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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, CO₂ 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 CO₂ 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 CO₂ concentration enhanced total modelled VOC emission by 81.8% (isoprene +82.1%, monoterpenes +81.6%, ORVOC +81.1%), whereas a simulated doubled CO₂ 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 CO₂ (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
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 CO2 concentration; (c) simulated changes in species distribution pattern; and (d) the combined influences of temperature, doubled CO2 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 CO2 atmosphere. The effect of a doubled CO2 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 (Nielson 1995). The changes in vegetation characteristics (NPP, foliar density, vegetation type) under each of the climate scenarios (increased temperature; doubled CO2 concentration, altered vegetation distribution; and a combination of all three) were
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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 CO2 atmosphere. The grid size for the UKMO simulations was 2.5° × 3.75°, each of which were decomposed to estimate the temperature increases at the finer-scale VEMAP grid of 0.5° × 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° × 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 monoterpane 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, foliage phenology, specific leaf weight (SLW, g dry mass per m² 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 CO2 concentration results in an increase in SLW that could change VOC emissions through an alteration in canopy structure. Although the effects of CO2 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
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 = 1 × 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 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) | Area coverage (10^3 km^2) |
|------------------------|--------------------------------------------------|------------------------|---------------------------|
| Tundra                 | 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                       |

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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 ~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\( \times 10^6 \) 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). 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

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**Table 2** Vegetation base emission rates of isoprene (Isop. Emis.) and monoterpenes (Mono. Emis.) (µg C g\(^{-1}\) h\(^{-1}\)) and specific leaf weight (SLW, g m\(^{-2}\) projected area) for growth under current (350 µL L\(^{-1}\) CO\(_2\)) and elevated (700 µL 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   |

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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 5) 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),
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 CO₂ scenarios. An increase in CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ concentration on VOC emission. The effects of increased growth CO₂ 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 monoterpenes 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 CO₂ 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 CO₂ 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 CO₂ concentration is due to
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 CO2. 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 CO2 (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). 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

| 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)         |

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

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.

| Vegetation Category | Current | Elevated Temp. | Elevated CO₂ | Altered Vegetation Distribution | Future |
|---------------------|---------|----------------|--------------|---------------------------------|--------|
| 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  |

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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 monoterpenes 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, CO₂ 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 CO₂ 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, CO₂ 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.
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 CO₂ 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, CO₂ 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

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**Plate 1** Percentage change in isoprene emission from current climatic conditions due to elevated temperature (a); elevated CO₂ concentration (b); altered distribution of vegetation (c); and the combination of all three factors representing a future climate (d).

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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 plate.

Plate 2 Percentage change in monoterpane emission from current climatic conditions due to elevated temperature (a); elevated CO₂ concentration (b); altered distribution of vegetation (c); and the combination of all three factors representing a future climate (d).
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 CO2 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 CO2 concentration amounted to only 12%. The limited influence of elevated CO2, 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 CO2 are also likely to result in decreased 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 CO2 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 CO2. 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 CO2 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 CO2 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 CO2 concentration is uncertain. The influence of growth CO2 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 CO2 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 CO2 on LAI. Open-top chamber studies with tree species have documented increased LAI after multiple years of growth at elevated CO2 in ponderosa pine (Tingey et al. 1996) and loblolly pine (Tissue et al. 1997). An increase in foliage mass when grown at elevated CO2 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 CO2 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 CO2 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.

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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, CO₂ 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 CO₂ 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, CO₂ 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 CO₂ 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 CO₂ reference(s) for SLW                                                                 | Notes |
|-------------------------------------------------------|---------------------------------------------------------------------------------------------------|-------|
| 1 Tundra                                              | Troeng & Linder (1982) *Physiologia Plantarum* **54**, 15                                        | 1     |
| 2 Boreal Conifer Forest                               | Brown & Higginbotham (1986) *Tree Physiology* **2**, 223                                        | 2     |
| 3 Maritime Temperate Conifer Forest                   | Teskey (1997) *Plant Cell and Environment* **20**, 373                                          | 2     |
| 4 Continental Temperate Conifer Forest                | Tolley & Strain (1984) *Canadian Journal of Forest Research* **14**, 343                      | 2     |
| 5 Cool Temperate Mixed Forest                         | Norby & O’Neill (1991) *New Phytologist* **117**, 515                                          | 2     |
| 6 Warm Temperate/Subtropical Mixed Forest             | Williams *et al*. (1994) *Oecologia* **98**, 64                                                 | 2     |
| 7 Temperate Deciduous Forest                          | Teskey (1997) *Plant Cell and Environment* **20**, 373                                          | 2     |
| 8 Tropical Deciduous Forest                           | Tolley & Strain (1984) *Canadian Journal of Forest Research* **14**, 343                      | 2     |
| 9 Tropical Evergreen Forest                           | Norby *et al*. (1992) *Nature* **357**, 322                                                    | 2     |
| 10 Temperate Mixed Xeromorphic Woodland               | Callaway *et al*. (1994) *Oecologia* **98**, 159                                                 | 2     |
| 11 Temperate Conifer Xeromorphic Woodland             | Smith *et al*. (1987) *Functional Ecology* **1**, 139                                           | 2     |
| 12 Tropical Thorn Woodland                            | Ziska *et al*. (1991) *Oecologia* **86**, 383                                                   | 2     |
| 13 Temperate/Subtropical Deciduous Savanna            | Cippolini *et al*. (1993) *Oecologia* **96**, 339                                                | 3     |
| 14 Warm Temperate/Subtropical Mixed Savanna           | Arnone *et al*. (1995) *Oecologia* **104**, 72                                                  | 3     |
| 15 Temperate Conifer Savanna                          | Smith *et al*. (1987) *Functional Ecology* **1**, 139                                           | 3     |
| 16 Tropical Deciduous Savanna                         | Ziska *et al*. (1991) *Oecologia* **86**, 383                                                   | 3     |
| 17 C3 Grassland                                       | Tremmel & Patterson (1993) *Canadian Journal of Plant Science* **73**, 1249                    | 4     |
| 18 C4 Grassland                                       | Campbell *et al*. (1988) *Plant Physiology* **88**, 1310                                      | 4     |
| 19 Mediterranean Shrubland                            | Ziska & Bunce (1994) *Physiologia Plantarum* **91**, 183                                         | 4     |
| 20 Temperate Arid Shrubland                           | Campbell *et al*. (1988) *Plant Physiology* **88**, 1310                                      | 4     |
| 21 Subtropical Arid Shrubland                         | Ziska & Bunce (1994) *Physiologia Plantarum* **91**, 183                                         | 4     |

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