13 Impacts of Climatic Changes on Biogeochemical Cycling in Terrestrial Ecosystems

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Abstract: Global climate change has profound effects on biogeochemical cycling in terrestrial ecosystems. This chapter summarizes the existing state of knowledge on how climate change affects biogeochemical cycling, specifically carbon cycling, as the carbon cycling has long been recognized as important for understanding climate change. The review draws largely on knowledge gained from manipulated experiments, modeling, and meta-analysis studies. This chapter starts with a brief description of current changes in several climate factors such as atmospheric carbon dioxide (CO_2) concentration, temperature, precipitation, and ozone (O_3) and their effects on terrestrial ecosystems. Then approaches commonly applied in global change research such as natural observation, experiment, ecosystem modeling, and meta-analysis are described. The advantages and disadvantages of these approaches and general procedures are also summarized. The impacts of global change such as elevated CO_2, global warming, and changes in precipitation and O_3 on carbon cycling in different terrestrial ecosystems are further synthesized. In addition, issues related to global climate change such as single factor versus multiple factor studies, graduate versus step increase experiments, and inverse modeling are briefly discussed. At the end of the chapter, some recommendations for future global change research in terrestrial ecosystems are provided.

## Introduction: Global Climate Change and Terrestrial Ecosystems

The atmospheric carbon dioxide (CO_2) concentration has gradually increased from 280 ppm in preindustrial times to ~379 ppm in 2005 and is expected to exceed 700 ppm in 2100 [1], mostly due to land use change and fossil fuel combustion. As a consequence of rising CO_2 and other greenhouse gases, the Earth's surface temperature has increased by 0.74°C in the twentieth century and is expected to increase by another 1.8–4.0°C by the end of this century [1]. Precipitation is also anticipated to increase by about 0.5–1% per decade over most of the middle- and high-latitude land areas in the northern hemisphere in this century [1]. The tropospheric ozone (O_3) level has been increasing at local, national, continental, and even global scales. Future projections indicate that the trends in greenhouse gases, temperature, and precipitation will continue, resulting in a warmer, wetter, yet drier world in the twenty-first century [1, 2].

Changes in atmospheric CO_2 concentration, O_3, and other climatic factors have the potential to trigger complex influences on terrestrial ecosystems with feedbacks to climate change [3–5]. Carbon dioxide, for example, is not only one of the main greenhouse gases, but also a substrate of plant photosynthesis. Rising atmospheric CO_2 concentration can directly affect photosynthetic rates, plant growth, and ecosystem productivity. Temperature influences all physical, chemical, and biological processes. Global warming can affect ecosystem structure and function, such as ecosystem carbon cycling. Precipitation, O_3 concentration, and nitrogen fertilization also regulate plant growth and ecosystem carbon cycling in terrestrial ecosystems [6–9]. The amount of carbon stored in terrestrial ecosystems will feedback and influence future atmospheric CO_2 concentrations. Thus, it is very

important to assess the impacts of global climate change on ecosystem carbon cycling and processes [10].

Ecosystem carbon cycling and fluxes between the atmosphere and terrestrial ecosystems are controlled by the processes of photosynthesis, plant autotrophic respiration, and soil heterotrophic respiration (❷ *Fig. 13.1*). The total of plant photosynthesis in terrestrial ecosystems is gross primary productivity (GPP). Soil respiration includes root respiration and heterotrophic respiration (i.e., soil microbial respiration). Ecosystem respiration includes both soil respiration and aboveground autotrophic respiration. The difference between plant photosynthesis and respiration is defined as net primary production (NPP). The difference between NPP and soil heterotrophic respiration, defined as net ecosystem production (NEP), represents the net carbon flux from the atmosphere to ecosystems. Ecosystem carbon processes and productivity are also influenced by plant phenology, nitrogen conditions, land use changes, and disturbances such as fire, drought, and insect outbreaks. Among many factors affecting these processes, the most obvious are elevated CO_2 concentration and climate change, which directly and indirectly influence and interact to control the carbon fluxes from ecological and physiological processes [5, 11, 12].

Climate and atmospheric CO_2 concentration are key regulators of most terrestrial biogeochemical processes and have the potential to markedly modify the carbon cycling in terrestrial ecosystems [10]. Responses of terrestrial ecosystems to elevated CO_2 concentration and global climate change are complex and thus, require different approaches, such as observation, manipulated experiment, ecosystem biogeochemical modeling, and meta-analysis [2]. Long-term observations over large spatial areas provide invaluable insights and background information on ecosystem response to climate changes. Manipulated experiments allow us to seek the different effects and mechanisms of climate change on terrestrial ecosystems. Ecosystem modeling is a very powerful tool to synthesize
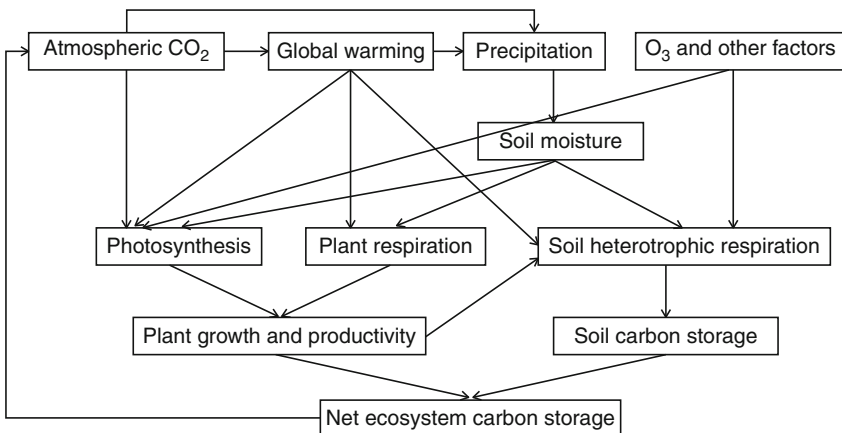
■ **Fig. 13.1**
Impacts of climate change on terrestrial ecosystem carbon processes and feedback

experimental results and assist extrapolation of leaf, plant, and ecosystem-level research results to project changes in ecological processes at regional and global scales [10–12]. Meta-analysis provides a quantitative synthesis and generates a general conclusion of many individual and often inconclusive studies [3, 14, 15].

Many studies have been conducted on the responses of terrestrial ecosystems to elevated CO_2 and global climate change during the past several decades using these different approaches. Results from these studies have greatly improved our understanding of the responses of terrestrial ecosystems and the feedback to future climate change. This chapter reviews global climate change studies on the impacts of biogeochemical cycling, specifically carbon cycling, in terrestrial ecosystems, and attempts to provide a comprehensive and up-to-date overview in the field. The complexity of responses is often confounded by other concurrent human-induced global changes such as nitrogen and sulfur deposition, invasive species, and land use changes, but these are not covered in this review. This chapter starts with a description and comparison of different approaches commonly applied in global change studies. Then the impacts of elevated CO_2, global warming, precipitation, and other climate change factors on ecosystem carbon cycling are reviewed. Issues related to global climate change such as single factor versus multiple factor studies, graduate versus step increase experiments, and inverse modeling are also briefly discussed. Finally, some recommendations for future global change research in terrestrial ecosystems are provided.

Approaches to Evaluate the Impacts of Climate Change on Terrestrial Ecosystems: Observation, Experiment, Model, and Meta-analysis

Several approaches have been used to evaluate the impacts of rising atmospheric CO_2 concentrations and climate change on terrestrial ecosystems in the past several decades at different spatial scales. Generally, these approaches can be classified into four categories: observation, experiment, model, and meta-analysis. Among these approaches, experimental study is a powerful tool to evaluate the responses of climate changes on terrestrial ecosystems and to understand the mechanisms underlying these responses. It will continue to be a major tool and has been extensively used, in global change studies. With the advancement of sensor technology, automatic recording, and satellite images, more and more observations and measurements on terrestrial ecosystems under natural conditions can be made over long term and at large spatial scales. Ecosystem modeling becomes more and more important, especially at scaling up from plot-level experiments to large spatial scales and forecasting future responses. As more and more data accumulates, meta-analytic techniques provide another means to quantitatively integrate the individual studies and generate a grand conclusion on a common topic. Recently, Rustad [2] summarized some of these approaches (❯ *Table 13.1*), particularly on experimental studies (see also Fig. 1 and Table 1 in [2]). In this section, the four approaches are briefly discussed, with a focus on terrestrial ecosystem carbon cycling.

◘ **Table 13.1**

Advantages and disadvantages of different approaches to evaluating global change impacts on terrestrial ecosystems [2]

Approach	Advantage	Disadvantage
Observations	1. Suitable for long-term research	1. No true control, effects of climate are confounded
	2. Good for model validation	2. Quality of study depends on data availability
	3. Relative low costs	3. Future responses are unknown
Experiments	1. Suitable for evaluating cause–effect relationships	1. Can only generate short-term data on short-term response due to costs
	2. Can study past, current, and future climate change	2. Step increase is not realistic
	3. Good for model validation	3. Can only realistically alter two to three factors
Models	1. Integrating existing knowledge	1. Not possible to validate longer-term effects
	2. Extrapolating to long term and large scales	2. Need to incorporate heterogeneity, disturbance, etc.
	3. Testing of conceptual and process understanding	3. Uncertainty related to model structures, parameters, and predictions
Meta-analyses	1. Integrate multiple individual experimental results	1. Only limited levels and single factor experiments are synthesized
	2. Provide quantitative conclusions	2. Not provide novel insights

Observation

Observations can provide background information on ecosystem responses to climate changes. To be valuable, these observations/measurements need to be made over long term or at large spatial scales, or both. With long-term observational data, the relationships of ecosystem responses and climatic factors can be developed. For example, using long-term climate data and satellite observations of vegetation activity, Nemani et al. [16] report that the global changes in climate have eased several critical climatic constraints to plant growth, as that as NPP increased by 6%. The largest increase was in tropical ecosystems. They also estimate that water availability most strongly limits vegetation growth over 40% of Earth's vegetation surface, where temperature limits growth over 33% and radiation over 27% of Earth's vegetated surface. With observations at large spatial scales, different ecosystem responses to climate change may be derived.

Individual observational studies are often made along climate gradients, such as temperature gradient along mountain slopes, precipitation gradient with

elevations/longitudes, or CO_2 gradient near natural CO_2 springs. These natural climate gradients provide unique opportunities to study responses of ecosystems to a range of climate factors, and trade space for time.

Many observation networks have been built in recent years, due to the advancement of sensor technology and collaborations among scientists. For example, FluxNet is an international network of micrometeorological tower sites that use eddy covariance methods to measure the exchanges of CO_2, water vapor, and energy between terrestrial ecosystem and the atmosphere [17]. The goal of FluxNet is to understand the mechanisms controlling the exchanges of carbon, water vapor, and energy across various ecosystem types and over long-term timescales. The network spans a wide cross section of climate zones and ecosystem types. Synthesis of data from EuroFlux, a part of FluxNet network, confirms that many European forests act as carbon sinks, and ecosystem respiration determines net ecosystem carbon exchanges [18]. These data also provide a unique opportunity for researchers to identify the response patterns and the underlying mechanisms of ecosystem carbon fluxes to climate changes. Another example is the Long Term Ecological Research (LTER) network supported by the National Science Foundation (NSF). LTER provides insight on ecosystem responses to global climate change at broad spatial and temporal scales [2]. Other similar networks also demonstrate the value of the collaborative studies. Data from Afritron (African Tropical Rainforest Observatory Network), which includes 79 inventory plots, show that aboveground carbon storage in live trees increased by 0.63×10^6 g carbon (C) ha^{-1} year^{-1} between 1968 and 2007 [19]. Widespread changes in resource availability, such as increasing atmospheric CO_2 concentrations, may be the cause of the increase in carbon stocks. In the near future, National Ecological Observatory Network (NEON) will be built with the support from the NSF to make observations across the continental United States [20]. It is a continental-scale research platform for understanding and forecasting the impacts of climate change, land use change, and invasive species on ecological processes. At large spatial scales, satellite-based remote sensing plays an indispensable role in terrestrial ecosystem observations. Satellite-derived land products such as net primary production (NPP), NDVI, and leaf area index are important products toward a global observation capability. NPP derived from Moderate-resolution Imaging Spectroradiometer (MODIS) and NDVI data sets derived from satellite images can be used to derive the relationships of ecosystem carbon fluxes with climate changes.

The advantages of observational study include: (1) Data over long term and at large spatial scales can be collected, thus allowing to evaluate long-term effects across different ecosystems (❯ *Table 13.1*). (2) For pure observational studies, the costs for experimental site construction are low. Funds are required only for observations and measurements and thus, it is desirable to run for a long time. (3) Regional and international observation networks can be formed to focus on a centered theme to study climate change at large spatial scales across different ecosystems. The disadvantages of the observational study include: (1) There is no true control, thus, the effects of climate changes are often confounded with other environmental factors. (2) Quality of the study depends on the availability of data. The long-term records dating back to more than 100 years (which is

very long compared to experimental study, but short in terms of climate change) are rarely available [2]. (3) Observational studies mostly lack the ability to predict the future responses.

Experiment

Numerous manipulated experiments have been conducted in the laboratories and under field conditions [21–24]. For example, an international research coordination network – Terrestrial Ecosystem Response to Atmospheric and Climatic Change (TERRAC) – includes 135 field experimental sites in 25 countries [2, 24]. These studies include one, two, and multiple climatic factor experiments and consider atmospheric CO_2 concentration, temperature, precipitation, and nitrogen addition. Ecosystems include deciduous forest, coniferous forest, grassland, wetland, shrubland, tundra, and desert.

In global climate change research, most experimental studies use a perturbation approach that creates treatment levels (i.e., magnitudes in changes of treatment factors) that are large enough to generate detectable ecosystem responses [10]. For example, ecologists usually double CO_2 concentration, increase it by 200 ppm, or set a specific level at the onset of experiments conducted in greenhouses, growth chambers, open-top chambers, and Free Air CO_2 Enrichment (FACE) facilities (❯ *Fig. 13.2*) [21]. In the early years, researchers used closed chambers such as growth chamber to grow plants under control and elevated CO_2 levels. These studies were criticized as growth chambers cannot really mimic the real world environment, thus generate responses that are different to those under natural conditions. Open-top chambers provide natural light and precipitation for plants to grow, but often modify air and soil temperature inside the chambers. Open-top chambers have not been used successfully in the studies of ecosystems with large vegetation. They are mostly useful for low-stature systems (e.g., tundra, grassland, tree seedling). FACE is the state-of-the-art facility for studying the effect of elevated CO_2 on terrestrial ecosystems, as it creates a high CO_2 environment without altering other environmental factors [21]. Scientists measure responses of plants, soil, and ecosystem processes to such a step increase in CO_2 concentration through time [10].

Similar to elevated CO_2 studies, in order to examine the effects of climate warming on ecosystem processes and community structures, researchers usually raise soil/air temperature instantaneously by 1–4°C in treatment plots than that in the control. The methods used to manipulate temperature include soil warming [25], infrared heaters [26–28], passive heating, and open-top chambers with heated air (❯ *Fig. 13.2*) [29]. Most of the experiments with infrared heaters also have constant energy input to the ecosystem, resulting in increases in soil surface temperature being higher at night than during daytime. A comparison and discussion of the warming facilities can be found in Wan et al. [27].

Although other global change factors, such as precipitation and nitrogen deposition, may not evolve gradually in a regular fashion over time and/or uniformly over space as atmospheric CO_2 concentration does, experimental studies mostly use the step-change
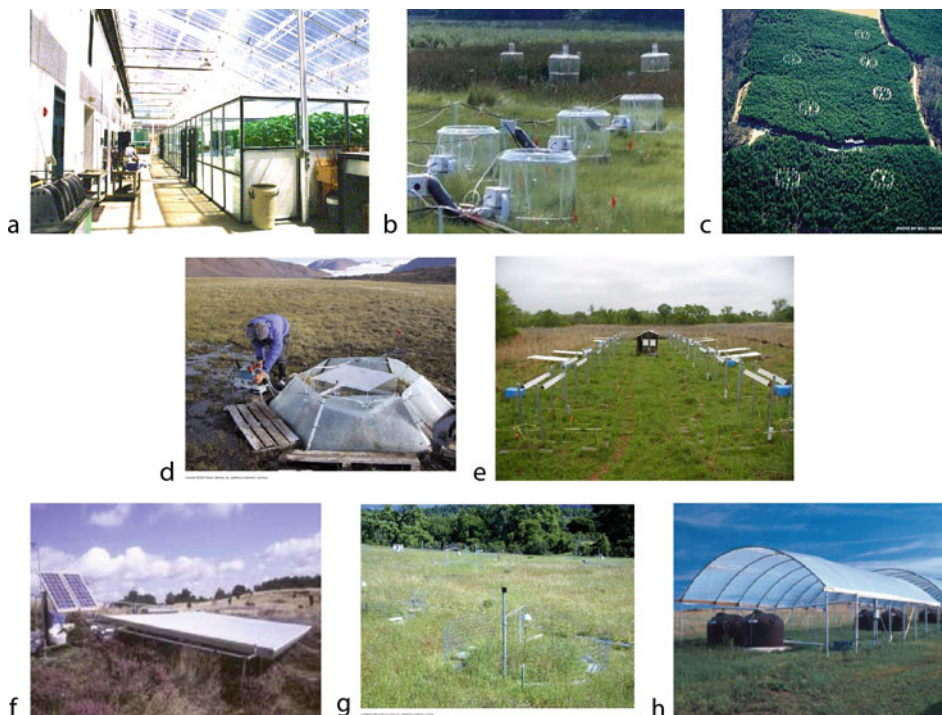
■ Fig. 13.2

Examples of field facility in global change research. (a). EcoCELLs, Ecologically Controlled Enclosed Lysimeter Laboratories, photo credit: Jay Arnone III; (b). Open-top chambers (OTCs) on a Florida Scrub-oak Ecosystem, photo credit: Bert Drake; (c). FACE (Free Air CO$_2$ Enrichment) experiment in Duke loblolly pine forest, photo credit: Will Owens; (d). The open-top-chamber (OTC) warming facility in the International Tundra Experiment (ITEX) warming study, photo credit: Greg Henry; (e). Global warming experiment in tall grass prairie in Oklahoma, photo credit: Yiqi Luo; (f). Rocky Mountain Biological Laboratory Meadow Warning Experiment, photo credit: John Harte (With kind permission from Springer Science+Business Media: Plant Ecology, Vol. 182, 2006, Rustad, photo); (g). Jasper Ridge multiple factors (CO$_2$, warming, precipitation and nitrogen) Global Change Experiment, California, photo credit: Chris Field; (h). Precipitation shelter in tallgrass prairie at the Konza Prairie Research Natural Area, Kansas, photo credit: Philip A Fay

approach as well [10]. Precipitation amounts were doubled in a grassland experiment in central US Great Plains and reduced by 30%, 55%, and 80% in Argentina [30]. Precipitation amounts were also changed together with timing in some of the studies [6].

Multiple factor experiments are logistically and financially challenging [2]. There are only a small number of experiments that consider more than two climatic factors in the same study. But these studies quantify not only the main effects of climatic factors, but also the interactive effects of these factors. Results from some experimental and modeling

studies also demonstrate interactive responses to the combinations of treatments and underscore the need for multifactor experiments at different ecosystems and over long term [2, 31–33].

The major advantages of experimental study are: (1) to reveal true ecosystem responses to climate change. As other factors are controlled and kept at relative same levels, the results are considered as the direct effects of climatic change; (2) to help understand the mechanisms of these responses; since only one or a few climatic factors are manipulated, it is relative to track the influences of climatic factors on ecological processes and components; (3) as treatment levels can be set at different levels, the effects of climate change factors in the past, current, and future can be evaluated; and (4) to provide data to parameterize and validate models, and generate mechanisms to be built into models. The disadvantages include: (1) Short terms. Majority of the experiments last less than 5 years. The results from these studies may be transient, and both magnitude and direction of responses may change over time [2, 22]. (2) Using a step increase rather than gradual increase in climatic factors. Many climatic factors such as CO_2 concentration, O_3, and temperature are increasing gradually over years. But experiments usually expose ecosystems to future high CO_2 concentrations, O_3, or temperature abruptly. The responses of ecosystems to step increases may be different to those of gradual increases in natural conditions. (3) Climatic factors change simultaneously, but most experiments can only consider one or a few climatic factors, and set two or a few treatment levels. (4) High costs for large global change projects, for example, FACE experiments. The financial costs also limit the number of climate factors that can be considered and the number of years an experiment can take.

Model

Process-based ecosystem models provide appropriate tools for integrating the existing knowledge, scaling experimental results up in time and space, and investigating multiple, interacting factors of global change [2, 5, 11, 12, 32–34]. They also represent a key method for testing hypotheses about the response of terrestrial ecosystems to multiple climatic factor changes [34, 35]. Many ecosystem models have been developed with different complex and ecological processes, and applied to assess the impact of climatic change on terrestrial ecosystems [31, 35]. Several model comparison studies also compared model structures, ecological processes, and model performances using one set or sets of experimental/observational data [32, 35]. Here two specific models, one at the stand level and one at large scale, are described to illustrate some common ecological processes included in ecological models.

Terrestrial Ecosystem (TECO) Model

TECO is a biochemical and ecophysiological model that uses daily meteorological data to simulate ecosystem carbon dynamics at site level (❯ *Fig. 13.3*). It has been applied to
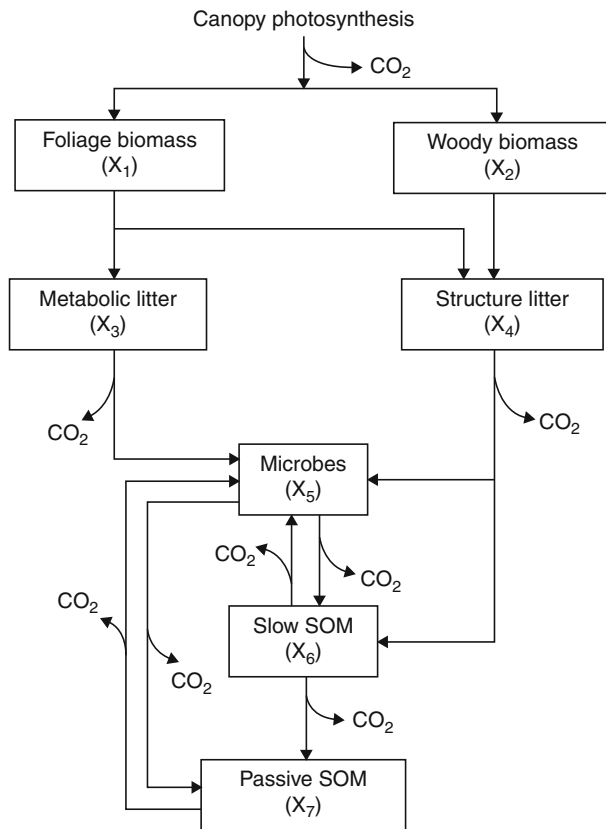
◘ Fig. 13.3

Diagram of the carbon processes of terrestrial ecosystem (TECO) model ([39]. With permission from AGU). SOM stands for soil organic matter

predict ecosystem responses to rising atmospheric CO_2 concentration, climate warming, and altered precipitation frequency and intensity in grasslands and forests [32]. TECO has two major components: a canopy photosynthesis model and an ecosystem carbon dynamic model. The canopy model is a multi-layer, process-based model of an even-aged mono-specific plant stand. The carbon dynamic model considers plant growth, respiration, and soil carbon movement. Allocation of assimilates over the plant components bases on the priority principle and varies with phenology.

The effects of climatic factors such as atmospheric CO_2 concentration, temperature, and precipitation are built in the model, as these factors will influence most biological processes. For example, precipitation will influence evapotranspiration and soil moisture directly, and then influence leaf photosynthetic rate and soil respiration. Temperature plays an important role in biological processes. It affects photosynthesis, respiration, and transpiration.

The main time step of TECO is 1 day. Light penetration, photosynthesis, and transpiration are simulated in half-hourly time steps. Input meteorological driving variables

(from half-hourly to daily values) are short-wave radiation, rainfall, wind speed, relative air humidity, air temperature, and soil temperature to be collected at the experimental site. The main outputs of the model include ecosystem productivity, ecosystem carbon exchange, soil respiration, and soil carbon pools.

Dynamic Land Ecosystem Model

Dynamic Land Ecosystem Model (DLEM) is a highly integrated process-based ecosystem model that simulates the fluxes and storage of carbon, water, and nitrogen among/within the terrestrial ecosystem components with the consideration of multiple natural and anthropogenic perturbations (e.g., climate change, CO_2 concentration, atmospheric composition, land use, and management practices), working at multiple scales in time from daily to yearly and space from meters to kilometers, from region to globe.

The DLEM includes five core components (❯ *Fig. 13.4*): (1) biophysics; (2) plant physiology; (3) soil biogeochemistry; (4) dynamic vegetation; and (5) disturbance, land use, and management. Briefly, the biophysics component simulates the instantaneous fluxes of energy, water, and momentum within land ecosystems and their exchanges with the surrounding environment. The plant physiology component simulates major
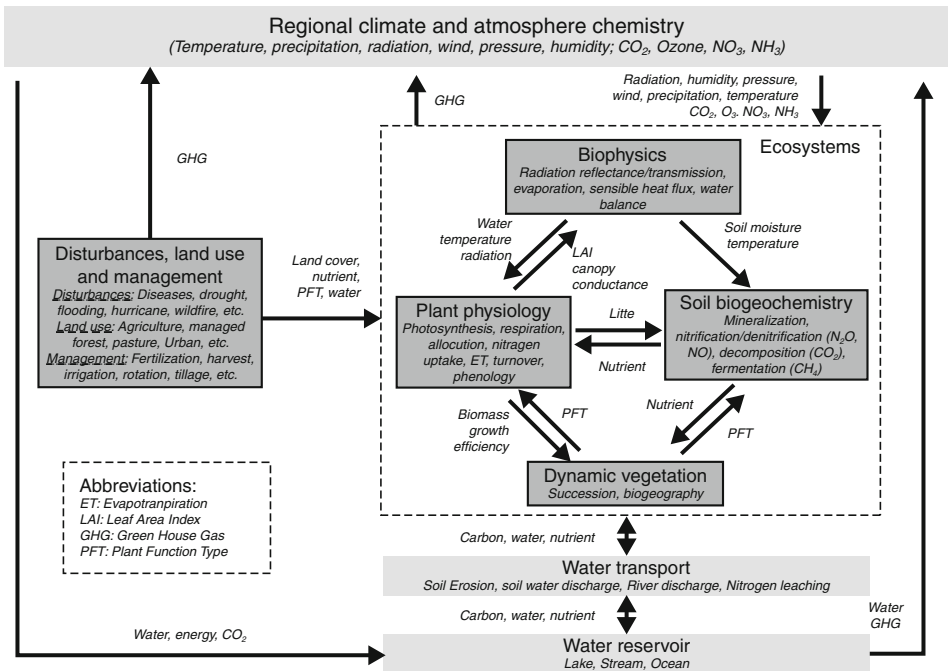
◻ **Fig. 13.4**
Framework of the Dynamic Land Ecosystem Model (DLEM) (Adapted from [70]. With permission)

physiological processes, such as plant phenology, C and N assimilation, respiration, allocation, and turnover. The soil biogeochemistry component simulates the dynamics of nutrient compositions and major microbial processes. The biogeochemical processes, including the mineralization/immobilization, nitrification/denitrification, decomposition, and methane production/oxidation are considered in this component. The dynamic vegetation component simulates the structural dynamics of vegetation caused by natural and human disturbances. Two processes are considered: the biogeography redistribution when climate change occurs, and the recovery and succession of vegetation after disturbances. Like most dynamic global vegetation models, the DLEM builds on the concept of plant functional types (PFT) to describe vegetation distributions. The disturbances, land use, and management component simulates cropland conversion, reforestation after cropland abandonment, and forest management practices such as harvest, thinning, fertilization, and prescribed fires. The DLEM has been extensively used to study the terrestrial carbon, water, and nitrogen cycles around the world in response to global change, and the detailed assumptions and processes are well documented in previous work [36–38].

Model Parameterization and Inverse Modeling

Traditionally, model parameters need to be derived from individual experimental studies or are based on previous knowledge. The inverse analysis is an approach that fundamentally focuses on data analysis for the estimation of parameters and their variability [10, 39]. It can also be used to evaluate model structure and information content of data. Inverse modeling usually starts with data and asks what the observed responses to a perturbation can tell us about the system in question. By combining prior knowledge about the system, processes underlying the observations can be incorporated into a model for an inverse analysis. The latter is implemented with optimization algorithms to adjust parameter values to the extent that differences between model predictions and observations (i.e., a cost function) are minimized. Those parameter values that satisfy the minimized cost function are considered the optimized parameter estimates, given the observations and model structure [39]. The optimized parameter values can be used in forward analysis, which is usually implemented using simulation models. Generally speaking, the forward analysis asks what a model can tell us about the ecosystems whereas the inverse analysis asks what the data can tell us about the same system. The combination of the two approaches allows us to probe mechanisms underlying ecosystem responses to global change [10].

   The major advantages of modeling study are [2] to: (1) integrate existing knowledge into models; (2) provide quantitative estimations and predictions of ecosystem responses; (3) help explain experimental results, formulate predictions, and guide future research; and (4) extrapolate ecosystem responses to large spatial scales over long term. The disadvantages include (1) lack of available data to drive and validate model results; (2) need to incorporate heterogeneity, disturbance, etc., into models; (3) there is usually large uncertainty related to model structures, parameters, and predictions.

Meta-analysis

Meta-analysis is a quantitative method used to compare and synthesize results of multiple independent studies with an attempt to address a common question or to test a common hypothesis [3, 14, 15, 41]. It has been widely applied in the fields of psychology, education, economics, and medical sciences. Since the early 1990s, the use of meta-analysis in the field of ecology and global climate research has increased exponentially [40–43]. As the experimental data accumulates, the number of meta-analysis increases dramatically. Over the last decade, approximately 50 papers using meta-analytical techniques have been published to synthesize the results of the large number of ecological CO_2 studies [41]. In 2007, Lei et al. [15] reviewed the application of meta-analysis in global change research. Here a brief overview of the procedure of the method is provided, followed by the discussion of the advantages and disadvantages of meta-analysis. Results from some meta-analysis studies on ecosystem carbon responses to elevated CO_2, temperature, and O_3 are then summarized. The detailed methods of meta-analysis can be obtained in [3, 14, 40, 42].

In conducting a meta-analysis, formal methods of sampling, partitioning of variance and statistical comparison are applied in order to evaluate the magnitude and distribution of treatment effects across many individual experiments [40]. The general procedure of conducting meta-analysis includes formulating research question, collecting and coding data, analyzing data, and interpreting the results (❯ *Fig. 13.5*) [15]. Like an experimental study, the first step in meta-analysis is to generate a research question/hypothesis needed to be addressed. Then collect data from relevant individual studies. Criteria for
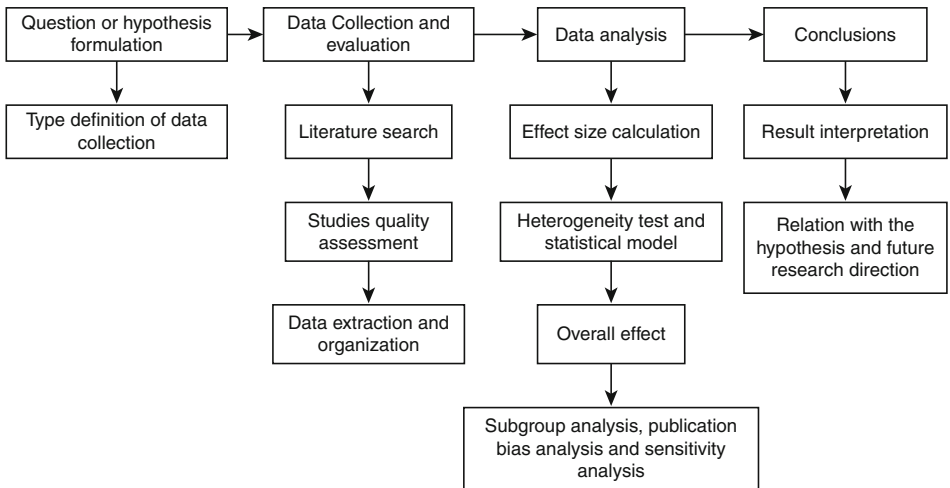
◼ **Fig. 13.5**

Procedures of meta-analysis (With kind permission from Springer Science+Business Media [15], Fig. 1. © 2007, Science in China Press and Springer-Verlag)

inclusion of studies should be explicitly documented. After quality control (e.g., delete these with missing data), data should be organized and coded. To analyze data, effective size metrics and analysis models have to be selected. A response ratio (RR, the ratio of means for a measured variable between the treatment group and the control group) is often used as an index of the estimated magnitude of the treatment effect [3, 14]. The significance of RR can be statistically tested to determine whether a response variable of the treatment group is different from that of the control group. The heterogeneity of RR is often calculated to examine whether all studies share a common magnitude of the treatment effect. Finally, the RR is grouped according to independent variables (e.g., vegetation type and time after treatment) for the purpose of detecting the differences in RRs among groups.

The major advantages of meta-analysis, compared to traditional narrative reviews, include: (1) It allows a more objective assessment of many individual research results. (2) It provides a more precise, overall estimate of a treatment effect, and increases power to detect true effects. (3) It can explain heterogeneity between the results of individual studies. Meta-analysis often does not provide much novel information. Debates over the meta-analysis include mixing apples and oranges (mixing experiments with different background information or purposes), biased estimates of effects due to publication bias (e.g., negative results are often not published), pooling of heterogeneous studies with different qualities, selection of nonindependence among studies (i.e., multiple entries from one study), and inclusion of unpublished data. Recently, Hungate et al. [43] compared four meta-analysis studies on the effect of elevated CO_2 on soil carbon and found that the approach to independence has the largest influence on the results. They recommend that meta-analysts critically assess and report choices about effective size metrics and weighting functions, and criteria for study selection and independence. Overall, when applied adequately, meta-analysis may draw more general and quantitative conclusions on some controversial issues compared to single studies, and provide some new insights and research directions [3, 14].

Impacts of Elevated Atmospheric CO_2 Concentration on Carbon Cycling in Terrestrial Ecosystems

Experimental Studies

Numerous experimental studies have been conducted over the past several decades considering some aspect of the effects of elevated CO_2 on plants and ecosystems across different terrestrial ecosystems [40]. These studies generally show that elevated CO_2 concentrations stimulate plant and canopy photosynthesis and respiration, reduce transpiration, and increase water use efficiency, leading to increased plant biomass and ecosystem productivity in terrestrial ecosystems. However, the magnitudes, sometimes even the direction of the change, vary among studies with different plant species, functional types, ecosystems, CO_2 experimental facilities, pot/plot sizes, and the length of experiments.

Photosynthesis, Respiration, and Stomatal Conductance

The response of plants to elevated CO_2 depends on the photosynthetic pathway. For C_3 plants (i.e., plants such as wheat, rice and most trees use C_3 photosynthetic pathway), photosynthetic CO_2 uptake rate are normally increased under high CO_2 concentrations. With the C_4 photosynthetic pathway, the enhancements of photosynthetic uptake in these C_4 plants (e.g., corn and sugarcane) due to elevated CO_2 are relatively lower. Experiments under optimal conditions show that doubling the CO_2 concentration increases leaf photosynthesis by 30–50% in C_3 plant species, but 10–25% in C_4 plant species [42, 44]. However, some studies show no difference between C_3 and C_4 plants, or even instances of effects in the opposite direction. Plants under high CO_2 concentrations can partially close their stomata, thereby reduce water loss and increase water use efficiency (WUE, the ratio of the weight of dry matter produced to the amount of water transpired).

Acclimation is a non-heritable, reversible change in the physiology or morphology of an organism in response to changing environmental conditions [24]. Photosynthetic downregulation in response to elevated CO_2 was initially reported in dozens of CO_2 enrichment studies and was generally attributed to decreases in leaf nitrogen and ribulose 1,5-biphosphate carboxylase/oxygenase (Rubisco) that lead to declines in photosynthesis. But the role of photosynthetic downregulation has been questioned, and its prevalence, particularly in earlier pot or chamber studies has been attributed, in part, to root restriction within experimental pots and inadequate N supply.

The effect of elevated CO_2 on plant respiration is much less clear, and experiments show opposite effects with different species [45]. CO_2 stimulation of root exudation can speed up rhizosphere decomposition, causing soil respiration to respond more strongly to photosynthetic rate than to soil temperature. Elevated CO_2 can also give rise to litter that has lower nitrogen concentration and is more resistant to microbial breakdown [46]. CO_2 effects on litter quality and nutrient availability have proven important in stand- and regional-scale models, but other indirect effects of CO_2 have yet to be tested in ecosystem-scale models.

Results from Duke FACE experiments from 1998 to 2000 showed a significant increase in estimated annual rates of total soil respiration of $\sim$0.30 kg C m^{-2} year^{-1} in the elevated CO_2 plots compared to the controls [13]. However, this initial stimulation of soil respiration declined to $\sim$0.12 kg C m^{-2} year^{-1} in 2003 after 7 years of manipulations.

Plant Growth, Biomass, Ecosystem Productivity, and Carbon Storage

Plant growth, biomass, and aboveground production generally increase with elevated CO_2. The enhancement of biomass is lower than photosynthesis responses. For example, on average across several species and under unstressed conditions, compared with current atmospheric CO_2 concentrations of 380 ppm, crop yields increase at 550 ppm CO_2 in the range of 10–20% for C_3 crops and 0–10% for C_4 crops. Increases in aboveground biomass

for trees range from 0% to 30% with the higher values observed in young trees and little to no response observed in the few experiments conducted to date in mature natural forests. Observed increases of aboveground production in C_3 pasture grasses and legumes are $\sim$+10 and +20%, respectively. Atmospheric CO_2 increases to 550 ppm have been shown to increase NPP by about 23% across a range of temperate forest sites [47], but the long-term outcome is unclear, especially when interactions with nitrogen availability are considered.

Since atmospheric CO_2 concentration increases gradually, there are a few studies that tested whether plants and ecosystems respond differently to step versus gradual increase in CO_2 concentrations [10]. For example, Hui et al. [23] grew *Plantago lanceolata* for 80 days before treating plants with ambient CO_2 (as the control), gradual CO_2 increase, and step CO_2 increase for 70 days and found that the step CO_2 treatment immediately resulted in an approximate 50% increase in leaf photosynthesis in week 3 after the CO_2 treatment. The gradual CO_2 increase caused much less stimulation of photosynthesis and less decrease in leaf N concentration than did the step CO_2 increase. Klironomos et al. [48] conducted an experiment with *Bromus inermis* and its associated mycorrhizal community over a period of 6 years during which CO_2 concentration increased either abruptly as is typical of most CO_2 experiments or gradually over 21 generations. They found that plant photosynthesis did not differentially respond to step versus gradual CO_2 increases. Belowground plant production was higher in the step than the gradual CO_2 treatments. Experiments using multiple CO_2 levels or a CO_2 tunnel to create CO_2 gradients [49] also demonstrate ecosystem responses to step CO_2 changes as, in most, manipulative experiments are different from those in response to a gradual CO_2 increase that occurs in the real world. New approaches such as inverse modeling may be needed to improve predictive understanding of ecosystem responses to gradual global change in the real world [10].

Modeling Studies

Ecological models have been developed at different scales from leaf, plant canopy, ecosystem, regional to global scales to study climate effects on terrestrial ecosystems. Most of the models simulate the processes of plant photosynthesis and respiration, stomatal conductance, evapotranspiration, nitrogen uptake, carbon allocation among plant organs, litter production, nitrogen mineralization, and soil organic carbon decomposition, and uses these to calculate the carbon fluxes between vegetation, soils, and the atmosphere. At leaf and canopy levels, Farquahar model has been widely used to simulate leaf photosynthesis [10, 35]. This model considers several key processes of CO_2 assimilation: diffusion of CO_2 into leaf and uptake of CO_2 by Rubisco enzyme into carbon-containing molecules. The model has also been built into global models. At regional or global scales, some biogeochemical models use a simplified light use efficient model to simulate photosynthesis and ecosystem productivity [50, 51].

Some ecological models specifically simulate the impacts of elevated CO_2 on terrestrial ecosystem carbon processes, while most of the biogeochemical models consider multiple factor impacts and have the capability to simulate the effects of multiple climatic factors

on terrestrial ecosystem carbon cycling. Several inter-model comparison studies also compared the features, ecological processes built in the models, and model simulation results among some ecosystem models. Several typical modeling results of elevated CO_2 impacts on ecosystem carbon processes are summarized below.

Similar to experimental results, modeling studies show that elevated CO_2 concentrations stimulate plant growth and ecosystem productivity. For example, Luo et al. (2001) simulated gross primary productivity (GPP) in the Duke Forest at both ambient and elevated CO_2 (ambient + 200 ppm) concentrations using a physiologically based canopy model (MAESTRA). They found that elevated atmospheric $[CO_2]$ resulted in increase of canopy C fixation by 35% in 1996, 39% in 1997, and 43% in 1998. The modeled GPP and its response to elevated $[CO_2]$ were sensitive to parameter values of quantum yield of electron transport, leaf area index, and the vertical distribution of LAI within the canopy. Hui and Luo [13] evaluated soil respiration in the same Duke Forest using a process-based modeling approach. Elevated CO_2 increased soil respiration by 18–26% (❷ *Fig. 13.6*), mainly due to root respiration caused by increased fine root biomass and microbial respiration through increased aboveground litter fall.

At large spatial scales, Cao and Woodward [11] used a terrestrial biogeochemical model (CEVSA), forced by simulation of transient climate change with a general circulation model to quantify the dynamic variation in ecosystem carbon fluxes induced by
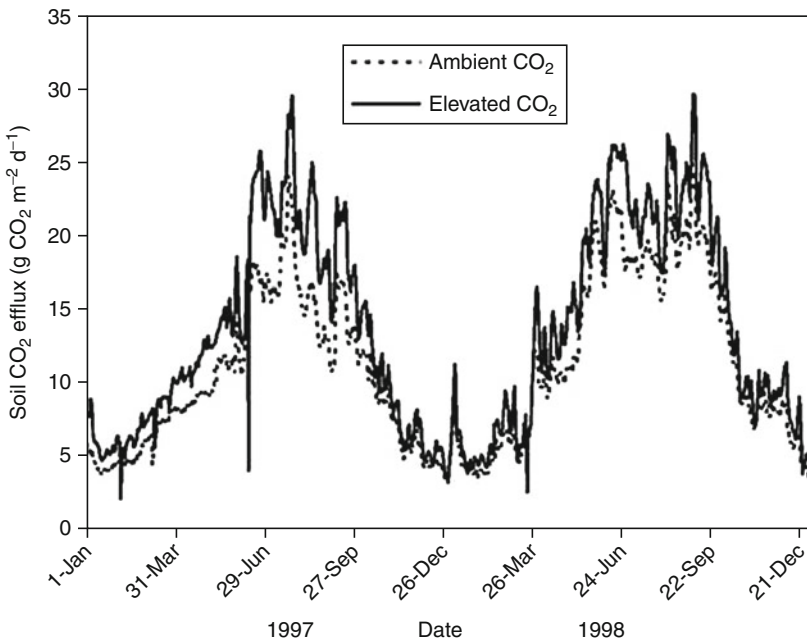
■ Fig. 13.6

Comparison of simulated soil CO_2 efflux (soil respiration) by PATCIS model at the elevated CO_2 treatment with that at the ambient CO_2 treatments in the Duke Forest, North Carolina ([13]. With permission from AGU)

changes in atmospheric CO_2 concentrations (from 288 to 640 ppm) and climate change from 1861 to 2070. They found that NPP, NEP, and carbon stocks are predicted to increase substantially under CO_2 increase alone. NPP increases by 45% in tropic ecosystems, 20% in temperate ecosystems, and 36% in northern ecosystems over the period 1861–2070. The CO_2 fertilization effect is found to decrease as CO_2 increases. The stimulation of photosynthesis by elevated CO_2 diminishes at high CO_2 concentration, but respiration increases as carbon accumulates in vegetation and soil. As a result, NEP falls rapidly as CO_2 exceeds 600 ppm.

Tian et al. [12] studied the effect of interannual climate variability on carbon storage in Amazonian ecosystems using a process-based biogeochemical model (Terrestrial Ecosystem Model – TEM) and found that soil moisture appears to be an important control on carbon storage. Climate variability with CO_2 fertilization generally resulted in a higher annual NEP than did climate without CO_2 fertilization. The strength of CO_2 fertilization effect for the Amazon Basin was between 0.1 and 0.4×10^{15} g C year^{-1}.

Field et al. [52] simulated present-day global NPP to be in the range 46.6–49.5×10^{15} g C year^{-1}, at the low end of the range estimated by others (44.4–66.3×10^{15} g C year^{-1}; [53]). Over the period $1860\sim2100$, global NPP increased by 23.3×10^{15} g C year^{-1} or 56% in the HadCM2 model–driven simulations and by 17.5×10^{15} g C year^{-1} or 43% in the HadCM3-driven simulation. NEP increased after about 1970 to $0.6\sim1.8 \times 10^{15}$ g C year^{-1} in the 1990s, to $2.5\sim4.5 \times 10^{15}$ g C year^{-1} in the 2030s, and then fell to below zero by 2100. Thus, model Hybrid predicted a growing terrestrial carbon sink, roughly in line with inventory and deconvolution estimates but a collapse and reversal of this sink during the next century.

In a multiple model evaluation of the response of climate-carbon cycle models to future CO_2 emissions, all 11 models demonstrated a decline through time in the capacity of terrestrial ecosystems to absorb increases in atmospheric CO_2 [53]. Terrestrial ecosystem carbon storage increases with higher atmospheric CO_2 in all models, driven by a 12–76% increase in NPP with CO_2 doubling (multi-model mean, 48%), offset slightly by enhanced heterotrophic respiration [53].

Using the TECO, Zhou et al. [54] examined the patterns and mechanisms of ecosystem responses to changes in CO_2, temperature, and precipitation. Simulated NPP, heterotrophic respiration, and NEP all show parabolic-curve responses to temperature, asymptotic responses to CO_2 concentration, and threshold-like curves to precipitation. Ecosystem response to combined temperature, CO_2, and precipitation anomalies differed considerably from the responses to individual factors in terms of patterns. Luo et al. [32] used four ecosystem models and simulated NPP in response to treatments of elevated CO_2 (C), elevated temperature (T), doubled precipitation (DP), halved precipitation (HP), summer drought (SP), and their combinations at seven ecosystems and found that elevated CO_2 enhanced NPP at all sites (❯ *Fig. 13.7*).

Randerson et al. [55] presented a systematic framework, the Carbon-LAnd Model Intercomparison Project (C-LAMP), for assessing terrestrial biogeochemistry models coupled to climate models using observations that span a wide range of temporal and spatial scales and evaluate two biogeochemistry models that are integrated within the
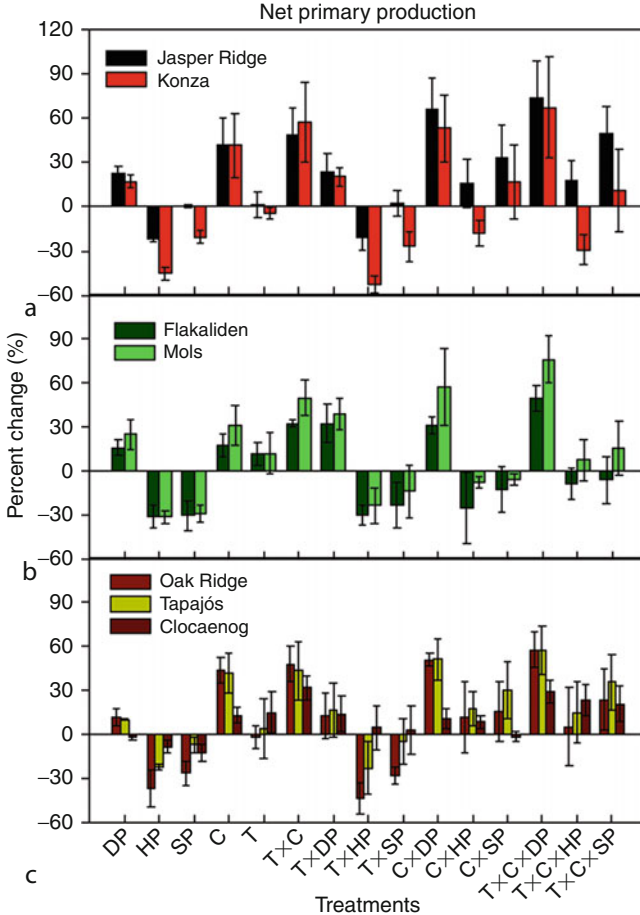
▣ Fig. 13.7

Percent changes relative to control in modeled net primary production (NPP) in response to treatments of doubled precipitation (DP), halved precipitation (HP), summer drought (SP), elevated CO_2 (C), elevated temperature (T), and their combinations at Jasper Ridge and Konza (a), Flakaliden and Mols (b), Walker Branch, Tapajo's and Clocaenog (c). Data indicate the mean 1 SE calculated from simulated values of NPP by the four models (Adapted from [32]. With permission from John Wiley and Sons)

Community Climate System Model (CCSM) – Carnegie-Ames-Stanford Approach (CASA') and carbon-nitrogen (CN). In response to an instantaneous increase in CO_2 mixing ratio to 550 ppm in 1997, both models exhibited a positive step change in NPP, with CASA' increasing globally by 17% and CN by 10% during the first 5 years after CO_2 enrichment. The disproportionately large NEP response in CASA' (almost threefold larger than CN) can only be partly attributed to the higher sensitivity of NPP to CO_2 enrichment; other important factors included a higher baseline NPP and similar turnover times in pools involved with initial carbon storage.

Recently, Friend [56] conducted sensitivity analysis using Hybrid 6.5, a global scale process-based ecosystem model, and found that leaf phenology has large effects on C_3 crop and needle-leaved cold deciduous tree production. An increase in CO_2 concentration from current to 720 ppm by the end of this century and climate change increase global NPP by 37.4%. Significant uncertainties concern the extent to which acclimative processes may reduce potential future increase in primary production.

These modeling studies and many others demonstrated that NPP and NEP will increase under elevated CO_2 conditions, but differ in the magnitudes of the enhancement from stands to global scales. As demonstrated by Hanson et al. [35], which evaluates the efficacy of 13 stand-level forest ecosystem models for predicting the carbon and water budgets of an upland-oak forest in eastern Tennessee, the mean of all model outputs showed better fit than any individual models. While improving individual model capability is still a vital task for ecosystem modelers, ensembles from multiple model simulations might be an adequate approach to reduce model uncertainty.

Meta-analysis Studies

Most of the meta-analysis studies in global climate change are performed on the effects of elevated CO_2 on terrestrial ecosystems. One reason may be the data availability. During the past decades, numerous individual studies of CO_2 effects have been conducted in terrestrial ecosystems. Since most studies consider only two levels of CO_2, one is ambient CO_2 ($\sim$350 ppm) and another one is elevated CO_2 at a level between 550 ppm and 700 ppm. This data structure is also suitable for meta-analysis, which was originally designed to test treatment effect with a control. The first meta-analysis of CO_2 effects was done by Curtis et al. (1996). Since then, there are more than 50 meta-analysis studies conducted [3, 15, 41]. Research using meta-analysis has addressed many ecological processes such as plant photosynthesis and respiration, growth and productivity, soil respiration, and accumulation of soil carbon and nitrogen in terrestrial ecosystems. In 2007, Lei et al. [15] provided a comprehensive study reviewing the applications of meta-analysis in global climate change research. While meta-analysis often provides a general conclusion and a precise effective size, the values also vary among different meta-analysis studies with different sample sizes, effective size metrics, and other issues. Certainty rules may need to be established to facilitate the comparison among different meta-analysis studies. Here the effects of elevated CO_2 on ecosystem carbon processes are summarized.

Photosynthesis, Respiration, and Stomatal Conductance

Similar to the conclusions from experimental studies, the effects of elevated CO_2 on plant photosynthesis and growth based on meta-analysis are generally positive. Facility type and the lengths of CO_2 exposure also modify the responses. Both species and size variability in the experimental populations are also a vital factor influencing ecosystem responses.

In the first meta-analysis of CO_2 effects on ecosystems physiology, Curtis and Wang [40] synthesized studies with 41 plant species grown in growth chamber, greenhouse, or open-top chamber, and reported a significant and large increase of net CO_2 assimilation ($\sim$50%). Average light-saturated photosynthesis rate and production increased by 34% and 20%, respectively, in C_3 species.

Leaf dark respiration under elevated CO_2 demonstrates a significant decrease [40, 57]. Similar conclusion was reached in Wang and Curtis [58]. For plant respiration, Wang and Curtis [58] found that mass-based leaf dark respiration was significantly reduced by 18%, while area-based leaf dark respiration marginally increased approximately 8% under elevated CO_2. An overall decline in the ratio of heterotrophic component to soil carbon dioxide efflux for increasing annual soil carbon dioxide efflux was also reported.

Curtis and Wang [40] reported that stomatal conductance decreased by 11%, not significantly under elevated CO_2. Using data collected from 13 long-term (>1 year), field-based studies of the effects of elevated CO_2 on European tree species, Wang and Curtis [50] reported a significant decrease of 21% in stomatal conductance, but no evidence of acclimation of stomatal conductance was found. Wand and Strain [59] also found a significant decrease in leaf stomatal conductance, and increased water use efficiency and carbon assimilation rate.

Plant Growth, Biomass, Ecosystem, Productivity, and Carbon Storage

Curtis and Wang [40] used meta-analytical methods to summarize and interpret more than 500 reports of effects of elevated CO_2 on woody plant biomass accumulation. They found total plant biomass significantly increased by 28.8% and the responses to elevated CO_2 were strongly affected by environmental stress factors and to a less degree by duration of CO_2 exposure and functional groups. Wand and Strain [59] show that total biomass has increased by 33% and 44% in elevated CO_2 for both C_3 and C_4 plants, respectively. Potter et al. [60] evaluated the effects of increased atmospheric CO_2 concentrations on vegetation growth and competitive performance using meta-analysis. Responses of fast-growing herbaceous C_3 species were much stronger than those of slow-growing C_3 herbs and C_4 plants. Norby et al. [47] report a meta-analysis of four FACE studies on temperate forests and conclude that the primary productivity of these forests at predicted 2050 CO_2 levels is 23% higher than today's CO_2 level. Allocation is increased to leaf and fine root tissues.

Ainsworth et al. analyzed 25 variables describing physiology, growth, and yield of soybean. They found the rates of acclimation of photosynthesis were less in nitrogen-fixing plants, and stimulation of photosynthesis of nitrogen-fixing plants was significantly higher than that of non-nitrogen-fixing plants. Pot size significantly affected these trends. Biomass allocation was not affected by elevated CO_2 when plant size and ontogeny were considered. Ainsworth and Long [42] also synthesized physiology and production data in the 12 large-scale FACE experiments across four continents and found that light-saturated

carbon uptake, diurnal carbon assimilation, growth and aboveground production increased, while specific leaf area and stomatal conductance decreased in elevated CO_2. Different results showed that trees were more responsive than herbaceous species to elevated CO_2 and grain crop yield increased far less than anticipated from prior enclosure studies. The results from this analysis may provide the most plausible estimates of how plants growing in native environments and field will respond to elevated CO_2 [52].

Jastrow et al. [61] showed a 5.6% increase in soil carbon over 2–9 years, at rising atmospheric CO_2 concentrations. Luo et al. [3] synthesized 104 publications and demonstrated that averaged litter and soil carbon pool sizes at elevated CO_2 were 20.6% and 5.6% higher than those at ambient CO_2. Averaged carbon pool sizes in shoot, root, and whole plant have increased by 22.4%, 31.6%, and 23.0%, respectively [3].

Impacts of Global Warming on Carbon Cycling in Terrestrial Ecosystems

Experimental Studies

Most of ecosystem carbon processes such as photosynthesis and respiration are regulated by temperature. As a result, ecosystem productivity, carbon sequestration and storage will be influenced by global warming. The responses of terrestrial ecosystem to global warming vary due to differences in ecosystem composition, ecosystem structures, and locations. Difference in experimental designs such as intensity of warming (or temperature level), warming methods and the length of warming, and other environmental factors such as precipitation and nitrogen may also contribute to diverse changes observed in global warming experiments [5].

Photosynthesis, Respiration, and Soil Respiration

In a recent synthesis, Luo [5] reviewed field experimental studies and found diverse effects of warming on photosynthesis, including increases, decreases, and no apparent change. Warming air temperature by 3–5°C, for example, increased photosynthesis in four vascular species in arctic tundra [62] and two dominant tree species and a shrub species in a boreal forest [63]. In contrast, a 3.5°C increase in air temperature did not significantly impact the photosynthesis of *Polygonum viviparum* in arctic polar semi-desert. Zhou et al. [64] also found that leaf photosynthesis increased in spring, decreased in early fall, and did not change in summer and late fall for four species exposed to an air warming of 0.5–2.0°C in the southern Great Plains of the United States. The variable responses are considered as the results of different methods and/or levels of warming, diverse temperature sensitivities and optimal temperatures of photosynthesis among species and ecotypes, and the confounding effects of drought, leaf age, and nutrient availability [5]. Photosynthetic acclimation to increased temperature has long been recognized including both shifts in temperature optima and uniform shifts across all temperatures, due to different thermal

properties of key photosynthetic enzymes, different temperatures at which membranes are damaged, and differential thermal stability of photochemical reactions [65].

Soil respiration is generally responsive positively to temperature changes. As temperature increases, soil respiration generally increases [25], as warming generally directly increase both autotrophic and heterotrophic soil respiration. For example, with 5°C soil temperature increase above the ambient temperature, Peterjohn et al. [66] reported a dramatic 26–75% increase in soil respiration in the first 4 years. However, 10 years after the initiation of treatments, soil respiration in the warmed plots in 2000 was no longer significantly different from the control, a trend that has continued through the latest period of record [24]. There are a few studies that have also reported decrease in soil respiration under warming. But the decrease at the Rocky Mountain meadow in Colorado [68] was attributed to indirect effect of global warming, as warming induced a decline of soil moisture [24]. Similarly, soil respiration in Norway spruce stands was initially stimulated by experimental warming but then declined, perhaps due to substrate depletion of labile C pools and downregulation of heterotrophic activity [67, 69]. Dorrepaal et al. [70] investigated the climate-change response of ecosystem respiration rates using open-top chambers in a subarctic blanket-bog in Abisko, north Sweden. They show that approximately 1°C warming accelerated total ecosystem respiration rates on average by 60% in spring and by 52% in summer and that this effect was sustained for at least 8 years. Global warming studies also found that soil respiration acclimates to elevated temperature, as soil temperature sensitivity decreases under warming [22, 25]. The acclimation may be caused by warming-induced changes in aboveground and belowground biomass; soil moisture; nitrogen mineralization; substrate quality/quantity; and microbial community activity, biomass, and composition [5, 24].

The warming times of a day may also influence the effects of warming on soil respiration. Xia et al. [71] recently compared the effects of day warming, night warming, and diurnal warming on soil respiration in a temperate steppe and found that day warming showed no effect on soil respiration, while night warming significantly increased soil respiration. Changes in soil respiration and gross ecosystem productivity under diurnal warming are smaller than the summed changes under day and night warming. In the same experiment, Wan et al. [72] found that nocturnal warming increased leaf respiration, stimulated plant photosynthesis, and shifted the steppe ecosystem from a minor carbon source to a carbon sink.

Plant Growth, Biomass, Ecosystem Productivity, and Carbon Storage

The effects of warming on plant growth are highly variable [5], similar to photosynthesis responses. Experimental warming increased leaf production by 50% and shoot production by 26% for *Colobanthus quitensis* but decreased leaf production by 17% for *Deschampsia antarctic* in Antarctica [73]. By warming a tallgrass prairie 0.5–2°C high using electronic heater, Luo [5] found warming stimulated growth of C_4 plants over

a 6-year experiment. While the growth of C_3 plants increased in the first 2 years, the growth decreased in the last 2 years [5]. Field soil-warming experiments showed that herbs and grass were more responsive to elevated temperature than shrubs, whereas tree species were less sensitive in a temperate forest [74]. The individualistic responses to warming reflect differences in optimum growth temperatures across species, as well as the limitations on growth by other factors than temperature [5].

The effects of warming on ecosystem primary production are also diverse. Experimental warming increased NPP by up to 25% in a tallgrass prairie [5]. Soil warming increased the yields of crops by 19–50% and vegetables by 19–100% [75], and increased the stem-wood growth of trees in heated plots by 50% relative to controls after 5 years [76].

Total aboveground biomass was largely unresponsive to temperature manipulation in tundra [77]. Along a gradient of increasing infrared heating, shrub production increased, whereas graminoid production decreased in a bog. In a fen, graminoids were most productive at high infrared heating and forbs were most productive at medium infrared heating.

The net ecosystem production and long-term carbon storage in ecosystems may be influenced by different warming methods. Buried heating cables only warm soil and have generally caused net carbon loss, such as in experiments at the arctic tundra [78] and Harvard Forest [25]. Ineson et al. [79] also showed a net carbon reduction of approximately 10% after 3 years of heating an upland grassland ecosystem at Great Dun Fell in the United Kingdom. The responses to whole-ecosystem warming using infrared heaters or greenhouse chambers show different responses, including decrease and increase, or cause no changes in net ecosystem exchange [5]. Using infrared heating, Marchand et al. [80] found a 24% increase in canopy carbon uptake and a nearly 50% increase in net carbon sink under warming in comparison with that under control in high-arctic tundra. Johnson et al. [81] reported that warming did not cause much change in canopy photosynthesis, ecosystem respiration, and net ecosystem carbon exchange in arctic tundra. The warming experiment at the southern Great Plains did not cause significant changes in net ecosystem production and soil carbon stocks [5]. But Saleska et al. [82] observed a decrease of soil organic carbon by $\sim$200 g C m^{-2} in warmed plots relative to control plots in a Rocky Mountain meadow.

Modeling Studies

Modeling studies generally have predicted a positive feedback between carbon cycling and global warming [5, 54]. Using a global biogeochemical model, Cox et al. [83] projected that while terrestrial ecosystems will sequester $\sim$400 $\times$ 10^{15} g C due to CO_2 fertilization in the twenty-first century, warming stimulates carbon loss, and results in a net source of 60 $\times$ 10^{15} g C from terrestrial ecosystems to the atmosphere. As a result, temperature will increase by 8°C, that is, 2.5°C greater than the climate-model simulation alone. Friendlingstein et al. [53] compared 11 coupled climate-carbon models and found that carbon cycle-climate feedbacks increase atmospheric CO_2 at the end of the twenty-first

century by 4–44% (multi-model mean, 18%), equivalent to an additional 20–224 ppm (multi-model mean, 87 ppm) [1, 53]. With temperature increase, almost all models predict carbon losses from terrestrial ecosystems (20–177 $\times$ 10^{15} g C $°C^{-1}$). Other ecosystem models also projected a loss of carbon from terrestrial ecosystems in response to global warming [5, 10]. Global NEP responds positively to changes in CO_2 concentration and precipitation, but negatively to changes in temperature [11].

Huntingford et al. [83] simulated ecosystem responses to global change using a simple terrestrial ecosystem model. They reported that soil respiration increases more rapidly with warming than net primary production, causing a gradual switch from a weak positive NEP initially to a weakly negative NEP. Die-back can occur at high temperatures and cause a large pulse of negative NEP.

Using TECO, Zhou et al. [84] simulated NPP, heterotrophic respiration Rh, and NEP and all simulations show parabolic-curve responses to temperature anomalies from $-2°C$ to $+10°C$ compared to current condition. NPP and Rh increased with temperature, reached a peak at $+8°C$ (NPP) or $+6°C$ (Rh), and then declined, while NEP had an adverse trend with a lowest value at $+7°C$.

Tian et al. [85] quantified ecosystem NPP and water use efficiency (WUE) in the Southern US by employing the integrated process–based ecosystem model (Dynamic Land Ecosystem Model, DLEM). They found that the mean regional total NPP was 1.18×10^{15} g C $year^{-1}$ (525.2 g C m^{-2} $year^{-1}$) during 1895–2007. NPP increased consistently from 1895 to 2007 with a rate of 2.5 $\times$ 10^{12} g C $year^{-1}$ or 1.10 g C m^{-2} $year^{-1}$. The average WUE was about 0.71 g C kg^{-1} H_2O and increased about 25% from 1895 to 2007. They also found that NPP and WUE showed substantial inter-annual and spatial variability, which was induced by the nonuniform distribution patterns and change rates of climate factors across the Southern US (❷ *Fig. 13.8*).

Using a process-based terrestrial biosphere model (ORCHIDEE) and satellite vegetation greenness index observations, Piao et al. [86] find that both photosynthesis and respiration increase during autumn warming, but the increase in respiration is greater. In spring, however, warming increases photosynthesis more than respiration. As a result, northern terrestrial ecosystems may currently lose carbon dioxide in response to autumn warming, with a sensitivity of about 0.2 $\times$ 10^{15} g C $°C^{-1}$, offsetting 90% of the increased carbon dioxide uptake during spring. If future autumn warming occurs at a faster rate than in spring, the ability of northern ecosystems to sequester carbon may be diminished earlier than previously suggested.

Meta-analysis Studies

There are a few meta-analysis studies conducted on the effects of global warming on terrestrial ecosystems [87]. A meta-analysis of 13 tundra experiments shows that the vegetative growth of herbaceous species was more responsive to warming than woody species [88]. They found that the primary forces driving the response of ecosystems to soil warming do vary across climatic zones, functional groups, and through time. Herbaceous

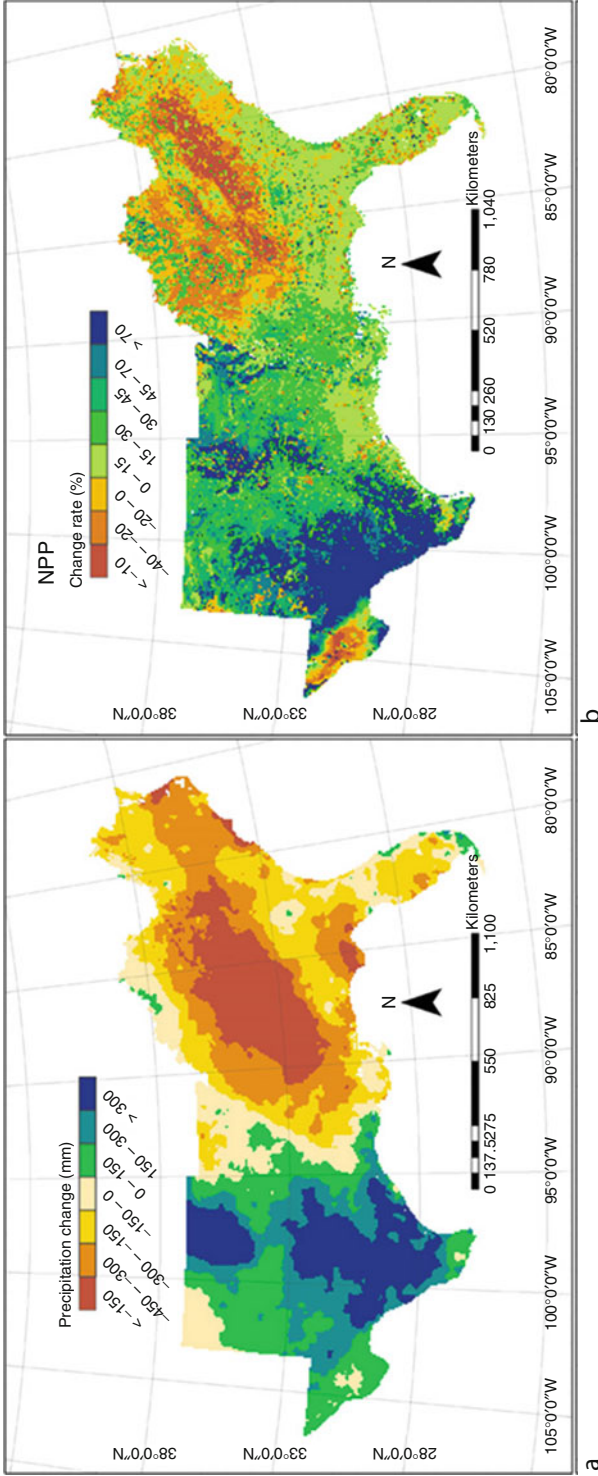**Fig. 13.8**

Precipitation (mm, A) and NPP (g C m^{-2} year^{-1}, B) anomalies (relative to 1961–1990 mean) in 2007 in the southern United States (Reprinted from [85]. Model estimates of net primary productivity, evapotranspiration, and water use efficiency in the terrestrial ecosystems of the southern United States during 1895–2007, Copyright 2010. With permission from Elsevier)

plants have stronger and more consistent vegetative and reproductive response than woody plants. Rustad et al. [4] synthesized experimental warming studies in a meta-analysis and found that 2–9 years of experimental warming of whole ecosystems or ecosystem components (e.g., soils) in the range 0.3–6.0°C significantly increased soil respiration rates by 20% and plant productivity by 19%. Among the 17 sites from tundra, grassland, and forest, soil respiration under experimental warming increased at 11 sites, decreased at one site, and did not change at five sites [4]. Walker et al. [88] tested plant community response to standardized warming experiments at 11 locations across the tundra biome and found that height and cover of deciduous shrubs and graminoids have increased, but, cover of mosses and lichens has decreased, and species diversity and evenness have decreased under the warming. Raich et al. [89] applied meta-analyses to evaluate the effects of temperature on carbon fluxes and storages in mature moist tropical evergreen forest ecosystems. They found that litter production, tree growth, and below-ground carbon allocation all increased significantly with the increasing site mean annual temperature, but temperature had no noticeable effect on the turnover rate of above-ground forest biomass. Soil organic matter accumulation decreased with the increasing site mean annual temperature, which indicated that decomposition rates of soil organic matter increased with mean annual temperature faster than rates of NPP.

Impacts of Precipitation, Ozone, and Multiple Climatic Factors on Carbon Cycling in Terrestrial Ecosystems

May other environmental factors, such as O_3 concentration, UV, and precipitation also play an important role in ecosystem productivity, but these factors are less studied in natural terrestrial ecosystems, compared to elevated CO_2 and warming. A few precipitation manipulation experiments have been initiated over the past several decades, and to date, no global synthesis of existing results has been undertaken [2]. Unlike atmospheric CO_2 concentration and temperature, changes in precipitation include timing, intensity, and interval of precipitation. All these changes may have different influences on terrestrial ecosystems. There is also less confidence in precipitation prediction and the changes of precipitation vary from place to place. As a result, there is not a clear focus of precipitation study [2]. Only a few studies explicitly focused on precipitation effects see (❯ *Table 13.1*, [2]). The studies of O_3 and UV have been conducted mostly in cropland ecosystems. A few studies also consider multiple climatic factors, such as warming, precipitation, O_3, nitrogen, and elevated CO_2.

Experimental Studies

Plant Photosynthesis, Respiration, and Soil Respiration

Of the existing experiments with precipitation, the Konza Praire irrigation study in Kansas, USA is one of the longest, continuously running precipitation manipulation

experiments [2]. Initiated in 1991, the treatment involves the addition of supplemental water to meet plant–water demand in a tallgrass prairie ecosystem. Results from the first 8 years of the study (1991–1998) showed that (1) water availability limited aboveground NPP (ANPP) 6 of the 8 years, (2) supplemental water increased ANPP by 25% in the irrigated plots compared to the controls, and (3) the response was due to physiological changes in the dominant plant species [90]. Results for the next 5 years (1999–2003), however, showed that (1) supplemental water increased ANPP by 70% compared to the control and (2) the response was due to an increased cover of *Panicum virgatum*, and thus a shift in community composition [90]. These results once again highlight the importance of decadal-scale responses in ecosystem manipulation experiments [2, 10].

There are many experimental studies on O_3 effects in terrestrial ecosystems, but mostly in managed croplands such as soybean, rice, and wheat. Changes in stratospheric O_3 and hence in solar UV-B (280–315 nm) radiation have many different effects on global carbon cycling. Longer wavelength UV-A radiation (315–400 nm) is little affected by O_3 depletion, but can be affected by global climate change [91]. UV (280–400 nm) radiation modifies carbon cycling through changes in photosynthesis and respiration. Certain plant species and communities are vulnerable to increased UV-B radiation. UV-B was also found to affect soil microbial community structure and the chemistry of leaf litter.

More and more experiments now consider more than one climatic factor of elevated CO_2, temperature, precipitation, O_3, and nitrogen. For example, Zhou et al. [92] reported the effects of warming and precipitation on soil respiration in a grassland ecosystem. Warming increased soil respiration by 22.9% with a 4.4°C increase. Double precipitation resulted in an increase of 9.0%. Warming decreased soil temperature sensitivity, while the precipitation slightly increased soil temperature sensitivity in warmed plots. Wan et al. [93] studied the effect of elevated atmospheric CO_2 concentration, air warming, and changing precipitation in an old-field grassland in eastern Tennessee, USA. They found that higher CO_2 concentration and soil water availability significantly increased mean soil respiration by 35.8% and 15.7%, respectively. There were no interactive effects on soil respiration among any two or three treatment factors irrespective of time period. Treatment-induced changes in soil temperature and moisture together explained 49%, 44%, and 56% of the seasonal variations of soil respiration responses to elevated CO_2, air warming, and changing precipitation, respectively. Additional indirect effects of seasonal dynamics and responses of plant growth on C substrate supply were indicated. Given the importance of indirect effects of the forcing factors and plant community dynamics on soil temperature, moisture, and C substrate, soil respiration response to climatic warming should not be represented in models as a simple temperature response function, and a more mechanistic representation including vegetation dynamics and substrate supply are needed.

While the importance of multiple factors has been well recognized, there are still not many studies that have been conducted, due to many reasons such as experimental costs of facility construction and maintenance, difficulty in experimental design implementation, requirement of large homogeneous lands, and time and efforts for measurements. One of the longest, continuously running and most complex multi-factor experiment is the

Jasper Ridge Global Change Experiment in the Santa Cruz Mountains of California, USA [2]. Initiated in 1998, the experiment includes a full factorial combination of warming, nitrogen deposition, elevated carbon dioxide, and increased precipitation, with eight replicates of each experimental unit. Important results from this experiment include the existence of nutrient constraints on NPP responses to global changes, shifts in plant and microbial species composition, and associated changes in productivity [94], changes in phenology, and a surprising CO_2- and warming-induced increase in growing season soil moisture. Perhaps the most important contributions of this long-term, multi-factor experiment are, however, to highlight the inherent complexity of natural ecosystems (even one as "simple" as an annual grassland in California, USA), the plethora of additive and non-additive responses to various global change factors, and the importance of inter-annual variations in climate drivers in determining overall ecosystem responses [2].

Modeling Studies

Precipitation and soil moisture have been recognized as important factors regulating photosynthesis, respiration, and ecosystem carbon sequestration. Most of the ecosystem biogeochemical models consider precipitation/soil moisture impacts on ecosystem carbon processes, through the limitation on leaf photosynthesis, soil respiration, and water/nutrient uptakes. Impacts of precipitation are also considered together with other climatic factors. Recently, Shen et al. [34] evaluated precipitation impacts on soil respiration and soil carbon pool size change in dryland ecosystems. The effects of O_3 on ecosystem productivity and carbon sequestration have also been investigated [37]. Below are a few recent modeling studies considering precipitation, O_3, or their interactions with other climatic factors.

Gerten et al. [95] studied effects of precipitation on ecosystem carbon dynamics using four process-based ecosystem models (TECO, LPJ, ORCHIDEE, and DayCent) and found that NPP response to precipitation changes differed not only among different sites, but also within a year at given sites. Humid sites and/or periods were least responsive to any change in precipitation as compared with moderately humid or dry sites/periods. Using the same four models, Luo et al. [32] showed that two-way interactive effects on NPP, R_h, and NEP were generally positive (i.e., amplification of one factor's effect by the other factor) between temperature and elevated CO_2 or between temperature and double precipitation (❯ *Fig. 13.7*).

Zhou et al. [54] simulate responses of NPP, R_h, and NEP to precipitation changes from −40% to +100% compared to current condition and reported that the responses increased with precipitation at the beginning and then reached a plateau. If "threshold" is defined as a point at which there is an abrupt change in response to external stimuli, the modeling results indicate that precipitation threshold values were about +30% for NPP and NEP and near current condition for R_h.

Shen et al. [34] used a process-based ecosystem model (PALS) to simulate how dryland soil respiration (R_s) and soil C pool size responded to precipitation changes at multiple

temporal scales. They found that increases in precipitation amount stimulated R_s and increased the contribution of R_a to R_s, whereas reductions in summer rainfall and strong increases in rainfall event size reduced total R_s and decreased the contribution of R_a to R_s. Increases in annual rainfall and decreases in summer rainfall benefited dryland soil C sequestration, whereas strong increases in rainfall event size resulted in a loss of soil C, with labile soil C pools being more responsive to precipitation regime changes than recalcitrant C pools at a decadal scale. These simulation results implied that dryland soils may act as C sinks with increased precipitation amount or C sources with decreased precipitation amount, but the strength of the sink/source may be mediated by accompanying shifts in rainfall seasonality and event size distribution.

Several studies considered the effects of O_3 on terrestrial ecosystems. For example, using the DLEM, Ren et al. [37] investigated the effects of O_3 along with climate change, increasing CO_2, and land use change on NPP and carbon storage in terrestrial ecosystems in China during 1961 and 2000. They found that elevated O_3 results in a mean of 4.5% reduction in NPP and 0.9% reduction in total carbon storage. Under the influence of O_3 and CO_2, the simulation results illustrate that mean annual NPP in the 1990s increased by 140.6×10^{12} g C compared to the 1960s; the total carbon storage increased by 46.3×10^{12} g C. The increased carbon storage may be attributed to the direct effects of increasing atmospheric CO_2 [96]; however, O_3 can partially compensate for the positive effects of CO_2 fertilization [37].

Meta-analysis Studies

Meta-analysis has not extensively applied on other climatic factors. So far, there is no meta-analysis of precipitation effects on terrestrial ecosystems [2]. But quite some studies have been conducted on the effects of O_3 on terrestrial ecosystems, particularly croplands. In general, elevated O_3 significantly decreased photosynthesis rates, decreased wheat grain yield and aboveground biomass. But the magnitudes of changes vary with different cropland ecosystems. Ainsworth [97] synthesized the research on rice responses to two elements of global change, rising atmospheric carbon dioxide concentration and rising tropospheric O_3 concentration. On an average, elevated CO_2 concentration (627 ppm) increased rice yields by 23%, but 62 ppb O_3 showed a 14% decrease in yield. Many determinants of yield, including photosynthesis, biomass, leaf area index, grain number and grain mass, were reduced by elevated [O_3]. Feng et al. [98] quantitatively evaluated the effects of elevated concentration of O_3 (31–59 ppb) on growth, gas exchange, and grain yield using a database of 53 peer-reviewed studies published between 1980 and 2007. They found that elevated O_3 decreased wheat grain yield by 29% and aboveground biomass by 18%. Grain yield decreased by 18% and biomass decreased by 16% relative to the control. Using another data set of 39 effective references, Feng et al. reported that the elevated O_3 decreased grain yield and grain weight by 26% and 18%, respectively. Light-saturated photosynthetic rate, stomatal conductance decreased by 40% and 31%, respectively. Feng et al. [99] also assessed the effects of rising O_3 concentrations on yield and yield

components of major food crops: potato, barley, wheat, rice, bean, and soybean in 406 experimental observations. They reported that with potato, current O_3 concentration (31–50 ppb) reduced the yield by 5.3%, and it reduced the yield of barley, wheat, and rice by 8.9%, 9.7%, and 17.5%, respectively. In bean and soybean, the yield losses were 19.0% and 7.7%, respectively. They also found that compared with yield loss at current O_3, future O_3 (51–75 ppb) drove a further 10% loss in yield of soybean, wheat, and rice, and 20% loss in bean. These findings confirm the rising O_3 as a threat to food security for the growing global population in this century [98, 99].

Future Directions: New Experiments, New Models, and New Approaches

Responses of terrestrial ecosystems to climate change play an important role in regulating future climate change. Biogeochemical cycling, specifically carbon cycling in terrestrial ecosystems, may have significant influences on future atmospheric CO_2 concentrations and global warming. Lack of knowledge about feedback from the biosphere is a major limiting factor to our forecast of future climate change. Due to the complexity of biogeochemical processes and components and each of these research approaches has some shortcoming, different approaches are needed and could be integrated together to minimize their weaknesses. Results from observations, experiments, modeling, and meta-analyses reveal one common: ecosystem responses to global change are complex, varying across different plants, functional types, ecosystems, and interact with many other environmental factors. More studies need to be conducted to fully understand climate impacts on terrestrial ecosystems.

For experimental study, field and controlled experiments will continue to be an important approach, particularly, the long-term and multi-factor experiments are urgently needed. As both experimental and modeling results indicated, the magnitude and even direction of response may change over time. It is imperative to provide long-term support for long-term global change experiments [6]. Terrestrial ecosystem responses to multiple, interacting factors of global change can be nonlinear and non-additive [34]. It is imperative to continue to initiate and support multi-factor experiments to explore these interactions at different ecosystems and different locations [2]. The gradual change of climatic factors in nature versus step-increase in experiments for some climatic factors and changes in the timing and intensity of other climatic factors should also be considered.

For ecosystem biogeochemical modeling study, data-model need to be better integrated. Inverse modeling techniques need to be applied to better parameterize the model. Uncertainty analysis in terms of measurement error, model structures, model parameters and parameter combinations need to be conducted to improve confidence of model estimation and prediction. Applications of inverse analysis to Duke Forest FACE experimental data demonstrated that uncertainty in both parameter estimations and carbon sequestration in forest ecosystems can be quantified to improve our understanding of

ecosystem carbon responses to climate change. As more data are accumulating in long-term manipulative experiments, inverse modeling and data assimilation will play a more important role in global change ecology. Besides climate variability, climate disturbances such as drought, cold-spell, heat-wave, fire, and biological disturbances such as disease, insect outbreak need to be built into biogeochemical models. Recently, Medvigy et al. [100] assess the significance of high-frequency variability of climatic factors (temperature, precipitation, and solar radiation) for terrestrial ecosystems under current and future climate, and report that the terrestrial ecosystems will be affected by changes in variability almost as much as by changes in mean climate. At large scale and for long-term prediction, dynamic changes of vegetation need to be considered in the models.

For meta-analysis study, the applications need to go beyond CO_2. As more experimental data and modeling results accumulate, meta-analysis needs to be performed on other climatic factors, such as precipitation. New analytic methods need to be developed to be able to deal with multiple treatment levels and multi-factors. At present, many global change meta-analyses consist of sets of contrasts, functionally equivalent to performing multiple sets of single classification analysis of variance (ANOVA) or Student's *t*-test [41]. More advanced statistical approaches (e.g., two-way ANOVA, analysis of covariance (ANCOVA), regression, and multivariate analysis) are rarely undertaken in ecological and global change meta-analyses [41], but need to be applied. The inconsistence among different meta-analyses highlights the need for careful selection of effective size metrics and weighting functions, and criteria for study selection and independence. Such decisions need to be justified carefully because they affect the basis for inference [43]. How to use meta-analysis to generate true and meaningful insights beyond only providing a general picture also needs to be considered when conducting meta-analysis.

Closing Remarks

Considerable progress has been made during the past several decades to better understand ecosystem responses to global change. In order to advance the field of research, it is necessary to better integrate observational, experimental, ecosystem modeling, and meta-analysis techniques into a multidisciplinary approach [2, 5, 24, 31]. Adequately conducted meta-analyses will summarize individual experimental results and provide general conclusions that are helpful for public and policy makers, but mechanisms of diverse response across different ecosystems and at different locations need to be understood using experiments and built into ecosystem models. Better communication between experimentalists and modelers would improve data-model integration by not only improving the model simulations, but also generating testable hypotheses [2, 5]. Uncertainty in ecosystem modeling can be reduced by improved experimental data and better understanding of biogeochemical processes. New experimental studies designed with multi-factor, multi-level of climatic factors and conducted over long-term are still needed to understand the complex impacts of climate change in terrestrial ecosystems. New meta-analysis methods are also to be developed to handle multi-factor and multi-level of

treatment factors. The mechanisms of climate change, climate interannual variability, and climate disturbances should be built into biogeochemical models to improve our understanding of climate impacts on terrestrial ecosystems. For long-term prediction, ecosystem biogeochemical models also need to consider indirect effects of climate change such as phenology and vegetation dynamics and the impacts of human activities such as land use change and urbanization. With the improved understanding of carbon cycling in terrestrial ecosystems and its feedback to global climate built into the earth system models, we will have a better and more accurate understanding of our future climate change.

Acknowledgments

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