Ecosystem–atmosphere CO_2 exchange: interpreting signals of change using stable isotope ratios

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Changes in the concentration and stable isotope ratio of atmospheric CO_2 can be used to study variations in the net exchange of carbon dioxide in terrestrial ecosystems (net difference between total photosynthesis and respiration). Changes in the timing of seasonal fluctuations in atmospheric CO_2 concentration have suggested that net uptake of carbon dioxide has been increasing in northern latitude ecosystems in association with warmer temperatures and a lengthening of the growing season. Stable isotope techniques allow a more detailed separation of differences between ecosystem photosynthesis and respiration because these two processes have contrasting effects on both the carbon and oxygen isotope ratio of atmospheric CO_2. Future applications of stable isotope analyses include documenting and monitoring the influence of global environmental change on ecosystem CO_2 exchange at regional scales (10–1000 km²).

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Interaction between terrestrial ecosystems and the atmosphere occurs via a number of processes including CO_2 exchange during photosynthesis and respiration. A number of well documented, ongoing global changes have the potential to alter ecosystem functioning through their effects on these gas exchange processses. For example, increases in atmospheric CO_2 concentration and alterations to the global nitrogen cycle could change ecosystem physiology because of the tight coupling of carbon and nitrogen cycles during primary production and decomposition[1]. Other important global issues associated with land-use change (agricultural and forestry expansion[2]) and interannual variability (El Niño/La Niña events[3]) could also have substantial effects on the timing and magnitude of ecosystem photosynthesis and respiration. To understand the influence of these current global changes on ecosystem function, we need tools to study whole-ecosystem functioning on large spatial scales. Stable isotope analyses of atmospheric carbon dioxide are one possible tool, which scales CO_2 exchange from the soil and individual plant level (scale of approximately 1 m) through to the troposphere (scale: 10^3 m).

Measuring large-scale ecosystem–atmosphere CO_2 exchange

The terrestrial biosphere exerts strong influences on the atmosphere. Recent studies have shown that measurements of atmospheric CO_2 concentration can be used to study net ecosystem carbon dioxide exchange on regional (10–1000 km²) or larger scales[4–6]. The slow mixing of the atmosphere, and the non-uniform distribution of uptake (photosynthesis) and release (respiration) of CO_2 in space and time, cause local changes in atmospheric CO_2 concentration from the global average value (Fig. 1). For example, superimposed on the annual increase of atmospheric CO_2 are large seasonal fluctuations, which become most apparent in the high latitudes of the northern hemisphere (Fig. 1). These seasonal fluctuations result because of differences in the timing and magnitude of photosynthesis and respiration in terrestrial ecosystems[5,6]. In contrast, tropical latitudes show less seasonal change in atmospheric CO_2 because of minimal differences in the timing of photosynthesis and respiration in these latitudes. In the southern hemisphere, the seasonal fluctuations in atmospheric CO_2 are opposite in sign and much reduced in magnitude compared to variation in the high northern latitudes. The reduced seasonal CO_2 variation observed in the southern hemisphere is because of the smaller overall land mass and because terrestrial vegetation in the southern hemisphere occurs primarily in tropical and subtropical latitudes[4–6].

The magnitude of the seasonal oscillation in atmospheric CO_2 in northern latitudes is increasing over time[5,6]. Over the past 15–20 years, there has been a 20% increase, with even larger increases recorded at more northerly latitudes. Changes in both the magnitude and the timing of the seasonal fluctuation of atmospheric CO_2 imply an imbalance between ecosystem photosynthesis and respiration associated with a lengthening of the growing season[6]. However, based on changes in CO_2 concentration alone, it is impossible to separate these ecosystem effects since changes in atmospheric CO_2 are the result of a net difference in photosynthesis and respiration. For example, a reduction in CO_2 concentration can result from an increase in photosynthesis and/or a decrease in respiration, and the concentration measurement alone cannot differentiate between these possibilities. In terms of ecosystem function, it is essential to differentiate between the effects of changes in photosynthesis from those affecting respiration. This is because photosynthesis and respiration respond differently to important environmental changes, such as temperature and CO_2 concentration. Stable isotope techniques offer great promise for differentiating between the effects of changes in CO_2 uptake and loss.

Associated with the seasonal and latitudinal changes in CO_2 concentration are fluctuations in the carbon and oxygen stable isotope ratios of atmospheric CO_2 (Refs 7–9) (Fig. 2). These changes in the stable isotope composition of atmospheric CO_2 result from isotope effects that occur during ecosystem–atmosphere CO_2 exchange. Photosynthesis and respiration have very different and contrasting effects on the

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stable isotope ratio of atmospheric CO_2. Thus, monitoring shifts in both the concentration and stable isotope ratio of atmospheric CO_2 can be used as a tool to study regional ecosystem CO_2 exchange processes[9,10]. Interpretation of the stable isotope signal recorded by the upper atmosphere requires an understanding of fractionation processes that occur during ecosystem CO_2 exchange. Previous studies have made use of the different isotope effects that occur between terrestrial and oceanic CO_2 exchange to determine the relative influence of the oceans and terrestrial biosphere as net sinks for anthropogenic CO_2 emissions[11–13]. Progress in understanding the mechanistic basis for isotope effects during photosynthesis and respiration potentially allow the separation of these components of net CO_2 exchange in terrestrial ecosystems on local and regional scales[10]. Since the processes controlling the ^{13}C composition of atmospheric CO_2 are completely independent from those affecting the ^{18}O composition[8,11,14], measurements of both isotopes can be used to check the consistency and accuracy of inferred changes in CO_2 exchange processes.

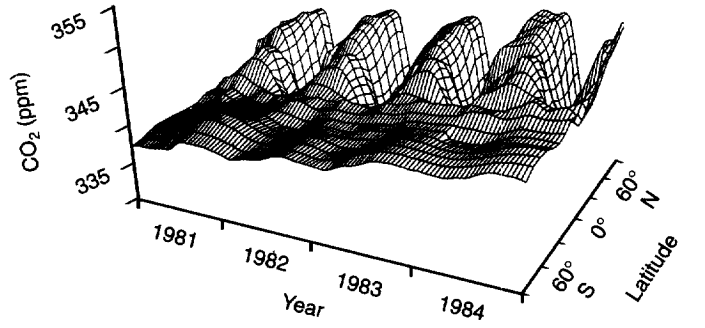

Fig. 1. Seasonal changes in the concentration of atmospheric CO_2 shown as a function of 10° latitudinal bands. *Reproduced with permission from Ref. 33.*

Factors affecting the carbon isotope ratio of atmospheric CO_2

Detailed mechanistic models have been developed that successfully explain the isotope effects that occur during photosynthetic gas exchange in C_3, C_4 and CAM plants[15]. These models can be used to determine the effect of different terrestrial ecosystems on the $^{13}C/^{12}C$ ratio of atmospheric CO_2, because of differences in photosynthetic pathway, genotypic variation, and environmental influences[16]. During photosynthesis, plants preferentially assimilate $^{12}CO_2$, resulting in an increase in the $^{13}C/^{12}C$ ratio of CO_2 remaining in the atmosphere[15]. There are two primary processes that cause the carbon isotope ratio of atmospheric CO_2 to change during C_3 photosynthesis: (1) diffusional fractionation ($^{13}CO_2$ diffuses slower than $^{12}CO_2$) and (2) enzymatic fractionation associated with ribulose-1,5-bisphosphate carboxylase (Rubisco)[15]. Shifts in the relative importance of diffusional and enzymatic fractionation are determined by the ratio of chloroplast CO_2 concentration (c_c) and atmospheric CO_2 concentration (c_a), which is a function of leaf physiological characteristics, photosynthetic capacity and stomatal conductance to CO_2. In plants with C_4 and CAM photosynthetic pathways, the initial fixation of atmospheric carbon dioxide is catalyzed by phosphoenol pyruvate carboxylase, which has a much smaller isotope effect than Rubisco. As a result, photosynthesis in C_4 and CAM plants causes a smaller change in the $^{13}C/^{12}C$ ratio of atmospheric CO_2 than C_3 photosynthesis[15]. The small isotope effect during terrestrial C_4 and CAM photosynthesis is similar to the isotopic change during the dissolution of atmospheric CO_2 into the ocean. The similar magnitude of these two isotope effects is a major barrier in trying to separate terrestrial and oceanic carbon dioxide sinks in tropical latitudes where C_4 agricultural plants are replacing C_3 forest vegetation[2].

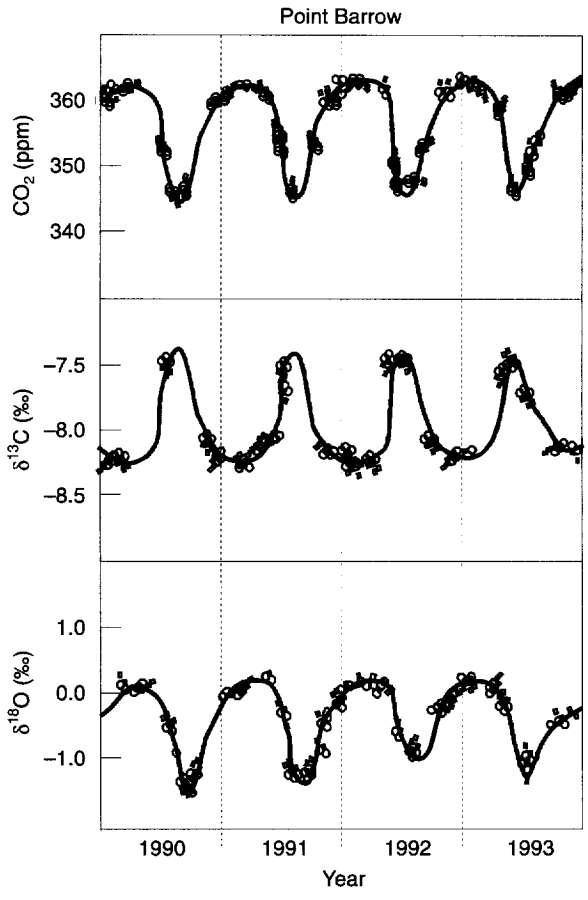

Fig. 2. Seasonal changes in the concentration, $\delta^{13}C$ and $\delta^{18}O$ of atmospheric CO_2 during 1990–1993 at Point Barrow, Alaska. *Adapted from Ref. 7.*

There is no significant isotope effect associated with respiration[17], so the carbon isotope ratio of respired CO_2 is dependent on the isotopic composition of the carbon substrate broken down during respiration. Plant carbon compounds have a lower $^{13}C/^{12}C$ ratio than atmospheric CO_2 because of fractionation during photosynthesis, so respiration releases CO_2 that is relatively depleted in ^{13}C, resulting in a reduction in the $^{13}C/^{12}C$ ratio of atmospheric CO_2. However, there is a great deal of variation among the carbon isotope ratios of different carbon compounds that are broken down during plant and soil respiration[18,19]. Many enzymes involved in secondary carbon metabolism have isotope effects so that different chemical components have different carbon isotope ratios (for example, lipids have lower ^{13}C contents than whole plant tissue[15,19]). Because of differences in the timing and magnitude of plant and soil respiratory processes, and associated variation in the chemical nature of the carbon-containing molecules that get broken down, significant spatial and temporal variation can occur in the carbon isotope ratio of respired CO_2 in terrestrial ecosystems[20–24].

Spatial and temporal variation in the $^{13}C/^{12}C$ ratio of CO_2 in boreal forest ecosystems

Respiration from black spruce (*Picea mariana*) ecosystems in northern Canada can be separated into two major components: respiration from the foliage of the dominant trees and respiration originating from the forest floor. There is little variation in the carbon isotope ratio of black spruce foliage collected at different heights within the vegetation canopy or foliage collected at different times within a growing season[20,25]. As a consequence, the carbon isotope ratio of CO_2 respired by foliage is expected to be quite uniform within a black spruce ecosystem. In contrast, the respiratory CO_2 released from the forest floor can be quite variable both spatially and temporally for several reasons. Respired CO_2 released from the forest floor can originate from several different sources including: (1) moss respiration – and mosses have extensive ground coverage in these ecosystems; (2) vascular plant root respiration; and (3) heterotrophic microbial respiration. The CO_2 molecules that are respired by these different components can have substantially different carbon isotope ratios. For example, boreal moss species have very low $\delta^{13}C$ values, approximately –32‰ to –30‰, while black spruce tree roots and mineral soil organic matter have higher $\delta^{13}C$ values, approximately –26‰ (Ref. 20). The isotopic signature of carbon dioxide released from heterotrophic processes in soils is expected to represent a weighted average of CO_2 released from sources with a range of $\delta^{13}C$ values. Soil organic matter is composed of different chemical fractions that turnover at different rates[26,27]. These different carbon pools should have different isotopic compositions because of reduction in the $\delta^{13}C$ value of source atmospheric CO_2 over time[11] (which would cause a change in the ^{13}C content of carbon fixed during photosynthesis), and because various chemical components of plant tissue and soil organic matter can have dissimilar ^{13}C contents (for example, lignin is depleted in ^{13}C relative to whole cellulose[18])[11]. In addition, the timing and magnitude of moss, plant root and heterotrophic respiration can vary substantially within a growing season and interannually. The spatial and temporal variability in the carbon isotope ratio of CO_2 respired by different components within boreal ecosystems, creates the potential for stable isotope techniques to be useful in studying the contributions of different components to overall ecosystem function and to changes in our atmosphere (Box 1).

Recent measurements of the $\delta^{13}C$ value of respired CO_2 show that CO_2 released from the forest floor is more enriched in ^{13}C than CO_2 released from the entire ecosystem (Fig. 3, Box 1). This observation is consistent with the hypothesis that older soil carbon (fixed during periods when atmospheric CO_2 was more enriched in ^{13}C) is a significant fraction of the soil respired CO_2 (Ref. 11). It is also consistent with the slow turnover time of some soil components[26,27], which are generally more depleted in ^{13}C than other carbon molecules that turnover at faster rate. Aircraft measurements[29] made over the boreal forest illustrate interannual variation in the $\delta^{13}C$ value of respired CO_2 (Fig. 3), perhaps associated with environmentally induced differences in the relative influences of different ecosystem components on respiration.

Factors affecting the oxygen isotope ratio of atmospheric CO_2

While much of the previous work with stables isotopes of atmospheric CO_2 has focused only on carbon isotopes, ecosystem CO_2 exchange can also have a significant influence on the oxygen isotope ratio of atmospheric CO_2 (Refs 8,14, 30,31). Two main isotope effects occur during photosynthesis: (1) a diffusional fractionation occurs because of the difference in mass between CO_2 containing ^{18}O and ^{16}O, and (2) an isotope exchange reaction occurs in the chloroplast between oxygen in CO_2 and oxygen in H_2O. During this exchange reaction, or equilibrium isotope effect, the oxygen isotope ratio of CO_2 becomes enriched in ^{18}O relative to that of the chloroplast water. A portion of the CO_2 that enters a leaf during photosynthetic gas exchange, equilibrates with chloroplast water and diffuses back out of the leaf with an altered $\delta^{18}O$ value, before having a chance to be fixed into carbohydrate. The amount of CO_2 that escapes from the leaf, which can be approximately two-thirds of the total that diffuses in, depends on the concentration of CO_2 in the chloroplast and the resistances to diffusion along the path from the chloroplast to the atmosphere[14]. This apparent discrimination against $C^{18}O^{16}O$ during photosynthesis acts to enrich atmospheric CO_2 in ^{18}O. Similar to the situation for carbon isotope discrimination, discrimination against $C^{18}O^{16}O$ is a function of changes in the c_c/c_a ratio, and so is controlled by differences in leaf photosynthetic capacity and/or stomatal conductance to CO_2 (Ref. 14).

The magnitude of the increase in the $^{18}O/^{16}O$ ratio of atmospheric CO_2 during photosynthetic gas exchange is dependent on factors affecting water balance in terrestrial ecosystems. For example, the oxygen isotope ratio of CO_2 equilibrating with chloroplast water is dependent on the $\delta^{18}O$ value of the chloroplast water[14,30], which changes because of isotope enrichment that occurs during transpiration. The oxygen isotope ratio of water in plant leaves will also depend on the source water taken up from the soil

Box 1. Determining the stable isotope ratio of respired CO_2

A simple technique developed by Keeling[28] can be used to determine the isotope ratio of CO_2 respired from ecosystems based on diurnal changes in the concentration and isotopic ratio of atmospheric CO_2 within a vegetation canopy. At night, the CO_2 concentration within the forest boundary layer is increased because of the input of respiratory CO_2. The CO_2 released from plant and soil respiration is depleted in ^{13}C and so causes a decline in the $^{13}C/^{12}C$ ratio of atmospheric CO_2 within the forest boundary layer.

Keeling[28] showed that by plotting the mixing relationship between $\delta^{13}C$ and $1/CO_2$ of atmospheric CO_2, a linear relationship was obtained and the intercept of this relationship was the isotope ratio of the respired CO_2 input into the forest canopy (see Fig. 3). At the forest canopy scale, the intercept represents a spatially integrated measure of the $\delta^{13}C$ of CO_2 respired from above-ground vegetation and soil components. The spatial area integrated by the calculation depends on the height at which the air samples are collected, or the footprint of the air sample mast. The calculated intercept also represents a temporal integration because it includes contributions from different aged carbon pools in plants and soil, that have different turnover times and different $\delta^{13}C$ values.

It is possible to use the 'Keeling plot' approach to calculate separately the isotope ratio of respired CO_2 at different spatial scales, both above and below that of the forest canopy. For example, chambers sealed on top of collars inserted into the soil can be used to calculate respiration by soil and forest floor components by measuring the increase in CO_2 concentration within the chamber over a short period. New analytical approaches make it possible to collect and analyze the $\delta^{13}C$ value of small subsamples of CO_2 from the chamber headspace during the increase in CO_2 concentration. This approach allows the separate calculation of the $\delta^{13}C$ value of CO_2 released from forest floor respiratory components, which can then be compared to the isotope ratio of CO_2 respired by the entire forest ecosystem to determine the relative contribution of the different ecosystem components.

In a similar manner, the 'Keeling plot' approach can be applied to the analysis of air samples collected by aircraft in vertical profiles through the nocturnal planetary boundary layer (Fig. 3). The aircraft samples will provide an integrated regional measurement of the $\delta^{13}C$ value of respired CO_2.

(groundwater or recent precipitation), which reflects variation in precipitation inputs[8,14,31]. Simple mechanistic models have been developed that can be used to calculate the isotope ratio of plant leaf water using global data bases for relative humidity, temperature and the stable oxygen isotope composition of precipitation[8,14].

Ecosystem respiration acts in opposition to photosynthesis by releasing CO_2 depleted in ^{18}O to the atmosphere. The primary factor influencing the oxygen isotope ratio of respired CO_2 is the equilibrium isotope effect that occurs between oxygen in CO_2 and oxygen in plant and soil water. In general, recent measurements of the $\delta^{18}O$ value of respired CO_2 show that CO_2 released from the boreal forest ecosystems is more depleted in ^{18}O than atmospheric CO_2 (Ref. 31). This is consistent with soil-respired CO_2 being in isotopic equilibrum with a water pool less enriched in ^{18}O than water in leaves of the above-ground vegetation. Regional measurements of the $\delta^{18}O$ of respired CO_2, based on samples collected by aircraft flights over the boreal forest[29], also illustrate that respired CO_2 in northern latitudes is depleted in ^{18}O. Significant spatial and temporal variability among the oxygen isotope ratios of the components of ecosystem respired CO_2 may allow an analysis of their relative importance to ecosystem gas exchange, analogous to what can be accomplished using carbon isotope techniques.

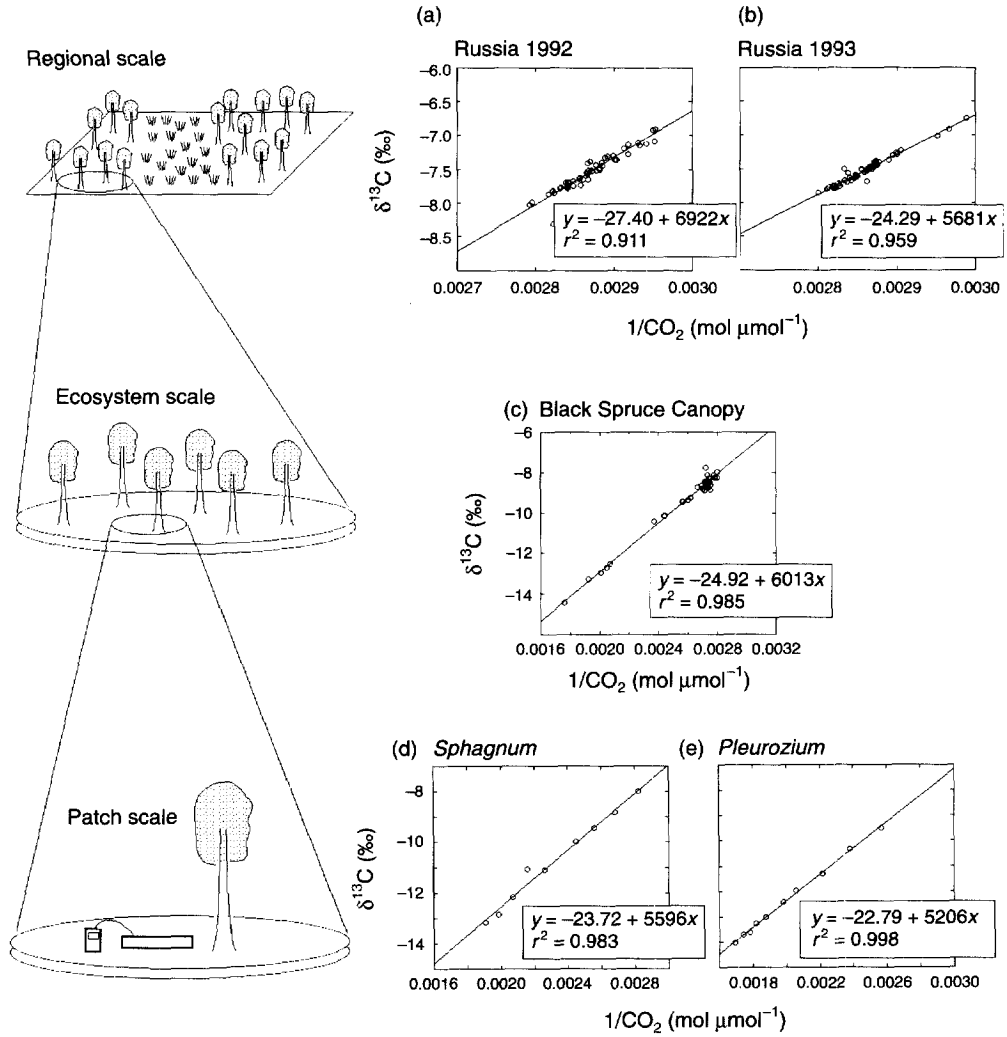

Fig. 3. Comparison of the carbon isotope ratio of respired CO_2 at different spatial scales, from analysis of the relationship between $1/CO_2$ concentration and the carbon isotope ratio of atmospheric CO_2 (see Box 1 for the theory behind the technique). Aircraft air sample data (a,b) are from Ref. 29. The forest floor (d,e) and canopy (c) data come from samples collected in a black spruce forest in northern Canada (see Ref. 20).

Analysis of the effects of global change on ecosystem function

Understanding the impact of global change on ecosystem function at the landscape and regional levels requires an approach for integrating changes in photosynthesis and respiration across different land surfaces with possibly distinct land-use histories and stages of development. We believe that measurement and analysis of the stable isotope ratio of atmospheric CO_2 offers a promising approach to document and study terrestrial ecosystem CO_2 exchange processes on large spatial scales. The mixing of CO_2 from the biosphere with the atmosphere at different scales provides a means of approaching this flux integration. Changes occur in CO_2 concentration at different time scales within the soil, the plant canopy, the convective boundary layer, and the troposphere, reflecting the balance between respiration and photosynthesis, and the dissimilar turnover rates of carbon at these distinct spatial scales.

There are good reasons to believe that the impact of land-use changes on ecosystem CO_2 exchange will be quantifiable using stable isotope approaches, because disturbance will result in shifts in stable isotope ratios of atmospheric CO_2. For example, changes in land-use practices resulting in the replacement of tropical forest (C_3 vegetation) with pasture (C_4 vegetation) or seasonal burning of savannas will have significant effects because C_4 plants have much lower carbon isotope discrimination during photosynthesis[16]. In addition, the isotope ratio of respired CO_2 from above-ground C_4 vegetation will be very different from soil-respired CO_2, which will continue primarily to represent the carbon fixed by the original C_3 vegetation[11,16,22]. Increases in temperature may have differential effects on photosynthesis and respiration, and result in faster turnover times of soil carbon in northern latitudes[27], with subsequent changes in the carbon isotope ratio of ecosystem-respired CO_2 because of the relatively high ^{13}C content of old soil carbon. Detecting shifts in the oxygen isotope ratio of atmospheric CO_2 will provide an independent check on changes in ecosystem photosynthesis and respiration inferred by using carbon isotopes, since the processes that control the ^{13}C and ^{18}O content of atmospheric

CO_2 are completely different[8,11,14]. The $\delta^{18}O$ value of atmospheric CO_2 could also provide information on changes in stomatal conductance associated with increases in atmospheric CO_2 or other global changes[32].

Continued research on the mechanisms causing isotope effects during ecosystem photosynthesis and respiration will allow us to better interpret the important global signal recorded in the stable carbon and oxygen isotope ratios of the slow-mixing tropospheric CO_2. While still in its infancy, the linkage of mechanistic ecophysiological approaches with tropospheric isotope ratio studies provides a means of understanding the dynamics and constraints that ecosystems play on influencing global carbon cycle dynamics. This mechanistic understanding of isotope effects sets the stage for the use of stable isotope techniques in documenting and monitoring the influence of global environmental change on ecosystem function over large spatial scales.

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