
	Total	13306	15706	13967	13314	16133
Vegetation Class						
1	Tundra	35	40	38	25	0
2	Boreal Conifer Forest	443	617	458	322	0
3	Maritime Temperate Conifer Forest	834	1146	867	775	362
4	Continental Temperate Conifer Forest	973	1352	1017	1474	1442
5	Cool Temperate Mixed Forest	865	1276	882	1202	305
6	Warm Temperate/Subtropical Mixed Forest	2589	2879	2647	2958	5583
7	Temperate Deciduous Forest	2233	2734	2326	4443	585
8	Tropical Deciduous Forest	0	0	0	0	0
9	Tropical Evergreen Forest	0	0	0	10	9
10	Temperate Mixed Xeromorphic Woodland	92	111	101	110	439
11	Temperate Conifer Xeromorphic Woodland	187	228	196	46	30
12	Tropical Thorn Woodland	0	0	0	0	2
13	Temperate/Subtropical Deciduous Savanna	2247	2293	2392	508	2621
14	Warm Temperate/Subtropical Mixed Savanna	332	243	349	270	1055
15	Temperate Conifer Savanna	12	16	13	1	0
16	Tropical Deciduous Savanna	0	0	0	0	0
17	C3 Grassland	699	829	768	99	116
18	C4 Grassland	1194	1213	1311	942	3435
19	Mediterranean Shrubland	18	34	20	13	6
20	Temperate Arid Shrubland	381	509	406	85	99
21	Subtropical Arid Shrubland	172	187	176	30	44

expansion of savannas is the result of a 250% increase in coverage of a single vegetation class, the warm temperate/subtropical mixed savanna (class 14) (Fig. 4). The increase in area of C4 grasslands produced an expansion of grasslands, whereas all the shrubland vegetation classes are significantly reduced in areal coverage (Fig. 4). The changes in area coverage by each vegetation class are further reflected by alteration in NPP of each vegetation class (Table 5).

Effects of altered vegetation distribution on VOC emission. The alteration of vegetation distribution reduced the total modelled annual U.S. VOC emission by 10.4%, driven by reductions in emission of isoprene (– 11.7%), and monoterpenes (– 18.6%), whereas the emission of ORVOCs are unchanged (Fig. 1). The alteration of vegetation distribution resulted in a ≈84% decline in the area coverage of the vegetation classes that emit isoprene at the greatest rates (classes 7 and 11). These declines were offset by warm temperate/subtropical mixed forests (class 6) and warm temperate/subtropical mixed savanna (class 14) that emit isoprene at a medium high rate and increase in area coverage from 16.2% of the land area in present potential conditions to 32.1% in future potential conditions. The remaining vegetation classes emitting isoprene at medium-high rates all declined in area coverage. There is an expansion in the coverage of vegetation emitting isoprene at a medium-low rate (classes 4 and 10 increase in coverage 24% and 350%, respectively). In contrast to the decline in areal coverage of vegetation emitting isoprene at greater rates, the areal coverage of C4 grasslands (class 18) that emit isoprene at low rates expanded by 130%.

The alteration of vegetation distribution (Fig. 4) significantly influences the role of certain vegetation classes in contributing to the modelled total annual U.S. VOC emissions. Altered vegetation distribution reduced isoprene emission in 13 of the 18 vegetation

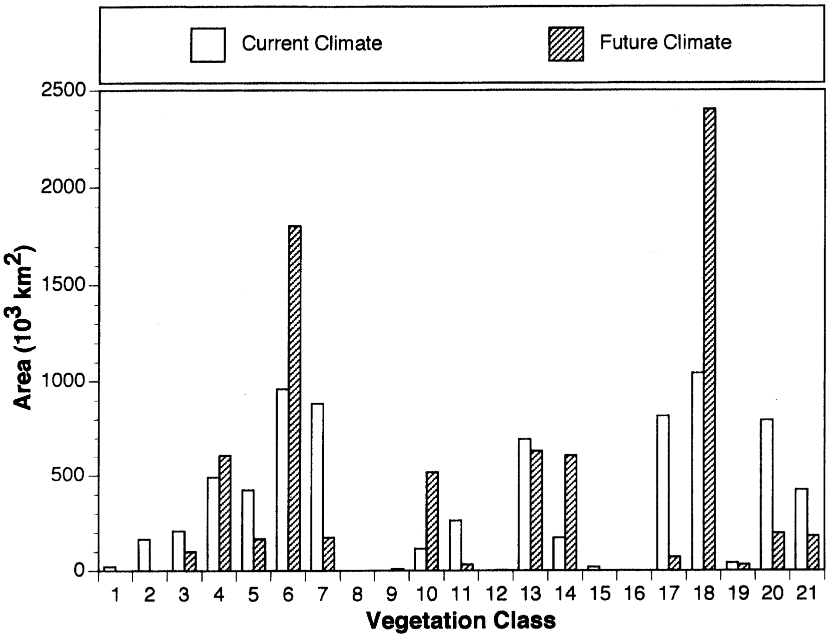

Fig. 4 Area coverage (10^3 km^2) of major vegetation classes of current potential (open bars) and future potential (shaded bars) vegetation determined using the MAPSS biogeography model.

classes represented in both the present potential and future potential vegetation distribution patterns. However, isoprene emission increased 36.5% from warm temperate/subtropical mixed forest (class 6), + 178% from temperate mixed xeromorphic woodlands (class 10), + 72% from warm temperate/subtropical mixed savanna (class 14), and + 140% from C4 grasslands (class 18). The same pattern of emission increase was also noted for monoterpenes. The influence of changes in vegetation coverage is also evident in the contribution to simulated total U.S. annual VOC emissions by each vegetation class. Emission of VOCs is still dominated by warm temperate/subtropical mixed forest (class 6) that emits 47.3% of the total VOCs, but the emissions contributions of warm temperate/subtropical mixed savanna (class 14) and C4 grasslands (class 18) increase in importance. One of the most pronounced effects of changes in vegetation distribution is a large rise in isoprene and monoterpene emission in the central and northern Great Plains due to greater vegetation coverage by temperate mixed xeromorphic woodlands (class 10), warm temperate/subtropical mixed savanna (class 14), and C4 grasslands (class 18) (Plates 1c and 2c).

Future climate scenarios. The individual effects of changes in temperature, CO_2 concentration, and a redistribution of vegetation have significant effects on the simulated annual total VOC emission of the U.S., however, the effects on VOC emission in each climate scenario are mediated by different mechanisms. The alteration of climate will have a large impact on the total annual biogenic VOC emission from the U.S. through the combined effects of temperature, NPP, foliar density and vegetation distribution that interact in nonlinear manners. It is already apparent that the effect of changes in temperature have a profound effect on VOC emissions, whereas the effects of CO_2 concentration and vegetation redistribution are more subtle. How these different factors interact will be highly dependent upon the covariance patterns among vegetation class, NPP, foliar density and the magnitude and spatial distribution of temperature increases, and the changes in each due to the alteration of climate.

Effects of future climate scenarios on VOC emission. The combination of elevated temperatures, CO_2 concentration and the redistribution of vegetation classes in the U.S. quantitatively alter the annual total VOC emissions in a manner that is similar to that predicted from temperature increases alone (Fig. 1). The simulated annual isoprene emission remained essentially unchanged from those predicted by an elevation of temperature alone as the additional positive effects of NPP on isoprene emission are offset by a combination of (a) the increased foliar density and (b) the decline in total area covered by high isoprene emission vegetation classes. A different situation occurred with respect to emission of monoterpenes, in which temperature still caused a large increase in emission, but the increase is less than that predicted from

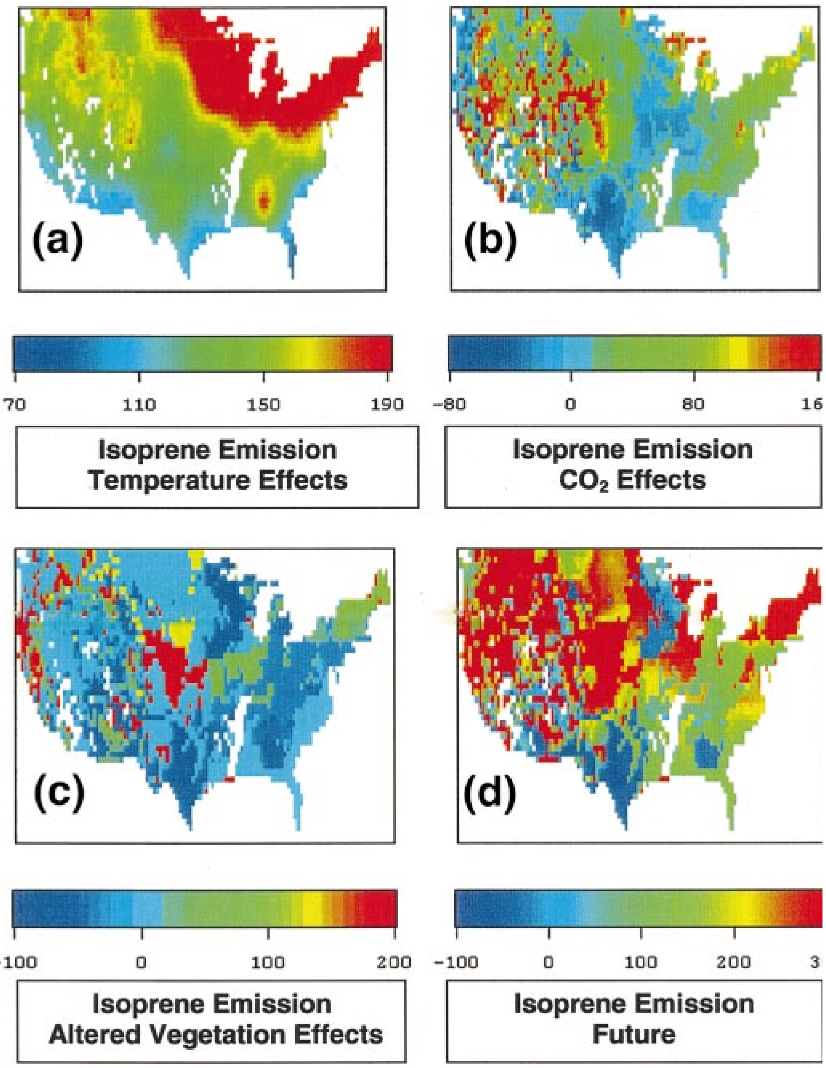

Plate 1 Percentage change in isoprene emission from current climatic conditions due to elevated temperature (a); elevated CO_2 concentration (b); altered distribution of vegetation (c); and the combination of all three factors representing a future climate (d).

temperature effects alone (Fig. 1) due to the net loss in areal coverage by monoterpene-emitting vegetation classes (Fig. 4). The combination of elevated temperature and CO_2 in conjunction with the redistribution of vegetation representative of a future scenario increased modelled VOC emissions only marginally more than those produced by temperature alone (Fig. 1), but, the spatial distribution of the increases differed between the two scenarios (Plates 1 and 2). The largest percentage increases due to temperature elevations occurred around the Great Lakes (Plates 1a and 2a), whereas the largest percentage increases in the future scenario occurred in the central plains and the western United States (Plates 1d and 2d).

In response to changes in temperature, CO_2 concentration, and vegetation redistribution emission of VOCs from specific vegetation classes are predicted to change markedly. Although the modelled total annual emissions increase relative to present potential conditions (Fig. 1), the increase is driven by emission enhancements within a relatively few vegetation classes. The large increases occurred in continental temperate conifer forests (class 4, + 113%), warm temperate/subtropical mixed forest (class 6, + 171%), temperate mixed xeromorphic woodlands (class 10, + 436%), temperate/subtropical deciduous savanna (class 13, + 91%), warm temperate/subtropical mixed savanna (class 14, + 347%), and C4 grasslands (class 18, + 320%). In contrast, VOC emission from the majority of remaining vegetation classes declined.

Discussion

An understanding of how alterations in climate will affect vegetation and ecological processes form a cornerstone for assessing the potential impact of climate change on humans. One of the greatest uncertainties involves the interaction between climate and vegetation as mediated by the emission of VOCs from vegetation. This study suggests that climatically induced changes in

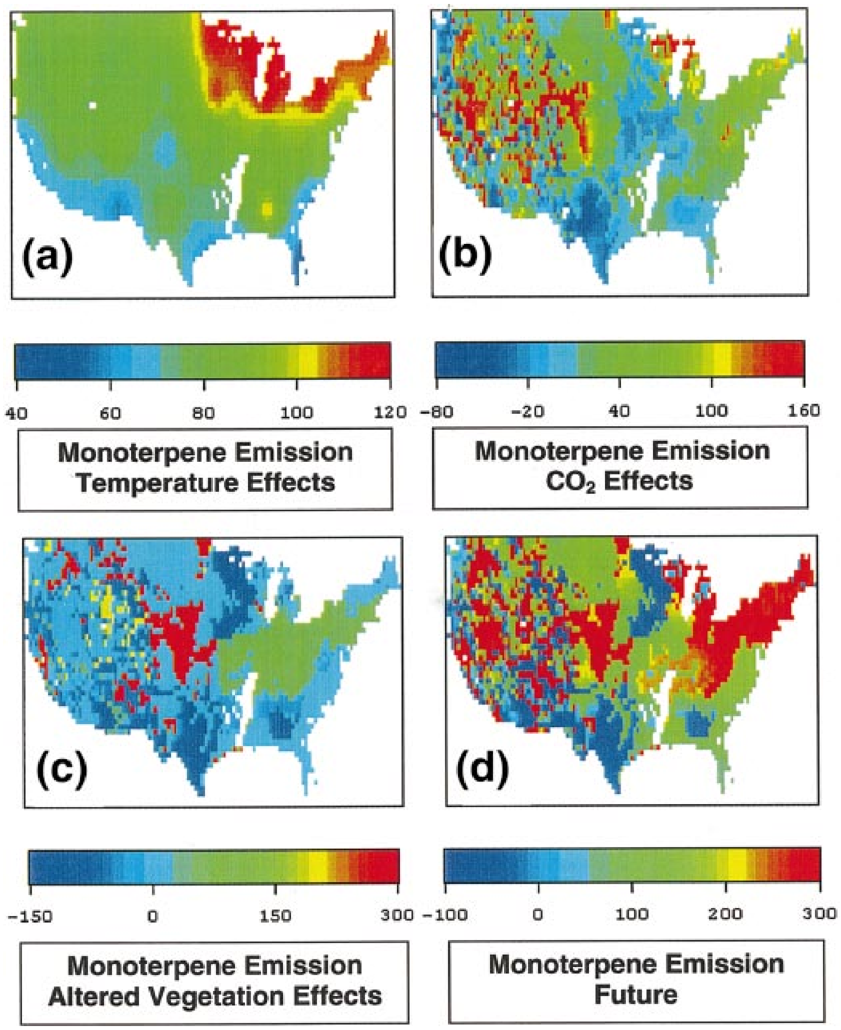

Plate 2 Percentage change in monoterpene emission from current climatic conditions due to elevated temperature (a); elevated CO_2 concentration (b); altered distribution of vegetation (c); and the combination of all three factors representing a future climate (d).

plant processes and distribution patterns may increase the emission of biogenic VOCs by ≈ 80%. The simulated increase in biogenic VOC emission of the future could have significant impacts on atmospheric chemistry by affecting the concentrations and lifetimes of CO (Hatakeyama *et al.* 1991), the oxidative balance of the atmosphere (Jacob & Wofsy 1988; Fehsenfeld *et al.* 1992) and aerosol formation (Andreae & Crutzen 1997).

Within the limitations of the VEMAP models with respect to spatial resolution and vegetation classifications, the current study estimates that under current climatic conditions and potential vegetation distribution that annual total U.S. biogenic VOC emission is ≈ 24 $Tg\,y^{-1}$ with isoprene, monoterpenes, and ORVOCs contributing 15.4 $Tg\,y^{-1}$, 3.9 $Tg\,y^{-1}$, and 4.9 $Tg\,y^{-1}$, respectively. The annual emission of isoprene predicted by this study is comparable to regional models developed by Zimmerman (1979) and Lamb *et al.* (1993), but threefold greater than the model of Lamb *et al.* (1987). Although the U.S. isoprene emission predicted by this study is at the high end of the expected range relative to other models, it is 36% less than that predicted for the U.S. from the global model of Guenther *et al.* (1995). In contrast to isoprene, the predicted U.S. emission of monoterpenes is lower than estimated by other regional models; < 10% of the values predicted by Zimmerman (1979) and approximately half those of Lamb *et al.* (1993). These discrepancies between the models are likely related to (i) methodological advances since the early VOC emission measurements that increase algorithm accuracy; (ii) estimation of VOC emissions from ecosystems that have not been experimentally measured; (iii) variation between and within species with respect to baseline VOC emission rates; and (iv) inclusion of emission of other reactive VOCs (ORVOCs) such as methyl-butenol and other oxygenated or polar hydrocarbons that are not present in other models (Ciccioli *et al.* 1993; Goldan *et al.* 1993; MacDonald & Fall 1993). The results presented here reflect only a single climate change and vegetation redistribution scenario within the larger VEMAP study. The use of alternate GCMs to predict climate or biogeography models would alter the results. For example, the use of the Oregon State University GCM that predicts lower temperature elevations than the UKMO GCM would predict a proportionally lower temperature-driven effect on VOC emission. Similarly, the use of a different biogeography model that produces different boundaries between vegetation classes could affect VOC emission if higher VOC-emitting vegetation types coincide with regions of high temperature elevation.

Of all the variables tested in this modelling exercise, the alteration in mean annual temperature and its associated increase in NPP appears to have the greatest single impact on modelled VOC emission. Integrated across the year for the entire U.S., VOC emission increased by 80% under the simulated temperature elevations predicted by the UKMO GCM, however, not all vegetation types contributed equally to this increase. Estimation of how VOC emission may change in the future requires sound information on not only the spatial distribution of temperature increases, but also biological aspects of VOC emission including vegetation class, vegetation class NPP, vegetation class foliar density and the effects of climatic variables other than temperature (e.g. drought, pollution, precipitation). More recent versions of the UKMO GCM include not only the positive forcing effect of greenhouse gases to increase global temperature, but also the counteracting negative forcing effect of sulphate aerosols that reduce global temperatures. Therefore, the temperature-elevation scenarios used here represent a maximum increase in VOC emission that may be somewhat ameliorated by the formation of VOC-derived aerosols that limit warming.

The effects of increased CO_2 on vegetation have been studied in detail with respect to changes in biochemistry and growth characteristics (Sage *et al.* 1989; Norby & O'Neill 1991; Farnsworth & Bazzaz 1995). In contrast to the large increase in modelled total VOC emission due to temperature, the increase stimulated by growth at a doubling of atmospheric CO_2 concentration amounted to only 12%. The limited influence of elevated CO_2, despite increases in NPP, is caused by the compensatory effects of increased foliar density that limits isoprene emission due to increased shading within the canopy. Changes in NPP in response to elevated CO_2 are also likely to result in decreased in isoprene emission relative to the U.S. average. The NPP increase for high (+4.7%) and medium-high (+2.9%) isoprene emission vegetation classes is less than is predicted for the average of all other vegetation classes (+5.0%). This suggests that growth at elevated CO_2 will promote growth of vegetation with lower base isoprene emission rates to a greater extent than vegetation with a high base isoprene emission rate. This is supported by the fact that NPP of the two lower isoprene emission vegetation categories increased ≈2-fold greater than the NPP increase of the two higher isoprene emitting vegetation categories. Emission of VOCs could be further influenced by an increase in leaf temperature due to stomatal closure at elevated CO_2. Although such an effect is not addressed here, a detailed understanding of the interaction between stomatal aperture, leaf temperature, and VOC emission could improve the modelling of VOC emissions in the future.

Increases in growth CO_2 concentration caused isoprene emission rates to decline in red oak, but increase in aspen (Sharkey *et al.* 1991). This is in contrast to monoterpene emission that exhibited no response to elevated growth CO_2 in either ponderosa pine or douglas-fir (Constable *et al.*, in press). How the emission of more exotic VOCs may respond to a doubling of CO_2 concentration is uncertain. The influence of growth CO_2 on VOC emission is likely to be further modified by changes in canopy structure that influence leaf area index (LAI), thereby changing the foliar emitting surface area per unit of ground area. An increase in SLW at elevated CO_2 is well-documented in a range of species covering many functional groups. Here altered SLW caused an increase in foliar density that increased canopy shading and lowered isoprene emission, but assumed no effect of growth CO_2 on LAI. Open-top chamber studies with tree species have documented increased LAI after multiple years of growth at elevated CO_2 in ponderosa pine (Tingey *et al.* 1996) and loblolly pine (Tissue *et al.* 1997). An increase in foliage mass when grown at elevated CO_2 occurs in deciduous tree species (Norby & O'Neill 1991; Norby *et al.* 1995), but the effect on LAI was not examined. Interpreted conservatively, these studies suggest that growth at elevated CO_2 may have differential effects on LAI in open canopy as opposed to closed canopy forests. An increase in LAI of open canopy vegetation classes [e.g. xeromorphic woodlands and forests (classes 10–12) and shrublands (classes 19–21)] or young forest plantations could increase VOC emissions proportionally more than observed in forests with closed canopies. Although accurate simulation of canopy structure in response to increased growth CO_2 concentration could affect VOC emission, simulations under current climatic conditions suggest otherwise. Simpson *et al.* (1995) constructed a VOC emission summary for Europe using several modelling methodologies. They determined that incorporation of detailed canopy structure increases VOC emission ≈30% due to the greater emission factors and greater leaf temperatures inside the canopy that promoted VOC emission. However, these increases in VOC emission were largely offset by lower light level within the canopy that lowered VOC emission.

The influence of climate change on the spatial distribution of vegetation has received considerable study (Prentice *et al.* 1992; Mellilo *et al.* 1993; Neilson & Marks 1994; Neilson 1995) as increased temperatures may promote shifts in agricultural zones to cooler latitudes (Schulze & Kunz 1995; Kaiser *et al.* 1994). Equally significant with respect to VOC emission, however, may be alteration in the distribution of vegetation to change the total area covered by vegetation classes of differing VOC emission potential. Total modelled VOC emission declined when the simulated vegetation redistribution patterns of the MAPSS biogeography model in a future climate were superimposed onto the current climatic conditions. The decline was driven by the reduction in area, ≈ 84%, of high isoprene emission vegetation (classes 7 and 11), however, the decline in total VOC emissions was partially offset by large increases in land coverage by vegetation that emitted isoprene at medium-high rates (classes 6 and 14) and medium-low rates (class 10). Due to uncertainty of ORVOC emission rates, temperature response and the use of common emission rates for all vegetation classes, the simulated annual ORVOC emission did not change in response to vegetation redistribution. Although not addressed here, there is also a potentially significant effect of alterations in land use that have changed vegetation from forest classes to either agriculture or urban/suburban vegetation that emit VOCs at lower rates and have lower LAIs than found in forest ecosystems. Considering the importance of changes in VOC emission with regard to atmospheric chemistry and the potential for driving further climatic change, this study suggests the role of biogenic VOCs in affecting atmospheric chemistry and the lifetimes of greenhouse gases will increase in the future. This conclusion is supported by the global study of Turner *et al.* (1991) who estimated a 25% increase in global isoprene emission driven by a combination of increased temperatures and the areal expansion of tropical forests. However, the actual global increase in isoprene emission may be greater if temperate latitude vegetation responds similarly to climate change as demonstrated in the current study.

Conclusions

The sum effect of future climate change scenarios including changes in temperature, CO_2 concentration and the redistribution of vegetation classes resulted in a significant increase in modelled total VOC emission from the vegetation of the U.S. However, the total annual U.S. VOC emission in the future climate scenario differs little from that predicted by temperature alone as the effects of CO_2 on NPP that increases VOC emissions are approximately offset by reductions in VOC emission caused by increased foliar density and reduced areal coverage by high isoprene-emitting vegetation. The approximate 80% increase in modelled VOC emission predicted for a future climate due to the combined effects of increased temperature, CO_2 concentration, and vegetation distribution could have a profound impact on global warming by affecting atmospheric oxidative capacity and concentrations of greenhouse gases.

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Appendix 1

Table 1 Determination of changes in specific leaf weight (SLW, g m^{-2} projected area) for each of the VEMAP vegetation classes under elevated growth CO_2 concentration. Notes: (1) Change in SLW assumed equal to mean of all grasslands; (2) Change in SLW assumed equal to mean of all forests; (3) Change in SLW assumed equal to vegetation class 14; (4) Change in SLW assumed equal to the mean of all vegetation classes.

Vegetation Class		Elevated CO_2 reference(s) for SLW	Notes
1	Tundra		1
2	Boreal Conifer Forest	Troeng & Linder (1982) *Physiologia Plantarum* **54,** 15	
		Brown & Higginbotham (1986) *Tree Physiology* **2,** 223	
3	Maritime Temperate Conifer Forest		2
4	Continental Temperate Conifer Forest		2
5	Cool Temperate Mixed Forest		2
6	Warm Temperate/Subtropical Mixed Forest	Williams *et al*. (1994) *Oecologia* **98,** 64	
		Teskey (1997) *Plant Cell and Environment* **20,** 373	
		Tolley & Strain (1984) *Canadian Journal of Forest Research* **14,** 343	
		Norby & O'Neill (1991) *New Phytologist* **117,** 515	
		Norby *et al*. (1992) *Nature* **357,** 322	
7	Temperate Deciduous Forest		2
8	Tropical Deciduous Forest		2
9	Tropical Evergreen Forest	Reekie & Bazzaz (1989) *Oecologia* **79,** 212	
		Arnone *et al*. (1995) *Oecologia* **104,** 72	
		Oberbauer *et al*. (1985) *Physiologia Plantarum* **65,** 352	
		Ziska *et al*. (1991) *Oecologia* **86,** 383	
10	Temperate Mixed Xeromorphic Woodland		2
11	Temperate Conifer Xeromorphic Woodland	Callaway *et al*. (1994) *Oecologia* **98,** 159	
		Smith *et al*. (1987) *Functional Ecology* **1,** 139	
12	Tropical Thorn Woodland	Ziska *et al*. (1991) *Oecologia* **86,** 383	
13	Temperate/Subtropical Deciduous Savanna		3
14	Warm Temperate/Subtropical Mixed Savanna	Cippolini *et al*. (1993) *Oecologia* **96,** 339	
		Arnone *et al*. (1995) *Oecologia* **104,** 72	
		Farnsworth & Bazzaz (1995) *Oecologia* **104,** 454	
15	Temperate Conifer Savanna	Smith *et al*. (1987) *Functional Ecology* **1,** 139	
16	Tropical Deciduous Savanna	Ziska *et al*. (1991) *Oecologia* **86,** 383	
		Ziska & Teramura (1992) *Plant Physiology* **99,** 743	
		Arnone *et al*. (1995) *Oecologia* **104,** 72	
17	C3 Grassland	Tremmel & Patterson (1993) *Canadian Journal of Plant Science* **73,** 1249	
		Campbell *et al*. (1988) *Plant Physiology* **88,** 1310	
		Ziska & Bunce (1994) *Physiologia Plantarum* **91,** 183	
		Sage *et al*. (1989) *Plant Physiology* **89,** 590	
		Farnsworth & Bazzaz (1995) *Oecologia* **104**: 454	
18	C4 Grassland	Tremmel & Patterson (1993) *Canadian Journal of Plant Science* **73,** 1249	
		Ziska & Bunce (1994) *Physiologia Plantarum* **91,** 183	
		Campbell *et al*. (1988) *Plant Physiology* **88,** 1310	
		Sage *et al*. (1989) *Plant Physiology* **89,** 590	
		Farnsworth & Bazzaz (1995) *Oecologia* **104,** 454	
19	Mediterranean Shrubland		4
20	Temperate Arid Shrubland		4
21	Subtropical Arid Shrubland		4