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REVIEW

Radiocarbon and the Transit Time of Carbon in Terrestrial Ecosystems

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Abstract

Purpose of Review The transit time of carbon quantifies the time that it takes carbon atoms to travel through an ecosystem, from fixation of atmospheric CO_2 via photosynthesis until loss of carbon, mostly via respiration by plants and microorganisms, but also by methane emissions, and by leaching as dissolved inorganic or organic matter. Transit times are relevant to predict the future behavior of carbon sinks and how they would respond to changes in the environment. As most carbon is lost to the atmosphere as CO_2, measurements of radiocarbon in respired carbon dioxide can be used to approximate the mean transit time of carbon in ecosystems. We review here an increasing number of studies that use radiocarbon to obtain the age of respired carbon from ecosystems, and their use as a constraint for carbon cycle models.

Recent Findings Measurements of radiocarbon from vegetation pools and soils indicate a mixture of ages of carbon in ecosystem respiration. For example, respiration to support metabolism and growth in trees comes from very recently fixed substrates in leaves, but organs like stems and roots can mix recent substrates with older storage reserves. From detrital necromass and soils, the age of respired carbon integrates large variations in the age of carbon in substrates available for decomposition, ranging from less than one year (leaf litter in tropical systems) to a few hundred years for slowly decaying wood, or carbon stabilized by mineral sorption. Integrated at the soil or ecosystem level, the age of respired carbon is generally a highly 'right' skewed distribution, with most CO_2 released through faster cycling processes (plant respiration and rapid decomposition), but with a small component derived from very slow processes (slower decomposition). Thus, the mean age of respired CO_2 can be one to two decades old, while the median age can be much younger. Linking measured radiocarbon to modeled processes requires translation of either measured values to transit times or prediction of radiocarbon by models.

Summary Evidence from radiocarbon observations and models shows that the distribution of transit times of carbon in terrestrial ecosystems is key to understand what fraction of fixed carbon will be respired quickly, what fraction can be stored for decadal to century timescales, and what fraction can accumulate over longer timescales and influence long-term carbon storage.

Keywords Terrestrial carbon cycle · Radioisotopes · Carbon age · Ecosystem models · Climate change mitigation · Carbon dioxide

Introduction

Terrestrial ecosystems fix annually about 125 Pg C yr^{-1} from the atmosphere via photosynthesis [1], a flux of carbon that is of global significance for regulating Earth's climate. The large majority of this carbon returns back to the atmosphere in the form of CO_2 after begin incorporated and transferred through different ecosystem compartments such as leaves, wood, roots, and soil organic matter. A small fraction can be lost via processes like weathering and leaching. The time that it takes photosynthetically fixed carbon to pass through an ecosystem is defined as the *transit time of carbon* [2], a concept that is fundamental to understand the timescales at which carbon is cycled and the timescales of response of the terrestrial biosphere to human-driven perturbations [2–7].

The concept of transit time of carbon is also of relevance to understand feedbacks between ecosystems and the climate system. During the time carbon is stored in ecosystems as organic compounds, it is removed from the radiative forcing effects of CO_2 in the atmosphere and does not contribute

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to atmospheric warming [8–10]. Therefore, it is of relevance to obtain estimates of the transit time of carbon through the terrestrial biosphere, and to determine how human activities could modify transit times for different ecosystems. Models of the land surface and the global carbon cycle are developed for the purpose of attributing processes underlying ecosystem carbon sinks, but currently they diverge greatly in their predictions of transit times [11, 12].

Transit times of carbon through an ecosystem can be understood from two different perspectives [13, 14]. One is from the perspective of the current flux of carbon entering from photosynthesis and the time that this new carbon will need to pass through all ecosystem components until it is respired back to the atmosphere. The other perspective is from the current respiration flux as the time it took this carbon to pass through the ecosystem. For ecosystems that are close to an equilibrium state where the total amount of photosynthetic inputs is approximately equal to the total amount of respiratory outputs, both perspectives coincide in their estimates of transit times [13]. For systems out of equilibrium, the time required for new inputs to transit the ecosystem may differ from the transit time reflected in current outputs. From a practical point of view, it is easier to determine the transit time of current outputs by looking at the past history of an ecosystem, than to predict the future unknown behavior of current inputs [14]. Therefore, approaches for determining the age of respired carbon from ecosystems provide a way to estimate transit times of carbon, and also serve as an important diagnostic to evaluate the performance of terrestrial carbon models.

Radiocarbon measurements in respired CO_2 from plants and soils provide valuable information on the age of respired carbon from ecosystems [15, 16], and can be used to obtain estimates of the transit time of carbon. In fact, radiocarbon measurements in ecosystem compartments and in respired CO_2 offer a powerful approach to understand the wide range of timescales at which carbon is cycled in terrestrial ecosystems. In this review, we compile recent advances in the use of radiocarbon for the estimation of transit times of carbon in ecosystems. We focus mostly on the recent literature from the past 10 years, and for older studies we refer the reader to [16] who reviewed a large set of studies published before the year 2016. While previous reviews have focused on methodological aspects on the use of radiocarbon in ecosystem studies, we focus here on the set of approaches that are useful for the quantification of transit times of carbon in ecosystems and their components.

The main questions driving this review are: *How can radiocarbon measurements be used to estimate the transit time of carbon in ecosystems? What is the range of values of transit times obtained from empirical studies and how do they compare with model-based estimates?* To address these questions, we will first review the main theoretical aspects concerning the concept of transit time. We will then review studies that have provided radiocarbon and model-based estimates of transit times, and we will end with a discussion about potential issues and opportunities for new research.

Age and Transit Time Distributions of Carbon

Before reviewing the main methodological uses of radiocarbon for the estimation of transit times, we present first a short review of the concepts of age and transit time distributions.

The carbon cycle in ecosystems can be understood, and is normally modeled, as a set of compartments that exchange carbon with the atmosphere and transfer carbon among compartments such as foliage, wood, roots and soils (Fig. 1) [17, 18]. Nearly all carbon enters ecosystems through plant leaves (the foliage compartment) through the process of photosynthesis, a flux of carbon from the atmosphere to terrestrial ecosystem called gross primary production (GPP). The organic products of photosynthesis can be directly respired from leaves, or allocated to different plant organs where they can support processes like metabolism, the fueling of respiratory demands in living cells, be stored for later use, or used to grow structural tissues like cellulose or lignin. Carbon may also be transferred to symbiotic organisms through exudates, most notably it can rapidly be transferred from leaves to mycorrhizal fungi in the soil. The carbon allocated to grow plant tissues enters the soil as necromass, either as surface litterfall or via rhizodeposition. Soil heterotrophs obtain energy by oxidizing the reduced carbon in organic matter, and in turn become necromass that can be recycled and respired, or can be absorbed to mineral surfaces and stabilized for a time. Because these processes occur continuously in ecosystems, there is always a mixture of carbon of different ages stored in the different ecosystem compartments.

We define the *system age* as the mixture of all the ages of all carbon atoms stored in an ecosystem at any given time. The system age can be characterized by a distribution function that represents the proportion of carbon of different ages stored in the ecosystem. For individual compartments, we define the *pool age* as the mixture of all ages of carbon atoms stored in a particular pool or compartment. Typically, the largest carbon stocks are found in compartments such as wood or sorbed soil organic carbon, which accumulate slowly over a long time and have older system ages. Similarly, the smallest carbon stocks are found in compartments such as plant carbohydrates that tend to be used and replenished rapidly.

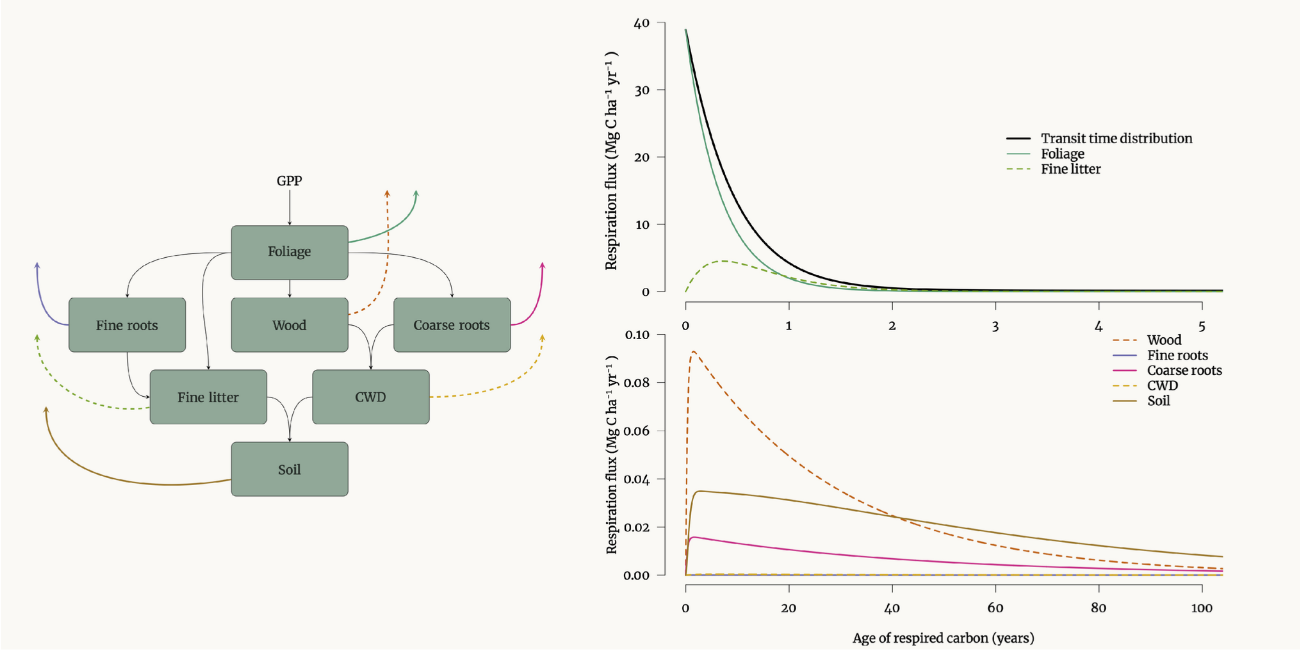

Fig. 1 The transit time of carbon in ecosystems represented as a distribution of different contributions from ecosystem compartments to the total ecosystem respiration flux. The carbon cycle in ecosystems is represented as a set of compartments that transfer carbon among each other and release carbon back to the atmosphere through respiration. Carbon enters ecosystems through the process of gross primary production (GPP) and photosynthates are allocated to different plant parts, and organic matter is later transferred to the litter layer and soils (left). Carbon released out of the compartments through respiration spends different amounts of time in the ecosystem since photosynthesis, and this heterogeneity in the age of respired carbon is captured by the transit time distribution (right). Distribution functions from a tropical forest ecosystem [6, 19]

The carbon that is respired from all living cells of plant parts, macro- and micro-organisms is composed of a mixture of carbon atoms that spend different amounts of time stored in different ecosystem compartments since they entered through photosynthesis. We define the *transit time* as the mixture of all ages of carbon in the respiration flux out of the ecosystem. The transit time can also be characterized by a distribution function that represents the sum of carbon respired from all compartments across the age range (Fig. 1). The mean transit time is a flux-weighted mean of the ages of carbon in the respiration flux from different compartments. Typically, the largest respiration fluxes are contributed by the smaller compartmental pools with lower carbon ages.

In systems with multiple compartments, the system age and the transit time are different. If an ecosystem would be characterized by one single well-mixed compartment, the system age would be equal to the transit time. But when ecosystems need to be represented with more than one compartment (e.g. fresh photosynthates versus storage reserves in vegetation, or fresh plant detritus versus mineral-associated organic matter in soil), the system age and the transit time will always be different [2]. In most ecosystems, the age is larger than the transit time – in other words, the ecosystem releases most of the carbon quickly after assimilation and only small amounts of carbon are retained over longer timescales [3, 20, 21].

The concepts of system age and transit time are generally different than the concept of *turnover time* [2], which is defined as the ratio of the stock of carbon divided by the input from photosynthesis or the output from respiration. However, the turnover time is equal to the mean transit time for a system in equilibrium. Therefore, if the carbon balance of an ecosystem is close to an equilibrium state (photosynthesis equal to ecosystem respiration), the turnover time can be used to approximate the mean of the transit time distribution of carbon.

The distribution functions of system age, pool age, and transit time can be obtained from carbon cycle models expressed as compartmental dynamical systems [17], and mathematical methods for their computation were developed recently for the case in which the model is in equilibrium (steady-state) [22], or for the case in which the model is out of equilibrium and forced by a time-dependent signal [14].

These distributions can also be obtained through numerical simulation using impulse-response experiments [3], in which a carbon cycle model is brought close to an equilibrium state and a sudden prescribed ‘pulse’ increases the amount of carbon added to the system via the leaf compartment over a very short period of time. The response of the system is observed and recorded as this pulse of 'new carbon' transits the ecosystem compartments over time, with some being stored and some contributing to increases in the respiration flux. Plots of the time series of 'new' carbon in, and respired by, the different compartments approximate the system age distribution and the transit time distribution, respectively [3]. However, this approach is prone to numerical errors and the tails of the distributions are cut off depending on the time span of the simulation after the addition of the pulse.

It is also possible to obtain age and transit time distributions for relatively simple models in which their equations can be manipulated to obtain the Laplace transform of the system of differential equations [20]. This approach provides exact analytical solutions for the distribution functions of age and transit time, but it is difficult to use for models with many compartments and connections among them.

Previous estimates of the transit time distribution of ecosystem models have shown that these distributions are highly asymmetrical [3, 19, 20], with a large proportion of carbon leaving the ecosystem via plant metabolic respiration at a young age, and very small proportions of the fixed carbon surviving to be respired at old ages. If these model predictions are accurate, it would imply that empirical estimates of transit times of carbon in ecosystems would have to address the issue that carbon is respired over a wide range of ages, with more carbon respired of young ages and less carbon of older ages. Sampling methods based on the assumption of an underlying Gaussian distribution of transit times would not be useful, and sampling methods would have to consider the large skewness of the expected underlying distributions.

Radiocarbon-Based Methods to Obtain the Age of Respired Carbon from Ecosystems

Over the last decades, an increasing number of studies have used radiocarbon methods to estimate the age of respired carbon from entire ecosystems, plant parts, and soils, which in turn can be used to obtain estimates of transit times of carbon in terrestrial ecosystems (Table 1).

Radiocarbon is a very useful isotopic tracer that can be applied to study the temporal dynamics of carbon in terrestrial ecosystems on two distinct timescales. As a naturally occurring radioisotope with a half-life of 5700 years, the depletion of the ^{14}C to ^{12}C ratio in organic samples with respect to that of pre-industrial atmospheric CO_2 is indicative of the preservation of carbon on timescales of centuries to millenia. However, making inferences of carbon transiting ecosystems on centennial to annual timescales requires a different approach that takes advantage of the radiocarbon bomb-spike generated by nuclear-weapon tests conducted in the 1950s and 1960s. In total, the atmospheric radiocarbon inventory was nearly doubled during this brief period, before concerns about radioisotope fallout led to a test ban treaty that ended nearly all atmospheric weapons tests in 1964. By tracing the dynamics of this 'excess' ^{14}C through the different ecosystem compartments, it is possible to obtain estimates of the rates of carbon exchange on annual to centennial timescales [16, 28, 29].

There are two approaches to estimating the radiocarbon signature of ecosystem respiration. One approach consists of performing a comprehensive radiocarbon budget of the radiocarbon signature of bulk organic material and the

Table 1 Previous studies reporting the Δ^{14}C signature of ecosystem respiration, isotopic disequilibrium with the atmosphere, and age of respired CO_2

Reference	Study site	Ecosystem type	Method	Δ^{14}C in ecosystem respiration (‰)	Measurement dates	Isotopic disequilibrium (‰)	Age of respired CO_2 (years)
Trumbore and de Camargo [23]	Multiple sites, Central Amazon Region, Brazil	Terra Firme Tropical Forests	Inventory of ^{14}C from respiration sources		2000s		3–7
Phillips et al. [24]	Willow Creek AmeriFlux site, Northern Wisconsin, USA	Boreal forest	^{14}C-CO_2 measurements and Keeling plots	121.7	June 2012	90	16–19
Phillips et al. [24]	Willow Creek AmeriFlux site, Northern Wisconsin, USA	Boreal forest	^{14}C-CO_2 measurements and Keeling plots	42	August 2012	10	1–4
Phillips et al. [24]	LEF Tower, Northern Wisconsin, USA	Boreal forest	^{14}C-CO_2 measurements and mixing model	76.8	May 2011 to December 2012		4–12
LaFranchi et al. (2016) [25]	LEF Tower, Northern Wisconsin, USA	Boreal forest	^{14}C-CO_2 measurements, transport model, and biospheric model	126	2010–2012	86	13.5–30
Tangarife-Escobar et al. [26]	Svartberget experimental forest, Sweden	Boreal forest	^{14}C-CO_2 measurements and Keeling plots	42.8	August 2022	45.1	4–9
Chanca et al. [27]	Amazon Tall Tower Observatory, Brazil	Terra Firme Tropical Forests	^{14}C-CO_2 measurements and Keeling plots	33	October 2019	25	4–8
Chanca et al. [27]	Amazon Tall Tower Observatory, Brazil	Terra Firme Tropical Forests	^{14}C-CO_2 measurements and Keeling plots	74	December 2021	74	14–22

respiration source from each ecosystem compartment. The total respiration radiocarbon signature is then obtained as a weighted average of the radiocarbon signatures from the respiration from each compartment. This approach requires the development of specific methodologies to capture the radiocarbon signature of respired CO_2 for diverse material such as leaves, wood, roots and soil.

The other approach uses the local atmosphere to integrate and mix respired CO_2 with that of 'background' air. Locally, or at night when a stable boundary layer allows for accumulation of higher CO_2 concentrations, the change in ^{14}C together with CO_2 concentrations allows estimating of the net ecosystem respiration ^{14}C signature. However, just as there is a distribution of transit times across the different compartments of an ecosystem, there will also be a distribution of radiocarbon being respired [30], with ^{14}C-CO_2 respired from plant metabolism having values close to that of the atmosphere from which it was recently fixed, to higher ^{14}C-CO_2 from the decomposition of dead wood built from carbon fixed years to decades previously, to lower ^{14}C-CO_2 derived from decomposition of carbon fixed hundreds of years previously and stabilized in soils.

Below, we provide several examples from the recent literature about what has been learned by measuring different ecosystem components (stem, root, litter and soil respiration) to perform comprehensive radiocarbon budgets. We also review a different set of studies where the radiocarbon signature of total ecosystem respiration in tropical and boreal forests has been estimated 'bottom up' from measuring components of respired ^{14}C-CO_2 and 'top-down' using samples from local atmosphere.

Sampling and Estimating the Mean Age of Respired Carbon

Analysis of the radiocarbon in CO_2 respired from leaves, stems, roots, litter and soils rely on two methods: attachment of an enclosure to trap living tissues inside a sealed chamber in the field (see for example [31]); or excision and collection of roots, stem cores, leaves, and soil samples, followed by field or laboratory incubation in closed chambers [32, 33]. In both cases, chambers are normally flushed with CO_2 free air and the respired CO_2 is allowed to accumulate to sufficiently high concentrations for radiocarbon measurement by accelerator mass spectrometry (AMS). The gas sample to be transported to the laboratory is often stored in a flask or septum-sealed vial containing headspace air with accumulated CO_2. Alternatively, the headspace air is passed over a molecular sieve trap that sorbs and stores CO_2 [34, 35].

The 'mean age' of the respired CO_2 is often estimated by comparing the ^{14}C of respired CO_2 with the recent record of atmospheric ^{14}C-CO_2 [e.g. 36]. In these comparisons, the 'mean age' is estimated as the amount of time elapsed since the atmospheric CO_2 in the past had the same ^{14}C value as the CO_2 that is now being respired. However, it is important to recognize that this is an approximation and there are several associated limitations. These limitations are: (1) An implicit assumption of the ecosystem carbon cycle as a well-mixed one-pool model, which helps to relate the radiocarbon signature of what is respired with the radiocarbon signature of the atmosphere in the past, but ignores differences in the rates of carbon cycling of ecosystem compartments. (2) A potential mismatch between the ^{14}C-CO_2 signature of the local atmosphere that serves as source of CO_2 for photosynthesis than the signature of the reference background site where this information is available. (3) The annual decline of the atmospheric ^{14}C-CO_2 signature is within the detection limit of most AMS systems.

Fundamentally, the idea of the comparison between respired and reference atmospheric CO_2 began with the recognition that the rate of annual ^{14}C-CO_2 decline during the period from the 1990s to early 2000s was relatively constant, such that the comparison of measured ^{14}C-CO_2 with the past atmospheric record gave essentially the same transit time as running a one-pool model as long as the mean age obtained was $<$ 15 years [for details, see 37]. However, as demonstrated in the studies below, the single (homogeneous) pool assumption in many cases is not valid. For both plant and soil incubations, it has been observed that the ^{14}C signature of respired CO_2 differs from that of the bulk material being incubated. This is important because it indicates that only a fraction of the bulk material may be easily metabolizable. In the case of plants, extracted nonstructural carbon contains compounds that are not metabolized in incubations [32, 33]. In most published studies using soil incubations, the respired carbon is 'younger' than the bulk soil carbon [5, 38, 39], reflecting stabilization mechanisms that slow decomposition rates of organic matter.

It is important that studies conducted in heavily populated or urban regions, where the 'background' atmosphere can have potentially high and/or variable contributions from fossil fuel CO_2 sources [40], quantify the local background atmospheric ^{14}C-CO_2, either averaged [e.g. in latewood of tree rings at the site; see [32]] or directly at the time of sampling. In these cases, the contribution of the polluted background atmosphere should be corrected for estimating the mean age of respired CO_2.

Finally, the precision of radiocarbon measurements often approaches the year-to-year change in $\Delta^{14}C$-CO_2 (now between 2–4 ‰ per year), limiting this method to detecting contributions from storage reserves that are older than 2 or 3 years.

Respiration Sources from Living Plants

Studies of plant respiration using radiocarbon generally focus on long-lived vegetation like trees that can store carbon or build tissues that last for many years. Recently fixed carbon used to support metabolic demands in leaf tissues and supporting growth of mycorrhizal fungal fruiting bodies [41] have the ^{14}C signature of atmospheric CO_2 of the year of sampling and show that fresh photosynthetic products can be transported quickly from leaves to roots. However, both ^{13}C-pulse labeling and radiocarbon studies that measured respiration from tree stems and roots have demonstrated that years to decades-old storage reserves can be mixed with the fresh photosynthates to fuel respiration [e.g. 42–44]. Carbon fixed years to decades previously and stored as carbohydrate reserves can also be mobilized for survival during times when supply of new carbon from leaves is limited. For example, such reserves are used to fuel winter metabolism and growth in temperate deciduous trees, but also when an early frost defoliates trees temporarily [45], or when phloem transport is cut off by experimental tree girdling [46–48]. In fact, most of the experimental evidence shows that respired carbon from tree stems and roots is one to several years old [49] due to this capacity of trees to re-mobilize storage reserves.

Observed seasonal changes in the radiocarbon signature of non-structural carbon (NSC) of temperate trees suggest that at least two compartments that cycle at different rates are necessary to accurately model NSC dynamics [50, 51]. The two-NSC-pool structure indicates that one pool is continually used to fuel respiratory demands while a second pool is used slowly and can be accessed during times of physiological stress [51, 52]. The rate of accessibility and mobilization of NSCs may depend strongly on wood physiological traits. Previous work with tropical forest trees has shown that species storing NSCs in their parenchyma tissue are able to mobilize NSCs faster than species storing them in fibers [52, 53]. Future work is needed to expand to other tree species and environments and to determine if there are links between the transit times for plant respiration and tree mortality and response to stress.

Importance of Multi-Year to Decadal Storage Reserves in Trees

The demonstration that respiration in tree stems and roots even in unstressed trees can be fueled by multi-year to decadal storage reserves mixed with fresh products of photosynthesis provides insights into the resilience of these long-lived organisms to periodic stresses such as drought, defoliation, insect damage, or fire [33, 45]. Comparisons of extracted nonstructural carbohydrates show increasing ages with depth in the tree stem [54], but subsequent work comparing the age of extracted carbon with the age of respired CO_2 shows that much of what is extracted is not metabolized [32, 33]. However, inward and outward mixing of metabolizable reserves varies with tree species according to anatomical traits such as where storage occurs and on recent disturbance history [53].

The ability to mobilize and use stored reserves increases the resilience of trees against environmental conditions that can reduce photosynthesis such as drought or defoliation. Experimentally, this is evidenced by the fact that girdled trees can take up to several years to die [47, 48], using increasingly older reserves to maintain metabolism in the absence of new photosynthetic products. Translocation of reserves belowground also maintains living roots of girdled trees that otherwise would run out of carbon reserves [32]. Belowground storage reserves can be used for new root growth – not only in response to emergency stress such as defoliation [55], but also in roots of unstressed trees [56].

Ecosystem transit times may be underestimated by models that do not account for time lags between photosynthesis and respiration, particularly in trees and woody tissue. For example, delays caused by storage reserves in long-lived trees should result in longer transit times for forests compared to grasslands [57]. Given the importance of plant respiration as a global carbon flux (estimated at ~ 50% of gross primary production), these delays may influence interannual variations of land–atmosphere CO_2 fluxes and buffer potential relationships between net ecosystem exchange measurements with other measures like net primary production. Given recent declines in the rate of atmospheric ^{14}C-CO_2, studies on the role of older reserves in plant respiration are particularly important to undertake in the next decade [58].

Pulse Labeling Experiments for Fast Transit Times

In cases where more information is needed about the timescales of carbon allocation to plant respiration on timescales below several years, tracking bomb radiocarbon can be of limited value. In such cases, transit times can be assessed by following a pulse-labeling of new photosynthates with ^{13}C-CO_2 or low-level ^{14}C-CO_2. ^{13}C isotope labeling studies that trace new photosynthetic carbon have demonstrated rapid (within days to weeks) transport and metabolism of ^{13}C isotope labels taken up by leaves [59]. These studies also show dilution of the label as it transits the stem [57], and have been used to estimate rhizodeposition fluxes [60] and to study the potential for dark CO_2 fixation in soils to introduce younger carbon into deep soil microbial communities [61]. Use of ^{13}C for labeling experiments is less expensive than low-level ^{14}C labeling, but ultimately limited by the time the label can be detected with confidence.

A useful approach consists of combining a ^{13}C labeling that can be measured with greater sensitivity and temporal resolution, together with a low-level ^{14}C pulse measured by AMS. Such a double label approach can extend the time period for estimating transit times to more than a year [62, 63]. With this approach it is possible to capture the fast respiratory response expected within one year of a pulse addition chasing the ^{13}C label, with the slower response of ^{14}C that travels across multiple compartments and needs years to decades to appear in the respiratory flux. For timescales of multiple years to decades, the bomb ^{14}C pulse is the most reasonable method available.

Pulse labeling experiments must take into consideration issues of reporting corrections for isotopic fractionation. For samples with a ^{14}C or ^{13}C label, the standard assumption used to correct ^{14}C data for mass-dependent isotope fractionation, that ^{14}C is fractionated twice as much as ^{13}C, does not apply. To address this issue, one needs to use the ^{13}C values measured for 'control' (unlabeled with ^{13}C) samples to correct for isotope fractionation in the measured ^{14}C samples in both ^{14}C unlabeled and labeled samples [see 64 for details].

Labeling with ^{14}C can provide orders of magnitude greater sensitivity compared to ^{13}C labeling. Usually, for ^{13}C it is possible to go from 1% to a maximum close to 100% of the samples' carbon, while the natural abundance of ^{14}C is about 1 part per trillion and the level of labeling is normally limited by radioactivity and safety regulations [65]. For experiments such as Free-Air CO_2 Enrichment (FACE), the sensitivity is generally from 1 ppt to the minimum measurable in the control treatment to a value that depends on the FACE concentration—for example 100% modern in control (400 ppm) to 550 ppm, whereas normally the ^{13}C label is about 20 ‰. In FACE experiments, the difference in ^{14}C sources can make sensitivity equal to or greater than ^{13}C differences in source [see 66].

Soil Respiration

The CO_2 released from soils to the atmosphere, collectively called soil respiration, integrates at least two fundamentally different sources of CO_2: respiration of living roots and associated mycorrhizae and rhizodeposits that tend to have been fixed recently from the atmosphere, and CO_2 derived from decomposition of necromass that contains carbon fixed from the atmosphere in the last years to decades. Incubation of roots are typically used to estimate the radiocarbon signature of autotrophic respiration, while incubations of soil and litter are used to estimate the ^{14}C signature of heterotrophically respired CO_2.

The difference in the radiocarbon signatures of these sources has facilitated the estimation of the contribution of root/rhizosphere respiration versus heterotrophic respiration. This has also enabled the investigation of seasonal variations in source partitioning [67, 68]. One previous study [43] compared the radiocarbon partitioning method with a method based on continuous measurement of fluxes in 'control' collars versus collars where roots had been cut by trenching. There were systematic differences between the two methods, with higher estimates of root respiration resulting from the differences between trenched and untrenched fluxes compared to the partitioning of respiration using radiocarbon. Interestingly, the root-respired CO_2 at this site (a temperate forest) was measurably higher (by about 15 ‰) than the atmospheric $^{14}C\text{-}CO_2$ measured at the same time, indicating the importance of time lags associated with mixing of modern and older storage reserves even in unstressed plants. Muhr et al. [67] observed that drought-related soil drying was associated with a reduction in heterotrophic but not autotrophic respiration in a spruce forest. Methods have been developed to sample radiocarbon over winter in tundra soils, and demonstrate the importance of winter heterotrophic fluxes to the annually averaged age of soil respired CO_2 [69].

Respiration measurements have been made in association with manipulative experiments to help explain reasons for changes in soil respiration rates in response to changes in litter inputs, soil warming [70–72], and root trenching [43]. In addition, experiments using laboratory manipulations of temperature and moisture have specifically investigated the potential for changing the age of carbon being respired [73]. Studies conducted in Arctic regions have shown that older organic matter that is thawed and warmed does not necessarily decompose rapidly after it is destabilized [74, 75]. Beem-Miller et al. [76] explored potential effects of storage and re-wetting of soils to create artifacts in the ^{14}C measured in respired CO_2. They found that differences between previous and current measurements of archived samples are small, and the analysis of archived samples is a useful approach to reconstruct time series of radiocarbon incorporation in soils.

Another important use for radiocarbon measurements of respired CO_2 is to demonstrate the mobilization of different carbon sources for soils that are not in equilibrium. An example is in a 19-year study that documents the increased contribution of older (pre-bomb) carbon associated with thawing permafrost [77]. The radiocarbon signature of ecosystem respiration in tundra soils has also demonstrated strong heterogeneity associated with patterned landscapes [78] that likely also reflects long-term disequilibrium associated with landscape evolution.

Recent studies have called to the attention potential contributions of ancient carbon derived from petrogenic sources that can be incorporated into soil organic matter, potentially affecting estimates of the age of soil organic carbon [79–81]. Radiocarbon free sources from rocks and incorporated by microorganisms in organic compounds can have a strong effect on the average radiocarbon values of soil carbon, particularly in the subsoil and under sedimentary-rock substrates [81, 82]. Thus, it is likely that under some circumstances the ^{14}C-CO$_2$ signature in soil respiration has contribution of ancient carbon from petrogenic sources, which would bias estimates of mean transit times towards larger values. However, the proportional contribution of petrogenic sources to soil respiration must be assessed carefully for different soils, and in the context of the skewness of the age distribution of soil carbon and the distribution of transit times. Since soil microorganism preferentially consume young carbon from plant-derived material, the contribution of petrogenic sources to microbial respiration should be quantified with respect to the much larger contribution of young carbon. In a recent study, Heinze et al. [82] found that incubation of crushed rocks resulted in leaching and microbial incorporation of old but not ancient organic carbon, which was likely of plant origin and stored in rock fractures. Under these experimental conditions, microorganisms still preferentially consumed and released CO$_2$ of younger plant origin, in comparison to the ancient petrogenic carbon available in the rocks.

Weighted Average of Radiocarbon from Respiration Sources

The different methods presented above and used to obtain the radiocarbon signature in respiration from individual compartments can be combined to obtain an average signature of total respired radiocarbon, weighted by the contribution of each compartment to the total respiration flux. Although such a weighted average can be laborious to obtain, it is in many cases possible to obtain by combining results from different studies that address individual components for a particular site.

At a central Amazon tropical forest, Trumbore & de Camargo [23] estimated the age of respired carbon in total ecosystem respiration by estimating the age of respiration components (plant respiration, litter, soil respiration) from radiocarbon measured using incubations, together with a model of decomposition of dead trees [83]. Respiration fluxes from the different ecosystem components were estimated separately [83]. Using this approach, they estimated a mean age of total respired carbon of 3 - 7 years (Table 1), assuming that autotrophic respiration contributed approximately 70% of ecosystem respired carbon with ages of 0.01–1 years, with the other 30% contributed by heterotrophic respiration and having ages averaging 15–29 years. This empirical 'bottom-up' estimate of the age distribution of respired carbon from an ecosystem is consistent with both modeled and integrated flux approaches [19, 27]. Therefore, this method has large potential for being replicated in other ecosystems provided that information on the relative contribution of autotrophic and heterotrophic respiration is available.

Below Canopy Air and Isotopic Mixing Models

The radiocarbon signature of total ecosystem respiration can also be obtained by combining direct sampling methods of atmospheric radiocarbon in below canopy air with isotopic mixing models to separate the contribution of the ecosystem respiration signal from the atmospheric background. Methods based on isotopic mixing models to estimate the δ^{13}C signal of respiration from the background have been successfully applied in ecosystem studies for several decades [84], but have only recently been applied using Δ^{14}C-CO$_2$ measurements.

There are two approaches to estimating the ecosystem respiration isotopic signature. The so-called "Keeling-plot" method [84, 85] is based on a linear regression between the inverse of the mole fraction of CO$_2$ versus its isotopic signature, and the intercept term of the regression provides an estimate of the isotopic signature of the source of CO$_2$ separated from the background. A similar approach was proposed by Miller & Tans [86] for cases in which the background concentration of CO$_2$ changes over time, using a different form of linear regression, which in this case the regression slope provides the isotopic signature of the source.

Working at a temperate deciduous forest, Phillips et al. [24] collected air samples below the canopy at six different heights during nighttime in summer 2012. They used the Keeling-plot method to separate the radiocarbon signature of ecosystem respiration from the atmospheric background, obtaining an average value of Δ^{14}C in respired CO$_2$ of 122 ‰ for samples taken in June 2021, and a value 42 ‰ for samples collected in August 2012. They obtained an average isotopic signature of ecosystem respiration of 77 ‰ for the period between May 2011 and December 2012. With both the Keeling plot and the Miller-Tans methods, the source signature of ecosystem respiration was higher than the 2012 background atmosphere by values ranging from 5 to 38 ‰ and indicating a mean age of ecosystem respiration of between 1 to 19 years (Table 1). Measurements of radiocarbon in air samples below the canopy were also conducted at a Boreal Scots pine forest in Scandinavia [87]. Isotopic mixing models were not used in this study to separate the source signature from the background, but the measurements were conducted over full diurnal cycles and over different seasons, showing an important level of variability between night- and day-time samples as well as across different seasons. These results indicate that the age of respired CO_2 in forests can differ with changes in the main contribution of sources of carbon to total respiration. During nighttime and winter months, respiration from soils seems to dominate the total $\Delta^{14}\Delta^{14}C\text{-}CO_2$ signal, with a stronger isotopic disequilibrium (larger difference between respired CO_2 and the background atmosphere) compared to measurements performed during the day in the summer season.

At a tropical rain forest site in Brazil, Chanca et al. [27] obtained the radiocarbon signature of ecosystem respiration using a similar approach as in the previous studies, collecting samples in a vertical profile below the canopy during entire diurnal cycles. The authors also had access to samples well-above the canopy, at a height of 324 m above ground level (agl) that provided information on the atmospheric radiocarbon background. Using the Keeling-plot and the Miller-Tans methods [85, 86], they obtained $\Delta^{14}C$ values in total respired CO_2 ranging between 24 to 41 ‰ during a campaign conducted in 2019, and values ranging between 53 to 102 ‰ for a campaign in 2021 (Table 1). These values of $\Delta^{14}C$ were enriched in radiocarbon compared to the atmospheric background, which was measured as 8 ± 2 ‰ in 2019, and 0 ± 2 ‰ in 2021. By comparing the radiocarbon signature of the respired carbon with the values of the atmospheric background from previous years, the authors concluded that the mean transit time for this forest was around 6 ± 2 years in 2019, and 18 ± 4 in 2021. The difference in mean transit time between the two sampling campaigns may reflect seasonal differences in respiration sources [87], but more measurements would be needed to better understand inter-annual variability in mean transit times. Nevertheless, the results indicate that the mean transit time for these tropical forests is on the order of one to two decades.

A separate study in a boreal forest conducted during the summer of 2023 using a combination of air sampling and isotopic mixing models [26], found only a small isotopic disequilibrium between the ecosystem-respired CO_2 (13 ‰) and the atmospheric background (−2 ‰) indicating a respiration source dominated by carbon respired within the last few years. Although this result may seem surprising for a boreal forest, it is also not unexpected if the seasonality of respiration sources is taken into account [50, 87]. During the peak of the growing season in summer time, organisms are at their peak of metabolic activity and experience the warmest temperatures of the year, and therefore autotrophic respiration sources likely dominate the total respiration flux [88]. To more fully understand the ecosystem respiration budget, measurements in other seasons would be required.

Model-Data Assimilation

Radiocarbon measurements of different components of ecosystems, particularly from roots and soils, have been used to parameterize models of the terrestrial carbon cycle [89–95]. Once parameters of a model have been found, it is possible to obtain transit time distributions from the model using equations for compartmental systems at equilibrium [22]. This approach makes use of any available data on carbon stocks and radiocarbon from any compartment, not necessarily from respired CO_2, to estimate the transit times that would most likely match the observations. Once the model that best matches the available data is identified, inferences on transit time and age distributions are made on the model.

An example of this approach is the simple carbon model developed for tropical rain forests in Colombia using data from a chronosequence of carbon stocks from vegetation and soils [19]. The model has seven carbon pools, foliage, wood, fine roots, coarse roots, fine litter, coarse woody debris (CWD), and soil organic carbon (Figs. 1 and 2). Using the average of a posterior distribution of parameter values for this model, we obtained the age and transit time distributions using the formulas of Metzler & Sierra [22]. This approach showed that the mean age of carbon for the entire ecosystem is approximately 41 years while the mean transit time is 11 years (Fig. 2); i.e. the carbon respired from the ecosystem is much younger than the carbon stored. The median of the transit time distribution of this model is 0.5 years, which indicates that 50% of GPP is respired in half a year.

Once a parameterized model is available, it is also possible to obtain predictions of the radiocarbon stocks in biomass and soils as well as in ecosystem respiration. This can be done by running a similar version of the model that only adds a radiocarbon decay term to the original system of differential equations [96]. Alternatively, one can take the numerical predictions of the model for all carbon pools and all fluxes connecting them, and reconstruct an equivalent model for which radiocarbon can be obtained [97].

For the tropical forest example, predictions of radiocarbon in ecosystem respiration show that the respiration flux back to the atmosphere is enriched with bomb radiocarbon since the 1980s, with an isotopic disequilibrium that increases over time as the atmospheric $\Delta^{14}C$ of CO_2 decreases due to fossil-fuel influence and the forest respires radiocarbon assimilated over the course of decades (Fig. 2). These model predictions are possible to test with direct radiocarbon observations (at least for future predictions), and can help to improve the original model if the data shows that the ecosystem is releasing carbon too fast or too slow back to the atmosphere.

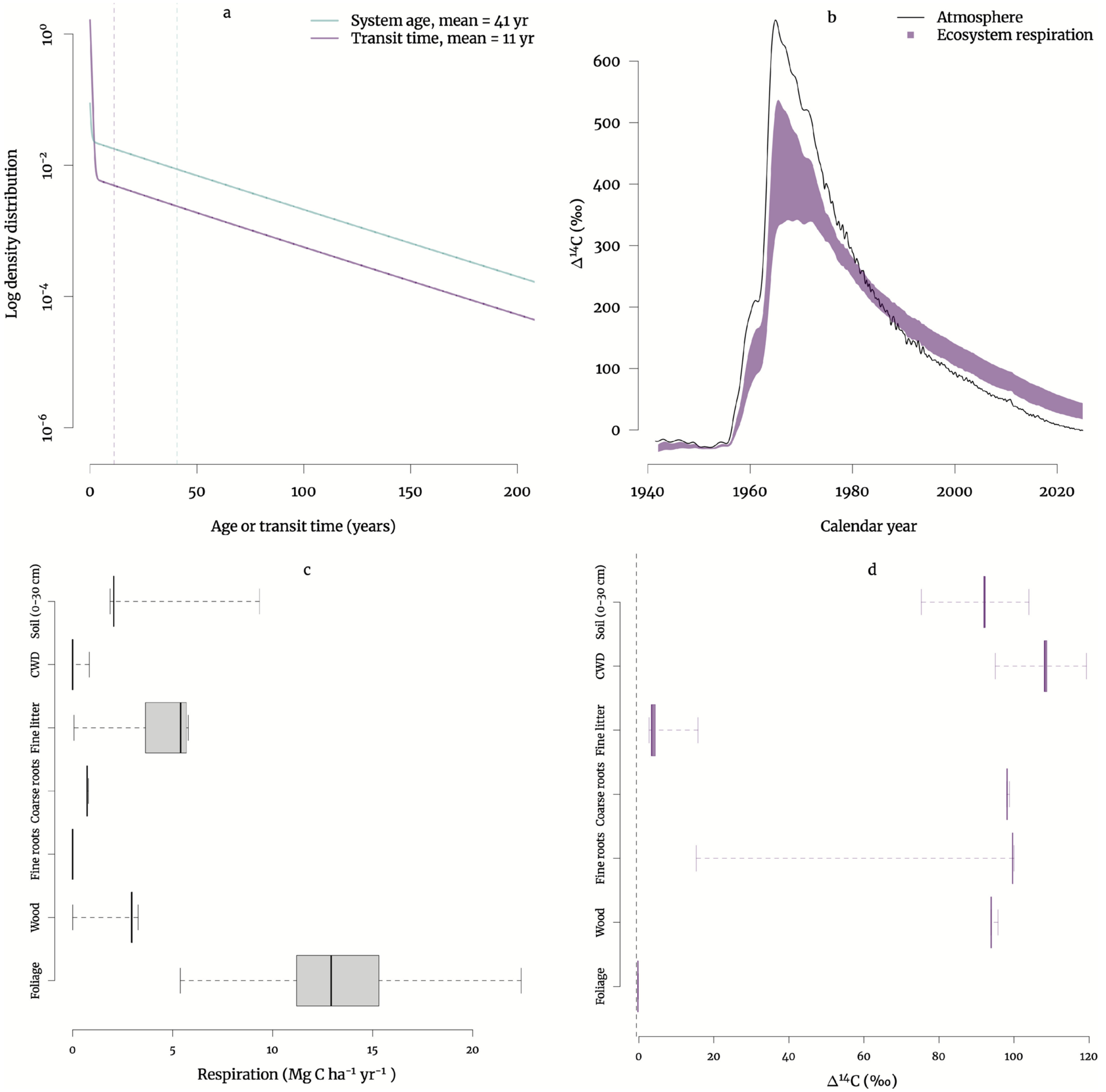

Fig. 2 (**a**) System age and transit time distribution of carbon for tropical rain forests in the foothills of the central Andean mountains in Colombia. (**b**) Radiocarbon signature of CO_2 in total ecosystem respiration predicted by the model. Notice that the difference between the radiocarbon signature of respired CO_2 and the atmospheric CO_2 changes over time while the transit time of carbon is constant in the model. (**c**) Respiration from each individual compartment predicted by the model at equilibrium. The variability in respiration flux is due to variability in GPP fluxes and uncertainty in model parameters. (**d**) Radiocarbon contribution of each individual compartment to the respiration flux predicted for the year 2025. Sources of variability similar as in (**c**). Vertical dashed line in (**d**) represents the atmospheric ^{14}C-CO_2 for the year 2025. Model parameters for a tropical forest [6, 19]

More importantly, the difference between the radiocarbon signature in respired CO_2 and the atmospheric signature changes over time even though the transit time distribution of the model, with its mean, are time invariant (Fig. 2). This isotopic disequilibrium changes because the atmosphere gets diluted over time due to the fossil fuel influence, and the respiration signal changes due to different timescales of carbon cycling, storage, and transfer among the different ecosystem compartments. The implication is that empirical studies that have used the isotopic disequilibrium signal to estimate a mean transit time without the aid of a model have likely introduced an error due to these different factors that affect the isotopic disequilibrium. Ideally, one should obtain the transit time of carbon from an ecosystem using a well parameterized model, preferably informed by radiocarbon data.

Several global-scale terrestrial carbon cycle models include a radiocarbon component that helps to evaluate the performance of the model with respect to radiocarbon observations [98–100]. Simulation results from these models can be compared with databases of radiocarbon observations such as ISRaD [101] to determine whether a model incorporates carbon too fast or too slow, or whether or not it performs well in certain geographical regions; thus, indicating issues that should be improved in a model. At the global scale, analyses of radiocarbon predictions from earth system models suggest that most models likely underestimate the uptake of carbon on land [100], and incorporate carbon too slowly in the oceans [99].

Discussion

Radiocarbon Observations and Transit Times of Carbon in Terrestrial Ecosystems

The transit time of carbon in terrestrial ecosystems can be approximated by obtaining an estimate of the radiocarbon signature of respired CO_2. In turn, the radiocarbon signature of respired CO_2 can be obtained by two separate approaches: (1) by a radiocarbon budget that estimates the radiocarbon contribution of each ecosystem compartment to the total respiration flux as a weighted average, or (2) by direct measurements of radiocarbon in CO_2 collected below forest canopies and partitioned between respiration signal and background using isotopic mixing models. The approach based on a radiocarbon budget of respiration components can be tackled to span different timescales by (a) purposeful isotopic labeling experiments combining ^{13}C and ^{14}C labels for timescales from days to a few years; (b) measurements of the radiocarbon signature from plants and soils using chambers installed in the field to integrate timescales of a year to decades; (c) radiocarbon in CO_2 obtained from laboratory incubation methods of live tissue and soils that can also investigate how temperature and moisture conditions can affect the age of substrates being respired.

Most of these empirical methods attempt at obtaining an average value of the radiocarbon signature of respired CO_2, and by using the radiocarbon signature of atmospheric CO_2 during the bomb period as a reference, match the obtained radiocarbon value with a previous value in the atmospheric curve (for transit times $<$ 10–15 years). The difference between the year of measurement and the matched atmospheric radiocarbon year provides an approximation of the mean transit time of carbon.

As the isotopic disequilibrium between the atmosphere and the terrestrial respiration flux increases over time (Fig. 2b), the direct match between the radiocarbon in respired CO_2 and a previous atmospheric value becomes less reliable as a method for obtaining the mean transit time of carbon in ecosystems. For this reason, methods that combine empirical measurements of radiocarbon and other components of an ecosystem's carbon cycle, with a carbon cycle model, offer a more robust approach to obtain transit times. With a model, it is possible to obtain entire transit time distributions, not just the mean value, which can provide very important insights on the range of timescales of carbon cycling in ecosystems.

What is the Range of Values of Transit Times Obtained from Empirical Studies and How They Compare with Model-Based Estimates?

While the carbon respired from ecosystems consists of a very wide range of ages that spans from days and months to centuries and millennia, the mean transit time obtained in published studies is in a range between one year to two decades (Table 1). Most of the evidence suggest that the large majority of respired carbon from ecosystem is very young, with a *median* transit time ranging from months up to a few years. The contribution of very old carbon to ecosystem respiration seems to be very small, but sufficient to skew the *mean* transit time of carbon to a range of decades instead of months or years. Even in permafrost soils, where the amount of very old carbon is large, measurements of radiocarbon in respired CO_2 show that the total respiration flux is dominated by very young carbon from plant material [69]. However, in disturbed ecosystems, the older carbon losses can become larger [77].

Overall, empirical estimates of the transit time of carbon based on radiocarbon observations agree on the decadal timescales of transit times obtained with ecosystem and land-surface models. At the global scale, models predict mean transit time of about one to two decades on average [3, 7, 12, 102, 103], but with strong differences among individual models and in spatial patterns. For instance, Lu et al. [102] obtained average values of mean transit time ranging between 13 to 341 years with the CABLE model. Mean transit times in the range between one to three decades were predominant in their simulations for most of the land surface covering the tropics and the temperate zone, while values higher than four decades were only obtained for boreal and arctic regions.

Despite this overall agreement at the decadal timescale, there are important limitations for comparing estimates of mean transit time between models and observations. One issue is that often the models obtain their estimates of mean transit time taking the ratio of the total stock of carbon divided by the GPP or the total respiration flux as in the definition of turnover time. However, it is well known that for systems out of equilibrium, as in a transient model simulation, the turnover time and the mean transit time do not match and they can differ considerably [5, 102]. Another issue is related to the way that allocation is computed in models, where often the total autotrophic respiration flux is subtracted from GPP immediately after photosynthesis, returning this flux to the atmosphere without allocating it to plant parts. As a consequence, the transit time obtained from these models is long because it is biased to the heterotrophic component only [3, 49] and this needs to be accounted for when comparing to field measurements of radiocarbon that integrate both autotrophic and heterotrophic sources.

Emerging Understanding and Potential Research Opportunities

Measurements of radiocarbon in respired CO_2 consistently show values enriched in radiocarbon in comparison with the background atmosphere (positive isotopic disequilibrium, Table 1). This is consistent with previous modeling studies that inferred a shift of the terrestrial biosphere, from being a sink of bomb radiocarbon to a source, approximately 20 years after the radiocarbon bomb spike [104, 105]. Currently, the terrestrial biosphere is returning bomb radiocarbon that took about one to two decades to pass through terrestrial ecosystems. Most of this bomb radiocarbon was incorporated in plant biomass, litter, and the top layers of soils. There is strong evidence for comparatively little incorporation of bomb radiocarbon to date in subsoils, which are dominated by radiocarbon highly depleted with respect to pre-industrial CO_2 [26, 106, 107].

A large proportion of bomb-produced radiocarbon still remains stored in topsoils, wood biomass, coarse woody debris, and wood products harvested during the last decades. Oxidation of organic matter in these compartments, either by biological activity or fires, will release to the atmosphere CO_2 enriched with ^{14}C in comparison to the oxidation of organic matter from other fast cycling compartments of the terrestrial biosphere. This source of radiocarbon to the atmosphere may play a role in the future trajectory of atmospheric ^{14}C-CO_2. Little attention has been given to the dynamics of carbon in woody debris and wood products, which at the current time likely contain a significant part of the bomb radiocarbon fixed in ecosystems during the last decades. There are opportunities to study these carbon compartments in more detail, and better explore their role in storing carbon at decadal to centennial timescales. In fact, these woody compartments have been shown to have a large potential for removing anthropogenic carbon from the atmosphere at timescales relevant for climate change mitigation [108].

The effects of ecosystem management on the transit time of carbon remain largely unexplored for a wide range of management practices and ecosystem types. Previous studies have shown that fertilization [94, 95], irrigation [94], and crop rotations [109] have a strong effect on the transit time of carbon in some agricultural ecosystems. However, a more systematic evaluation of the effects of management in croplands, grasslands and forests across biomes still needs to be done to better explore how changes in transit times due to ecosystem management may impact carbon dioxide removal at the global scale.

Methodological challenges still remain for obtaining transit times of carbon in ecosystems both from empirical measurements of radiocarbon and from models. For empirical estimates, the main challenge is to move away from estimates of transit times based on a comparison with previous values of radiocarbon in the atmosphere. For modeling studies, the main challenge is to move away from estimates based on turnover times, which make an assumption of equilibrium, while the simulations are run for transient conditions. There are however methodological approaches available to address these challenges and provide more robust estimates of transit times. For empirical studies, the best approach is to combine observations with models and obtain transit times from the model structure and its parameterization, and not from the data alone. For modeling studies, recent mathematical developments for the computation of time-dependent transit times [4, 14, 97, 110] can be implemented as part of model-output processing frameworks.

Conclusions

The transit time of carbon in ecosystems is a key metric to study carbon dynamics from an integrative perspective. Measurements of radiocarbon from ecosystem compartments and in respired CO_2 offer possibilities to estimate transit times of carbon. There are a number of approaches to estimate the radiocarbon signature of respired CO_2 combining measurements of the radiocarbon signature of respiration from individual compartments or from the entire ecosystem. However, to obtain values of transit times from estimates of the radiocarbon signature of respired CO_2, the most robust approach implies the use of an ecosystem carbon model that reliably incorporates field measurements. The estimate of the transit time of carbon, i.e. the entire transit time distribution, can be inferred from the model structure and its parameters, providing valuable information on the proportions of carbon that are cycled at a continuum range of timescales.

The few available estimates of transit time of carbon in forest ecosystems based on radiocarbon methods suggest that the mean transit time is on the range from one year to two decades, but methodological uncertainties remain. To our knowledge, estimates of transit times for ecosystems such as deserts, wetlands, grasslands, among others, have not been conducted yet and remain a major uncertainty for global carbon studies. Seasonal and inter-annual changes in transit times also remain unexplored– though measurements suggest they can be potentially large. In addition, effects of ecosystem management on transit times are also potentially assessable with radiocarbon studies. Progress in sampling methodologies, technological improvements on radiocarbon measurement devices, and in model development, could expand the range of estimates of transit times for diverse ecosystems as well as the study of its environmental controls. More importantly, future studies likely would improve our understanding on the time that carbon atoms need to pass through the terrestrial biosphere, and how this time is related to the time carbon atoms spend in the atmosphere where they contribute to the greenhouse effect.

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Declarations

Competing interests The authors declare no competing interests.

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