

Chapter 7

General discussion

7.1. Value of the Sim-CYCLE approach as an original study

There are actually about 20 models which address the global carbon cycle of terrestrial ecosystems (cf. Chapter 2), utilized to understand and predict the interaction between the atmosphere and biosphere. Some of earlier ones are exceedingly simple and based on empirical relationships, but contemporary ones are being more and more elaborated and incorporate recent ecophysiological findings. Then, it is necessary to clarify the advantages and originality of Sim-CYCLE approach.

Model The first emphasis is unambiguously put upon the fact that Sim-CYCLE is based on the dry-matter production theory in calculating photosynthesis, respiration, allocation, and growth, enabling the author to construct a process-based model. Most ecosystem models have hitherto utilized only a part of the theory, i.e. the exponential attenuation of irradiance within a canopy, and then they may not express the carbon dynamics in an ecophysiological manner. Although many of the ideas in the dry-matter production theory were discovered by classic researches (e.g. Monsi and Saeki, 1953; Monsi, 1960), establishment of an integrated view of ecosystem carbon dynamics is one of the recent achievements of ecophysiology. Sim-CYCLE has an intermediate complexity, so that it may fully utilize global data available to date, and does not demand minute data at the biochemical scale. Such important quantities as *NPP* and *NEP* are obtained as a result of the component fluxes (i.e. *GPP*, *AR*, and *HR*), regulated at the physiological scale. The 5-compartment system adopted is both necessary and satisfactory to capture the carbon dynamics in terrestrial ecosystems, although some elaborated models may divide carbon into more functional compartments. For example, TEM, one of the representative models, has only two compartments (one for plant and another for soil). The high spatial resolution of global simulations ($0.5^\circ \times 0.5^\circ$) and fine vegetation classification (33 types) are also an important

property for an accurate estimation. Although the spatial resolution of 0.5° (i.e. 55 km) is not sufficient to retrieve the features at the landscape scale, the integration of 86,705 grid-cells within a viable time (i.e. hours to days) became possible only if the model has the intermediate complexity and spatial resolution.

Simulation

The equilibrium simulation in Chapter 4 has been addressed a number of models (e.g., Foley, 1994a; Kohlmaier et al., 1997), but Sim-CYCLE pointed out several distinctive properties; e.g. water use efficiency at the biosphere scale was firstly investigated (cf. Fig. 4-19). Moreover, Sim-CYCLE could disaggregate the component fluxes by C_3 and C_4 plants (cf. Fig. 4-17). In Chapter 5, one of a few studies of interannual change in terrestrial carbon budget was presented. The model analysis covers a longer period (41 years) than other studies (e.g., Maisongrande et al., 1995; Kindermann et al., 1996), and suggests firstly the mechanism of the CO_2 anomaly in 1998 in relation to the strong ENSO event. In addition, the long-term analysis in Chapter 5 suggests a fertilization effect of the atmospheric CO_2 increase during the recent decades on the terrestrial carbon budget, in relation to the potential mechanism of the missing carbon sink. The prediction study in Chapter 6 would be valuable, because Sim-CYCLE gave one of a few estimations of the future role of the terrestrial biosphere (e.g. Melillo et al., 1996; Cao and Woodward, 1998a), reducing the uncertainty of the anticipation.

7.2. Direct and supporting evidence of model validity

In this thesis, model validity was revealed firstly by comparing with field measurements at the plot scale (cf. Chapter 3; Figs. 3-7 and 3-9), and secondarily by correlating with other model estimations at the global scale (cf. Chapter 4; Fig. 4-20). The seasonal cycle of *NEP* and its latitudinal variation were qualitatively reasonable, compared with the seasonal change in atmospheric CO_2 concentration (Fig. 4-13). And, Sim-CYCLE revealed the correspondence between the estimated anomaly in *NEP* and the observed anomaly in the growth rate of atmospheric CO_2 concentration (Chapter 5).

In addition, Table 7-1 provides a supporting evidence for comparison with other

estimations, in terms of *NPP*, plant C, soil C, and radiation use efficiency. Of the 18 estimations of global annual *NPP* (dispersed widely from 39.9 Pg C yr⁻¹ by HYBRID to 66.3 Pg C yr⁻¹ by GLO-PEM, after Cramer et al., 1999), Sim-CYCLE one seems moderate (or slightly higher). Similarly, plant biomass and soil carbon storage look like moderate among the current estimations. Plant biomass of 646 Pg C is smaller than that by Whittaker and Likens (1975), who presented the biomass of 835 Pg C (or 1837 Pg dry matter) based on field surveys, but the difference is attributable to their overestimation of forest biomass. The estimations by Friedlingstein (1992), and Adams et al. (1990) are apparently larger than Sim-CYCLE one, because they assumed the potential vegetation mapping (without croplands). Using the average forest biomass of 137.2 Mg C ha⁻¹ and the cropland area of 19.7 x 10⁶ km², Sim-CYCLE gave the biomass of potential vegetation as 889 Pg C, i.e. close to those by Adams (1990) and Friedlingstein (1992). The *RUE* estimations in Table 7-1 were derived from the intercomparison study by Ruimy et al. (1999), who summarize the workshop in Potsdam, 1997 (Cramer et al., 1997). Obviously, Sim-CYCLE gave an intermediate estimation among all, suggesting the moderateness of the simulation in Chapter 4.

7.3. The role of terrestrial ecosystems in the global carbon cycle

Sim-CYCLE showed that the terrestrial biosphere surely plays an important role in the global biogeochemical carbon cycle: the carbon storage of 2150 Pg C and *NPP* of 61.8 Pg C yr⁻¹ (cf. Chapter 4). Although these estimations correspond to the equilibrium state, the quantitative importance may not be reduced by incorporating the effects of disturbance and environmental change. The magnitude of gross CO₂ fluxes (*GPP*, *AR* and *HR*) is comparable to those of the ocean exchange (about 100 Pg C yr⁻¹), and overwhelms those of the lithospheric exchange (weathering and volcanic emission, less than 1 Pg C yr⁻¹). Total carbon storage of 2150 Pg C is smaller than that of the ocean (about 4 x 10⁴ Pg C) and the lithosphere (8 x 10⁷ Pg C), but is three-fold larger than that of atmosphere (750 Pg C) (Schlesinger, 1997). The carbon dynamics of the terrestrial biosphere has several remarkable properties, as shown by Sim-CYCLE simulations. (1) Mean resident time of carbon is generally short, i.e. 10.5

years of biomass and 24.7 years of soil organic carbon, although a portion of soil carbon is buried to be passive humus. (2) CO₂ fluxes are sensitive to environmental condition, and acutely respond to daily to monthly climatic change (cf. Chapter 5). This responsiveness may be reflected in the seasonal and interannual change in the concentration and isotopic composition of atmospheric CO₂. (3) There is substantial spatial heterogeneity in the responsiveness to environmental change, making a broad generalization difficult. (4) The responsiveness can change with time; the response to seasonal climate change is different from that to decadal change. Additionally, the terrestrial carbon cycle has been and will be most severely disturbed by human activities.

7.4. Impacts of the global environmental change on terrestrial ecosystems as predicted by the carbon cycle model

The experiment 3 (cf. Chapter 6) shows that terrestrial ecosystems will be largely affected by the global warming induced by atmospheric CO₂ doubling. The interactive effects of CO₂ rise, warming, and precipitation change made prediction difficult, but Sim-CYCLE provided a reasonable estimation: the resultant *NPP* increase by 25 % and carbon sequestration of 78 to 137 Pg into the biosphere. Remarkably, the increase of *NPP* is larger than expected from the sole CO₂ doubling (+21 %), whereas the increase of carbon storage is smaller than the sole CO₂ doubling (+206 Pg C). The large response of global *NPP* was attributable to those in northern boreal forest and tundra ecosystems, because climatic warming enhanced production during their growing period. Nevertheless, they emitted a large amount of soil organic carbon simultaneously, because warmer soil temperature accelerated the decomposition rate. The net balance of these countering mechanisms appears to be subtle.

The high responsiveness of the biospheric carbon budget to climate change was partly exemplified in Chapter 5; *NEP* responded to such climatic perturbations as El Niño event and volcanic eruption. Based on the ΔT - ΔNEP relationship, global warming by 3°C may bring about approximately 9 Pg C yr⁻¹ of emission from the biosphere, although this emission may be offset by CO₂ fertilization effect to some extent.

All of the experiments in this thesis were carried out as off-line simulations, i.e. ecosystem change had no effect on the atmospheric system. However, terrestrial ecosystems can exert feedback effects, as implied by the Sim-CYCLE study. (I) After the doubling of atmospheric CO₂, terrestrial ecosystems are capable of accumulating 74 to 128 Pg of additional carbon, due to the CO₂ fertilization effect on plants. The carbon uptake could offset 10 to 17 % of the atmospheric CO₂ increase, and alleviate the global warming to some extent. (II) As a result of doubled CO₂ concentration, *LAI* was estimated to increase by 17 to 19 %, while stomatal and canopy conductance decreased considerably (cf. Fig. 2-10). These changes in *LAI* and conductance can affect such surface processes as latent and sensible heat fluxes, and finally influence the growth of boundary layer (McNaughton and Jarvis, 1991) and soil water drainage (Idso and Brazel, 1984; Field et al., 1995a). The interaction between the biosphere and atmosphere through canopy exchange will further be discussed in the next section.

7.5. Interaction between the atmosphere and the biosphere

Although Sim-CYCLE focused on the atmosphere-biosphere CO₂ exchange, other interaction processes (water and energy exchanges) were simply included as subschemes, because they are essentially linked with carbon dynamics in terrestrial ecosystem. In atmospheric science, the atmosphere-biosphere exchange is also recognized as an important process, but focusing on energy and momentum exchanges. Those climatological ecosystem models are called Land Surface Parameterization (LSP) and incorporated in many GCMs (e.g. Manabe, 1969; Dorman and Sellers, 1989; Noilhan and Planton, 1989; Henderson-Sellers, 1993; Sellers et al., 1997; Mabuchi et al., 1997). Early LSPs were so simple that they could not evaluate the response of terrestrial ecosystems to climatic change, but contemporary LSPs (e.g., SiB2 by Sellers et al., 1996a and BAIM by Mabuchi et al., 1997) have been developed to calculate the atmosphere-biosphere CO₂ exchange. Then, an interactive simulation between the atmosphere and the biosphere is progressively possible (Sellers et al., 1996), although the LSPs are still too simple to estimate the carbon dynamics within ecosystem. For example,

Henderson-Sellers et al. (1995) and Pollard and Thompson (1995) simulated the climatological change induced by the doubling of plant stomatal resistance. On the other hand, several studies attempted to incorporate a carbon cycle model into GCM (e.g. Xiao et al., 1997), for a similar purpose to LSP studies. In spite of the fundamental discrepancy in approach, integrating ecological models like Sim-CYCLE and climatological LSPs are likely possible, or necessary to simulate the interaction. Ideally, the integrated ecosystem model should deal with the exchanges of momentum, energy, water, and CO₂ (or other trace gases) in a mechanistic manner, and regard *LAI* and canopy conductance as prognostic variables. The IBIS model by Foley et al. (1996) is one of the attempts to construct an integrated model, on a basis of cooperation of biologists and earth scientists. To improve Sim-CYCLE toward the direction of the integrated model, it is necessary to shorten simulation time-step (one hour or shorter), to include momentum transport by turbulence, to sophisticate soil hydrology, to parameterize sensible heat and soil heat fluxes, and so on. These modifications are sufficient to perform a short-term simulation (days to years), but another factor of biome shift becomes important in long-term simulations (decades or longer). This implies that some biogeography scheme should be additionally incorporated into the integrated model; the linkage between carbon cycle model and biogeography model will be discussed in the next section. In sum, the Sim-CYCLE simulations suggest that the carbon dynamics of the terrestrial biosphere is an important component of the Earth System, and then more integrated approach is needed to understand and appraise the atmosphere-biosphere interaction.

7.6. Potential model deficits and future direction of the study

(1) Intrinsically, compartment models have their own limitation; it can not consider such community properties as population density, species composition, and individual size distribution. And, minor carbon pools (e.g. animals) are often neglected, although they can play an important role as a keystone of ecosystem processes. The compromise between simplicity and fineness of the compartment system of Sim-CYCLE will be reconsidered in the forthcoming study.

(2) Many studies suggest that dynamics of nutrient, especially nitrogen (N), is coupled with carbon cycle in terrestrial ecosystems (e.g. Norby et al., 1986; Melillo et al., 1989; Vitousek and Howarth, 1991). Concentration of photosynthetic enzymes and photosynthetic capacity are proportional to N concentration (Evans, 1989; Schulze et al., 1994). This mechanism leads to an ecologically interesting phenomenon; leaf nitrogen concentration shows a gradient from the top to bottom along with the gradient of irradiance in canopy, to optimize carbon economy (Field, 1983; Hirose and Werger, 1987). Moreover, Kelliher et al. (1995) showed that maximum stomatal conductance is proportional to N concentration and then photosynthetic capacity, across a variety of biomes. Specific dark respiration rate is also proportional to N concentration (Ryan, 1995; Reich et al., 1998). Thus, there is physiological modulation between C and N metabolisms (Atkins, 1987; Chapin, 1991). The N dynamics is also meaningful in considering underground carbon dynamics, because decomposition rate is dependent on litter N concentration (Melillo et al., 1982). Indeed, nitrogen nutrition is one of the most severe limiting factors for most of natural ecosystems (Vitousek and Howarth, 1991), and then deposition of anthropogenic nitrates may have stimulated plant growth (Hudson et al., 1994; Nadelhoffer et al., 1999). Additionally, accelerated N mineralization due to global warming may ameliorate the N deficit in natural ecosystems, and enhance carbon assimilation and plant growth, at least during a short-term period (Melillo et al., 1993; McGuire et al., 1995). Therefore, coupling N cycle with the C cycle should be a prospective modification for Sim-CYCLE, leading to higher predictability.

(3) After the milestone work by Monsi and Saeki (1953), heterogeneities of light environment and physiological property have been studied intensively, leading to more elaborated models of plant canopy. For example, the current *GPP* model of Sim-CYCLE assumes the spherical distribution of leaf orientation, and the homogeneous photosynthetic property among leaves. These simplifications may be modified on a basis of the recent outcomes of ecophysiology (e.g. Kuroiwa and Monsi, 1963; Hozumi and Kiritani, 1970; Monsi et al., 1973; Oikawa and Saeki, 1977; Hirose and Werger, 1987; Kurachi et al., 1992). A part of oversimplification in canopy expression will be ameliorated by adopting a multi layer model. Recently, De Pury and

Farquhar (1997) showed that division of canopy into the two-layer model (i.e. sunny layer and shade layer) would apparently improve the model accuracy.

(4) Adoption of the multi-layer model can lead to another advantage for Sim-CYCLE; i.e., this may enable us to simulate population dynamics. For example, the tropical rain forest model of Oikawa (1986), who adopts a three-layer canopy (i.e. upper, middle, and lower stories), showed that the lower story plants may undertake an unfavorable effect by atmospheric CO₂ rise, through aggravated shading by the upper story. DeLucia et al. (1999) observed the corresponding phenomenon by the FACE experiment at a loblolly pine forest site.

(5) Although Sim-CYCLE simulations in this thesis assumed a stationary biome distribution, biome shift induced by the global warming is one of the focal points of the global ecology (Woodward, 1987). Then, several semi-mechanistic models estimating biome distribution have been developed and used to predict the future biome shift (Prentice et al., 1992; Haxeltine and Prentice, 1996; Neilson, 1993). Moreover, recent attentions are directed toward constructing the Dynamic Global Vegetation Model (DGVM), in which transitional migration of ecotones is simulated (Beerling et al., 1997; Potter and Klooster, 1999). Not only biome distribution but also C₃/C₄ composition in rangeland ecosystems may change as a result of atmospheric CO₂ increase and climate change (Henderson et al., 1995; Ehleringer et al., 1997; Collatz et al., 1998). Thus, linkage with biome models is important for a long-term simulation with high spatial resolution, under changing environments. For example, when using 1-km mesh model, forest expansion and replacement with grassland can take place in a few years (Daly et al., 2000).

(6) The seasonal change in zonal *NEP* was qualitatively consistent with the change in atmospheric CO₂ concentration. More sophisticated examination will be possible by coupling Sim-CYCLE with an atmospheric transport model (Heimann and Keeling, 1989; Taguchi, 1996), so that the spatio-temporal distribution would be appropriately simulated. Additionally, inverse atmospheric models provide an estimation of surface CO₂ exchange (e.g. Enting et al., 1995; Kaminski et al., 1999; Bousquet et al., 1999), which is useful for Sim-CYCLE

validation.

(7) The current version of Sim-CYCLE regards carbon as a single mass, which is composed of two stable isotopes (^{12}C and ^{13}C). Many studies suggest that the isotope composition ($\delta^{13}\text{C}$) is strongly related to CO_2 exchange, due to the fractionation effect in photosynthetic pathway (Farquhar et al., 1982; Lloyd and Farquhar, 1994), as reflected in $\delta^{13}\text{C}$ of atmospheric CO_2 (Nakazawa et al., 1993; Troler et al., 1996; Bakwin et al., 1998). Particularly, there is a significant difference of $\delta^{13}\text{C}$ between C_3 and C_4 plants (Hattersley, 1982; Buchmann and Ehleringer, 1998). Then, incorporating the carbon isotopes into Sim-CYCLE will enable us to simulate the atmosphere-biosphere CO_2 exchange with a stronger constraint.

(8) Keeling and Shertz (1992) showed that seasonal variation of atmospheric O_2 concentration is inversely corresponding to CO_2 concentration. Since ocean O_2 exchange is negligible unlike CO_2 exchange (Heimann, 1997), the O_2 variation is attributable to terrestrial exchange, such as plant metabolisms and fossil fuel combustion. Based on the interannual changes in O_2 and CO_2 concentration, Keeling et al. (1996) successfully divided the ocean and land CO_2 exchange. In addition, stable oxygen isotope composition ($\delta^{18}\text{O}$) is used to distinguish between photosynthetic and respiratory CO_2 fluxes (i.e. $\text{C}^{18}\text{O}^{16}\text{O}$; Farquhar et al., 1993; Tans, 1998), and between evaporation and transpiration (i.e. H_2^{18}O ; Yakir et al., 1994). Thus, information in oxygen will serve as a constraint of the global carbon cycle (Nakazawa et al., 1997; Ciais et al., 1997a,b).

(9) Simulating the past state is both a common application and a validation of model, as Chapter 5 exemplified the analysis from 1958 to 1998. Indeed, two lines of simulations have been done by other modelers for reconstruction of the past state: (I) historical change in carbon budget after the Industrial Revolution, focusing on the human land-use change (Houghton, 1999; Houghton et al., 1983; Emanuel et al., 1984; Ramankutty and Foley, 1999), and (II) estimation of the carbon budget at the Last Glacial Maximum (LGM, ca. 18,000 years before present (BP); Friedlingstein, 1992; Crowley, 1995; François et al., 1999) and the following Hypsithermal period (ca. 6,000 years BP; Foley, 1994b; Peng et al., 1995). A preliminary result of Sim-CYCLE simulation of the carbon budget at the LGM showed that

terrestrial carbon storage might be smaller by 170 to 590 Pg C than the contemporary state (Ito, unpublished data), and the reconstruction of the past states will be increasingly addressed by the forthcoming researches.

7.7. Recommendation to field and laboratory studies

Apparently, modeling study must intimately communicate with field surveys and laboratory experiments, since these empirical researches provide a sound standpoint for exploring ecosystem phenomena and a large amount of indispensable data for validation and parameterization. Reversely, this section attempts to point out some problems and recommendations in terms of empirical studies, to facilitate the interaction between the research fields.

(1) *Requirement of wider coverage of measurements.*

The satisfactory agreement between Sim-CYCLE and field measurements (cf. Chapter 3) may be reconsidered with caution, because the number of experimental sites (21 sites) may be insufficient to validate the global Sim-CYCLE with 33 biome types. A few biomes (e.g. tropical rain forest) had a multitude of datasets, while many biomes (desert, wetland, and mixed forest) are destitute of field data. And, it is highly uncertain that the surveyed plots were representative of respective biome. In addition to the bias of biomes surveyed, Churkina and Running (1999) suggest that the field surveys to date have underrepresented the climatic diversity over the world. As a consequence of data shortage, a comparison with individual data could not be performed, perhaps leading to a significant bias of parameter calibration. Additionally, the wide coverage of field measurement is necessary for scaling up to the regional scale by using remote sensing data (Seller et al., 1995; Asner et al., 1998; Olson et al., 1999).

(2) *Scrutinizing underground carbon dynamics.*

In most models, dynamics of soil organic matter is parameterized in a simpler way than plant biomass; in Sim-CYCLE, biomass of 646 Pg C was divided into 3 compartments, while soil carbon of 1503 Pg C was divided into only 2. In the prediction study of Chapter 6, uncertainty in soil carbon storage (from -40 to +17 Pg C) was larger than plant biomass (from +115 to +148 Pg C), after the 70-

year global change. The oversimplification of underground soil carbon dynamics is one of the sources of uncertainty in simulation studies, and then more researches are needed. Jenkinson et al. (1991) suggest that the accelerated decomposition rate by global warming may act as a substantial potential of feedback mechanism, while some recent studies cast question on the temperature dependence of soil decomposition rate (Liski et al., 1999; Kirschbaum, 2000; Giardina and Ryan, 2000). Finally, it should be noted that the uncertainty of underground carbon dynamics is regarded as a critical problem in estimating the carbon balance of the Kyoto forests (IGBP Terrestrial Carbon Working Group, 1998).

(3) *Physiological mechanism of acclimation.*

Many field and laboratory experiments revealed that plants acclimate to environmental change (including atmospheric CO₂ rise), such that initial responsiveness would decrease with time (Sims et al., 1998; Wolfe et al., 1998). The acclimation may have a significant meaning in estimating the response of plants to global environmental change, because extrapolation of short-term experiments can result in an overestimation of long-term trend (Luo and Reynolds, 1999). As to the photosynthetic acclimation to elevated CO₂, two lines of hypothesis have been proposed: (I) diluted nitrogen concentration, leading to lower photosynthetic capacity (Pettersson and McDonald, 1994; Zhang et al., 1997), and (II) sink restriction of assimilated carbohydrates, especially root limitation (Arp, 1991; Thomas and Strain, 1991). However, there remain great uncertainties in the physiological mechanisms of acclimation, preventing the process from general parameterization. Although some ecophysiological models addressed the nature of acclimation (Thornley, 1991; Rastetter and Sgaver, 1992; Hikosaka, 1997), no global model could introduce the process into simulation exercise. If the acclimation mechanism includes the regulation of gene expression (Van Oosten and Besford, 1996; Moore et al., 1998), modeling will need further information at the molecular scale.

(4) *CO₂ dependence of respiration.*

Not only stomatal conductance and photosynthesis, but also respiration can change with increasing ambient CO₂ level (Amthor, 1991), as suggested by many experimental researches (e.g. Amthor et al., 1992; Ziska and Bunce, 1994; Drake et al., 1999). Since autotrophic plant respiration is also a substantial

component in the ecosystem carbon dynamics (86 Pg C yr^{-1} , cf. Chapter 4), variation in the process can complicate the estimation of atmosphere-biosphere CO_2 exchange under changing environment. The mechanisms of respiratory response to CO_2 increase are composed of two processes: (I) direct inhibition at the biochemical level, and (II) indirect reduction via diluted nitrogen concentration (Wullschleger et al., 1994). Although some studies imply that the respiration reduction under elevated CO_2 level would acclimate with time (Drake et al., 1997), it is uncertain that the respiration change is negligible in a simulation of the future carbon dynamics (as done in Chapter 6).

(5) *General view of the modulation of canopy conductance.* Leaf area index (*LAI*) and canopy conductance have special importance in considering the atmosphere-biosphere interaction (Ito and Oikawa, 1999). While *LAI* is accessible by optical procedures at plot to regional scales, vegetation conductance can be measured only at the single-leaf scale (i.e. stomatal conductance by porometric study), although some indirect methods applicable to larger scales have been designed (e.g. Omasa et al., 1985; Granier and Breda, 1996). In consequence, most models adopt semi-empirical parameterizations of stomatal conductance at the ecosystem to global scales (e.g. Jarvis, 1976; Ball et al., 1987). Although these parameterizations imitate the instantaneous behavior of stomatal closure under elevated CO_2 level, they lack the ecological view of water use efficiency (Cowan, 1977, 1986) and then may be insufficient for the purpose of prediction. (Fortunately, Drake et al. (1997) suggest that there is little evidence that stomatal conductance acclimates to elevated CO_2 .) The author believes that establishing a general mechanistic parameterization of vegetation conductance is one of the challenges of high priority.

(6) *Phenological regulation.* In the current models, plant phenological cycle has been incorporated only in empirical ways; e.g. leaf emergence and shedding happen in prescribed days of the year (Janecek et al., 1989; Kaduk and Heimann, 1996). In addition, no global model considers the phenological shift of herbaceous plants during their growing period, from vegetative stage to reproductive stage. However, several recent studies suggest that global warming induced by atmospheric CO_2 rise can change the phenological schedule

of natural ecosystems, especially at middle to high latitudinal zones (Navas et al., 1997; Starr et al., 2000). The elongation of growing period owing to climate change has been emphasized since the study of Myneni et al. (1997), who pointed out the relationship between plant growth, satellite vegetation index, and atmospheric CO₂ concentration. Therefore, additional field studies to parameterize the phenological cycle are strongly required.

(7) *Importance of high latitude tundra and wetland.* The equilibrium simulation in Chapter 4 showed that northern ecosystems may accumulate a huge amount of below-ground carbon, and the prediction in Chapter 6 suggests that northern latitudes would be severely affected by global warming. Accordingly, carbon dynamics in the northern ecosystems, i.e. boreal forests, tundras, and wetlands, should deserve investigations. Indeed, a vast area of northern tundras and wetlands (in North America and Siberia) gather attentions from researchers (e.g. Oechel et al., 1993; Christensen et al., 1999), in terms of the current and future carbon balance.

(8) *More sensitive regions to environmental change.* The correlation analysis in Chapter 5 showed that there are considerable heterogeneities in the ΔT - ΔNEP relationship; such subtropical regions as eastern Australia, western South Africa, western India, and middle South America realized stronger negative correlation coefficients. These regions exhibited remarkable anomalies in the ENSO years. On the other hand, the prediction run in Chapter 6 showed that there are especially sensitive or vulnerable regions to global environmental change. As a result of CO₂ doubling (cf. Fig. 6-7a), such subtropical arid regions as India, southern Australia, and eastern South Africa increase *NPP* to large extent, and most of tropical forests in South America, Africa, and Southeastern Asia, accumulate a large amount of extra carbon. After incorporating the effect of global warming (cf. Figs. 6-7b to 6-7d), a part of North America and Siberia may undergo larger impacts in *NPP* and carbon storage, while the importance of tropical forests as a carbon sink may be reduced. The boreal regions, where are expected to lose a substantial amount of soil carbon (cf. Fig. 6-8), may be worth paying particular attention.

Table 7-1. Comparison of estimations among global studies, with respect to total *NPP* , radiation use efficiency (*RUE*), and plant and soil carbon storage.

[illegible]