



The contribution of reactive carbon emissions from vegetation to the carbon balance of terrestrial ecosystems

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Abstract

About 2.4 Pg (1 Pg = 10^{15} g) of carbon is emitted annually into the atmosphere as reactive compounds and most of it is eventually oxidized to CO_2 . Isoprene, α -pinene, methanol, carbon monoxide and other compounds emitted by terrestrial vegetation contribute about half of the total flux and are estimated to produce about 1 PgC as CO_2 per year. The global average for vegetated surfaces is about 7 g C m^{-2} per year but could exceed 100 g m^{-2} per year at some tropical locations. The magnitude of these fluxes on both the landscape and global scales are small relative to the total carbon emission or deposition but are significant relative to the net fluxes. Reactive carbon fluxes are very sensitive to landcover and climate change and may vary significantly due to future perturbations. This paper summarizes what is known about reactive carbon emissions from vegetation including the magnitude of local, landscape, and global scale fluxes and their contribution to atmospheric CO_2 . Reasons for including this term in carbon flux models are presented as well as the potential importance on various spatial scales. Past, present and future reactive carbon emissions are expected to differ significantly and the implications of this are discussed.

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1. Introduction

The global exchange of carbon between terrestrial surfaces and the atmosphere is dominated by the emission and deposition of carbon dioxide (CO_2) but there are other carbon containing compounds that comprise several percent of the total flow of carbon between landscapes and the atmosphere (Went, 1960) but have only recently been mentioned as a potentially significant term in analyses of carbon budgets (e.g., Clark et al., 2001). These compounds undergo chemical reactions in the atmosphere and are referred to in this paper as reactive carbon compounds (RCCs). Since the ultimate atmospheric fate of most of these compounds is oxida-

tion to carbon dioxide, these CO_2 precursors may need to be included in efforts to understand the processes controlling atmospheric global CO_2 concentrations. The annual global emission of all reactive carbon is estimated to be about 2.4 Pg (10^{15} g) of carbon (Muller, 1992; Guenther et al., 1995). These estimates include approximately 0.6 PgC as carbon monoxide (CO), 0.5 PgC as methane, 0.5 PgC as isoprene, and 0.8 PgC as other volatile organic compounds (VOC). About half of this total is associated with emissions from terrestrial vegetation; the remainder is primarily from technological sources, biomass burning, and microbes.

Since most RCCs are oxidized to CO_2 in the atmosphere, vegetation RCC emissions are likely to produce more than 1 PgC as CO_2 each year through chemical oxidation. This source is large relative to minor anthropogenic sources such as cement production, 0.06 PgC as CO_2 in 1990, and is nearly 20% of the 1990 total

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fossil fuel emission of about 6 PgC as CO₂ (Andres et al., 2000). The production of CO₂ from the RCC emissions associated with fossil fuels is already included in estimates of the fossil fuel source even though it is less than 0.1 PgC (Andres et al., 2000). Vegetation RCC emissions respond to changes in biophysical forcing differently than the terrestrial heterotrophic CO₂ respiration term used in carbon budget models and so should be considered separately in these models. This is particularly important since RCC fluxes are more sensitive to landcover and climate change than are CO₂ respiration fluxes (e.g., Constable et al., 1999; Guenther et al., 1999).

This manuscript describes the sources and types of RCC emitted from vegetation and discusses the current understanding of the processes controlling production and emission. The atmospheric fate of these compounds, including the fraction converted to CO₂, is also considered. The potential contribution of these compounds to the total carbon balance is then assessed at leaf, landscape, regional and global scales.

2. Reactive carbon compounds

All living organisms produce and emit RCCs. Plants produce a particularly wide variety (>10 000 compounds) of RCCs. Most of these compounds have a low volatility or are stored in structures that present substantial barriers to emission to the atmosphere. As a result, a relatively small number of the RCC occurring within plants contribute to the total RCC emission into the atmosphere. The major RCC emissions can be grouped into three categories: terpenoid compounds, other VOC, and other reactive carbon. The compounds and emission sources summarized here are described in more detail by Kesselmeier and Staudt (1999) and Guenther et al. (2000).

2.1. Terpenoid compounds

The terpenoids are an important class of organic compounds that include hemiterpenes (containing five carbon atoms), monoterpenes (10 carbon atoms), sesquiterpenes (15 carbon atoms) and diterpenes (20 carbon atoms). Only two hemiterpenes, isoprene and methyl butenol, are emitted from vegetation in significant quantities. Isoprene has the single largest contribution to the total global vegetation RCC emission and is the dominant emission from many landscapes (Guenther et al., 1995). Methyl butenol is the dominant RCC emission from some regions in western North America but makes only a small contribution to the global total (Harley et al., 1998).

Less than 20 of the more than 1000 monoterpene compounds found in plants are responsible for nearly all

monoterpene emissions into the atmosphere. Global total monoterpene emissions are dominated by α -pinene, β -pinene, Δ^3 -carene, d-limonene, camphene, myrcene, sabinene, β -phellandrene and p-cymene but other monoterpenes can be regionally important (Geron et al., 2000). About half of the total monoterpene flux is α -pinene. Only a few (e.g., β -caryophyllene) of the approximately 3000 sesquiterpenes and none of the approximately 2000 diterpenes are thought to be emitted into the atmosphere in significant amounts, although there have been few attempts to quantify emissions of these compounds.

2.2. Other VOC

In addition to terpenoids, there are many other VOC that are emitted by vegetation into the atmosphere. These include hydrocarbons such as alkanes (e.g., methane, ethane), alkenes (e.g., ethene, propene) and arenes (e.g., toluene). Of these compounds, only ethene, propene and butene are thought to have substantial emission rates. Additional VOC emitted by vegetation include sulfur (e.g., dimethyl sulfide) and nitrogen containing compounds (hydrogen cyanide). These compounds are typically emitted at relatively low rates but emissions can be high under certain conditions and in specific locations (Guenther et al., 2000).

Oxygenated compounds contribute about half of the estimated global total vegetation RCC emission (Guenther et al., 1995). These partially oxidized compounds include alcohols (e.g., methanol, ethanol, hexenol), aldehydes (e.g., acetaldehyde), ketones (e.g., acetone), organic acids (e.g., formic acid), ethers (e.g., 1,8 cineole), and esters (hexenyl acetate). As is the case for the other categories, a few of the many oxygenated VOC contribute most of the total RCC flux (Kesselmeier and Staudt, 1999). Methanol, acetone and acetaldehyde are among the major emissions (Guenther et al., 2000). However, there are very few emission rate measurements of most of these oxygenated compounds so there may be others that make a large contribution.

2.3. Other reactive carbon

Other RCC include CO and particulate carbon. Annual emissions of CO from living, senescing and dead plant leaves are estimated to be about 0.1 PgC (Tarr et al., 1995). There is both direct evidence of CO emission from vegetation, from enclosure measurements, and indirect evidence from atmospheric concentration distributions. The global total CO source is reasonably well constrained but there are large uncertainties associated with individual sources and their distributions.

Carbon is a large mass fraction of many of the particles that move between the atmosphere and terrestrial

surfaces. Some of this carbon is emitted directly from vegetation and consists of organic material, such as plant waxes (Rogge et al., 1996). Additional carbon in these particles originates from RCC that are emitted as volatiles and are later deposited to particles. It is possible that this source represents a significant RCC flux in some regions but there is a lack of quantitative flux estimates (Mazurek et al., 1997).

3. Production and emission pathways

Foliage (leaves and needles) is the primary source of RCC emissions from vegetation although other live tissues (e.g., stem, cortical, root and reproductive) are minor contributors. Trees are the major source of global emissions although shrubs and herbaceous plants also contribute. There are many different processes leading to the production and emission of RCC. Some pathways are responsible for the emission of many different RCC and some RCC can be emitted by more than one pathway. The production and emission pathways of these carbon compounds are described by Kesselmeier and Staudt (1999), Fall (1999) and Guenther et al. (2000) and are summarized here.

Compounds produced in plant chloroplasts dominate the global RCC flux. These compounds are produced in the presence of light by an enzymatic process and then emitted almost immediately (Silver and Fall, 1995). Only about a third of all tree species emit RCC in this manner but the relatively high emission rates allow these processes to dominate global VOC emissions. The compounds emitted by this pathway include isoprene, methyl butenol and, in some cases, monoterpenes (e.g., α -pinene). Investigations of the mechanisms responsible for the production and emission of these compounds have focused on isoprene, which accounts for the majority of the total RCC emitted in this manner. Isoprene moves from the chloroplast into the intercellular space of the leaf and then exits the plant via the stomata. Isoprene synthase activity is controlled primarily by leaf temperature and light (photosynthetically active radiation) with increased activity, resulting in increased isoprene emission, occurring at higher temperature and light (Silver and Fall, 1995). Isoprene emissions are near zero in the dark. Emissions depend both on the current temperature and light conditions and those to which a leaf has previously been exposed (Petron et al., 2001). Leaf age, phenology, nutrients, water stress, and other factors can also influence isoprene emission.

Additional RCCs are emitted from specialized tissues that have a role in plant defense (Fall, 1999). These compounds act as a solvent for creating a physical barrier and/or as feeding deterrents to pests and are dominated by monoterpenes (C_{10}) with a large number, but small quantity, of sesquiterpenes (C_{15}) found within

leaves. The biochemistry of these compounds and the genetic and ecological controls of these plant defense mechanisms have been studied for many economically significant plants (McGarvey and Croteau, 1995). Diurnal variations in emissions of these stored compounds typically range from about a factor of two to four and are primarily controlled by temperature. The relationship between emission and temperature is exponential and is dependent on the compound and the resistance properties of the plant.

Other RCCs emitted by vegetation are produced in unspecialized plant tissues. Some compounds (e.g., ethane, ethanol, methyl salicylate, octanone and methoxyphenol) act by either repelling pests or attracting predators. Other VOC (e.g., 2-hexenal, 3-hexenol, 3-hexenal, 3-hexenyl acetate, hexanal, and hexanol) may have antibiotic properties and can be emitted from damaged plants at high rates. There is a reasonably good understanding of many of the general mechanisms associated with the production and release of these VOC (Fall, 1999).

Ethene is a volatile hormone that controls numerous aspects of plant growth and development, including fruit ripening, seed germination, flowering, senescence, and plant defense. The biochemistry of ethene production is relatively well understood (Fall, 1999). Ethene production is widespread in plants, which should make it a significant emission from most landscapes.

There are a large number of VOCs that act as floral attractants including alkanes, alcohols, esters, aromatics, nitrogen compounds, monoterpenes and sesquiterpenes. These flower scent emissions are a small fraction of the annual global VOC emissions but could be a significant component in some locations at certain times. There are many other plant metabolic processes that produce VOCs that ultimately are emitted into the atmosphere. The emission of these compounds may be unintentional and due simply to the leakage of plant metabolites.

The formation and emission of CO by live plant foliage is the result of direct photochemical transformation and occurs inside the leaf (Tarr et al., 1995). Organic carbon particles can be formed from the crystalline-like surface waxes that are present on many leaves. These particles become dislodged by the wind and/or by abrasion resulting from leaves rubbing against each other.

In addition to carbon emissions from living vegetation, there are also significant emissions from leaves excised from the plant, whether naturally or during harvest. This includes emissions of VOC, CO and particles. Drying vegetation, in particular, is a large source of VOC (e.g., acetaldehyde, methanol, and acetone) (Warneke et al., 1999). These compounds are produced and emitted by abiotic processes and are not the result of microbial activity.

4. Atmospheric fate of reactive carbon compounds

Most, but not all, of the volatile RCCs emitted by vegetation are transformed into CO₂ in the atmosphere. The complete atmospheric oxidation schemes for most VOC are not well known and are complicated by a large number of chemical reactions and intermediate compounds and by the possibility of deposition to particles or the earth surface. In addition, the atmospheric fates of the many different compounds are dependent on conditions such as the atmospheric abundance of other chemical species (e.g., oxides of nitrogen).

The possible atmospheric fates of a RCC includes (1) deposition as the originally emitted compound, (2) oxidation and subsequent deposition as another RCC, (3) condensation on particles and subsequent deposition, and (4) oxidation to CO₂. The initial fate of most RCCs is oxidation in the atmosphere. The amount deposited without undergoing any chemical reactions is thought to be about 10% for less reactive RCCs such as CO (Granier et al., 2000) and about 5% for reactive compounds such as isoprene (Cleveland and Yavitt, 1997). The deposition of some VOC such as methanol may exceed 10%.

Some RCC emissions are at least partially converted to particles and eventually deposited in this form. The aerosol yields of these compounds range from less than 15% for some monoterpenes to over 80% for sesquiterpenes (Hoffmann et al., 1997). If we assume that 5–25% of total RCC emissions form at least some particles and that the average particle yield for these RCC is between 15% and 60% then the range for global annual particle production is about 1–15% of the total emission. A reasonable best estimate, based on the analysis of Griffin et al. (1999), is that about 5% of total RCC emissions are deposited as particles. The carbon deposited to particles could be chemically transformed into volatile compounds that are emitted and oxidized to CO₂ but most of this carbon is probably deposited in particulate form and so is a negligible source of atmospheric CO₂. However, since the carbon can be emitted and deposited in different locations there is the possibility for influencing local carbon budgets.

Although there are considerable uncertainties associated with estimates of CO₂ production from RCC emissions, it is likely that complete oxidation to CO₂ is the fate of a large fraction (>75%) of the total emitted RCC. This fraction has been estimated to be about 80% for the dominant biogenic RCC, isoprene (Granier et al., 2000). It is probably somewhat higher for some RCCs, e.g. CO, and somewhat lower for others such as monoterpenes and methanol. Developers of anthropogenic CO₂ inventories assume that much of RCC produced by fossil fuels is soon converted to CO₂ in the atmosphere and so include these emissions as CO₂ (Andres et al., 2000).

5. Leaf-level carbon balance

Leaves are responsible for both CO₂ and RCC exchange between terrestrial ecosystems and the atmosphere. Thus the carbon balance of an individual leaf provides a starting point for considering the role of RCCs in the carbon balance of these landscapes. The net exchange of carbon between the atmosphere and leaves can be quantified using dynamic leaf enclosure systems. The CO₂ flux measured by these tools is the net result of the uptake of CO₂ by photosynthesis and the emission of CO₂ by autotrophic respiration. Changes in one or both of these processes can result in net CO₂ fluxes that range from uptake to emission. Mature leaves exposed to moderate temperatures and daytime light conditions typically have net uptake rates. Net emissions occur at night and with some daytime conditions, e.g., high temperatures and low light. The relative contribution of RCCs to the leaf total carbon flux is highly dependent on the magnitude of the net CO₂ flux and comparisons of CO₂ and RCC fluxes should consider the range of typical environmental and phenological conditions.

The relative magnitude of the isoprene and net CO₂ fluxes from a single eucalyptus leaf is shown in Fig. 1 for a range of leaf temperatures (note different scales). These observations were made with the system described by Guenther et al. (1991). Isoprene tends to have a temperature maximum that is approximately 20 °C higher than the temperature maximum for photosynthesis (Guenther et al., 2000). The amount of isoprene emitted relative to the net CO₂ uptake is less than 1% for temperatures below the temperature maximum for photosynthesis, which is about 20 °C for the leaf shown in Fig. 1, but greater than 10% for temperatures above 40 °C. A better estimate of the relative carbon flux can be made by modeling fluxes over a realistic range of conditions. For this comparison, the photosynthesis and isoprene emission models described by Harley and Baldocchi (1995) and Harley et al. (1997) for oak leaves at a temperate site was used along with the leaf-level light and temperature variations recorded at this site by Guenther et al. (1996a,b) to estimate isoprene and CO₂ fluxes from several leaves over a one week period. The percentage of carbon emitted as isoprene ranged from less than 0.1% to over 8% of net CO₂ uptake while the daily values ranged from about 1% to 4%.

Only about a third of all woody plants, and very few herbaceous plants, emit isoprene at these high rates. However, there are many other forms of RCCs. Some (e.g., CO, ethene, hexenol) are widespread among plants but have much lower rates of emission. Other compounds including methyl butenol, acetone, and α -pinene can be emitted at high rates from the leaves of undisturbed plants (Guenther et al., 2000). The leaves of stressed plants (e.g., heat, drought, ozone, infections)

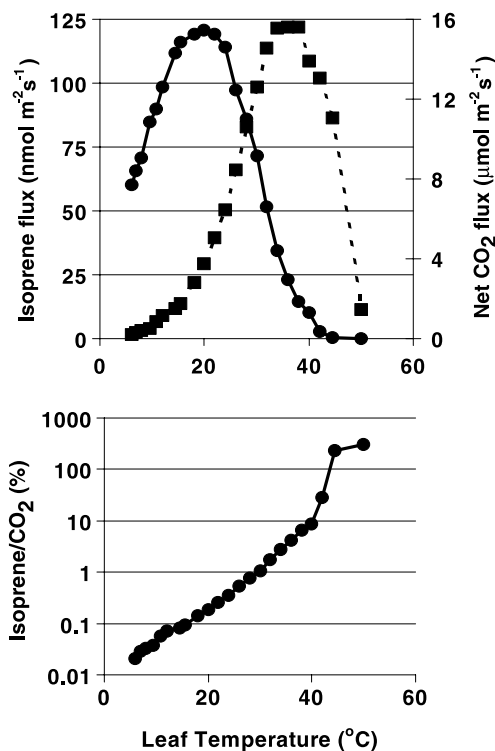


Fig. 1. Temperature dependence of net photosynthesis (circles and solid line) and isoprene emission (squares and dashed line) from a single eucalyptus leaf. The percent carbon ratio of isoprene to net photosynthesis is shown at bottom.

may have particularly high VOC emissions (Kesselmeier and Staudt, 1999).

6. Landscape level exchanges of carbon

Guenther et al. (1995) estimated area average annual VOC emissions from about 80 terrestrial ecosystems. Annual emission estimates ranged from less than 1 g C m^{-2} for landscapes with low productivity or short growing seasons, such as deserts and tundra, to about $40 \text{ g C m}^{-2} \text{ yr}^{-1}$ for tropical rainforests, which have a high productivity and long growing season. These estimates represent global ecosystem averages. Large variations in actual emission rates, both higher and lower, are expected for specific locations within a global ecosystem type.

Above-canopy flux measurements of RCCs have generally been limited to isoprene and a few monoterpenes although other compounds such as methyl butenol, ethene, propene, methanol, acetaldehyde and acetone have been measured in a few studies (Goldstein et al., 1996; Karl et al., 2001). The recent development of fast response analyzers for a larger range of RCCs has

greatly increased capabilities for eddy covariance measurements (e.g., Karl et al., 2001). Peak hourly isoprene fluxes measured in ten North American landscapes, primarily forests, ranged from 7 to $15 \text{ mg C m}^{-2} \text{ h}^{-1}$ with peak daily totals of about 0.03 – 0.1 g C m^{-2} (Lamb et al., 1985; Guenther et al., 1996a,b; Goldstein et al., 1998; Guenther and Hills, 1998; Fuentes and Wang, 1999; Fuentes et al., 1999; Westberg et al., 2000). Although none of these studies extended over an entire year, extrapolation of these fluxes using the model of Guenther et al. (1995) indicates that annual isoprene emissions at these sites are between 2 and 10 g C m^{-2} . If all of the trees at these sites were isoprene emitters, instead of the 20 – 35% that occur in these mixed forests and woodlands, the fluxes would be a factor of 3 – 4 higher. These higher fluxes are expected for monospecific plantations of isoprene emitting trees such as poplars, sweetgum and eucalyptus where the model predicts annual isoprene fluxes exceeding 30 g C m^{-2} . Tropical forest conversion to monoculture plantations of isoprene emitters, such as eucalyptus and oil palm, is expected to result in even higher annual isoprene emissions, $>60 \text{ g C m}^{-2}$, due to the much longer growing season. Since other RCC can be emitted at similar rates, it is likely that some tropical landscapes have annual emission rates that exceed 100 g C m^{-2} .

The highest annual CO_2 uptake rates measured by eddy covariance are between 200 and 600 g C m^{-2} (Malhi et al., 1999) indicating that RCC fluxes exceeding 50 g C m^{-2} would be significant even in these landscapes. Phillips et al. (1998) investigated tree inventories at 68 tropical forest sites and estimated an annual carbon flux of 68 g C m^{-2} . The average RCC emission estimated for all tropical forests by Guenther et al. (1995) is greater than 50% of this carbon flux. The generally lower RCC fluxes associated with temperate regions indicate that they will have a significant impact on net carbon exchange only in landscapes with low net carbon fluxes or very high RCC emissions.

7. Global carbon cycle

Direct measurements of carbon fluxes do not extend to regional or global scales. Instead, models are used to estimate the carbon balance of these areas. Modeling efforts have important political implications and could be used to direct and evaluate carbon management strategies. The Amazon basin has received considerable attention due to the large-scale landcover changes during the past several decades and because of recent reports that undisturbed forests in this region could be large carbon sinks (Malhi et al., 1999). For example, Tian et al. (1998) used a terrestrial ecosystem model to estimate annual Amazonian carbon fluxes for 1980–1994. They estimated an average annual net primary

production (NPP) for the entire Amazon basin of 5 Pg C and a heterotrophic respiration (R_H) of 4.8 Pg resulting in an average annual net ecosystem production (NEP) of 0.2 Pg C. The Tian et al. study demonstrated that there were large interannual variations in net Amazonian carbon fluxes with NEP ranging from an emission of 0.2 Pg C to an uptake of 0.7 Pg C. The model described by Guenther et al. (1995, 1999, 2000) predicts that the average annual RCC emission from Amazonian vegetation exceeds 0.2 Pg C. Using climate model predictions (NCAR CCM3) for a 14 year period, estimates of the annual total RCC flux varied between 0.18 and 0.24 Pg C. The predicted standard deviation for total RCC fluxes was about 10% of the mean. In comparison, the interannual variability presented by Tian et al. (1998) for a 14 year period was about 6% for NPP and 2% for R_H . These results illustrate the sensitivity of RCC fluxes to interannual changes in climate.

The estimated annual global RCC emission from vegetation predicted by the same model (Guenther et al., 1995, 1999, 2000) is about 1.2 Pg C. As discussed above, these emissions should result in the annual production of about 1 Pg C as CO_2 per year. This is a small flux relative to the global annual NPP of 40–78 Pg C (Melillo et al., 1993) but is significant relative to the annual carbon emission from fossil fuel and cement production (about 6 Pg in 1990), the atmospheric increase in CO_2 abundance (3.3 Pg C) and the “missing sink” (1.8 Pg C) that represents the imbalance of the known terms (Malhi et al., 1999). Given the large uncertainties associated with the individual terms estimated by models of global terrestrial carbon fluxes (e.g., leaf, above-ground wood, root, and heterotrophic respiration), the addition of another uncertain term, RCC emissions from vegetation, may not improve the accuracy of global estimates of carbon fluxes in the near future. The greater importance of including the RCC fluxes is that they are expected to respond differently to global changes in climate and landcover and so may be needed for an accurate understanding of future changes in the global carbon cycle.

Due to the large differences in emission rates associated with different vegetation types, there is a substantial potential for landuse change to influence RCC emissions (e.g., Guenther et al., 1999). Since woody plants tend to have much higher isoprene and monoterpene emissions rates, compared to crops and grasses, deforestation tends to reduce RCC emissions. However, the tree plantations and secondary forests that replace primary forests often have even larger emission rates. There is an equally large potential for perturbed RCC emissions as a result of climate change. Biogenic VOC emissions are very sensitive to temperature (Fig. 1) and an increase of as little as 2 °C could lead to an increase in biogenic VOC emissions of more than 25%. The overall result of expected future landuse and climate change is an in-

creased biogenic VOC production that could result in significant perturbations in trace gas distributions and global biogeochemical cycles (e.g., Constable et al., 1999).

8. Conclusions

The existence of large annual fluxes of RCCs from terrestrial vegetation was suggested by Went (1960) more than four decades ago. Vegetation RCC emissions are estimated to produce about 1 Pg C as CO_2 each year. The estimated global annual average is about 7 g C m^{-2} of RCC (Guenther et al., 1995) and this flux is thought to range from <0.1 to $>100 \text{ g m}^{-2}$ for specific locations but more long-term above-canopy flux measurements are needed to adequately characterize this range. Increasing concentrations of CO_2 in the atmosphere, and the potential impact on global climate, has generated considerable interest in quantifying CO_2 sources and sinks but RCC (mainly VOC and CO) emissions from vegetation are rarely included in estimates of local, regional or global carbon fluxes. The current understanding of vegetation RCC emissions does not allow us to rule out these fluxes as potentially significant components of the global carbon cycle and the carbon balance of at least some terrestrial sites.

Net CO_2 fluxes between terrestrial landscapes and the atmosphere are quantified using complex models of NEP, which treat explicitly carbon uptake by photosynthesis and losses through autotrophic and heterotrophic respiration. The allocation of carbon to RCC production and RCC emission losses are not included explicitly in these models. Reasons expressed for omitting RCCs in earlier carbon flux modeling included the uncertainties associated with RCC fluxes and that parameterization of CO_2 uptake in carbon models does not include the allocation of carbon to support the production of VOCs and so that carbon does not play a role in the carbon balance (Tian et al., 1999). Although RCC fluxes cannot be accounted for in NEP models by increasing heterotrophic respiration since they respond differently to biophysical drivers than do respiration processes, their omission was a reasonable first order approach for initial studies. RCC fluxes should be considered in future studies since they are of similar magnitude, and have similar levels of uncertainty, as other terms that now receive explicit treatment. Their relatively high sensitivity to climate and landcover perturbations makes their inclusion particularly important for global change studies. RCC emissions have been parameterized for global and regional models, primarily for use in numerical investigations of global tropospheric chemistry, and these estimates are improving (Guenther et al., 2000). Future studies of RCC emissions should take advantage of the resources focused on net

ecosystem carbon exchange by using facilities developed for CO₂ studies (e.g., flux towers, controlled manipulations of CO₂ and temperature conditions) and by incorporating RCC emissions into the sophisticated numerical ecosystem models that are being developed to investigate carbon fluxes. This will be a particularly effective strategy for characterizing future scenarios of potential climate and land-use change.

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