

Review Article

Understanding the Terrestrial Carbon Cycle: An Ecohydrological Perspective

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The terrestrial carbon (C) cycle has a great role in influencing the climate with complex interactions that are spatially and temporally variable and scale-related. Hence, it is essential that we fully understand the scale-specific complexities of the terrestrial C-cycle towards (1) strategic design of monitoring and experimental initiatives and (2) also developing conceptualizations for modeling purposes. These complexities arise due to the nonlinear interactions of various components that govern the fluxes of mass and energy across the soil-plant-atmospheric continuum. Considering the critical role played by hydrological processes in governing the biogeochemical and plant physiological processes, a coupled representation of these three components (collectively referred to as ecohydrological approach) is critical to explain the complexity in the terrestrial C-cycling processes. In this regard, we synthesize the research works conducted in this broad area and bring them to a common platform with an ecohydrological spirit. This could aid in the development of novel concepts of nonlinear ecohydrological interactions and thereby help reduce the current uncertainties in the terrestrial C-cycling process. The usefulness of spatially explicit and process-based ecohydrological models that have tight coupling between hydrological, ecophysiological, and biogeochemical processes is also discussed.

1. Introduction

The greenhouse effect of the Earth's atmosphere due to the radiative forcing of gas molecules contained in it was first reported by Joseph Fourier in France as early as in the 18th century [1, 2]. However, it was only in the works of Tyndall [3] followed by Arrhenius [4] that the first quantification on the influence of increasing atmospheric carbon dioxide (CO₂) on increasing the Earth's surface temperature was made. Since the industrial revolution, the mean global CO₂ concentration has risen from about 280 ppm to over 379 ppm [5, 6]. This rapid rise in atmospheric carbon dioxide concentrations occurred due to the imbalances between the rates at which anthropogenic and natural sources emit CO₂ and the rate at which the global C sinks remove CO₂ from the atmosphere [7].

The first-order effect of increased atmospheric CO₂ is the increase in surface temperature of the Earth which subsequently leads to climate change (e.g., [8, 9]). However, climate change will further enhance CO₂ emissions due the presence of several feedback mechanisms operating among various biogeochemical cycles thus leading to further intensification of climate change [10]. Potential consequences of elevated CO₂ concentrations include increasing air and ocean temperatures, melting of polar ice-caps, and rising of sea levels [11] and plant composition and ecophysiological changes [12]. Some other effects include decrease in areas of the surface of the Earth that are covered with snow and decrease in spatial extent of permafrost [13]. The globe overall acts as a net C sink. Of this, the oceanic C sink is larger than the terrestrial C sink because of both the two mechanisms (solubility pump and biological pump) that sequester atmospheric C [14].

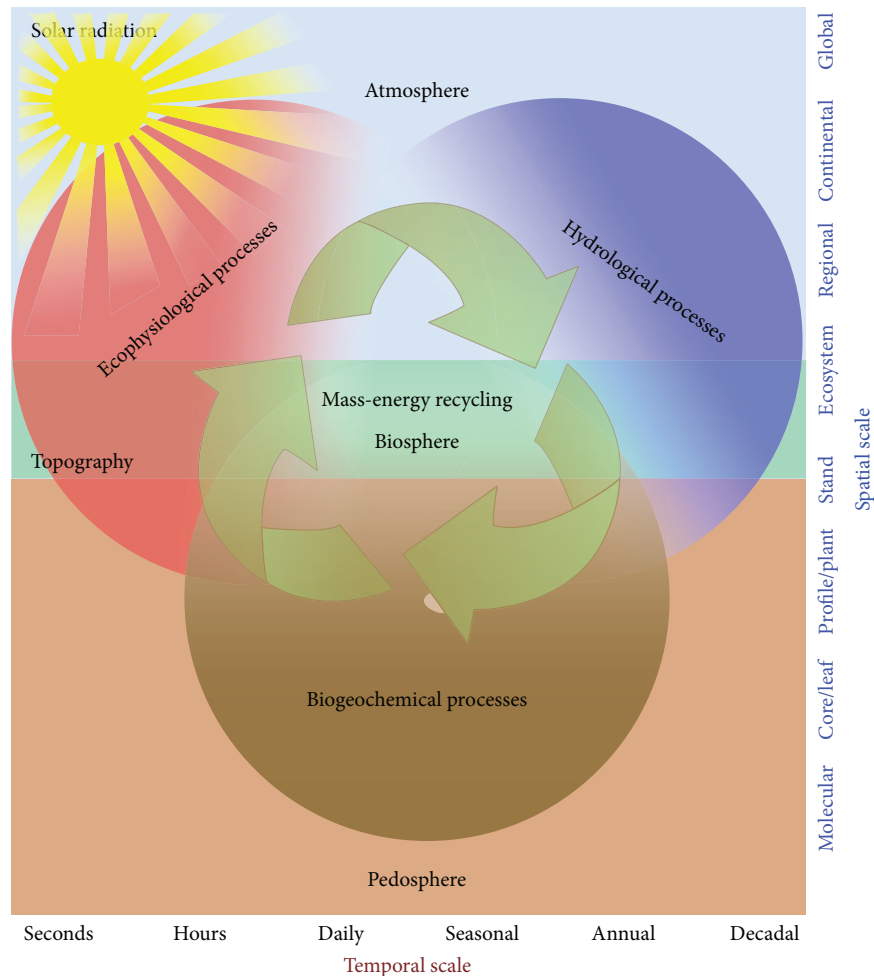


FIGURE 1: A conceptual sketch showing the close interaction between the ecophysiological, hydrological, and biogeochemical processes within the soil-plant-atmospheric continuum of mass and energy.

The terrestrial C sink, on the other hand, in spite of its smaller size and also being the habitat that supports humanity, shows some trends of saturation [15] and hence needs a greater understanding of the underlying dynamics.

Modeling studies have shown that the effects of global warming may change the status of the terrestrial biosphere from a Carbon (C-)sink to a C-source by the middle of this century due to the release of soil C stocks [16, 17]. On a long-term basis, the sizes of C-stocks present in a terrestrial ecosystem in its soil and vegetation depend on the disturbance history [18], atmospheric CO₂ concentration [19], nitrogen (N) deposition rate [20], stand age [21], soil texture [22], local hydrological regime [23], and climate [24, 25]. Terrestrial C-cycle is sensitive to climate change because of its direct and indirect connections to anthropogenic activities (due to factors such as deforestation, desertification, N-deposition, and land-use change) and also it is difficult to estimate the dynamics of the terrestrial C-cycle because of its heterogeneous nature and the complex nature of various

interactions that govern it. Hence, more attention needs to be given to this subject matter.

2. Complexity of the Terrestrial Carbon Cycle

Terrestrial ecosystems modify atmospheric C balance mainly at the biosphere-atmosphere-pedosphere (soil) interface through ecophysiological, hydrological, and biogeochemical processes (collectively referred to as ecohydrological processes). These three classes of processes have strong interactions and mass (C) and energy (e.g., latent heat) continuously gets exchanged among them as shown in Figure 1. The complexity with which these interactions occur vary substantially across the different scales in the spatial and temporal domains. For example, the ecohydrological complexity at a small spatial scale (e.g., forest stand) may not be the case while we deal with the ecohydrological complexity at the continental scale or the global scales. Similarly, the nature of ecohydrological complexity at the subdaily time step

could be much different than annual or decadal time scales when processes such as phenology and ecological successions need to be considered. Thus, scale is an important issue to be defined before we try to explore the nature of the complexity.

In pristine ecosystems, in general, the C balance is mainly controlled by the two main C fluxes, namely, photosynthesis and respiration. In recent years, scientists have learnt that terrestrial ecosystems' vegetation, soil [28, 29], and animals [30, 31] play key roles in mediating the C-cycle. Vegetation being the primary producer, it is from the plants whose mass and energy get transformed to other living beings, within an ecosystem [32]. The process of photosynthesis fixes atmospheric C into the biosphere. Atmospheric C enters the biosphere through stomatal openings of the vegetation that are controlled by a variety of environmental factors [25, 33]. These factors include the solar irradiance, humidity of the boundary layer, ambient temperature, atmospheric CO₂ concentration, nutrient availability, soil water availability, and forest age [34, 35]. Changes in the atmospheric C concentration and the corresponding changes in the climate have altered the magnitudes of terrestrial C balance. For example, a climate-induced enhancement of vegetation growth has been explained by the increased atmospheric CO₂ concentration [36] and satellite-based earth observation (e.g., [37]). Studies indicate that increase in atmospheric CO₂ enhances photosynthesis [38] and hence increase assimilation of atmospheric C by the terrestrial vegetation [39–42].

The photosynthetic C gained by the vegetation is used to build up the sizes of biomass C-pool (BCPs) such as wood, foliage, and the root system. A part of C in the BCPs is used for its growth respiration and maintenance respiration, collectively referred to as autotrophic respiration (R_a). A part of C from the BCPs is (1) transferred to the soil (in pristine settings) or (2) exported (in conventional agroecosystems) as litter, based on the mortality of the different BCPs (see [43]). Less frequently, BCPs also get transferred partly between the atmosphere and soil and across the landscape because of different types of ecosystem disturbances such as forest fire, wind-throw, and pest and disease infestations [18]. The C that is transferred to soil as litter gets associated with the different soil C-pools (SCPs) that eventually it gets "sequestered" in the soil due to its long residence time, although a part of it gets released back to the atmosphere based on microbial respiration, that is, often referred to as heterotrophic respiration. There have been a growing number of studies that indicate that the terrestrial biosphere is a net C sink [15].

Ecosystem respiration is one of the main processes by which C is added to the atmosphere from the biosphere. There are studies that indicate that total ecosystem respiration is a major determinant of terrestrial C balances [44]. Total ecosystem respiration (TER) includes respiration by autotrophic (plants) and heterotrophic (animals) components of the ecosystem. However, often, from a measurement point of view, the TER is studied as the contribution from (1) aboveground plant parts (boles, branches, twigs, and leaves) and (2) soil component, which is the sum of the heterotrophic respiration and root respiration including respiration of micro- and macroorganisms. The temporal variability of

respiratory metabolism is influenced mostly by temperature and humidity conditions [45]. Although ecosystem respiration has received considerable attention in recent decades, much less is known about the relative contributions of its subcomponents [46], and our understanding of how they will respond to global warming is poor. Soil respiration (root + heterotrophic respiration) is a dominant component of C exchange in terrestrial ecosystems which accounts for more than half of the total ecosystem respiration [47]. This is because soils of terrestrial ecosystems contain more C than atmosphere and live biomass together [48]. Components of respiration can have different responses to temperature and soil water content [49, 50]; thus, the effects of these environmental controls need to be understood in order to fully comprehend the soil C cycling mechanism. The biosphere consists of substantial amount of animal-based biomass (especially multicellular eukaryotic organisms, including man). However, the respiratory fluxes from these biomasses are not taken into account in the current estimates of terrestrial C budget. Perhaps this limitation is rendered because of the difficulty in modeling the dynamics of the eukaryotic biomass, primarily due to the complexity involved in factors such as the complex trophic interactions, competition, mobility and migratory trends, and more resilience to climate change.

Methane emission is yet another form of C-flux between the biosphere and the atmosphere (e.g., [51]). This mode of C-flux occurs mostly in anoxic conditions such as water-logged areas [52–55], peat lands [56, 57], permafrost emissions (e.g., [58, 59]), rice cultivation [60–62], and large animals both wild and domesticated [63, 64].

Another form of C-flux in almost all terrestrial ecosystems is the import and export of dissolved organic carbon (DOC) [65]. DOC fluxes include C in the form of simple amino acids to large molecules that are transported through water flows. Since these fluxes are very small compared to the C fluxes due to photosynthesis and respiration, DOC fluxes are not generally considered for the global C-cycle [35]. Moreover, since DOC fluxes are small compared to the total C stocks in the ecosystem and DOC fluxes do not affect the fluxing of C between the biosphere and the atmosphere, DOC is often not considered in the annual net ecosystem productivity (NEP) calculations. However, on a long-term basis, DOC can be considered as an essential component of the net biome productivity, NBP [66]. Fluxes of volatile organic compounds have also been reported to be a source of biosphere-atmosphere C flux [67–69].

Different types of ecosystem disturbances remove C from a landscape. Ecosystem disturbances can be broadly classified into natural and human-induced disturbances. Some examples of natural disturbances include forest fires, storm-based vegetation removal, sudden pest infestation [70, 71], and invasive species [72] to name a few. Examples of human-induced disturbances include land cover change [73, 74], reforestation, and agricultural and grazing activities [75]. Emission of large amounts of C to the atmosphere from vegetation can occur during forest fires [76–78] or biomass burning [79, 80]. These C emissions are of very high magnitudes although their duration is short. Forest fires and biomass burning also affect the nutrient status of the soil which could have

positive effects on the succeeding vegetation [81]. On the other hand, processes that are human-induced, but are not necessarily a direct disturbance to the ecosystem, include factors such as fossil fuel burning, industrial emissions such as calcination of limestone [82], fermentation processes [83–85], and deforestation. Because pristine vegetated ecosystems are spatially extensive at the global scale as opposed to human-influenced ecosystems (e.g., agroecosystems, urban landscapes), the C fluxes of pristine systems (GPP, Ra, and Rh) are generally considered to be more important (spatially) than other components of C fluxes.

Besides the above mentioned biophysical factors, several biogeochemical processes can also affect the terrestrial C-cycle. For example, nitrogen (N) availability to plants is an important factor that can affect photosynthesis. This is because N is a primary nutrient for plant growth [86, 87]. In the recent years, variations in plant N availability have also altered the trends in the terrestrial C-cycles. Variations in plant N availability occur mainly due to natural and anthropogenic N-deposition. Based on modeling studies, Townsend et al. [88], Asner et al. [89], and Holland et al. [90] have demonstrated that N-deposition is responsible for about $0.1\text{--}2.3\text{ GtC yr}^{-1}$ fixed by terrestrial vegetation which is almost half of the magnitude of C flux due to fossil fuel emission. Similarly, phosphorous also has been identified as an important controller of plant growth in several forest and agricultural crops [91, 92]. Another factor that determines the nature of terrestrial C balance of an ecosystem is the age effects of the vegetation. Schimel [35] has demonstrated that forest regrowth can account for part of terrestrial C uptake as much as $0.5 \pm 0.5\text{ GtC yr}^{-1}$, especially in northern mid and high latitude. This is because younger vegetation actively grows and hence sequesters more atmospheric C as opposed to mature forest stands.

In spite of the various mechanisms of exchange of C between biosphere and the atmosphere, many studies demonstrate that the terrestrial ecosystem is a net C sink due to the presence of soil C-pools having much longer residence times [15, 18, 93, 94]. The strength of the terrestrial C sink was estimated to be $0.5\text{--}2.0\text{ GtC yr}^{-1}$ [35]. By sequestering atmospheric C, the terrestrial ecosystems help decrease the rate of accumulation of anthropogenic CO_2 in the atmosphere and its associated climate change [95]. Terrestrial C sinks may be responsible for taking up about one-third of all the carbon dioxide that is released into the atmosphere [15]. The terrestrial C sink, as inferred on the basis of our current understanding, may not be permanent [16, 96]. Over the last few years there have been several studies suggesting that the size of this terrestrial C sink is vulnerable to global warming [15].

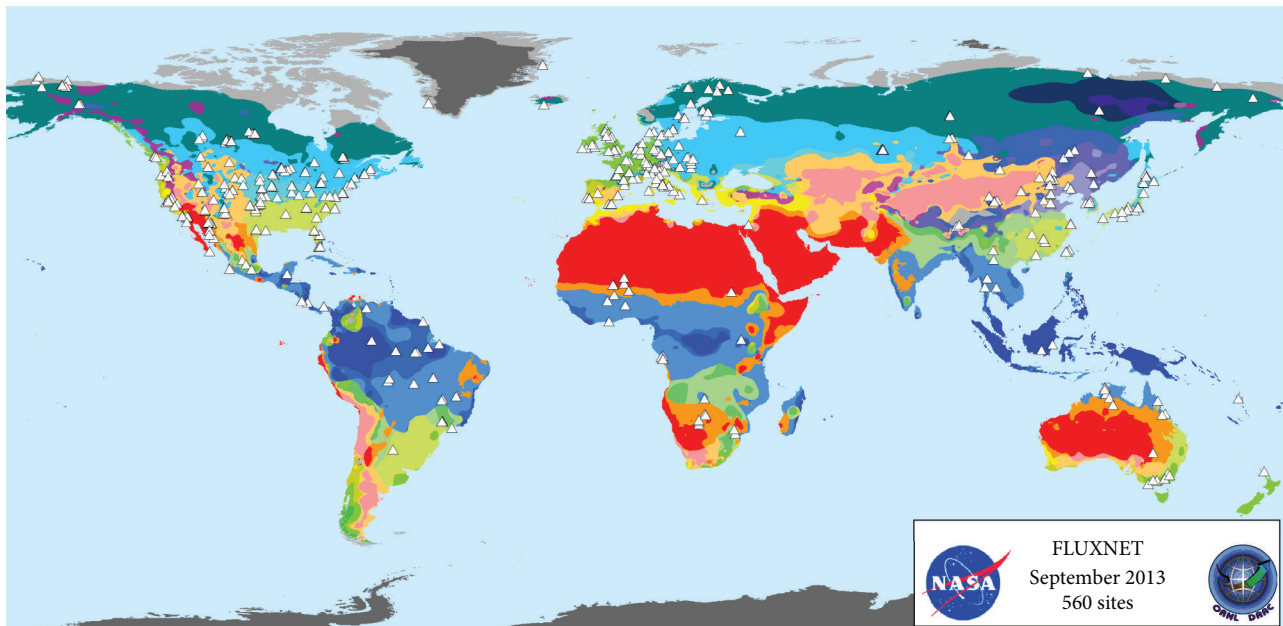
3. Monitoring Carbon Cycling in Terrestrial Ecosystems

Currently, several techniques exist for measuring the exchange of CO_2 from an ecosystem to the atmosphere at various spatial scales. The technique that is commonly used is the eddy covariance technique (EC), which directly

measures the fluxes of CO_2 , water vapor, and energy from a land surface. It is based on the principle that the vertical flux of an entity in the turbulent surface layer is proportional to the covariance of the vertical velocity and its concentration [97]. Over the last few years, EC measurements have provided vital information about terrestrial C balances on a variety of ecosystems such as boreal forests [98]; boreal and arctic peatlands [99–101]; tropical rainforest [102–104]; tropical savannah (e.g., [105]); tropical seasonal forest (e.g., [106, 107]); tundra (e.g., [108, 109]); tropical wetlands, mangrove, and tropical swamps [110]; temperate wetlands and peatlands [111–113]; temperate grasslands [114]; and even vegetated urban landscapes [79, 115, 116].

Since the early 1990s, there has been a large increase in the use of EC technique to monitor CO_2 exchange at the ecosystem level [117]. Ecosystems that have been subjected to natural and human-induced disturbances such as fire [98] and managed and regenerated stands [118] are also being studied using the EC technique. When an EC system is mounted on a tall structure, such as a scaffold tower, it is possible to estimate a spatially averaged flux for a “footprint” that extends 200–1000 m in radius, depending on the height of the tower and wind speed and direction [119, 120]. The EC measurements are done without disturbing the vegetation. The measurements made are continuous, long-term flux records. The EC technique measures the ecosystem response to short-term (subhourly) and long-term (seasonal and annual) variations. These important datasets provide a great deal of information on the processes controlling CO_2 and water vapor exchange, as well as ecosystem sensitivity to climate variability.

EC measurements also provide direct means of testing ecological models [86, 121, 122]. During the Boreal Ecosystem-Atmosphere Study (BOREAS) between 1994 and 1996, EC measurements of CO_2 and water vapor fluxes were made on towers in nine different boreal ecosystems [123], which provided invaluable data concerning the mechanism of C energy and water exchanges on boreal ecosystems. Consequently, scientists advocated that long-term EC flux measurements above terrestrial ecosystems could be undertaken on different ecosystems to better understand regional and global C and water budgets [124]. As a result, several EC flux networks in Europe (HAPEX-MOBILHY, Euroflux, CARBOEUROPE, and ICOS), United States (FIFE, Ameri-Flux, and NEON), Africa (HAPEX-Sahel and CarboAfrica), Canada (BOREAS 1 and 2 and Fluxnet-canada/Canadian C Program), South America (LBA and Eucflux), China (ChinaFlux), Korea (Koflux), Japan (Asiaflux), Thailand (Thaiflux), Australia (Ozflux), and India (National C Program of India started in 2011) were initiated. These networks were created under different multi-PI, multisite mega projects funded at the national or regional levels or were initiated (see Figure 2), although many of the projects discontinued (e.g., FIFE, Fluxnet-Canada) and many of them merged with newer consortia (e.g., BOREAS sites merged with Fluxnet Canada, Euroflux sites with CARBOEUROPE). Many of the currently operational ones are associated under the aegis of the global consortia called FLUXNET (~560 sites). However, there are



Koppen-Geiger climate classification (2006)

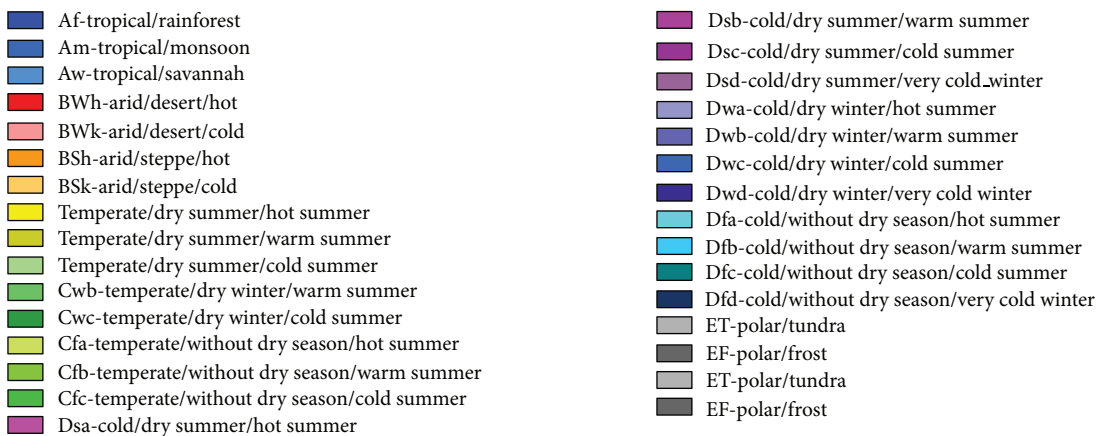


FIGURE 2: A global distribution of the EC-towers measures the fluxes of carbon, water, and energy fluxes between the biosphere and the atmosphere prepared by the Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) [26].

many EC sites around the world that operate independently without necessarily participating in the FLUXNET [125].

The network of EC flux towers around the world greatly assists in the better understanding of biosphere-atmosphere exchanges of carbon, water, and energy. However, it does not provide reliable evidence of the regional magnitude and location of C sinks because an EC tower does not operate over a large and sufficiently unbiased sample area to represent a land cover [126]. Furthermore, the method is limited to generally flat terrain with uniform vegetation [127]. In order to generalize the nature of mass and energy fluxes between the biosphere and atmosphere, use of techniques that operate at higher spatial scales are also warranted, in addition to the EC technique. These include the measurement of buildup of CO₂ concentrations above an ecosystem during temperature inversions [128]. At a much larger scale (~10⁶ km²), concentration measurements are made from tall

tower [129, 130] or balloons that reach the top of the boundary layer of the Earth. An example of a technique that infers flux at this intermediate scale is the Convective Boundary Layer (CBL) budgeting approach [131–133]. Aircraft based flux estimations can measure at scales larger than balloons [134, 135]. These measurements are very useful for validating large scale modeling efforts.

4. Need for Modeling of C-Cycle in Terrestrial Ecosystems

Thermodynamically, a terrestrial ecosystem is an open system. Therefore, biogeochemical cycles strongly interact with one another along with positive or negative feedback relationships [10, 136, 137]. Due to the complex nature of the system, simplified empirically based studies cannot provide

a complete description of the nonlinearity that exists in various aspects of terrestrial ecosystem responses. Interactions between components at different spatiotemporal scales are quite variable and, therefore, create uncertainties in our understanding of their behaviors as the climate changes with time [138]. The only way to improve our understanding of the nonlinearities and associated feedback mechanisms that exist in biogeochemical processes is to use a systems approach that adequately considers the scales at which these processes operate [139]. The dynamics of Earth as a system is modeled using complex systems models that have enormous number of models and submodels. The issues that we are talking about in this paper are those small models that mathematically conceptualize various natural interactions.

Recently, various modeling studies show that the feedback mechanisms between various processes could accelerate climate change [16, 96, 140]. Although such projections have much uncertainty, through model intercomparison studies (e.g., the PILPS project [141–143]), much of the uncertainty associated with models may be clarified and this may further aid in policy making. Moreover, with a large wealth of data on fluxes of mass and energy between the biosphere and the atmosphere, meteorological data, remote sensing technology, and rapidly increasing computational capabilities, simulation models can be used both to better understand how ecosystems function and to reduce uncertainty. The picture that is evolving from long-term measurement records is that different combinations of environmental factors affect the interannual variability of exchange of C between the biosphere and the atmosphere and generalizations are hard to make in ecosystem processes. Therefore, we need modeling tools to explain variability in a cogent manner.

5. Hydrological Controls on Terrestrial C and N Dynamics

Hydrological and biogeochemical processes are closely linked because of the unique physicochemical properties of water as a chemical compound. The association between hydrological and biogeochemical cycles is multifaceted and is often difficult to comprehend when based only on empirical studies. It is, therefore, necessary to employ simulation models that take a systems approach to better understand the intricacies involved [144, 145]. There are several ecological processes that are highly sensitive to hydrological controls, both directly and indirectly. These include hydrologically controlled primary production [98, 146], ET (e.g., [147, 148]), nitrogen cycling (e.g., [149, 150]), DOC export [151], methane production [51], and carbon sequestration [152]. These processes occur with different levels of complexities at various spatial and temporal scales.

Hydrological controls on biogeochemical cycles and their implications for global climate change have recently gained recognition, especially among regional and global scale modelers [123, 140, 153]. This body of work demonstrates that climate change may be explained by alteration in hydrological controls that govern the exchange of C between the atmosphere and the biosphere, with vegetative controls as

intermediate processes. Some studies also highlight that for high latitude ecosystems, it is possible that the melting of permafrost could intensify biogeochemical processes such as the decomposition of soil C [154–157] and the large amounts of methane emission [59]. This warrants serious attention to hydrological controls that affect biogeochemical processes, which could appreciably alter plant growth, nutrient and C dynamics, and physical growth conditions.

There are many studies that suggest that snow and the frozen water in the surface soils have the capacity to insulate the soil surface in high latitude ecosystems and this may significantly affect the C-cycling of these ecosystems by controlling winter soil respiration [45, 158, 159]. In arid and semiarid ecosystems, hydrological controls may be evident through conditions of water insufficiency. Dry conditions may directly or indirectly control biogeochemical cycles. Therefore, adequate representations of hydrological controls must be incorporated in models that predict biogeochemical processes.

6. Hydrological Controls on Photosynthesis and Respiration

Hydrological controls on photosynthesis are manifested through deficits or excesses of soil water [160–163]. Although there are many hypotheses regarding the physiological mechanism of the control of soil water on primary production, the most accepted school of thought is that of Schulze et al. [164] who hypothesized that abscisic acid (ABA), a phytohormone produced by stressed root tips when transported through xylem, triggers leaves to close stomata and reduce transpiration losses. During this process, the entry of CO₂ declines and photosynthesis decreases. Tardieu et al. [165] found that stomatal conductance (g_s) depends both on ABA and leaf water content and hence both factors are required to properly model this physiological control of stomatal conductance. Some models (e.g., [166]) attempted to simultaneously represent ABA and hydraulic signals from the roots to the stomata as proposed by Tardieu et al. [165]. But a quantitative description of the ABA is not yet developed for any of the models. To link soil water and stomatal conductance, various conceptualizations have been adopted by the modeling community.

There are two distinct approaches for modeling stomatal conductance, namely, (i) models based on empirical approaches and (ii) models based on the optimal hypothesis. The most popular empirical ones include the Ball-Berry [167, 168] and the Jarvis [33] approaches. The Ball-Berry types of models take the form

$$g_s = m \left[\frac{A_n \cdot h_s}{c_s} \right] + b, \quad (1)$$

where m and b are empirical constants, A_n is the photosynthetic rate, h_s is relative humidity at the leaf surface, and c_s is the CO₂ mole fraction at the leaf surface. Ball-Berry models adequately estimate C assimilation by simultaneously accounting for C assimilation and conductance response using a biochemical model of photosynthesis such as

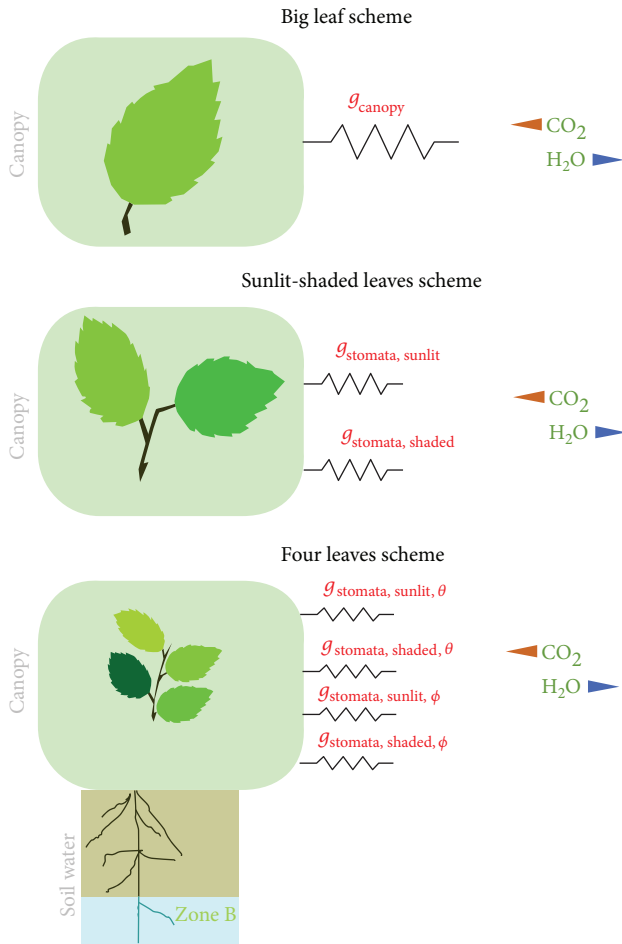


FIGURE 3: Conceptual representation of the various upscaling schemes used to model ecophysiological processes such as photosynthesis and evapotranspiration.

the Farquhar model [98]. These types of stomatal conductance models require iterative calculations to update current stomatal conductance by equilibrating photosynthesis at a previous time step against the ambient stomatal conductance for CO_2 . Ecological models that employ this formulation are SiB2 [169], CTEM [170], CN-CLASS [86], and Ecosys [121, 171] to name a few.

An alternative way to model stomatal conductance is to use the Jarvis [33] multiplicative algorithm. Jarvis-type models have the general form

$$g_s = g_{s,\max} \cdot \prod f_i, \quad (2)$$

where $g_{s,\max}$ is a species specific maximum stomatal conductance that may occur under optimal environmental and plant physiological conditions. A series of environmental factors in the form of scalars (f_i) constrain the potential stomatal conductance. The $g_{s,\max}$ parameter can vary widely among and within species [172–174] and g_s increases with $g_{s,\max}$ [23, 172–175]. Most of the ecological models currently use a process-based instantaneous biogeochemical leaf-level photosynthesis model postulated by Farquhar et al. [176] with

various modifications for upscaling the photosynthetic processes in space (leaf to canopy) and time (instantaneous to daily). Some of the spatial upscaling strategies (Figure 3) are “big-leaf” [169, 177] sunlit-shaded or two leaves (e.g., [178]), “multi-layered” [179], “multi-layered with sunlit-shaded,” and “four-leaves scheme” [27, 180–182] among others. An example for temporal upscaling (instantaneous to daily) is the analytical solution developed by Chen et al. [183]. All these approaches rely heavily on optimal estimates of g_s .

The model of g_s that employs the optimal hypothesis works on the principle of “economics of gas exchange” such that the stomata regulations are made to maximize their carbon gains while minimizing water losses [184–189]. The advantages of this approach are that it is a generic methodology and therefore could be applied across a wide range of species as opposed to the empirical approaches [185]. Moreover this approach offers closed form analytical expressions between g_s , assimilation rate, and intercellular CO_2 concentration and requires only a single parameter called the marginal water use efficiency [186].

In addition to the hydrologically controlled g_s , another biophysical parameter, the maximum carboxylation rate of the rubisco enzyme ($V_{c,\max}$) is used in photosynthesis modeling. $V_{c,\max}$ has a strong association with leaf nitrogen (N) content [86, 173]. Leaf N is directly related to the available soil N. Several environmental factors, such as temperature, precipitation, and soil moisture, directly or indirectly affect the availability of soil N. Some studies have reported that in northern ecosystems, particularly in forests, N availability limits plant growth [190]. In these ecosystems, decomposition of soil C-pools and the consequent N mineralization, atmospheric deposition, and biological N fixation are the sources of available soil N. Under conditions of global warming, as the decomposition of soil C-pools intensify due to increased soil temperature and moisture inducing increased heterotrophic respiration, N mineralization can increase [86, 150, 191]. Since water, N, and soil C-cycles are strongly linked, it is often difficult to separate the extent to which net primary production or net ecosystem productivity is controlled by the combined action of water or nutrient availability. N is mineralized in the soil when soil organic matter decomposes under optimal hydrothermal conditions [192]. Recently Govind et al. [182] demonstrated that mineralized N in soil may also be a factor that is responsible for the decomposition of some of the soil organic matter pools, which in turn mineralize N. In an ideal modeling domain, one needs to tightly couple N availability through organic matter decomposition as a function of soil temperature and soil water fluctuations on plant growth and C assimilation [86].

Ecosystem respiration is an important form of C flux. There are many environmental controls that affect respiration, especially soil respiration. They include soil temperature and moisture, substrate availability and quality, soil C decomposition and microbial growth dynamics, soil hydraulic properties, and root maintenance and growth requirements on rates of respired CO_2 from soils [45, 46, 50]. Soil respiration is highly controlled by soil water status. Studies demonstrate that at low soil water content, respiration is reduced [193–195]. This has been mainly attributed to a reduction in

decomposition of the soil organic matter due to microbial activity.

From this discussion it is clear that a proper representation of soil water dynamics, stomatal dynamics, photosynthesis, soil C dynamics, and soil N dynamics is required in a coupled manner to properly model the exchange of C between the soil-plant-atmospheric continuums. A set of other related processes should also be accurately represented, for example, radiation regimes, soil temperature, and the dynamics of snow depth. In the current ecosystem models, all of these processes are not explicitly described. Imbalances exist in the current models in terms of the processes they describe. For example, when one process is described in a sophisticated manner, another process is highly abstracted. This is mainly because of the inherent technical variations associated with models with regard to their ability to handle the variability in the scales and resolutions a model can handle in the spatial and temporal domains. The scientific background of the model developer also plays a vital role. Although significant progress has been made by the ecological modeling community in the area of representing the soil-plant-atmospheric continuum of mass and energy, the dynamics of soil water remain highly abstracted, despite being a crucial parameter of ecological processes.

7. Towards a Better Understanding of Terrestrial C-Cycle

Even though ambient soil water content is the net result of precipitation, soil characteristics (infiltration capacity, porosity, etc.), extraction of water by plants, and the topography of the landscape, an integrated approach representing the complete hydrological cycle is not often adopted in most ecological models [196]. Soil water can be accurately simulated only if the complete hydrological cycle is “well-represented” within a modeling domain. Hydrologists and ecologists differ in their view of soil water dynamics. While hydrologists consider the physical laws that determine water flow between locations in the soil body or landscape, ecologists and agriculturists are more concerned with the volume of water available for plant use during ecophysiological processes such as transpiration. They often ignore the amount of water that drains laterally across the landscape, which could significantly alter local scale hydrological regimes. Likewise, hydrologists also abstract vegetation controls on the hydrological cycle. For both hydrologists and ecologists, vegetation is the common bridge that links the water-potential gradient between soil and air.

Until now, ecological modeling studies focus either on point scale details [122, 197] or large-scale generalizations [198–201]. Most existing ecological models are lumped or point scale formulations that assume that a modeling unit is isolated from its neighboring areas [171, 197, 202–204]. As such, only vertical hydrological processes can be realistically modeled using “soil layers” employing some implicit procedures to account for the lateral water flow although the vertical movement of

water in between layers is modeled at various levels of sophistication.

On one hand, the conceptualizations used to describe the vertical movement of water in lumped models include single layered soil, double layered soils that demarcate saturated and unsaturated zones, multilayered soil, or multilayered soil with root water uptake schemes. Almost all of conventional models employ Richard’s equation to calculate the unsaturated flow of soil water fluxes. On the other hand, spatially distributed ecological models that are driven on a remote sensing framework, where modeling units (pixels) remain isolated, soil moisture is calculated simply as “available soil moisture” [199] or some form of scalars may be used to represent the soil moisture [198], in order to circumvent computational difficulties. Although most of the ecological models are sophisticated in terms of modeling the biophysical controls on plant growth, they still abstract the hydrological processes (especially the lateral water fluxes). Absence of or simplified representations of lateral hydrological processes make the current ecological models hydrologically incomplete. Hence, models that abstract hydrological controls have great vulnerability to simulate the terrestrial C-cycling processes in a biased manner.

Topographic variations on the Earth’s surface play a major role in governing the hydrological, geomorphological, and ecological processes [205]. At small spatial scales, although electrostatic and osmotic forces govern flow of water (e.g., a soil core or a soil profile) at large spatial scales, topography is the dominant factor that governs water flow [206, 207]. Conventional hydrological models use the digital elevation model (DEM) to simulate the landscape scale hydrological processes [208–213]. In earlier land surface models, the baseflow component was formulated as drainage under gravity [214] or a down-slope lateral drainage (e.g., [215]). Topographically driven lateral water flow could have significant influences on the local scale ecological processes such as the C balance [175]. To accurately represent the hydrological controls on biogeochemical processes within land surface (or ecological) models, the currently existing simplified representation of lateral hydrological processes needs to be improved. Lateral hydrological processes need to be explicitly described considering topography (often used as a proxy for water potential differences) and soil properties that govern the nature of lateral water flow over the landscape, that is, surface overland flow or subsurface baseflow. Ideally, hydrological processes should be simulated according to a hydrologist’s perception of the water cycle and should then be linked to an ecological model created according to an ecologist’s perception of ecological processes in order to accurately describe what happens in natural systems.

The question of linking ecology and hydrology can be conceptualized either as an ecohydrological or as hydroecological issue. It is only in the recent years that scientists have begun taking this approach. Hannah et al. [216] gives a vivid commentary on the dichotomy of this subject matter. In ecohydrology, ecology has prominence and this subject matter focuses mainly on plant-water relations that exist in terrestrial

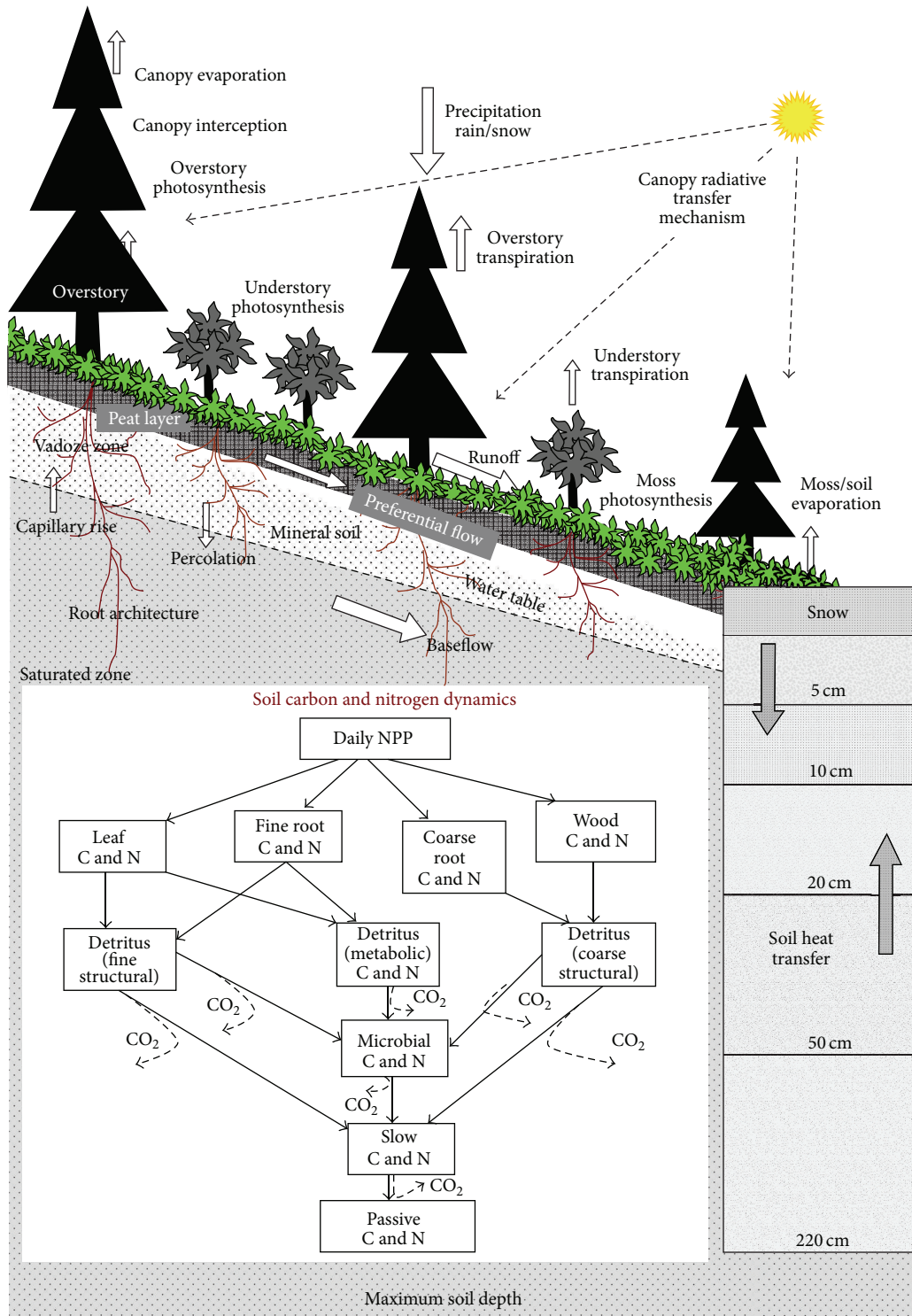


FIGURE 4: Conceptual representation of an ecohydrological model having a tight coupling between hydrological, ecophysiological, and biogeochemical processes, Figure reproduced from Govind et al. [27] with permission from Elsevier publishers.

ecosystems [121, 165, 217, 218]. In hydroecology, hydrological processes dominate and determine the conditions for ecological processes (e.g., [216, 219–221]). The hydroecological philosophy uses knowledge from hydrological,

hydraulic, geomorphological, and biological/ecological sciences to predict the response of ecosystems to variation in abiotic factors over a range of spatial and temporal scales [222].

8. Addressing the Feedback Effects in the Soil-Plant-Atmospheric Continuum

Because terrestrial primary productivity is limited by light, water, and nutrients, it is often difficult to separate the extent to which the C-cycle is controlled by the combined action of these governing factors and the feedback relationships that additively, synergistically, or antagonistically affect biogeochemical transformations. For example, hydrological and nutrient limitations govern plant physiological status and hence the plant growth. The availability of nitrogen to vegetation alters photosynthetic rates by affecting the activity of rubisco enzyme in the plant [86]. Soil water conditions control stomatal dynamics and hence the gas exchange between the biosphere and the atmosphere. Therefore, intuitively it can be seen that simplified light use efficiency type of models [223] that cannot address these nonlinear responses of environmental controls on plant growth. Ideally, models having a systems approach should be adopted in a remote sensing driven framework to better understand the integrated effects of various environmental controls on biogeochemical processes at larger spatial and temporal scales.

To date, modeling of ecological processes is being conducted at point scale [122, 197, 224–226], watershed scale [227–229], regional scales [198–200, 230], and global scales [223, 231, 232]. These approaches differ widely in their sophistications, complexities, temporal resolutions (half hourly to annual), and temporal spans (hourly to decadal). Most of the modeling studies focus on ecological indicators such as biomass [43, 233]; gross primary productivity, GPP [234]; net primary productivity, NPP [213, 230]; ecosystem respiration [235, 236]; N-fluxes [86, 237]; Leaf Area Index [86, 238]; DOC fluxes [65]; and water use efficiency [239] to demonstrate the hydrological effects on terrestrial C or biogeochemical cycles. Moreover, researchers have been employing either ecohydrological [217] or hydroecological approaches [228, 229] and hence models greatly differ in the manner in which the hydrological influences on C-cycle are represented. While ambient soil moisture is the net result of the magnitudes of various components of the water balance, hillslope hydrological processes that drive lateral flow are not explicitly conceptualized in most ecological models. In a recent study, it was shown by Morales et al. [240] that most of the ecosystem models inadequately simulated ecosystem processes because of the incompleteness in the representations of hydroecological processes. While stomatal conductance is conceptualized to be the primary link between biosphere and the atmosphere in most of the ecological models, this is not very much constrained by hydrological and biogeochemical interactions [27, 43, 182].

In order to adequately represent the hydroecological regimes, within the models, the local-scale soil moisture regimes should be modeled as a function of the landscape-scale hydrological processes, which consequently modulates the plant physiological status via stomatal dynamics and the consequent C-cycling process (GPP). Because local-scale ecophysiological and biogeochemical processes are governed by hydrological processes that occur at a landscape-scale and

also because interactions between vegetation, soil, hydrothermal factors, climate, and other feedback relationships could strengthen the nonlinearities, a realistic representation of all these processes in a coupled manner is required [241]. For example, studies suggest that, within modeling domains, the N cycle can be comprehensively explained only through proper hydrological and C-cycle representations. Soil moisture has an impact on soil C and nitrogen cycles through the processes of mineralization, leaching, plant uptake, and denitrification. It was in this spirit that BEPS-TerrainLab V2.0 [27, 182] was developed with an added capability to address some of the unique boreal hydrological processes that govern its primary production and the consequent biogeochemical processes. A tight coupling of ecophysiological, hydrological, and biogeochemical processes in a spatially explicit manner is quite necessary to capture the feedback relationships that govern water, nutrient, and light induced stress factors that affect the C-cycling patterns of the terrestrial vegetation as shown in Figure 4. The numerical experiment performed by Govind et al. [182] showed that models of terrestrial C dynamics that ignore hydrological processes are vulnerable to underestimate the sizes of C-sources rather than C sinks.

9. Conclusions

Terrestrial ecosystems determine the atmospheric C balance through many mechanisms. In the recent years, we have learned that terrestrial ecosystems play a significant role in taking up atmospheric C. Accurate assessments of regional and global-scale changes in the terrestrial biosphere are essential to better understand the anthropogenic impacts on the global climate and its direct consequence on social, economic, and geopolitical aspects. In pristine terrestrial ecosystems, at shorter temporal scales, they are controlled mainly by processes such as photosynthesis and respiration in addition to relatively minor processes such as methane fluxes and lateral transport of dissolved organic carbon (DOC). At larger temporal scales, however, spontaneous release of C in the event of forest fires and land-use changes as a function of various anthropogenic activities can also be significant. Until now, significant advances have recently been made in our understanding of the role of terrestrial ecosystems in the global C-cycle by a variety of approaches such as the eddy covariance-based measurements, forest biometric measurements, and simulation models. There are uncertainties regarding the dynamics of the terrestrial C-cycle. Water being the medium of mass and energy in the soil-plant-atmospheric continuum, it has a significant role in governing the terrestrial C-cycle. While we rely on computer-based simulation models to predict the dynamics of terrestrial C-cycle, most of these models ignore or simplify hydrological processes. Thus, incorporating hydrological processes is seminal to our better understanding of the terrestrial C-cycle. The heterogeneous nature of terrestrial ecosystems and the nonlinearities existing within ecophysiological, biogeochemical, and hydrological processes pose a major challenge in our effort to improve regional and global C-cycle estimation.

Inadequate information on the C budget poses a great challenge in improving our understanding of the global climate change because of the uncertainties in the terrestrial C balance. This issue has also become a major knowledge gap in formulating strong international policies related to climate change.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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