Chapter 1
General Introduction

1.1. Background

Terrestrial ecosystems and the atmospheric system Terrestrial ecosystems have various interactions with the atmospheric climate system, at different time scales ranging from minutes to millions years. The atmosphere-ecosystem interactions are expressed as exchange processes of energy, momentum, and materials such as water and trace gases. Indeed, the contemporary atmospheric composition, i.e. high partial pressure of oxygen molecule and low partial pressure of carbon dioxide (CO_2), is certainly a result of the unceasing functions of green plants. Recent studies have shown that these processes play a critical role in determining local and even global climate, in spite of their localization to a thin layer near the ground surface. Through simulation studies with global climate models (GCMs), the significance of the hydrological (i.e. water and energy exchange) processes of the terrestrial ecosystems in controlling the regional climate was revealed (e.g. Avissar and Pielke, 1991; Bonan et al., 1992; Dickinson and Kennedy, 1992). In addition, the exchange of trace gases, especially of such greenhouse gases as CO_2 and methane (CH_4) with the atmosphere, exerts an influence on the climate system, because terrestrial ecosystems are one of the most important components of the global biogeochemical carbon cycle.

As asserted by the Intergovernmental Panel on Climate Change (IPCC) (1996), the atmospheric CO_2 concentration has increased from about 270 ppmv to 360 ppmv since the Industrial Revolution, and is anticipated to increase to as high as 500 to 700 ppmv in the next century. During the last decade, the annual increase rate of atmospheric CO_2 is approximately 1.5 ppmv, or 3.3±0.2 Pg C per year. The most obvious cause of the atmospheric CO_2 rise is firstly anthropogenic fossil fuel combustion of 5.5±0.5 Pg C yr^{-1}, and secondarily land use change of 1.6±1.0 Pg C yr^{-1} (IPCC, 1996). The discrepancy between the gross human emission of 7.1 Pg C yr^{-1} and net increase in the atmospheric CO_2 of 3.3 Pg C yr^{-1} may be a matter of debate and is often attributable to net ocean uptake. On the other hand, there is no consensus about the role of terrestrial ecosystems in the "missing sink" issue, in spite of a couple of hypotheses for the mechanism of terrestrial carbon sequestration (Schindler, 1999). The uncertain carbon budget is substantially small compared with gross fluxes of terrestrial and oceanic carbon exchange of as large as 100 Pg C yr^{-1}, demanding our refined understanding on the global carbon cycle. The increase of atmospheric CO_2 poses us further questions, because this will cause a series of global environmental changes, typically global warming. How will the terrestrial ecosystems be affected (i.e. changes in productivity and biodiversity) by the elevated CO_2 and global warming? What is the feedback mechanism of terrestrial ecosystems to these environmental changes? In spite of the long history of ecology, in which plant-environment interaction is one of the fundamental issues, we can hardly give answers to these questions. Therefore, a new field of ecology, so called "global ecology", is urgently being founded, so that we may have supplementary knowledge and sufficient predictability for the global-scale issues.

Brief history of environmental science on the global change Generally, it was 1980s when we recoginized the true importance of global change isuue; until 1970s, local issues of poisonous pollutants gathered a majority of attentions (cf. UNCHD, Stockholm in 1972). The typical global environmental issues contain the problem of vanishing stratospheric ozone and the problem of increasing greenhouse gases. The former was recognized so broadly and swiftly that industrial use of chlorofluorocarbons, the key material of ozone depression, was prohibited by the Montreal Protocol as early as 1987. As increasing social interest in the ozone problem, a series of observational and modelling studies were performed, in terms of atmospheric chemistry of ozone and biological impacts of UV-B. Another problem of global warming induced by greenhouse gases became the focal point, when Keeling et al. (1984) presented an unambiguous evidence of the increasing atmospheric CO_2 concentration during the last decades. They continued to observe the atmospheric CO_2 since 1958 at Mauna Loa, Hawaii (this is the longest record of monitoring the historical behavior of greenhouse gas), and proved that the atmospheric CO_2 has increased steadily at a surprising rate during the last decades. Stimulated by the fact, much scientific interest was directed to the nature of greenhouse gases and global warming. In 1988, IPCC was founded by the United Nations and World Meteorological Organization (WMO), for the purpose of aggregating recent scientific comprehension of global change issues and providing a proper viewpoint for policy makers. In fact, the first report of IPCC (1990) gave a considerable impact not only on scientific society but also on the general society. This is because the report contained a projection of the course of future global warming, estimated by the representative three GCMs: GISS, GFDL, and UKMO. Along with the rapid development of computational ability, the numerical procedure was recognized to be a powerful tool not only for weather forecast (short-term) but also for climate prediction (long-term). Concomitantly, these predictions of atmospheric CO_2 rise and global warming directed the interest of ecologists toward the prediction of the effect of global change. Emanuel et al. (1985) conducted one of the earliest studies of estimating the impact at the global scale; they simulated the biome distribution before and after the global warming induced by CO_2 doubling, by means of the Holdridge scheme. In spite of some methodological deficiencies, such as the lack of direct impact of elevated CO_2 on ecosystems, their study brought about much attention to the impact at the global scale.

Future global warming and terrestrial ecosystems At present, most GCMs predict that mean surface temperature over the earth will rise by about 2 to 5 °C as a consequence of the greenhouse gas doubling projected in the future (IPCC, 1996). The severe climatic change should bring about various ramifications to terrestrial ecosystems, especially in their productivity and resultant distribution pattern. For example, the global warming can move the distribution of temperate and boreal biomes, poleward or upward (Woodward, 1987). The extent of the predicted global warming is fifth as large as the largest temperature perturbation in this century: warming of 0.58 °C in 1998, relative to the long-term mean (WMO, 1999). We know empirically that agricultural yield is considerably affected by weather conditions, e.g. temperature, precipitation, and sunshine hours. In natural ecosystems, similar environmental controls should be important in determining plant productivity and many ecological processes. If the climate change affects such plant processes as reproduction (e.g. fruition and germination) and competition, ecosystem structure and physiognomy would change significantly (Graham et al., 1990; Chapin et al., 1995).

Moreover, a large number of empirical and theoretical studies indicate that sole higher atmospheric CO_2 concentrations can exert influences on terrestrial ecosystems (Woodward et al. 1991; Bazzaz et al., 1996). At the organ scale, elevated CO_2 concentration alters single-leaf gas exchange, such that generally it enhances photosynthetic CO_2 assimilation and stomatal closure (Mott, 1990; Field et al., 1995a), leading to higher water use efficiency (Bunce et al., 1997). At the individual scale, plant growth rate is accelerated by the elevated CO_2 concentration, frequently accompanied with a change in photosynthate allocation (Ziska et al., 1991; den Hertog and Lambers, 1993). At these smaller scales, subject plants are usually exposed to higher CO_2 level by means of growth chamber and phytotron, in which growth conditions are conveniently controlled. However, their outcomes can not be applicable directly to natural ecosystems, where environmental and biological conditions are highly heterogeneous in time and space (Bazzaz et al., 1996). Therefore, the upscaling from individual or smaller scales to community scale is a matter of both practical and theoretical ecology. During the last decade, a couple of procedures of exposing natural ecosystems (from low-stature grasslands to high-stature forests) to higher CO_2 concentration is developed: open-top chamber with ventilation system (OTC) and free air CO_2 enrichment system (FACE). Most of these efforts are performed as a part of an integrating project, called the International Geosphere-Biosphere Programme (IGBP), especially for its core project, the Global Change and Terrestrial Ecosystems (GCTE) (Walker and Steffen, 1996). However, these studies are revealing that there is a substantial diversity in the responses to environmental change, among plant species and at least functional types, suggesting that we may require further investigations to accumulate fundamental ecophysiological knowledge.

Importance of modeling study in the global change study In addition to the experimental and observational studies, it is modelling study that is prospective and essential for the integration and prediction of global change issues. As regards simulating ecosystem dynamics, we have a lot of theoretical and applied studies stemming from such classic ones as Logistic model and Lotka-Volterra model. Although these studies focused chiefly on the biological interactions, e.g. competition and predation, we have relatively scarce knowledge about the interaction between organisms and surrounding environment. In particular, mechanistic analysis of the reaction (*sensu* Clements, 1916) from plants to environments has a history of only less than half century, while the action of the environment through temperature, water, light, and nutrient was fully recoginized and physiologically studies (e.g. Boysen-Jensen, 1932). The milestone work by Monsi and Seki (1953) gave a breakthrough for analyzing the productive structure in plant canopy, in which light environment is substantially changed by mutual shading of plant leaves. Their theory, called dry-matter production theory, lead to a mathematical technique to evaluate canopy gross photosynthetic production (*GPP*), and underlies most models that parameterize atmosphere-biosphere exchange. Through the International Biological Programme (IBP), we acquired a large amount of knowledge on the functioning of terrestrial ecosystems, and Lieth (1975) aggregated the worldwide data on net primary production (*NPP*) into an empirical model, termed Miami model. Simularly, using agrometeorological approach, Uchijima and Seino (1985) constructed another empirical *NPP* model, termed Chikugo model. Although the Miami model and Chikugo model are so convenient that it gave the first global map of plant primary productivity, it could not be applicable to estimate the impact of global change; the Miami model does not consider the effect of CO_2 concentration. In other words, we needed a mechanistic model of terrestrial ecosystems, in which ecological processes are described at lower levels, e.g. physiological scale. Indeed, based on a large amount of data, plant physiologists (e.g. Penning de Vries, 1972) constructed various models of plant processes, including photosynthesis, transpiration, respiration, scenescence, allocation, and so on. Nevertheless, these models hardly had effectiveness in estimating the ecosystem response to global environmental change, because (1): they are largely based on the data of crop species, and (2) these models need to determine numerous physiological parameters, making them impractical for simulating natural ecosystems.

State of the art of the modeling study A number of models have been constructed to simulate the biogeochemical carbon cycle, with a wide variety of procedures. There are roughly two approaches for developing the global model; one is the top-down approach, in which some empirical relationships are applied to the whole biosphere, and another is the bottom-up approach, in which a mechanistic ecosystem model is extended to the whole biosphere. Most of early studies employed the top-down approach, by which the terrestrial biosphere was expressed as a single box, and carbon exchange with the atmosphere was calculated with very simple equations (e.g. Revelle and Suess, 1957; Oeschger et al., 1975). These models were constructed by earth scientists, and then much attention was paid to the atmosphere-ocean exchange, while the importance and complexity of the biosphere were probably underestimated. The situation was the case for geochemical models (e.g. Berner et al., 1983), which simulate global carbon cycle at the geological time scale (e.g. millions years), focusing on the atmosphere-lithosphere interactions. The breakthrough was made in 1987, when the Osnabrück Biosphere Model (OBM) was presented by Esser (1987). The OBM had three important meanings; (1) OBM was virtually the first global model constructed by ecologist; (2) the NPP scheme in OBM was based on the outcomes of the IBP, suggesting that modeling is a data-intensive study; and (3) OBM would be the first model which has grid structure at the global scale (2.5° x 2.5° longitude-latitude). In spite of its top-down approach permitting empirical relationships, OBM was so successful that a revised version (High Resolution Biosphere Model, HRBM) has still been used in some recent studies (Heimann et al. 1998; Meyer et al. 1999). The next breakthrough, i.e. adoption of bottom-up approach, was firstly introduced by Raich et al. (1991) and McGuire et al. (1992) into the Terrestrial Ecosystem Model (TEM). Although several ecosystem carbon cycle models had been constructed at that time (e.g. McMurtrie and Wolf, 1983; Oikawa, 1985; Running and Coughlan, 1988; Valentine, 1988; Janececk et al., 1989; Rastetter et al., 1991; Thornley et al., 1991), TEM could perform at the continental scale on a high spatial resolution (0.5° x 0.5° longitude-latutude). Unlike the former top-down models, TEM included explicitly differences in ecophysiological properties related to photosynthesis and respiration, and then was thought to be applicable for prediction. Melillo et al. (1993) adopted TEM to estimate the impacts of atmospheric CO_2 doubling and accompanying climate change on terrestrial ecosystems. Similarly, other models attempted to scale up from ecosystem to the biosphere; FOREST-BGC of Running and Coughlan (1988) was generalized to BIOME-BGC by Running and Hunt (1993); the model of Janececk et al. (1989) was extended to Frankfurt Biosphere Model (FBM) by Ludeke et al. (1994). Additional models, which have a mechanistic structure but are designed for global application from the first, have been actively constructed in 1990s (e.g. Carnegie-Ames-Stanford Approach model (CASA) by Potter et al. 1993; DEMETER model by Foley 1994a; Carbon Assimilation in the Biosphere (CARAIB) by Warnant et al. 1994; Carbon Exchange betweenn Vegetation, Soil, and the Atmosphere model (CEVSA) by Cao and Woodward 1998b). One of the apparent improvements in this field is due to the development of remote sensing, which provides broad-scale, homogeneous data, e.g. Normalized Difference Vegetation Index (NDVI) (Running and Nemani, 1988; Field et al., 1995b). However, it is apparent that the research field of mechanistic modeling in global carbon cycle, has a history of as short as 15 years, and then is far from maturity. These models differ in even their most fundamental parts of ecosystem conceptualization, such as compartment system and growth scheme. In 1995 in Potsdam, principal model researchers tried to make an intercomparison of their models, especially with respect to *NPP* (Cramer et al., 1999). It was shown that existing models gave a broad range of estimation: global *NPP* from 39.9 to 80.5 Pg C yr^{-1}. The situation suggests strongly that more sophisticated model and validation practice are needed to reduce the uncertainty in quantifying the role of the biosphere in the global biogeochemical carbon cycle.

1.2. Scope of the present study

The present study focuses on the interaction between the atmosphere and the biosphere, especially CO_2 exchange, and on the carbon dynamics within terrestrial ecosystems. As a basic line of the study, the author will address the problems mostly at the global scale, because it is especially important to regard a variety of terrestrial ecosystems as a single integrated system (i.e. biosphere), in considering the atmosphere-biosphere interaction. For example, the influence of the terrestrial carbon budget on the atmospheric CO_2 concentration could obviously be addressed only at the global scale. As a general rule, such problems as described below will be investigated. (1) How is the equilibrium carbon dynamics of terrestrial ecosystems under a stationary condition? (2) What was the role of the terrestrial biosphere in the global carbon cycle in the past, as a sink or a source? (3) How will the terrestrial biosphere respond to the future global environmental change?

However, first of all, the author should ask what is the appropriate model to address the problems. Reynolds et al. (1996) concluded that the model, which is applicable to simulate the response of plants to changing environment, must be mechanistic, rather than empirical or phenomenological, because only mechanistic models may estimate the behavior of plants under the future unexperienced environment. A mechanistic model should deal with ecosystem processes in the physiological manner, along with an appropriate scaling strategy. For example, the CO_2 fertilization effect on ecosystems should be expressed not by an empirical function of CO_2 concentration (e.g. biotic growth factor β; Kohlmaier et al., 1987) but by a series of physiological processes (e.g. McMurtrie et al., 1992a; Lloyd and Farquhar, 1996; Luo and Mooney, 1996). On the other hand, mechanistic models, in general, require more information on ecophysiological properties, which should be obtained from the ecosystem at the cost of a great deal of efforts. The data deficiency limits the applicability of the model, although recent improvement of computer architecture will enable us to practice a huge scale of numerical experiments. The data collection and computer performance are especially serious for the global studies, because models become more and more complicated, and simulation is to be performed at higher spatial resolution in order to take heterogeneity and diversity of land ecosystems into account. As a result, simple structure to a sound extent is regarded as an advantage, rather than a shortage, of the model. Taking these conditions into account, the author constructed a new model, termed **Simulation** model of **C**arbon c**YC**le in **L**and **E**cosystems (Sim-CYCLE), which is a mechanistic model of biogeochemical carbon cycle in terrestrial ecosystems, originally based on the dry-matter production theory established by Monsi and Saeki (1953) and Oikawa (1985).

Using Sim-CYCLE, the author will access the problems mentioned above in general terms through more specific simulation problems, as follows.

(1) How does the model simulate the equilibrium carbon dynamics of worldwide terrestrial ecosystems simulated? Here, the author takes such features into consideration:

- how is the difference among biomes, in terms of their productivity and carbon storage?
- how is the latitudinal distribution of carbon exchange and carbon storage?
- how is the seasonal change in gross and net carbon fluxes?
- to what extent do C_4 plants contribute to the biospheric carbon dynamics?
- how effective do terrestrial ecosystems perform dry-matter production, at the cost of water and radiation energy?

Finally, the model outcomes should be examined by comparing with the former estimations by other researchers, for validation.

(2) How has been the interannual change in the biospheric net carbon budget during the recent years? This problem will be addressed by using actual meteorological data, and I would like to inquire into such specific questions:

- which carbon flux is most sensitive to environmental change?
- which environmental factor is most strongly related to the interannual change?
- is the interannual change related to some extreme climatic events, such as volcanic eruption and El Niño?
- to what extent does the interannual change in the terrestrial carbon budget account for the growth rate of the atmospheric CO_2 concentration?

(3) How does the model estimate the impacts of the prescribed global warming on terrestrial carbon dynamics? The climate scenarios are derived from GCM simulations, on an assumption that atmospheric CO_2 concentration increases at a rate of +1 % per year. The

author will pay attention to such features as:

- which regions and biomes are sensitive or vulnerable to the global change?
- how long is the time-lag of the ecosystem response?
- how is the difference in the responsiveness between C_3 and C_4 plants?
- which direction and how much is the biotic feedback to the atmospheric CO_2 increase (and potentially to climate change)?

1.3. Outline of the thesis

Chapter 1 clarifies the background and the objectives of the present study, as mentioned above. In Chapter 2, a comprehensive description of the model, Sim-CYCLE, is presented. Chapter 3 denotes how to validate Sim-CYCLE as an appropriate tool for the modeling study, by comparing with plot-scale measurements. In Chapter 4, Sim-CYCLE simulates the equilibrium carbon dynamics of terrestrial ecosystems, at the global scale with a high spatial resolution. A number of diagnostic properties of carbon dynamics, e.g. productivity, biomass, and turnover, are discussed. Chapter 5 gives consideration to the year-to-year change in the atmosphere-biosphere CO_2 exchange, and Sim-CYCLE is adopted to analyze the net carbon balance of terrestrial ecosystems. This simulation analysis covers the time period from 1958 to 1998. In Chapter 6, Sim-CYCLE predicts the responses of terrestrial ecosystems to the future climate change induced by atmospheric CO_2 increase. Three climate scenarios are derived from GCM simulations. Chapter 7 makes a general discussion with respect to the carbon dynamics in terrestrial ecosystems, based on a series of simulation studies.