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Multi-scale observation and cross-scale mechanistic modeling on terrestrial ecosystem carbon cycle

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Abstract To predict global climate change and to implement the Kyoto Protocol for stabilizing atmospheric greenhouse gases concentrations require quantifying spatio-temporal variations in the terrestrial carbon sink accurately. During the past decade multi-scale ecological experiment and observation networks have been established using various new technologies (e.g. controlled environmental facilities, eddy covariance techniques and quantitative remote sensing), and have obtained a large amount of data about terrestrial ecosystem carbon cycle. However, uncertainties in the magnitude and spatio-temporal variations of the terrestrial carbon sink and in understanding the underlying mechanisms have not been reduced significantly. One of the major reasons is that the observations and experiments were conducted at individual scales independently, but it is the interactions of factors and processes at different scales that determine the dynamics of the terrestrial carbon sink. Since experiments and observations are always conducted at specific scales, to understand cross-scale interactions requires mechanistic analysis that is best to be achieved by mechanistic modeling. However, mechanistic ecosystem models are mainly based on data from single-scale experiments and observations and hence have no capacity to simulate mechanistic cross-scale interconnection and interactions of ecosystem processes. New-generation mechanistic ecosystem models based on new ecological theoretical framework are needed to quantify the mechanisms from micro-level fast eco-physiological responses to macro-level slow acclimation in the pattern and structure in disturbed ecosystems. Multi-scale data-model fusion is a recently emerging approach to assimilate multi-scale observational data into mechanistic, dynamic modeling, in which the structure and parameters of mechanistic models for simulating cross-scale interactions are optimized using multi-scale observational data. The models are validated and evaluated at different spatial and temporal scales and real-time observational data are assimilated continuously into dynamic modeling for predicting and forecasting ecosystem changes realistically. In summary, a breakthrough in terrestrial carbon sink research requires using approaches of multi-scale observations and cross-scale modeling to understand and quantify interconnections and interactions among ecosystem processes at different scales and their controls over ecosystem carbon cycle.

Keywords: global climate change, terrestrial carbon sink, multi-scale observation, data-model fusion, cross-scale mechanistic modeling.

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The global terrestrial ecosystems have been taking up substantial CO_2 from the atmosphere, offsetting a part of human-induced increases in atmospheric CO_2 concentration and the greenhouse effect[1]. Being affected by numerous environmental, biological and human factors, the terrestrial carbon uptake has high spatial heterogeneity and temporal variations, accurate quantification of which is essential to realistic prediction of global climate change. The terrestrial carbon sinks that arise from human activities have been included in a legally binding framework in the Kyoto Protocol for stabilizing atmospheric greenhouse gases concentrations[2]. Effective implementation of the Kyoto Protocol requires country-based accounting, monitoring and verifying carbon emissions and sequestration. The terrestrial carbon sink, therefore, is an important international political as well as a scientific issue. Since the late 1990s, many countries and international organizations have given priority to the terrestrial carbon sink in the global change research.

Although extensive and intensive studies have been conducted, big uncertainties still existed in estimating the magnitude, spatial distribution, and temporal variation of the terrestrial carbon sink and in understanding the underlying mechanisms[1]. In order to reduce the uncertainties, a new series of international and national research projects have launched such as the Global Carbon Project[3], North America Carbon Program[4], and Chinese Terrestrial Ecosystem Carbon Cycle and its Driven Mechanism Research. To achieve the designed objectives, to continuously update the concept framework and research direction is necessary according to the progress in the global change science and techniques. In contrast to the previous projects that are of mostly disciplinary studies, the new projects employ multi-disciplinary and comprehensive approaches to study the terrestrial carbon sink as an integral part of the carbon cycle of the Earth system. For example, the Global Carbon Project[3] breaks the separation of the carbon cycle into terrestrial, atmospheric and oceanic sectors, regarding the Earth carbon cycle as a whole in a framework of carbon-climate-human interactions and using approaches that combines space- and land-based observations, controlled experiments, mechanistic modeling, and social science methodologies[3]. But, these projects have not put forward a clear solution for understanding, quantifying and predicting multi-scale and cross- scale interconnection and interactions among ecosystem processes over the terrestrial carbon sink[5, 6].

Terrestrial ecosystem carbon cycle depends on regional climate and ecosystem patterns and on small-scale environmental conditions and ecophysiological characteristics of organisms; is modulated by long-term changes in climate, biogeochemical cycle and ecosystem structure and by short-term climate variability and fast eco-physiological responses; and is affected by both natural and anthropogenic perturbations. As a typical complex system, the function and behavior of the ecosystems depends on the interconnections of processes at different levels or scales. To reduce the uncertainties in the terrestrial carbon sink requires understanding, quantifying and predicting cross-scale interconnections of ecosystem processes and their controls over the carbon cycle[5,6]. In the past decade, numerous experimental, observational and modeling studies on terrestrial ecosystem cycle have been conducted from site to global scales, however few cross-scaling studies are available to untangle ecosystem multi-scale interconnections[7]. The present paper first overviews experimental and observational studies at different scales using new techniques and the consequent progress in understanding the terrestrial carbon sink in the past decade, then discusses the development of cross-scale analysis and the new generation of mechanistic ecosystem models, and finally gives our perspective on the directions of using the approaches of multi-scale and cross-scale data-model fusion in quantifying the terrestrial carbon sink.

1 Multi-scale ecosystem experiment and observation

Until the early 1990s studies on mechanisms of ecosystem carbon cycle were limited to short-term responses of eco-physiological processes (e.g. plant photosynthesis and respiration) and the growth and development of individual organisms to changes in single environmental factors (e.g. increasing atmospheric CO_2 and global warming)[8]. Some studies at regional scales in that time, for example, on changes in regional pattern of terrestrial net primary productivity (NPP) and carbon stock used statistic and survey data of land cover changes[9] and empirical models[10,11]. The statistic data were usually lacking geo-referenced quantitative information, and the empirical models had no mechanistic description of ecosystem processes. Therefore, it was imperative to conduct ecosystem-level experiments, regional quantitative observations and mechanistic modeling on terrestrial ecosystem carbon studies. After about a decade, with the development of new techniques such as controlled environmental facilities, eddy covariance measurement and quantitative remote sensing, various ecosystem research networks have been established to study ecosystem carbon cycle across from site to global scales, obtaining a large amount of data that shed light on the terrestrial carbon sink. The multi-scale experiments and observation and the resulting understanding of the terrestrial carbon sink are introduced as the following.

1.1 Ecosystem-level experiments on the response to environmental changes

To understand mechanisms of terrestrial carbon sequestration requires information on ecosystem responses to global environmental changes, particularly to increasing atmospheric CO_2 concentration and climate warming. Experimentation is an effective way to obtain the information. However, traditional experimental facilities (e.g. closed growth chamber) limited the experimentation to small organisms (e.g. grasses or tree seedling) and produce biases and artifacts by disturbing the growth of organisms greatly[8]. From the 1990s, large environmental controlling facilities[8], e.g. Open-Top Chamber (OTC) and Free-Air CO_2 Enrichment (FACE)[12], have been used to conduct ecosystem-level experiments (fig. 1). Conventional techniques are unable to measure and distinguish carbon fluxes arising from photosynthesis, autotrophic and heterotrophic respiration, and hence cannot directly measure their responses to environmental changes. Recent development of stable isotope measurement makes the measurement possible based on the discrimination of those processes on the isotopic composition of CO_2[13]. The ecosystem experiments that use the large-scale environment controlling facilities and modern measurement techniques have formed regional or global networks, e.g. the Elevated CO_2 Network, the Network of Ecosystem Warming Studies, (NEWS), and the Biosphere-Atmosphere Stable Isotope Network (BASIN).

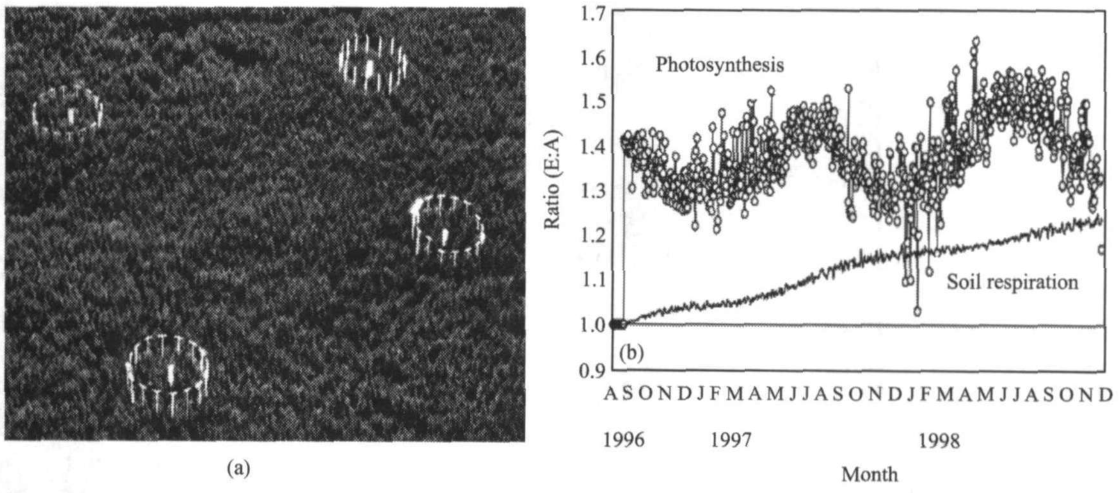

Fig. 1. A large-scale controlled environmental facility Free-Air CO_2 Enrichment (FACE, a) is used to study the response of forest ecosystem at natural status to elevated atmosphere CO_2. (b) shows the relative increases in forest photosynthesis and soil respiration to elevated atmosphere CO_2 concentration by 200 ppmv, indicating that forest carbon sequestration increased substantially in the early stage because of much higher increases in photosynthesis than soil respiration, but reduced in the later stage with the catching up of soil respiration[14].

The ecosystem experiments indicated that the initial responses of ecosystem carbon processes to environmental changes are set by their direct effects, but the long-term changes are largely modulated by indirect, interactive, and feedback effects[15]. For example, prolonged exposure of plants to elevated CO_2 results in down-regulation to the CO_2 fertilization to photosynthesis, which includes starch accumulation inhibition, source-sink limitations, and leaf N concentration and active Rubisco reductions[16,17]. The enhanced photosynthesis by elevated atmospheric CO_2 does not necessarily lead to significant increases in ecosystem carbon sequestration since most of the increased carbon fixed in photosynthesis is allocated into the carbon pools that will be decomposed quickly once getting into soils (e.g. leaves and fine roots)[18,19]. Increasing atmospheric CO_2 affects ecosystem carbon cycle through many indirect processes, e.g. increasing carbon allocation to roots and the C/N ratio of plant tissues, reducing litter decay rates and soil organic nitrogen mineralization[16,17,20,21], affecting ecosystem carbon uptake both negatively and positively. Atmospheric nitrogen deposition may enhance plant growth, but the increased nitrogen supply may finally reduce ecosystem carbon storage by decreasing the C/N ratio of plant biomass and soil organic matter and enhancing soil respiration[22], therefore has no significant contribution to the terrestrial carbon sink[23]. Climate warming in cool regions stimulates plant growth and mineralization of soil organic nitrogen and hence increase NPP[24,25]. The sensitivity of soil respiration to temperature may decrease with increases in temperatures, indicating the stimulation of global warming to soil carbon release may be overestimated in previous studies[26,27]. However, long-term observations showed that warming has increased soil respiration more than plant carbon fixation and has turned some ecosystems at high latitudes from a carbon sink in to a source[25, 28].

1.2 Measurements ecosystem-atmosphere carbon flux using eddy covariance technique

To estimate ecosystem carbon sequestration requires considering the temporal scale over which the estimate is made because of high variations at different time scales (e.g. diurnal, seasonal and year to year). Accounting the temporal variations needs to measure ecosystem-atmosphere carbon fluxes continuously for a long time period (e.g. for a life cycle of plants) at a whole ecosystem level. The continuous measurement has been made possible using the eddy covariance technique that determines CO_2 exchange between a whole ecosystem and the atmosphere through measuring the correlation between CO_2 concentration and vertical wind velocity across a spectrum of time scales from hours to years. Although eddy covariance measurements of CO_2 started in the early 1970s, it is the production of commercial infrared spectrometers in the late 1980s realized the long-term, continuous measurement of CO_2 fluxes[29]. Since a whole-year continuous measurement in the early 1990s [30], the technique has been used at over 250 sites globally, in which about 10 sites are of continuous measurements over 10 years, forming regional (EuroFlux, AmeriFlux, AsiaFlux, ChinaFlux, etc.) and a global CO_2 flux network (FluxNet).

The eddy flux measurements are particularly adopted as studying environmental and eco-physiological mechanisms over diurnal, seasonal, and interannual variations in ecosystem carbon cycle (fig. 2). Those studies indicated that the factors that modulate ecosystem carbon sequestration vary at different temporal scales: in the course of a day carbon sequestration essentially follows solar radiation[31,32]; over a year the length of the growing season that depends largely upon seasonal variations in temperature and soil moisture has a major influence on carbon sequestration[29,33], and decadal variations in ecosystem carbon sequestration, particularly of forests, are characterized by changes associated with plant life cycle and ecosystem succession and often depend on change in size of long-term carbon pools and their turnover times[32—34]. The variations in ecosystem carbon sequestration between flux sites often have weak correlation to the varying environmental factors but seem closely related to biological factors such as vegetation type and carbon pools[29, 33]. Measured net carbon exchange between ecosystem and atmosphere has high interannual variations up to 2—3 times of the mean

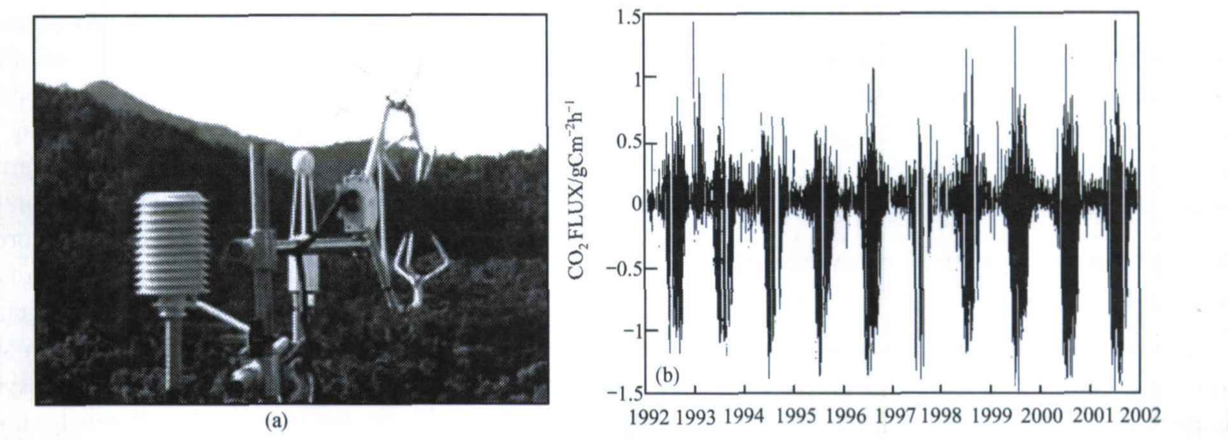

Fig. 2. Eddy covariance technique (a) has been used in continuous, long-term measurements of ecosystem-atmosphere carbon fluxes, providing a unique and effective tool for studying ecosystem carbon cycle. The hourly, 10-year eddy flux data obtained in Harvard Forest (b) reveal the characteristics of the diurnal, seasonal and interannual variations and the mechanisms in terrestrial ecosystem carbon sequestration[32].

value resulting from climate variabilities from year to year[29,35]. Therefore, short-time measurements cannot capture temporal characteristics and potential terrestrial ecosystem carbon sequestration.

Eddy flux measurements also provide new data for reassessing the spatial pattern and the underlying mechanisms of the terrestrial carbon sink. Atmospheric-based measurements generally indicated terrestrial carbon uptake at northern high latitudes[36,37] and carbon release in tropical regions[38], and satellite remote sensing supported the existence of the carbon sink in the north with detected consistent lengthening of plant growing season by warming[37]. However, data from 15 eddy flux sites of the EuroFlux showed that northern terrestrial ecosystems had low carbon uptake rates with high interannual variability. Mature arctic coniferous forests were near carbon-balanced and the young coniferous forests were carbon sink but with lower rates than the temperate forests in the Mediterranean. The forest biomass was increasing at all the sites, but some sites at high latitudes were a net carbon source[39]. Those observations found that with increases in latitude forest photosynthetic rates had litter change but the sensitivity of soil respiration to climate warming increased, thus forests at higher latitudes are likely to become a carbon source in response to ongoing warming. In contrast, eddy flux measurements indicated substantial carbon uptake by undisturbed forests in Amazon[40—42]. Studies based on the measurements estimated undisturbed tropical forests may take up 0.5—3.0 Pg C a^{-1}[43], although net carbon release was observed at some tropical sites[44].

Eddy flux measurement provides a unique tool for understanding eco-physiological mechanisms and environmental controls of ecosystem carbon processes, and the regional and global networks using the technique may reveal the terrestrial carbon sink at a broad spatial scales. However, the limited number of flux tower sites is far from capturing high spatial variability, and the measured results in the specific ecosystems under specific environmental conditions cannot extrapolate directly to regional scale. Moreover, the eddy covariance technique has some problems in quantifying ecosystem carbon fluxes. For example, the measurements are often not in energy closure, viz. the sum of measured sensible and latent heat is less by 10%—30% than the energy available[45], indicating that eddy flux measurements may underestimate ecosystem carbon fluxes. The drainage of CO_2 out of plant canopy at night causes the CO_2 flux from vegetation to atmosphere boundary less than the amount from respiration, thus eddy flux measurements often overestimate ecosystem carbon sequestration[35]. At sites with complex topography and unstable atmospheric condition, measured ecosystem carbon uptake with eddy covariance techniques differ 80%—200% from the results from other independent measurements such as carbon stock inventories[45]. At some sites the average net ecosystem carbon uptake for several years was as high as 500 g C m^{-2} a^{-1}, 2—3 times higher than the result from carbon stock inventory[46]. Eddy flux measurement may not an effective, economical way to measure long-term changes in ecosystem carbon cycle, the accuracy may be lower than that from conventional ecosystem inventories.

1.3 Satellite observation of ecosystem pattern and productivity

Development of satellite remote sensing, the data processing capacity, and relevant eco-physiological studies make large-scale, continuous quantitative observations of ecosystem patterns and activities possible[47—49]. Meteorological and resource satellites have had global land observations for 30 years. New-generation satellite systems (e.g. NASA's the Earth Observing System satellites) are providing more accurate and higher resolution data on changes in ecosystem patterns for the next 20 years. Since the pioneering work of Tucker et al. on the correlation between remote sensing-derived vegetation index (e.g. the Normalized Difference Vegetation Index, NDVI) and photosynthetic activity[47], satellite remote sensing has become a primary source of data on regional ecosystem patterns and productivity[48,49]. Until the late 1990s, studies on land use-induced carbon releases[50] mainly depend on statistical and survey data of land use for administrative areas (e.g. countries, provinces or states). Since then, remote sensing data were used in mapping the spatio-temporal patterns of regional and global land cover at fine resolution (500 m to 1 km)[51,52]. Remote sensing-derived absorption of photosynthetically active radiation (PAR) provides a mechanistic basis to quantify changes in vegetation productivity and rates of carbon fixation from space observations, and remote sensing-based ecosystem models have been developed and used widely in studies on ecosystem carbon cycle[53—55]. The studies were initially limited to estimating regional and seasonal pattern of terrestrial net primary and ecosystem productivity[53—55], now are focused on the interannual variations and long-term trend (fig. 3)[56—58].

Satellite remote sensing provides the first regional-scale, direct observational evidence to the existence and the increases in the terrestrial carbon sink in the northern terrestrial ecosystem[37], which were usually estimated based on atmospheric measurements. Remote sensing data showed that NDVI at latitudes higher than 45° N increased by 9%, and the growth

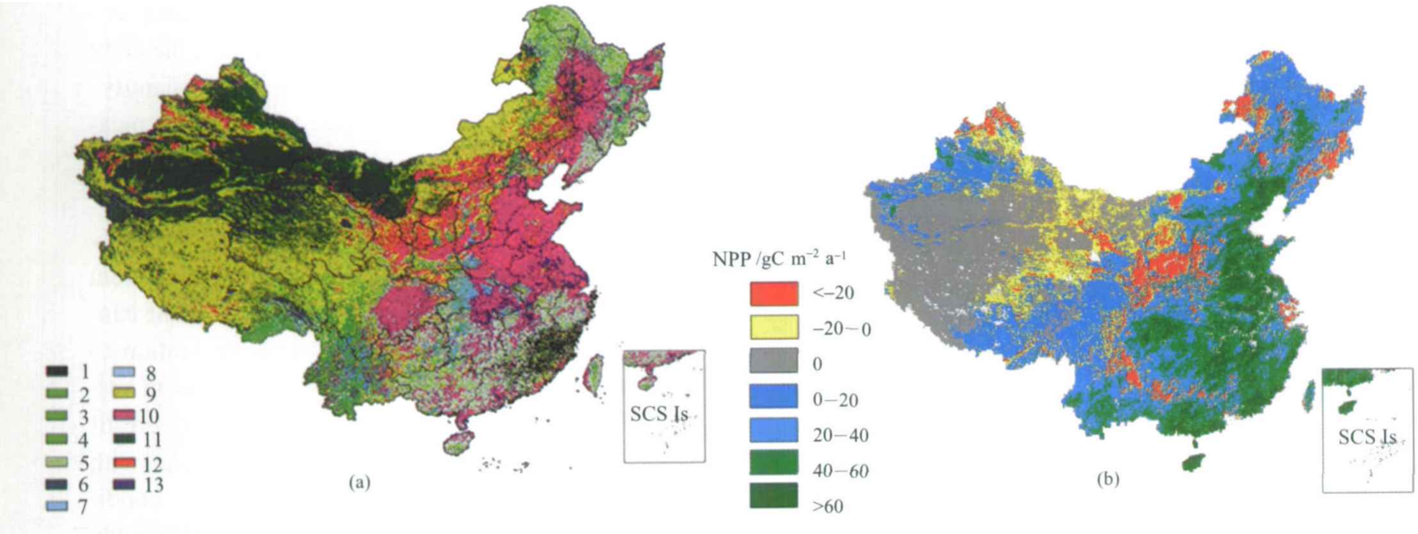

Fig. 3. Satellite remote sensing is currently the only means available to monitor change in ecosystem pattern and productivity at regional and global scales. The figure shows satellite-observed vegetation pattern in the 1980s (a) data derived from ref. [51] and (b) changes in NPP from the 1980s to the 1990s in China[59]. 1, Evergreen needleleaf forest; 2, evergreen broad-leaf forest; 3, deciduous needleleaf forest; 4, deciduous broad-leaf forest; 5, mixed forest; 6, woodland; 7, closed shrubland; 8, open shrubland; 9, grassland; 10, cropland; 11, bareland; 12, urban and built-up; 13, water.

period started earlier by 6 days in the 1980s; and in the 1990s NDVI increased by 8%, the growth period started earlier by 2 days[60]. Increases in NDVI and longer growing season implied higher plant productivity and more carbon fixation. The vegetation carbon storage in northern mid and high latitudes was estimated increasing 0.68 Gt per year in the last 20 years, in which 70% and 20% occurred respectively in Eurasia and North America based on remote sensing data[60]. According to observed consistent increases in NDVI, some studies inferred that the vegetation in the north provided a natural negative feedback to climate warming by taking up CO_2 from the atmosphere[61—63]. The NPP estimated using remote sensing-based ecosystem models increased by 0.5%—0.8% per year in the last 20 years and that in northern tropical regions was higher than in mid and high latitudes[57,58], consistent with land-based eddy flux measurements[40—42]. The NEP of northern boreal forests was estimated at 0.2 Pg C a^{-1} for the 1980s and 1990s using an NDVI-driven biogeochemical model[63]. Estimates using statistical data for land use-induced carbon release in the tropics was 2.2 Pg C a^{-1} and reduced by 10% in the last 10 years[64], in contrast, remote sensing-based studies indicated a release of only 0.9 Pg C a^{-1} and an increase of 12%[65,66]. If the remote sensing-based estimate was right, the global terrestrial carbon sink that is derived as a residual of the global carbon budget (as industrial emission + landuse release – the oceanic uptake) should be smaller than the value that was widely believed[66], closer to the results of ecosystem inventories[67] and reflecting the increasing trend in the past decades[68,69].

Although it is the only approach available to continuously and quantitatively observe ecosystem changes at large scales, remote sensing cannot directly measure changes in ecosystem carbon fluxes and carbon storage, which can only be obtained through a series of inverse analysis, empirical or process-based modeling from remote sensing data. The advantage of remote sensing in ecosystem carbon cycle studies is in providing quantitative, high resolution data at regional scales about changes in environment conditions (such as climate, radiation and soil moisture), vegetation pattern and activity (e.g. vegetation distribution, composition, leaf area index and PAR absorption), and land use (deforestation, reforestation, and cropping systems). Currently, the remote sensing data used in studying ecosystem carbon cycle are mainly from optical satellites, but data from radar and laser satellites can greatly increase the accuracy of the estimates by providing information on 3-dimension forest coverage and structure[70]. For example, the Vegetation Canopy Lidar satellite that will be launched soon will increase the accuracy of estimating vegetation distribution, height and biomass 5—10 times[70]. Even though, because of interferences by many factors (e.g. accuracy of sensors, atmospheric condition, cloudiness, and satellite orbital drift), remote sensing data and the estimated changes in ecosystem NPP and carbon stocks have big uncertainties, particularly, in the estimates of the long-term trend. Therefore, remote sensing-based estimates of ecosystem carbon cycle should be validated using data from ground measurements.

1.4 Atmospheric-based estimates of the terrestrial carbon sink

The global magnitude, regional distribution and interannual variations of the terrestrial carbon sink that are cited widely are mainly derived from measurements of atmosphere CO_2, carbon and oxygen isotope concentration and inverse modeling based on the measurements[68,69]. Seasonal variability in atmospheric CO_2 concentration follows the phonological cycle of plant growth, and the interannual variability depends largely upon vaiations of terrestrial ecosystem carbon uptake[1,36]. Because of the difference in carbon and oxygen isotopes composition in terrestrial and oceanic biological processes, measurements of the changes in the isotopes composition became a unique and effective way to distinguish the terrestrial and oceanic sink[71]. The networks of atmospheric measurements have been greatly extended, both the sampling site and frequency have a large increase. The data are used in atmospheric transport models to infer

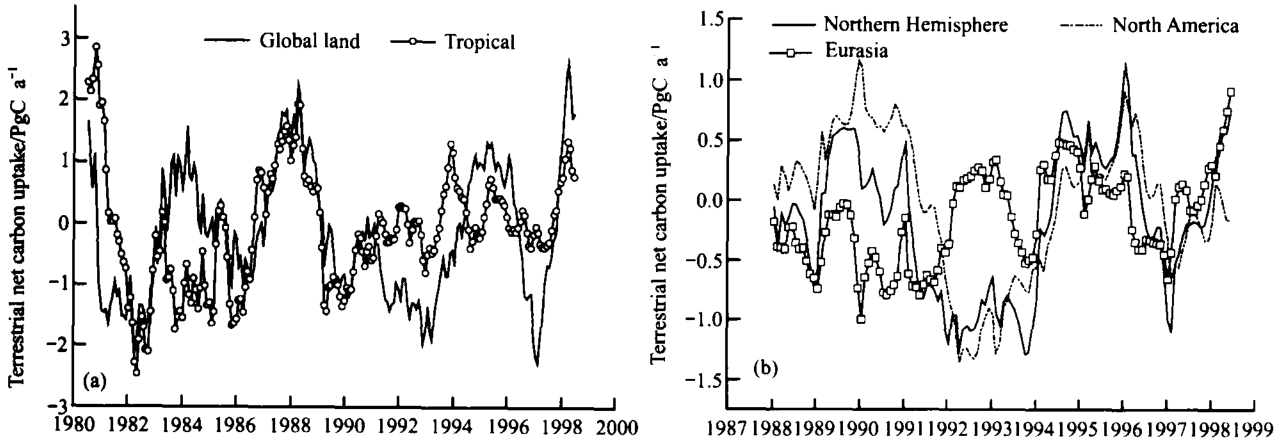

Fig. 4. Estimates of the global terrestrial carbon sink and its regional distribution and interannual variations are mainly based on atmospheric measurements and inverse modeling. The figure shows the estimated global (a) and regional (b) net land carbon flux in the past 20 years (the negative value indicates carbon uptake, and *vice versa*)[68].

spatial distribution and temporal variability of carbon sources and sink through inverse modeling based on atmospheric circulations and transport mechanisms.

Atmospheric measurements and inverse modeling have quantified regional distribution, seasonal, interannual variations in the land-atmosphere net carbon flux. Results[68,69] showed that the net terrestrial carbon uptake increased from 0.2—0.4 Pg a^{-1} in the 1980s to 0.7—1.4 Pg a^{-1} in the 1990s, and the terrestrial carbon sink (the net land uptake + carbon release from land use) varied greatly between 2.0—4.0 Pg a^{-1}[1]. Early atmospheric inverse modeling indicated that terrestrial carbon uptake occurred mainly in northern mid and high latitudes and that tropical terrestrial ecosystems were a large carbon source[36,38], however, recent studies estimated that tropical regions were carbon balanced or have moderate carbon uptake[72,73], implying that undisturbed tropical ecosystems were a substantial carbon sink[74] to offset the carbon release of up to 2.2 Pg a^{-1} from deforestation[64]. The results were supported by eddy flux measurements[40—42]. According to atmosphere inverse modeling, the terrestrial carbon sink was 0.8 Pg a^{-1} in North America, 1.7 Pg a^{-1} in Eurasia, and 0.4 Pg a^{-1} in the tropics and Southern Hemisphere, with no significant net carbon uptake or release in East Asia and the Pacific Ocean[1].

Atmospheric measurements and inverse modeling are an effective approach to quantify the terrestrial carbon sink in global and continental scales. Because of the rapid movement and mixing of CO_2 in the atmosphere and sparse atmospheric measurements, the method is limited to provide fine-resolution (e.g. at sub-continental or national scales) distribution of the terrestrial carbon sink[69]. At present, the understanding of historical changes in the atmosphere $^{13}CO_2$ background value is still poor, thus the estimates of terrestrial carbon uptake based on it have some uncertainties[75]. Moreover, as an indirect approach, atmospheric measurements and inverse modeling has not any physiological and ecological mechanisms involved in estimating the terrestrial carbon sink, thus are unable to give mechanic explanation for estimated changes.

2 Cross-scale mechanistic analysis and quantification of ecosystem carbon processes

2.1 Multi-scale observation and cross-scale mechanistic analysis

Ecosystem experiments and observations at multiple scales described above have obtained a large amount of data about ecosystem carbon cycle in the past 10 years, but the uncertainties in estimating the terrestrial carbon sink have not been reduced much. For example, the estimates of the terrestrial carbon sink and the regional distribution still vary greatly, and the range of the estimates increased with the emerging of new approaches and data sources. Atmospheric-based estimates of the global terrestrial carbon sink are twice of land-based[67,76]. The estimated net ecosystem carbon uptake or release for a same site using eddy covariance technique and carbon stock inventory differed by 60%—170%[29]. The studies based on remote sensing suggested warming has caused increases in the terrestrial carbon sink[61—63], but ecosystem experiments and observations indicated that warming caused net carbon release[25,28]. Land use-induced carbon release based remote sensing[65,66] was less than a half of the estimate based on statistical data[64]. Partitioning the effect of natural (e.g. climate change, atmosphere CO_2 concentration increase and N deposition) and anthropogenic mechanisms (e.g. reforestation, afforestation, and land management) on the terrestrial carbon sink is essential to effective implementation of the protocol, however, there have been clear estimates of their relative contribution[76—79].

The major cause of the uncertainties is that the existing estimates were based on the data observed at individual scales. Few studies have been conducted to investigate interconnections and interactions of ecosystem processes at different scales. Like in any complex system, the controlling factors and processes differ at different levels in ecosystems and their interactions, at a large extent, determine the whole ecosystem function and behavior[5,6]. The spatial heterogeneity in terrestrial ecosystem carbon cycle depends, on the one hand, on regional climate, vegetation, hydrology and land use pattern, and on the other hand, on micro-climate, soil conditions, land management, and eco-physiological processes. The temporal variation is affected by both fast processes from hourly to yearly climate variability and physiological responses (e.g. stomatal conductance, photosynthesis, and respiration) and slow processes (e.g. climate change, vegetation succession and species migration at temporal scales from decades to centuries). Micro-scale eco-physiological responses, ecosystem pattern shifts, and macro-scale energy transfer and material cycles jointly determine spatio-temporal variations in the terrestrial carbon sink. Individual-scale observations can not capture the interactions between different scales, and even cannot provide a full understanding of the processes at the specific observational scales because of the effect from the other scales. Therefore, to estimate spatial and temporal variability in the terrestrial carbon sink requires mechanistic understanding and quantitative analysis of the interconnections and interactions between ecosystem processes and pattern at different scales.

2.2 Mechanistic modeling of cross-scale ecological interactions

Experimentation and observation are always conducted at specific scales, thus they alone cannot result in understanding of the interconnections and interactions of ecosystem processes and pattern at different scales[7,15]. Experiments and observations at multiple scales provide the necessary data for the understanding, but to achieve the understanding requires bridging the data obtained at different scales. At present cross-scaling approaches used in ecosystem carbon studies are the traditional "Bottom Up" and "Scaling Down" [5]. The "Bottom Up" approach is to extrapolate results or mechanisms at small scales to large scales directly. Limited small-scale studies, on the one hand, cannot reflect high spatial and temporal variabilities in ecosystem carbon cycle and, on the other hand, cannot capture large-scale mechanisms that often concealed at high small-scale variabilities. For example, the CO_2 fertilization effect observed at plot-scale experi- ments is generally much higher than that observed at ecosystem levels[15]. The estimated net ecosystem carbon uptake or release using micro-level eddy flux measurements is more than twice of that from macro-level carbon stock measurements[29]. The "Scale Down" approach generally use statistical analysis to link changes in large-scale patterns and activities to the driving forces. So it is difficult to identify the underlying mechanisms, even often leading to misleading results due to the statistical errors and poor data quality at large scales[15]. For example, remote sensing-based studies indicated poor correlation of NPP with precipitation at the north mid and high latitudes, even in dry regions[53,63,80], but mechanistic studies showed that increasing precipitation was a major cause in the terrestrial carbon sink[81].

Cross-scale analysis shall reveal mechanistic, quantitative connection between ecosystem processes at different scales, e.g. the relationship of changes in plant stomatal conductance and photosynthesis to carbon allocation among plant organs and plant morphology, the effects of changes in the relative rates of plant carbon and nitrogen assimilation on C/N ratio of plant biomass and soil organic matter, litter decay, soil organic mater decomposition, and the carbon and nitrogen cycles in the soil-plant system, and shifts in vegetation structure, composition and distribution resulting from changes in the relative growth rate among different species and their competition advantage for limited resources. These cross-scale connections are often concealed in the processes at specific scales and hence are difficult to distinguish and quantify using empirical analysis. Process-based mechanistic modeling is the most effective approach to analyze and quantify the cross-scale interconnections and interactions[7].

Mechanistic modeling advanced rapidly during the last decade. Various mechanistic models have been developed, which are generally classified into biogeochemical models and dynamic global vegetation models (DGVM). The models have been widely used to estimate impacts of climate and land use changes on NPP, ecosystem carbon fluxes and storage (fig. 5). For example, Melillo et al. first used a mechanistic model to estimate global spatial pattern of terrestrial NPP and predicted a doubled atmospheric CO_2 concentration and the corresponding climate change would enhance NPP significantly[82]. Cao and Woodward for the first time simulated the transient, dynamic response of terrestrial net ecosystem productivity to climate change during the past and future 100 years, and found that the global terrestrial ecosystem became a carbon sink at the beginning of the last century, and the sink increased rapidly during the recent decades but would saturate in the middle of this century[83]. Mechanistic models are also used to estimate the effect of land cover changes on terrestrial ecosystem NPP and carbon stocks[84]. Cramer et al. used 6 DGVMs to predict dynamic response of global terrestrial ecosystem carbon cycle to climate change, estimating the terrestrial carbon sink varied from 0.6 to 3.0 Pg C a^{-1}

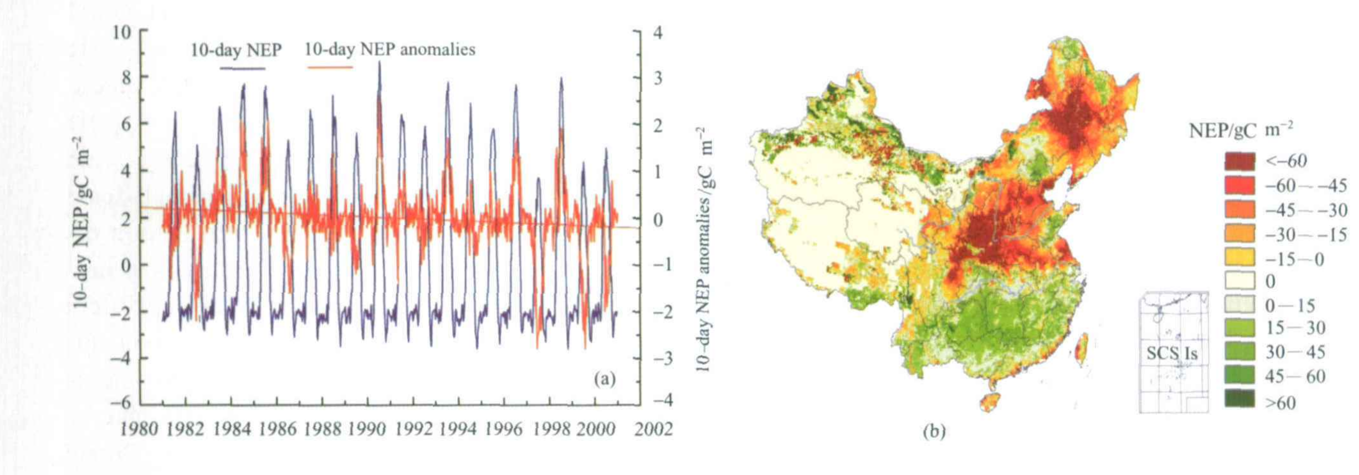

Fig. 5. Model-estimated spatial pattern and temporal variations in terrestrial net ecosystem productivity (NEP) in China during the past 20 years [59]. The results show that NEP had high seasonal and inetrannual variability and a decreasing trend because of higher increases in NPP than in soil respiration (a). The decrease from the 1980s to the 1990s occurred mainly in Northeast and North China where warming and drying concurred in the 1990s, whereas NEP increased in South and Northwest China because of increases in precipitation (b).

at present and from 0.3 to 6.6 Pg C a^{-1} in the end of this century[85]. Cox[86] and Friedlingstein et al.[77] used a coupled ecosystem and climate model to study the feedback between changes in the terrestrial carbon sink and in climate, predicting the terrestrial carbon sink would disappear or turn into a source in the late of this century.

Although mechanistic modeling has greatly advanced understanding of ecosystem carbon processes, the credibility of and confidence in the modeled spatial and temporal variations in the terrestrial carbon sink are very low. Most of existing models were established on small-scale experiments and observations before the middle of the 1990s when few long-term, large-scale experimental and observational data were available. The models focus on eco-physiological responses to environmental changes at individual plant or patch scales, and few of them have been validated fully. DGVM is designed to simulate ecosystem structural and functional changes from patch to regional scales, however those used in ecosystem carbon studies[85] are basically a combination of biogeographic and biogeochemical models, unable to describe the mechanistic connections between eco-physiological responses and vegetation patterns and structural shifts. Therefore, to quantify cross-scale interactions of ecosystem processes and their controls over carbon cycle requires new-generation mechanistic ecosystem models.

2.3 New generation of mechanistic ecosystem models

Development of new-generation mechanistic ecosystem models requires understanding and quantifying interactions between ecosystem processes at different spatial and temporal scales. Whereas numerous ecological experiments and observations focus on micro-scale eco-physiological responses to environmental changes, lacking of quantitative studies of transient dynamics of ecosystem pattern and structure prevent development of the new-generation mechanistic ecosystem models. In addition to direct responses, ecosystems have complex mechanisms to acclimate to environmental changes[16,21]. Ecosystem acclimation consists of a series of physiological and ecological adjustments to offset or adapt to the primary response to environmental changes[21,87]. It occurs at different levels from plant physiological processes to morphology to community levels but usually manifests at long-time scales (from years to decades). Acclimation is the mechanistic basis of ecosystem pattern and structural changes. Therefore, to develop the new-eneration models requires understanding the mechanistic transformation from micro-level eco-physiolo-ical responses to long-term, macro-scale acclimation.

An ecological theoretical framework is needed to modeling interconnection and interactions among ecosystem processes at different scales. Classic ecological theories, e.g. resources balance theory[88,89] and optimal allocation hypothesis[90,91], that are used to explain ecosystem acclimation are flawed in many aspects. For example, according to the resource theory, plant primary responses to environmental changes disturbs the balance of plant assimilation of different resources (e.g. carbon assimilation by leaves and water and nitrogen uptake by roots), the consequent adjustment of resource allocation among plant organs to keep and recover the balance resulting in changes in plant morphology and growth rate, which in turn cause vegetation structural changes and shifts in spatial pattern. Models that are based on the resources balance theory prescribe that ecosystems shift from an assumed equilibrium status toward another, however many ecosystems never reaches an equilibrium status, particularly under the ongoing rapid environmental changes and intense anthropogenic disturbance, and their changes are often not toward an equilibrium status. The optimal allocation theory assumes plants optimize resource allocation in a way that maximizes growth[90,91], but the models based on the theory cannot realistically simulate the carbon allocation among plant organs and the consequent morphological changes[92,93]. Therefore, more reasonable ecological theories should be developed to provide a mechanistic basis for understanding and simulating ecosystem acclimation, particularly for non-equilibrium ecosystems.

2.4 Multi-scale data-model fusion

Unlike existing ecological models that are established mainly based on single-scale, limited experiments and observations, the new-generation ecosystem models shall be based on a large number experimental and observational data obtained at different scales from regional and global ecological research networks. Appropriate approaches are needed to extract mechanisms and quantitative interconnections from data obtained at different scales for developing ecosystem models. Multi-scale data-model fusion is a new approach emerging in studies of ecosystem carbon cycle[94—97]. Firstly, data-model fusion uses data obtained at multiple scales to optimize model structure and parameters by combining “forward” and “inverse” modeling approaches[95,96]. Whereas “forward” modeling prescribes model structure and parameters from theoretical deduction or single-scale experiments directly, “inverse” modeling determines model structure and parameters using complex mathematical optimization methods based on data obtained at different scales[95,98]. For example, existing models simulated NPP based on the mechanisms and parameters about stomatal conductance and photosynthesis derived from leaf or individual-plant scales, the new-generation models shall use the mechanisms and parameters inferred multi-scale data, e.g. from ecosystem experiments, landscape eddy flux measurements and regional remote sensing. Second, data-model fusion uses multi-scale observational data to validate and evaluate models at different scales. This is particularly important to the new-generation models that simulate cross-scale interconnections and interactions. With accumulation of data about changes in ecosystem carbon flux and stocks, NDVI, leaf area index, and plant productivity from ecosystem experiments, eddy flux measurement and remote sensing, the effectiveness of the models at different scales can be validated and evaluated. Finally, the long-term observational data are continuously assimilated in dynamic modeling to achieve realistic simulation, prediction and forecasting of ecosystem changes.

3 Conclusions

During the past decade regional and global networks of ecosystem experiments and observations have been established using new techniques such as controlled environmental facilities, eddy covariance technique, stable isotope measurements and remote sensing, and a large amount of data have been obtained about ecosystems changes from site to landscape to regional scales. However, those intensive experiments and observations have not yet substantially reduced the uncertainties in quantifying and understanding the terrestrial carbon sink, and the range of the estimates of the sink increases with using new approaches and data sources. The major reason is lack of cross-scale mechanistic analysis of the data obtained from experiments and observations at individual scales. Uses of data obtained at different scales get different estimates of the terrestrial carbon sink and the underlying mechanisms. The ecosystem is a typical complex system, in which micro-level eco-physiological processes and behavior of individual organisms interact with the macro-level ecological pattern, energy transfer and material cycle to modulate ecosystem carbon cycle. Therefore, studies at any single scale cannot result in understanding and accurate quantification of the terrestrial carbon sink.

Experiments and observations are always conducted on a specific scale. Multi-scale experiments and observations provide data for but are not necessarily result in understanding interconnections and interactions of ecosystem processes at different scales, which are best achieved by using mechanistic modeling. However, existing ecosystem models mostly focus on micro-level eco-physiological processes and thus cannot realistically simulate transient dynamics in the ecosystem pattern and structure and the acclimation to long-term environmental changes. Therefore, new-generation models are needed to analyze and quantify cross-scale interconnections and interactions of ecosystem processes. Classic ecological theories are flawed in explaining cross-scale interactions, thus to understand and quantify the mechanistic transforma-

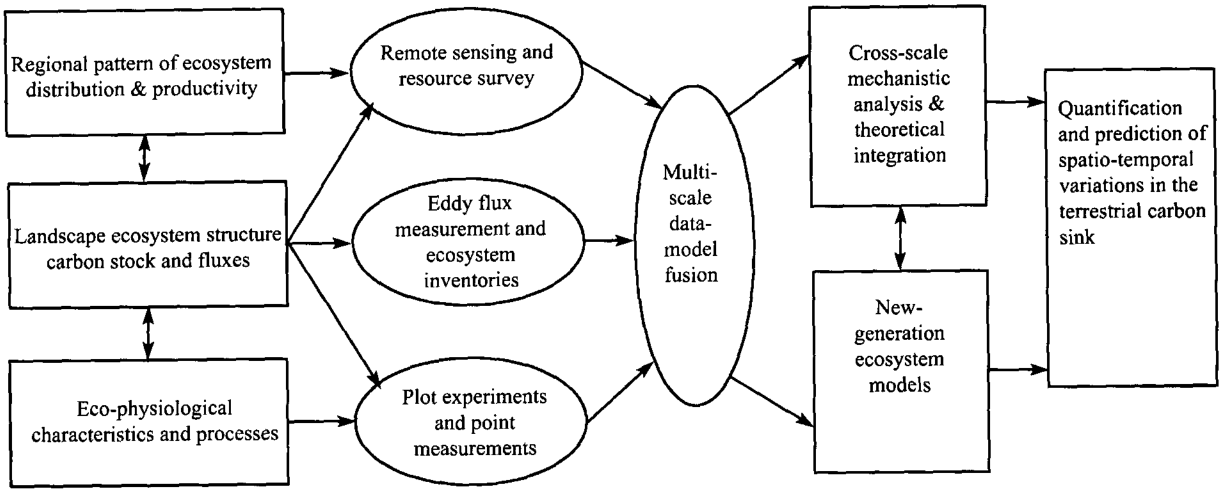

Fig. 6. A data-model fusion system based on multi-scale observation and cross-scale mechanistic analysis for studying terrestrial ecosystem carbon cycle.

tion of micro-scale process responses to macro-scale structural acclimation, particularly in disturbed ecosystems, requires new theoretical framework.

New methodologies are needed to use multi-scale data in developing the new-generation models. Multi-scale data-model fusion is a new approach recently emerging in ecosystem carbon studies, which includes optimization of model structure and parameters using multi-scale observational data; model validation and evaluation at different scales, and continuous data assimilation into dynamic modeling for realistically predicting and forecasting ecosystem changes.

In summary, a breakthrough in terrestrial ecosystem carbon cycle research requires understanding, integrating and quantifying interconnections and interactions between ecosystem processes at different scales. Cross-scale mechanistic modeling based on multi-scale experiments and observations is the approach toward achieving the objective (fig. 6).

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