Development and Validation of Hourly Based *Sim-CYCLE Fine* in a Temperate C₃/C₄ Coexisting Grassland

Lee, G. Z.*, P. Z. Lee, W. S. Kim[1] and T. Oikawa

Institute of Biological Sciences, University of Tsukuba, Tsukuba, Ibaraki 305-8572, Japan

[1]*National Institute for Agro-Environmental Science, 3-1-3 Kannondai Tsukuba-shi Ibaraki 305-8604, Japan*

ABSTRACT: We developed a local-scale ecophysiological model, *Sim-CYCLE Fine* by modifying *Sim-CYCLE* which was developed for a global scale simulation. *Sim-CYCLE Fine* is able to simulate not only carbon fluxes but also plant growth with various time-steps from an hour to a month. The model outputs of CO_2 flux and biomass/*LAI* were highly reliable; we validated the model results with measurements from the eddy covariance technique and the harvest method (R^2 values of around 0.9 for both). The results suggested that the phenology and the seasonal dynamics of the C₃/C₄ plant communities affected significantly the carbon fluxes and the plant growth during the plant growing season.

Key words: Biomass, CO_2 flux, Ecophysiological model, *LAI*, Plant seasonal dynamics

INTRODUCTION

Ecophysiological models have been developed to link with global circulation models (e.g. IBIS by Foley *et al.* 1998, LPJ by Sitch *et al.* 2003) and/or to use remote-sensing data (e.g. FOREST-BGC by Running and Coughlan, 1988). Nowadays researchers are making an effort to develop the models with higher resolution temporally and spatially, including various plant ecophysiological parameters (IPCC 2001). For developing high-resolution models, researchs are needed for the parameterization of such plant physiological features as dominant species, the ecological features with seasonality of these species, and the correlation among plant species in the community.

Generally, ecophysiological models are classified into global- and local-scale models. Models for global scale simulations (e.g. TEM by Raich *et al.* 1991, CASA by Potter *et al.* 1993, CEVSA by Cao and Woodward 1998, *Sim-CYCLE* by Ito and Oikawa 2000) have sparse temporal and spatial scales (around monthly-time-steps/ degree square) and are relatively simple in the application of ecophysiological parameters. On the other hand, models for the local scale simulations (e.g. G' DAY by McMurtrie *et al.* 1992, ASPECTS by Rasse *et al.* 2001, canok by Wang *et al.* 2002) were made with finer temporal and spatial scales (around hourly-time-steps/spot scale) and relatively finer parameterization for various species and seasonal change.

Considering the advantages and disadvantages of these models, it is suitable to use the structure, scheme, and parameters when developing high-resolution models, but there are some problems for the direct adaptation of the results from local scale models. At first, developed ecophysiological models lack interaction with each other, that is, developed model structures and schemes could not be easily applied to other models – e.g. allocation, phenology, and canopy integration method (cf. Arora 2002). The other problem is that most developed parameters for the purpose of high-resolution analysis were not directly applied to other regions. Until now, sufficient parameters for various regions/vegetations have not been developed. For example, the model research for grasslands on which is distributed various types of vegetation and the vegetation distribution is easily changed, was less sufficient than that for forests.

The aim of this research was to develop a high-resolution model, named *Sim-CYCLE Fine* (Simulation model of Carbon cYCle in Land Ecosystems for Fine resolution) using the structures and schemes of *Sim-CYCLE* (Ito and Oikawa 2000), and to validate the model reliance with data from the eddy correlation technique (CO_2 flux) and harvesting method (biomass and *LAI*). Also, we estimated the changes of the various carbon fluxes in a C₃ and a C₄ plant community.

MODEL DESCRIPTION

Outline

Sim-CYCLE Fine was designed for having finer temporal resolution than the original model, *Sim-CYCLE* by Ito and Oikawa (2000, 2002), which is a compartment, process-based, and prognostic model. The structure and basic processes of this model for carbon fluxes and plant growth are same with the original model.

* Corresponding author; Phone: +81-29-853-4531, Fax: +81-29-853-6661, e-mail: s005609@ipe.tsukuba.ac.jp, or gilzae@hanmail.net

However, *Sim-CYCLE Fine* differs from the original model in three ways: 1) the carbon fluxes of dominant species were calculated with an hourly time-step while *Sim-CYCLE* is done with a monthly time-step, 2) we used cumulative degree days (cf. Eq. 18) to estimate the seasonal changes of each vegetation type while *Sim-CYCLE* adopted the monthly average temperature, and 3) three ecophysiological parameters were changed seasonally (cf. Table 2) while these values were constant in the original model.

The items of input data (Fig. 1) are the same as those for the original model, which are hourly mean meteorological variables (cf. Appendix: List of Symbols and Abbreviations): *TA*, *TG*, *TS*, *PR*, *WV*, *Rs*, *VPD*, and CO_2 concentration. The initial values of prognostic variables were as follows: leaf and stem were 0 g C m^{-2} because they belonged to the temperate grassland; however, when F_{NEP} was going to near 0 g C m^{-2} year^{-1} using the micrometeorological input data of 1999 year in the experimental site (cf. Ito and Oikawa 2002), spin-up was carried out for the initial values of root, litterfall, and mineral soil.

Ecosystem Carbon Flux

Carbon pool (*WE*) in the given ecosystem is composed of plant biomass (*WP*) and soil organic carbon (*WS*). *WP* is composed of three compartments: foliage (*WP$_F$*), stem (*WP$_S$*), and root (*WP$_R$*). *WS* is comprised of two compartments: litter (*WS$_L$*) and mineral soil (*WS$_{MS}$*).

$$WE = WP + WS \tag{1a}$$
$$WP = WP_F + WP_S + WP_R \tag{1b}$$

$$WS = WS_L + WS_{MS} \tag{1c}$$

Atmosphere-biosphere CO_2 exchange occurs through three major processes: Gross primary production (F_{GPP}), Plant respiration (F_{RP}), and Soil respiration (F_{RS}) (see the functions in the next section). In this model, hourly net primary production (F_{NPP}) and net ecosystem production (F_{NEP}) are defined as follows:

$$F_{NPP} = F_{GPP} - F_{RP} \tag{2}$$
$$F_{NEP} = F_{NPP} - F_{RS} \tag{3}$$

Here, the value of F_{NEP} represents the CO_2 exchanges between atmosphere and plant community including soil, which is the same as the value of CO_2 flux measured by the eddy covariance technique.

Photosynthesis

Single leaf photosynthetic rate (*PC*) is the most fundamental process in F_{GPP}:

$$PC = \frac{PC_{SAT} \cdot QE \cdot PPFD}{PC_{SAT} + QE \cdot PPFD} \tag{4}$$

where PC_{SAT} is light-saturated single-leaf photosynthetic rate, QE is quantum yield, $PPFD$ is photosynthetically active photon flux density. PC_{SAT} is a function of temperature, CO_2 level, and soil water, and it is different among biome types between C_3 and C_4 species.
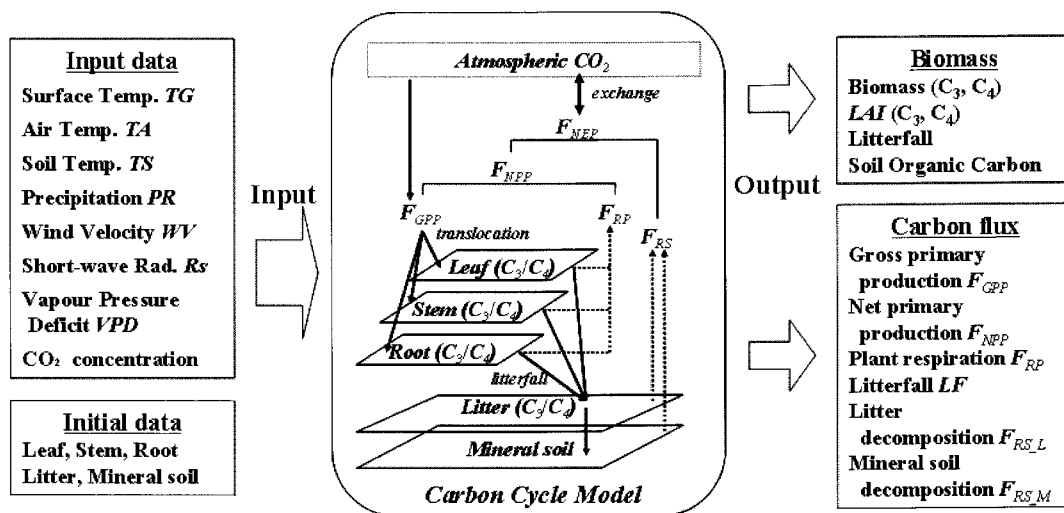

Fig. 1. The schematic carbon cycle of *Sim-CYCLE Fine*. The carbon storage of terrestrial ecosystems is divided into five compartments: foliage, stem, root, litter, and mineral soil. Carbon fluxes among the compartments include gross primary production F_{GPP}, translocation of photosynthate, litterfall, plant respiration F_{RP}, and soil heterotrophic respiration F_{RS}. The solid arrow from the atmosphere indicates the carbon input from the atmosphere to the plant community and the dotted lines indicate the carbon output.

$$PC_{SAT} = PC_{MAX} \times \frac{(TG - T_{MAX})(TG - T_{MIN})}{(TG - T_{MAX})(TG - T_{MIN}) - (TG - T_{OPT})^2}$$

$$\times \frac{CD_i - CD_{CMP}}{KM_{CD} + CD_i} \times \frac{SW_{LOW}}{KM_{SW} + SW_{LOW}} \quad\quad\quad (5)$$

where PC_{MAX} is the potential maximum value of PC_{SAT} under optimal conditions. TG is surface temperature and $T_{MAX, MIN, OPT}$ is maximum, minimum, and optimum temperature for photosynthesis (Table 1). It is well known that PC_{SAT} of C_4 species is higher than that of C_3 species (Pearcy and Ehleringer, 1984). CD_i is leaf intracellular CO_2 concentration and CD_{CMP} is the CO_2 compensation point of photosynthesis. SW_{LOW} is soil water in the lower part (10 cm deep). KM_{CD} (C_3 plant is 60 and C_4 plant is 5) and KM_{SW} (C_3 plant and C_4 plant are 0.30) are parameters. CD_{CMP} of C_3 species greatly differs from that of C_4 species: C_4 species have a low CD_{CMP} (here, 5 ppmv) but C_3 species have higher (around 50 ppmv) and variable CD_{CMP} (Brooks and Farquhar 1985).

Monsi and Saeki (1953) derived the hourly canopy photosynthetic rate (F_{GPP}) by scaling up Eq. (4):

$$GPP = \int^{LAI} PCdLAI$$

$$= \frac{PC_{SAT}}{k} * \ln \frac{1 + k_{leaf} \cdot QE \cdot PPFD_{IN} / PC_{SAT}}{1 + k_{leaf} \cdot QE \cdot PAR \cdot \exp(-k_{leaf} \cdot LAI) / PC_{SAT}} \quad (6)$$

Table 1. The constant parameters for ecophysiological characteristics of C_3 plants and C_4 plants in *Sim-CYCLE Fine*

Constant parameters		C_3 plants	C_4 plants
k_{leaf} (dimensionless)		0.7	0.35
Photosynthetically optimal temperature T_{OPT} (℃)		22	30
Photosynthetically maximum temperature T_{MAX} (℃)		40	50
Photosynthetically minimum temperature T_{MIN} (℃)		0	6
Specific growth respiration (at the case in 15℃) RM_X (mgCg^{-1}Ch^{-1})	Foliage	0.071	0.071
	Sterm	0.017	0.01
	Root	0.021	0.01
Specific growth respiration RG_X (gCg^{-1}C)	Foliage	0.4	0.3
	Sterm	0.15	0.13
	Root	0.15	0.15
Specific litterfall rate β_X (mgCg^{-1}Ch^{-1})	Foliage	0.096	0.063
	Sterm	0.029	0.042
	Root	0.042	0.042
Specific soil respiration $RS_{L,M}$ (mgCg^{-1}Ch^{-1})	Litter	0.038	
	Humus	0.008	
Q_{10}		4.9	4.9

where k_{leaf} is the light attenuation coefficient (C_3 plant is 0.7 and C_4 plant is 0.35), differing among plant species and the incident angle of light (Ito and Oikawa 2002). $PPFD_{IN}$ is incident photosynthetically active photon flux density in a canopy and is a function of k_{leaf} and LAI:

$$PPFD_{IN} = PPFD \cdot \exp(-k_{leaf} \cdot LAI) \quad\quad\quad (7)$$

Plant Respiration

The plant respiration rate (F_{RP}) is composed of maintenance respiration rate (F_{RP_M}) and growth respiration rate (F_{RP_G}) (e.g. Amthor 1989),

$$F_{RP\_M} = RM_X \cdot \exp \left[\frac{\ln(Q_{10})}{10} (TG - 15) \right] \cdot WP_X \quad\quad (8)$$

where WP_X is the biomass of each organ (subscript X becomes leaf, stem, or root) and TG is surface temperature.

$$F_{RP\_G} = RG_X \cdot \triangle WP_X = RG_X \cdot \frac{PT_X}{1 + RG_X} \quad\quad\quad (9)$$

where $\triangle WP$ is the hourly change of biomass (cf. Eq. 12) and PT is the photosynthate that is translocated into each organ (cf. Eq. 10). RM_X (mg C g^{-1}C h^{-1}) and RG_X (g C g^{-1}C) are specific respiration rates (cf. Table 1).

Translocation and Litterfall

Photosynthate translocations into each organ (PT_X) and litterfall from each organ (LF_X) are calculated as follows:

$$PT_{X = f, s, r} = \alpha_X(F_{GPP} - F_{RP\_M}) \quad\quad\quad (10)$$

where subscript f, s, and r indicate foliage, stem, and root and α_X is the allocation ratio (%) of foliage : stem : root (35 : 45 : 20 in C_3 plants and 35 : 20 : 45 in C_4 plants). This ratio, however, is changed through the relation with optimal leaf area index (LAI_{OPT}) (Kuroiwa 1966, Ito and Oikawa 2002), that is, the ratio for foliage decreased when LAI is close to LAI_{OPT} (LAI_{OPT} is the function of $PPFD_{IN}$, TA, SW, and CO_2 concentration), and then the residual PT goes to other organs.

$$LF_{X = f, s, r} = \beta_X \times WP_X \quad\quad\quad\quad (11)$$

where β_X is specific litterfall rates for each organ presented in Table 1.

Biomass and *LAI*

Hourly change of biomass ($\triangle WP$) is calculated by using hourly fluxes of photosynthate translocations (Eq. 10), plant growth respiration (Eq. 9), and litterfall (Eq. 11):

$$\triangle WP_{X=f, s, r} = PT_X - F_{RP\_GX} - LF_X \quad \text{(12)}$$

Monthly changes of plant biomass are the result of a chain series of microscopic carbon dynamics in the plant community.

$$WP_{X, i} = WP_{X, i-1} + \sum \triangle WP_X \quad \text{(13)}$$

where subscript *i* indicates the month.

The leaf area index (*LAI*) which is the prognostic variable for integrating canopy photosynthetic rate (Eq. 6) is obtained from the calculated leaf biomass (*WP*$_f$):

$$LAI = SLA \cdot WP_f \quad \text{(14)}$$

where *SLA* is the specific leaf area, and it changes seasonally (Table 2).

Decomposition

Because organic carbon composition of the litter layer differed greatly from that of the soil layer, soil respiration rate (F_{RS}) was divided into litterfall decomposition (F_{RS_L}) and mineral soil decomposition (F_{RS_MS}):

$$F_{RS\_L} = RS_L \cdot WS_L \cdot \exp\left[308.56 \left(\frac{1}{56.02} - \frac{1}{TS_{up} + 46.02}\right)\right]$$

$$\cdot \left(WA_0 + \frac{SW_{up}}{KM + SW_{up}}\right) \quad \text{(15)}$$

$$F_{RS\_MS} = RS_{MS} \cdot WS_{MS} \cdot \exp\left[308.56 \left(\frac{1}{56.02} - \frac{1}{TS_{low} + 46.02}\right)\right]$$

$$\cdot \left(WA_0 + \frac{SW_{low}}{KM + SW_{low}}\right) \quad \text{(16)}$$

where WS_L and WS_M are the amount of litter and mineral soil, WA_0 is the minimum value of soil water (C_3 plant is 20% and C_4 plant is 10%) and *KM* (C_3 plant is 0.2 and C_4 plant is 0.05) is a parameter related to responsiveness. RS_L (mg C g^{-1}C h^{-1}) and RS_{MS} (mg C g^{-1}C h^{-1}) are the specific respiration rates. The soil temperature TS_{up} is at 5 cm depth and TS_{low} is at 50 cm depth, and the soil water SW_{up} is upper part at 10 cm depth and SW_{low} is from 10 cm to 200 cm.

C₃/C₄ Mixed Community

Carbon fluxes and plant growth of each C_3 and C_4 plant community were calculated as follows:

$$X = X_{C3} \times PGC_{C3} + X_{C4} \times PGC_{C4} \quad \text{(17)}$$

where PGC_{C3} and PGC_{C4} are ground coverage by C_3 and C_4 plant communities ($PGC_{C3} + PGC_{C4} = 1$). *X* was applied to the items of carbon fluxes and plant growth.

Plant Ecophysiological Parameters

The fundamental model parameters were classified into constants and seasonally changing parameters. The constant parameters (Table 1) in *Sim-CYCLE Fine* followed mainly from the temperate grassland ones used in *Sim-CYCLE* (Ito and Oikawa 2000). However, some constants which specify ecophysiological characteristics of a C_3 and a C_4 plant altered to more realistically simulate the dominant species in the experimental site, for example, leaf angle (k_{leaf}) and Q_{10} by the measurements in Table 1 (Yokoyama and Oikawa 2000, Li *et al.* 2003).

Plant ecophysiological characteristics between germination and senescence are largely different (Murthy *et al.* 1997, Leuning *et al.* 1998, Verhoef and Allen 2000, Froking *et al.* 2002) even if these periods have similar climatic conditions such as temperature and soil water. However, many ecological models have neglected the seasonal changing parameters (or variables) of these characteristics because of the difficulty of application by insufficient data. In this model, three parameters which were treated as constant in original model were changed seasonally (Table 2) — the specific maximum photosynthetic rate (PC_{MAX}: Eq. 5), the specific leaf area (*SLA*: Eq. 14), and the ground coverage of C₃/C₄ plants (*PGC*: Eq. 17); Seasonally changing parameters were used as like variables in *Sim-CYCLE Eddy* however, we call these as 'seasonally changing parameter' for the comparison with original model. They were considered to largely affect the dynamics of plant ecophysiological cha-

Table 2. The seasonally changing parameters of the C_3 and C_4 plant communities

Seasonally Changing parameters		Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.
PC_{MAX}	C₃Plants	18.0	18.0	18.0	17.1	17.1	13.5	10.8
(μmolCO₂m^{-2}s^{-1})	C₄Plants	24.7	26.0	26.0	26.0	26.0	18.7	15.6
SLA	C₃Plants	156	149	143	137	131	125	119
(cm²g^{-1}DW)	C₄Plants	168	160	152	145	137	129	121
PGC	C₃Plants	60	60	56	48	41	40	40
(%)	C₄Plants	40	40	44	52	59	60	60

racteristics. The seasonal dynamic values of these parameters were decided as follows: the value of PC_{MAX} which was calculated using the changing ratio by Murthy (1997) with the mean value from Ito and Oikawa, (2002); and *SLA* and *PGC* were calculated by referring to the measured *LAI* and biomass (Yokoyama and Oikawa 2000).

Timing of emergence and senescence differ according to plant species and their differences are generally governed by cumulative temperature, which limits the potential growth period of each species as long as there is no water stress (Winslow *et al.* 2003). In this model, cumulative degree-days $(^{\circ}D_c)$ was used to estimate the plant growing season. Degree-days $(^{\circ}D)$ is estimated as follows:

$$^{0}D = T_m - x \quad\quad\quad\quad\quad\quad\quad (18)$$

where T_m is daily mean air temperature and x is the threshold temperature for initiation of emergence or senescence; the values of x are 5℃ for C_3 plants and 8℃ for C_4 plants. In the case of C_3 plants, emergence is started when the cumulative degree-days exceed 104 $^{\circ}D_c$ and in a case of C_4 plants, over 75 $^{\circ}D_c$. Senescence is started when cumulative degree-days has a negative value but it is only started after emergence. Also, senescence stops when $^{\circ}D_c$ turns positive during this stage. This scheme made this model more realistic when the temperature fluctuated occurred around the threshold temperature.

SITE DESCRIPTION

Model simulation was performed for a C_3/C_4 co-existing grassland located at the Terrestrial Environment Research Center (TERC), University of Tsukuba (36.1° N, 140.1° E, 2ha, 27m asl). This site was established in 1975 by clear-cutting of a red-pine (*Pinus densiflora*) forest to monitor long-term meteorological and hydrological processes and vegetation dynamics of the grassland. The field is circular with a diameter of 160m and has a 30 m tall meteorological observation tower at the center. The study area is in a zone of humid climate and has a rainy season (from mid June to late July). The annual short-wave radiation Rs is 4800 MJ m^{-2}, the mean annual air temperature (*TA*) is 14 ℃, the mean annual vapor pressure deficit (*VPD*) is 5.1 hPa, and the annual precipitation is 1,300 mm.

The grassland vegetation is composed of 54 perennials (46 C_3 species and 8 C_4 species), and the dominant species are *Solidago altissima* (C_3, *Compositae*), *Miscanthus sinensis* (C_4, *Gramineae*), and *Imperata cylindrica* (C_4, *Gramineae*) (Yokoyama and Oikawa, 2000). The dynamics of the species composition demonstrates seasonal succession repeatedly every year; the C_3 species dominates in the early growing period but the C_4 species dominates in the

summer and autumn. Such grassland commonly exists in fragments over areas of central and northern Japan (Hayashi 1994, Yamamoto *et al.* 1997).

VALIDATION DATA

The model validation was performed with data measured by two different methods in 1999; the data of eddy covariance method (Li *et al.* 2003) were selected under conditions of no-rain-event, proper wind condition (u* > 0.2), and wind direction (considering the fetch) as well as the data of harvesting method (Yokoyama and Oikawa 2000) were measured directly. The eddy covariance technique (micrometeorological method) is able to measure the continuous carbon flux of a whole community with high accuracy (Law *et al.* 2000, Baldocchi *et al.* 2001), but this technique has difficulty classifying the flux from each vegetation in multi-species communities (Baldocchi and Wilson 2001). The harvesting method, even though it had only monthly data of biomass and *LAI*, can classify C_3 and C_4 plant communities.

The comparison to the eddy covariance data was carried out using daytime CO_2 flux (F_{NEP}): hourly comparison during two different periods and daily (daytime mean) comparison during one year. Validation periods for hourly time-resolution were divided into two stages: the growing period of C_3 plants (30 May to 3 June) and the growing period of C_4 plants (2 to 6 August). The daily time-resolution measured data covered 119 days with no missing data; they covered most of the plant growing period from May to October. The nighttime data were excluded due to low friction velocity (Baldocchi and Meyers 1998, Anthoni *et al.* 1999, Aubinet *et al.* 2000). Gaps in the data were caused by rain or the insufficient fetch in the night time (Li *et al.* 2003).

The comparison to the harvesting data was carried out monthly. Biomass and *LAI* of C_3 and C_4 plant communities were compared with model outputs.

RESULTS AND DISCUSSION

Validation of CO$_2$ Exchange

We used daytime CO_2 flux from the eddy covariance technique to validate the whole plant community. The model validation of hourly CO_2 flux was conducted in spring and then again in summer (Fig. 2), under different micrometeorological and plant ecophysiological conditions. Period A was a fast growing period and plant growth was better for C_3 plants than for C_4 plants due to relatively low temperatures (15~25 ℃). Period B was more suitable for growth of C_4 plants due to higher temperatures (over 25 ℃). *LAI* of each period was 2.3 and 4.7, respectively.

The daily patterns of the measured and modeled F_{NEP} showed the good accordance (Fig. 2). A high coefficient of determination (R^2) was obtained from the regression analysis for both period A (R^2 = 0.89) and period B (R^2 = 0.93). This good correspondence was acquired owing to the distinctive schemes of the separated calculation for C_3 and C_4 plant community with the seasonally changing parameters (Table 2).

The regression results (slope, intercept, and determination coefficient) for period A were not as good as those for period B (lower panel in Fig. 2). The poorer fit was caused by the existence of various plant species that were sporadically distributed in the experimental site in addition to the dominant species (Yokoyama and Oikawa 2000). Consider the distribution of C_3 plants other than the dominant species in period A; *Artemisia princeps*, *Equisetuma rvense*, and *Festuca arundinacea* occupied 22%, 13%, and 10%, respectively. In period B, these percentages declined to 7%, 1%, and 0%, respectively. Other non-dominant species occupied just small percentages of the C_4 plant community; only 7% was occupied by *Andropogon virginicus* during period B. Since the model was calculated using only the ecophysiological characteristics for the dominant species, the model performance for period A was inferior than that for period B.

The value of the maximum F_{NEP} in period A was smaller than that in period B because the increasing rate of F_{GPP} by increased LAI was larger than the increasing rate of ecosystem respiration rate (F_{RE} = F_{RS} + F_{RP}). In the rapid growth period – period A was the rapid growth period for C_3 plants and period B for C_4 plants – plant growth was principally generated by leaf growth rather than stem and root in order to increase photosynthetic benefit more than neighbors (Kuroiwa 1966); thus, plant respiration rate increased less than photosynthetic rate. Moreover, in the case of this experimental site, the ecophysiological characteristics of each C_3 and C_4 plant community also affected the value of F_{NEP} of each period; LAI was changed from 1.2 to 1.6 in the C_3 plant community and changed from 0.9 to 3.1 in the C_4 plant community, because C_4 species maintained higher photosynthetic capability than C_3 species under the non-stress temperature and water conditions (Ehleringer and Björkman 1977, Sage *et al.* 1999).

The seasonal pattern of daytime F_{NEP} agreed well not only for the plant growing period but also for the senescence period (October and November) (Fig. 3). These results were mainly gained by applying the cumulative degree-days and the seasonal dynamic parameters (e.g. PC_{MAX} and SLA in Table 2). Even though the ecological features and physiological capacities changed rapidly
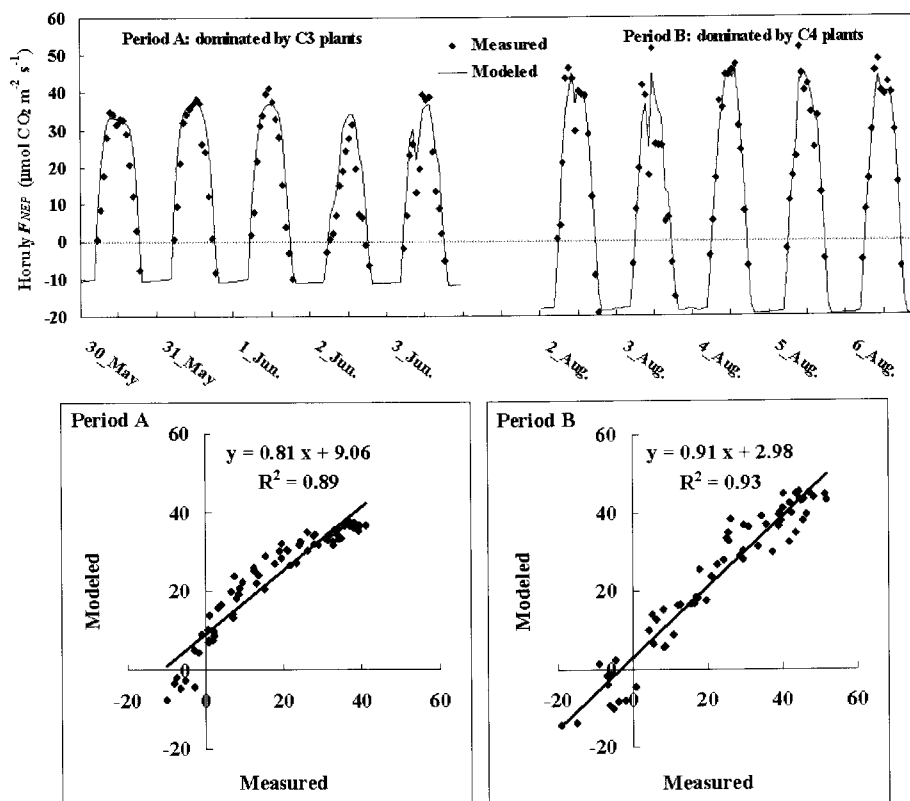

Fig. 2. Measurement and model hourly F_{NEP}: daily patterns (upper panel) and regression analysis (lower panel). The nighttime CO_2 flux is excepted when solar radiation Rs $\leq$ 0. Period A was from 30 May to 3 June and period B was from 2 to 6 August.
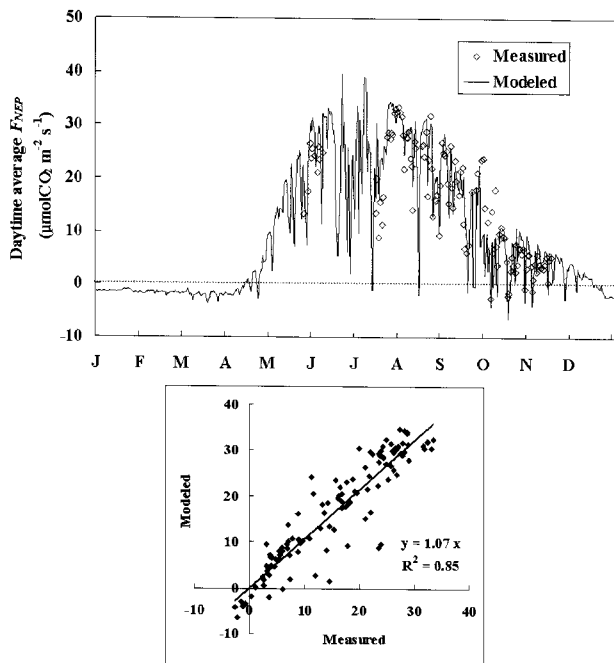
Fig. 3. Daytime mean measurement and modeled F_{NEP}: seasonal pattern (upper panel) and regression analysis (lower panel). Missing measured data was caused by instability of the fraction velocity, a rain event, and change of main wind direction. The number of measured days was n =119 days.

Fig. 4. The seasonal changes of F_{NEP} (CO_2 flux) between *Sim-CYCLE Fine* and the original model *Sim-CYCLE*.

during the senescence period — e.g. maximum photosynthetic rate (Murthy 1997), leaf area (Lenuing *et al.* 1998), and biomass (Froking *et al.* 2003) — the good agreement was encouraging because many comparable model studies have showed the low reproducibility for this period (cf. Arora 2002).

Although direct comparison is difficult, our result was better than other validation researches which showed relatively good agreement between measured and modeled data; a savanna (one month; CO_2 flux: slope = 0.82, r^2 = 0.81 by Verhoef and Allen 2000), a wheat crop (two months; CO_2 flux: slope = 0.71, r^2 = 0.71 by Lenuing *et al.* 1998), and a temperate broadleaved forest (whole growth period; CO_2 flux: slope = 1.14, r^2 = 0.83 by Baldocchi *et al.* 2001). Moreover, *LAI* which was the integrating variable for calculating F_{GPP} (Eq. 6), was obtained not by input but by calculation, and it was important by meaning of that the ecophysiological processing method was able to calculate the canopy photosynthetic rate with no use of measured *LAI*.

From the comparison of F_{NEP} (net carbon exchanges) between *Sim-CYCLE Fine* and *Sim-CYCLE* (Fig. 4), F_{NEP} of *Sim-CYCLE Fine* was higher than that of original model for the plant growing period; however, F_{NEP} of *Sim-CYCLE Fine* was smaller for the early growing period. The causes of these differences varied by season: At first, the difference of F_{NEP} between models for the early growth
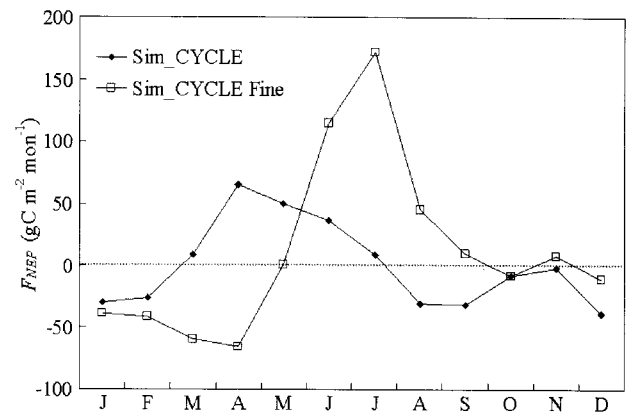
period from March to April was caused by the difference of starting time of emergence; the original model started emergence from March but our model started it from April; thus, the original model calculated higher plant growth rate as well as F_{NEP} in this period. Secondly, two factors caused the difference of F_{NEP} during the plant growth period from May to September. One was the ecophysiological parameters of *Sim-CYCLE Fine* which has lower *SLA* and higher PC_{MAX}; these differences made F_{GPP} of this model increase. The other was the increased F_{RP} (negative effect to F_{NEP}) according to plant growth. Here, the effect of F_{RP} was larger in the original model because of the earlier plant growth after emergence. Lastly, the difference of F_{NEP} for the senescence period after October was mainly caused by *LAI*. Although PC_{MAX} was decreased about 40% compared to the value of it in plant growing period in this model (Murthy 1997), *LAI* was still high in this period of this model (cf. Fig. 5).

While, the original model agreed well with measurements on various vegetation (Ito and Oikawa 2000, Ito and Oikawa 2002) and the difference of the integrated annual F_{NEP} between the two models was small, the monthly results suggest that a proper ecophysiological strategy to model a seasonal effects is important to estimate and predict the real seasonal change of plant communities (cf. Arora 2002).

Validation of Biomass and *LAI*

We measured the CO_2 flux for entire canopy level with the eddy covariance technique. However, in the case of communities with both C_3 and C_4 plants co-existing, origins of CO_2 flux are complex and the data from eddy covariance technique could not distinguish these fluxes (Verhoef and Allen 2000). For our study site, which is dominated by both C_3 and C_4 species (*Solidago altissima* and *Imperata cylindrical*, respectively), we needed the supplemental data to validate the activity of C_3 and C_4 plant functional types. In the

Sim-CYCLE Fine, *LAI* and biomass were able to be estimated by the dry matter theory (Monsi and Saeki 1953) and these model outputs were validated with the measured monthly *LAI* and biomass of each functional type by the harvesting method (Yokoyama and Oikawa 2000) (Table 3).

The measured data and model outputs of *LAI* and above-ground biomass had similar seasonal patterns and magnitudes, and showed very high determination coefficients (R^2 in Table 3) for both C_3 and

Fig. 5. Measured and modeled plant growth of *LAI* (a), leaf (b), and stem (c).

C_4 plant communities (Fig. 5). In addition to the regression analysis, we also used the value of MPD (Mean Percent Difference), which permits comparison of model errors with typical uncertainties associated with measurements (Table 3); MPD was defined as follows (Anderson *et al.* 2000);

$$MPD = 100 * (\text{modeled} - \text{measured}) / \text{measured} \quad \cdots\cdots (19)$$

The MPD values also showed good agreement for every month between measured and modeled except the early growth period (underlined in Table 3). Most large differences of MPD were for the early growth period (April and May). Although the differences of the underlined MPD (Table 3) were large, the gaps of absolute value were small.

For the plant growing period from June to October accordance was satisfactory not only for determinant coefficient but also for MPD values. This result suggests that the estimated *LAI* and biomass for the plant growing season were good in both seasonal patterns (high R^2 values) and magnitudes (MPD values near 0%). Even though some MPD values showed relatively low accordance, under 30% for the plant growing period, we also regard these as satisfactory results when considering the measurement error (Moncrieff *et al.* 1992, Anderson *et al.* 2000).

Estimated Carbon Fluxes of the C_3 and C_4 Plant Communities

Sim-CYCLE Fine could estimate not only carbon fluxes but also plant growth using a mechanistic method; it was able to simulate separately each functional type of plant community (Ito and Oikawa 2002). In this research, the carbon fluxes of the C_3 and C_4 plant communities could not be directly validated by eddy correlation technique measurements. However, the dynamics of *LAI* and biomass are closely related to changes in carbon fluxes (Verhoef and Allen 2000). We indirectly validated the estimated carbon fluxes of the C_3 and C_4 plant community (Fig. 6) using the data from the harvesting method (Fig. 5).
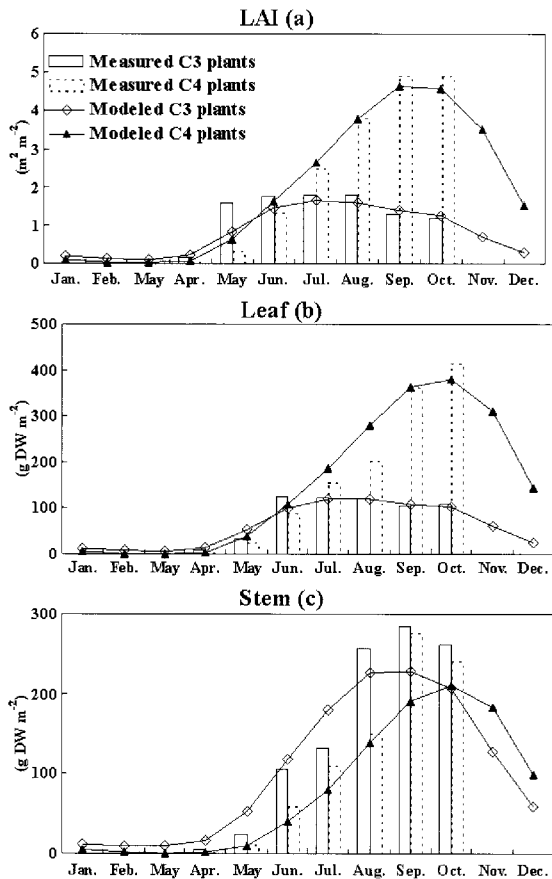
Table 3. Statistical analysis between measured and modeled plant growth during the plant growth period

Component		Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	R^2
	LAI	−150.0	32.7	6.3	8.3	12.2	−3.1	−1.7	0.90
MPD of C_3 plants (%)	Leaf	−84.6	−61.9	18.5	3.9	0.9	−2.5	4.8	0.95
	Stem	−277.4	−116.0	−11.9	−35.7	11.9	19.5	20.8	0.93
	LAI	−300.0	−197.0	−48.9	−16.4	−2.4	3.7	8.0	0.99
MPD of C_4 plants (%)	Leaf	−67.7	−53.6	−22.3	−18.8	−37.5	0.2	8.5	0.96
	Stem	7.0	13.9	33.4	27.8	8.0	30.2	13.0	0.96

MPD is mean-percent-difference. R^2 is the determination coefficient between measured and modeled data during the plant growth period.

The carbon fluxes of the C_3 and C_4 plant communities had similar seasonal patterns (Fig. 6): the both C_3 plant community and C_4 plant community had the peak values in July. However, in the case of C_3 plant community, the integrated F_{GPP}, F_{NPP} and F_{NEP} before July were larger than those after July. On the other hand, the C_4 plant community showed the opposite trend. This is because of the C_3 species have an advantage on the relatively low temperature conditions (15 to 25 ℃) and receive stress under the high temperature conditions (over 30℃), but C_4 species had a good activity at the high temperature condition (cf. Ehleringer and Björkman 1977, Pearcy and Ehleringer 1984). Additionally, C_3 species and C_4 species differ from each other during emergence (cf. Eq 18; C_3 plants started from late March and C_4 plants started from 20 April) and the photosynthetic availability (cf. Table 2; the specific maximum photosynthetic rate was larger in C_4 species than C_3 species).

The annual F_{GPP}, F_{NPP} and F_{NEP} were estimated to 3.0, 1.7, and 0.1 kg C m^{-2}year^{-1}, respectively. Here, the protion of F_{GPP} and F_{NPP} for the C_4 plants community was 57% and 56%, which was 14% and 12% larger, respectively, than those for the C_3 plants community. F_{NEP} of C_3 plants community showed net carbon source of -38.79 g C m^{-2}year^{-1} but that of C_4 plants community showed net carbon sink 155.8 g C m^{-2}year^{-1}. The magnitude of annual F_{NPP} is related to the length of the plant growing season (Baldocchi and Wilson, 2001), which is determined by the environmental conditions and plant species. The length of plant growing season in this experimental site (from April to November) was relatively longer than that of other temperate grassland regions; thus, the annual F_{NPP} in TERC was higher than that in other temperate grasslands (cf. Scurlock *et al.* 2001). However, the capacity of photosynthetic capacity of this plant community was similar to that of other temperate grassland regions without water stress. For example, the estimated maximum daily mean F_{GPP} in this experimental site (Day 188: 34.1 μmol CO_2 m^{-2} s^{-1}) was similar to that of the Shidler site in OK/USA (Day 182: 33.5 μmol CO_2 m^{-2} s^{-1}; Suyker and Verma 2001), which had relatively favorable annual precipitation (880 mm) and temperature (26.5 ℃) conditions. Moreover, although our F_{NPP} was large, in the case of grassland in Japan, the high F_{NPP} over 1.7 kg C m^{-2} year^{-1} (Scurlock *et al.* 2001) was often shown to be due to favorable temperature and precipitation, and abundant minerals in the soil.

CONCLUSION

In this paper, we developed the local scale ecosystem model named *Sim-Cycle Fine*, and simulated and validated CO_2 flux as well as biomass/*LAI* in a mixed C_3 and C_4 plant community.

This model had important characteristics as follows;

1) Each calculation was carried out with hourly-time-step

2) The C_3 and C_4 plant communities were simulated separately

3) Cumulative degree-days was used for deciding emergence and senescence

4) Seasonal dynamic parameters were applied to express the seasonal change of plant ecophysiological characteristics.

From the validation, the model outputs showed good agreement with the measurements. The hourly and daily CO_2 flux (F_{NEP}) accorded well with the data from the eddy covariance technique and the comparisons between them showed over 0.85 of determination coefficient. The estimated monthly *LAI* and biomass also showed good accordance in terms of MPD (magnitude) and determination coefficient (seasonal change) with the data from the harvesting method.

The seasonal dynamics were different between *Sim-Cycle Fine* and the original model even though the integrated annual F_{NEP} of the models were almost the same. Our results showed that the seasonal dynamics of carbon flux varied between C_3 and C_4 plant communities. Such results suggests that a proper model strategy and ecophysiological parameters are important to predict the real changes of plant community.
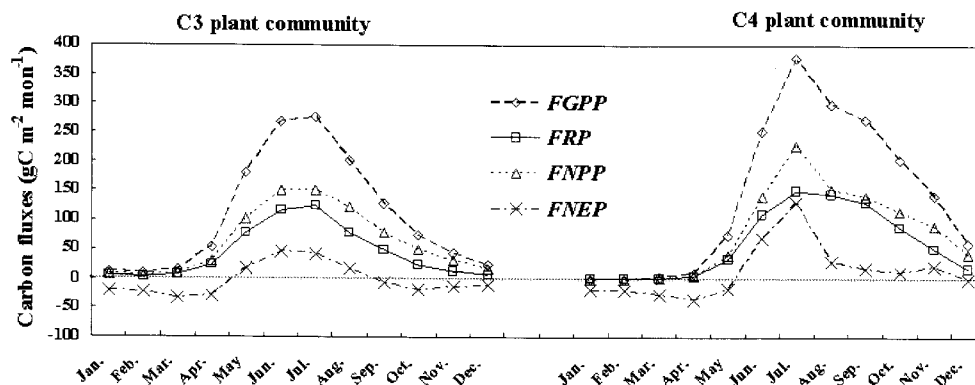

Fig. 6. The monthly estimated carbon fluxes in the C_3 and C_4 plant communities.

LITERATURE CITED

Amthor, J.S. 1989. Respiration and Crop Productivity. Springer, New York, 215 p.

Anderson, M.C., J. M. Norman, T.P. Meyers and G.R. Diak. 2000. An analytical model for estimating canopy transpiration and carbon assimilation fluxes based on canopy light-use efficiency. Agric. For. Meteorol. 101: 265-289.

Anthoni, P., B. E. Law and M. J. Unsworth, 1999. Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem. Agric. For. Meteorol. 95: 151-168.

Aubinet, M. 2000. Estimates of the annual net carbon and water exchange of European forests: The EUROFLUX methodology. Adv. Ecol. Res. 30: 114-175.

Arora, V. K. 2002. Modeling vegetation as a dynamic component in soil-vegetation-atmosphere transfer schemes and hydrological models, Rev. Geophysics, 40, 10.1029/2001RG000103.

Baldocchi, D.D., E. Falge, L. Gu, R. Olson, D. Hollinger, S. Running, P. Anthoni, C. Bernhofer, K. Davis, R. Evans, J. Fuentes, A. Goldstein, G. Katul, B. Law, X. Lee, Y. Malhi, T. Meyers, W. Munger, W. Oechel, U. K. T. Paw, K. Pilegaard, H. P. Schmid, R. Valentini, S. Verma, T. Vesala, K. Wilson and S. Wofsy. 2001. FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bull. Am. Meteorol. Soc. 82: 2415-2434.

Baldocchi, D.D. and K.B. Wilson. 2001. Modeling CO_2 and water vapor exchange of a temperate broadleaved forest across hourly to decadal time scales. Ecol. Model. 142: 155-184.

Baldocchi, D.D. and T.P. Meyers. 1998. The effects of extreme turbulent events on the estimation of aerodynamic variables in a deciduous forest canopy, Agric. For. Meteorol. 48: 117-134.

Brooks, A. and G.D. Farquhar. 1985. Effect of temperature on the CO_2/O_2 specificity of ribulose 1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. Planta 165: 397-406.

Cao, M. and F.I. Woodward. 1998. Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. Global Change Biol. 4: 185-198.

Ehleringer, J.R. and O. Björkman. 1977. Quantum yields for CO_2 uptake in C_3 and C_4 plants: dependence on temperature, CO_2, and O_2 concentration. Plant Physiol. 59: 86-90.

Foley, J. A., S. Levis, I. C. Prentice, D. Pollard and S. L. Thompson. 1998. Coupling dynamic models of climate and vegetation. Global Change Biol. 4: 561-579.

Forking, S., N.T. Roulet, T.R. Moore, P.M. Lafleur, J.L. Bubier and P.M. Crill. 2003. Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada. Global Biogeochemical Cycles 16(3): 1030-1051.

Hayashi, I. 1994. Experimental community ecology in *Miscanthus sinensis* grassland − change of species composition according to mowing frequency. Jap. J. of Ecol. 44: 161-170.

Intergovernmental Panel on Climate Change (IPCC), 2001. Climate Change 2001: the Scientific Basis. Cambridge University Press. Cambridge. UK. 48 p.

Ito, A. and T. Oikawa. 2000. The large carbon emission from terrestrial ecosystems in 1998: A model simulation. J. Meteorol. Soc. Jap. 78: 103-110.

Ito, A. and T. Oikawa. 2002. A simulation model of the carbon cycle in land ecosystems (Sim-CYCLE): A description based on dry-matter production theory and plot-scale validation. Ecol. Model. 151: 147-179.

Kuroiwa, S. 1966. Dry matter production of plants, Ecology and Evolution. A Series of Modern Biology. Iwanami Shoten. Tokyo. pp. 71-100. (in Japanese)

Law, B.E., M. Williams, P. Anthoni, D.D. Baldocchi and M.H. Unsworth. 2000. Measuring and modeling seasonal variation of carbon dioxide and water vapor exchange of a *Pinus ponderosa* forest subject to soil water deficit. Global Change Biol. 6: 613-630.

Leuning, R., F.X. Dunin and Y.P. Wang. 1998. A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. II. Comparison with measurements. Agric. For. Meteorol. 91: 113-125.

Li, S.G., C.T. Lai, T. Yokoyama and T. Oikawa. 2003. Carbon dioxide and water vapor exchange over a Miscanthus-type grassland: effects of development of the canopy. Ecol. Res. 18: 661-675.

McMurtrie, R.E., H.N. Comins, M.U.F. Kirschbaum and Y.-P. Wang. 1992. Modifying existing forest models to take account of effects of elevated CO_2. Aust. J. Bot. 40: 657-677.

Moncrieff, J.B., S.B. Verma and D.R. Cook. 1992. Intercomparison of eddy correlation carbon dioxide sensors during FIFE 1989. J. Geophys. Res. 97: 18,725-18,730.

Monsi, M. and T. Saeki. 1953. Über den Lichtfaktor in den Pfanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jap. J. Bot. 14: 22-52.

Murthy, R., S. J. Zarnoch and P. M. Dougherty. 1997. Seasonal trends of light-saturated net photosynthesis and stomatal conductance of loblolly pine trees grown in contrasting environments of nutrition, water and carbon dioxide. Plant Cell Environ. 20: 558-568.

Pearcy, R.W. and J.R. Ehleringer. 1984. Comparative ecophysiology of C_3 and C_4 plants. Plant Cell Environ. 7: 1-13.

Potter, C.S., J.T. Randerson, C.B. Field, P.A. Matson, P.M. Vitousek, H.A. Mooney and S.A. Klooster. 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. Global Biogeochem. Cycles 7: 811-841.

Raich, J.W., E.B. Rastetter, J.M. Melillo, D.W. Kicklighter, A.L. Grace, B. III Moore and C.J. Vörösmarty. 1991. Potential net primary productivity in South America: application of a global model. Ecol. Appl. 1: 399-429.

Rasse, D.P., L. Frncois, M. Aubinct, A.S. Kowalski, I.V. Walle, E. Laitat and J.C. Gérard. 2001. Modelling short-term CO_2 fluxes

and long-trem tree growth in temperate forests with ASPECTS. Ecol. Model. 141: 35-52.

Running, S.W. and J.C. Coughlan. 1988. A general model of forest ecosystem process for regional applications I. hydrologic balance, canopy gas exchange and primary production processes. Ecol. Model. 42: 125-154.

Sage, R.F., D.A. Wedin and M. Li. 1999. The biogeography of C_4 photosynthesis: patterns and controlling factors. In: Sage, R.F., Monson, R.K. (Eds.), C_4 Plant Biology. Academic Press, San Diego, CA. pp. 313-373.

Scurlock, J.M.O., G.P. Asner and S.T. Gower. 2001. Worldwide Historical Estimates and Bibliography of Leaf Area Index, 1932-2000. ORNL Technical Memorandum TM-2001/268, Oak Ridge National Laboratory, Oak Ridge, Tennessee, U.S.A.

Sitch, S., B. Smith, I.C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J.O. Kaplan, S. Levis, W. Lucht, M.T. Sykes, K. Thonicke and S. Venevsky. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Glob. Change Biol. 9: 161-185.

Verhoef, A. and S.J. Allen. 2000. A SVAT scheme describing energy and CO_2 fluxes for multi-component vegetation: calibration and test for a Sahelian savannah. Ecol. Model. 127: 245-267.

Wang, S.S., R.F. Grant, D.L. Verseghy and T.A. Black. 2001. Modelling plant carbon and nitrogen dynamics of a boreal aspen forest in CLASS – the Canadian Land Surface Scheme. Ecol. Model. 142: 135-154.

Winslow, J.C., E.R. Hunt and C.P. Stephen. 2003. The influence of seasonal water availability on global C_3 versus C_4 grassland biomass and its implications for climate change research. Ecol. Model. 163: 153-173.

Yamamoto, Y., Y. Saito, H. Kirita, H. Hayashi and N. Nishimura. 1997. Ordination of vegetation of Miscanthus-type grassland under some artificial pressure. Grassland Science 42: 307-314.

Yokoyama, T. and T. Oikawa. 2000. Seasonal changes of LAI and Biomass of a C_3/C_4 mixed Grassland in 1999 in the Terrestrial Environmental Research Center. Bulletin of Environmental Research Center, University of Tsukuba. No.1: 67-71. (In Japanese)

Appendix

List of Symbols and Abbreviations (unit)

CD_{CPM} compensation CO_2 concentration for photosynthesis (ppmv)

CD_i intercellular CO_2 concentration (ppmv)

F_{GPP} gross primary production (μmol CO_2 m^{-2} s^{-1} or gCm^{-2} time^{-1})

F_{NEP} net ecosystem production, which same with CO_2 flux from eddy covariance technique (μmol CO_2 m^{-2} s^{-1} or gCm^{-2} time^{-1})

F_{NPP} net primary production (μmol CO_2 m^{-2} s^{-1} or gCm^{-2} time^{-1})

F_{RP} plant autotrophic respiration [$=F_{RP\_G}$, + F_{RP_M}] (μmol CO_2 m^{-2} s^{-1} or gCm^{-2} time^{-1})

F_{RP_G} plant growth respiration (μmol CO_2 m^{-2} s^{-1} or gCm^{-2} time^{-1})

F_{RP_M} plant maintenance respiration (μmol CO_2 m^{-2} s^{-1} or gCm^{-2} time^{-1})

F_{RSL} total soil heterotrophic respiration (μmol CO_2 m^{-2} s^{-1} or gCm^{-2} time^{-1})

$F_{RS\_H, L}$ litter and soil heterotrophic respiration (μmol CO_2 m^{-2} s^{-1} or gCm^{-2} time^{-1})

$LF_{X=f,s,r}$ total and partial plant litterfall (g DW m^{-2})

LAI leaf area index (m^2 m^{-2})

PC single-leaf photosynthetic rate (μmol CO_2 m^{-2} s^{-1})

PC_{SAT} light-saturated single-leaf photosynthetic rate (μmol CO_2 m^{-2} s^{-1})

$PPFD$ photosynthetically active photon flux density (μmol photon m^{-2} s^{-1})

$PPFD_{IN}$ incident photosynthetically active photon flux density (μmol photon m^{-2} s^{-1})

PR precipitation (mm)

Rs short wave radiation (W m^{-2})

QE quantum yield, photochemical light-use efficiency (mol CO_2 mol^{-1} photon)

$SW_{X=UP,LOW}$ soil water content (%)

TA air temperature (℃)

$T_{OPT,MIN,MAX}$ optimum, minimum, and maximum temperature for photosynthesis (℃)

TG ground surface temperature (℃)

TS_{uplow} soil temperature at upper 5 cm and lower 5 cm ~50 cm depth (℃)

TS soil temperature (℃)

VPD vapor pressure deficit of air (hPa)

WE ecosystem carbon pool (g DW m^{-2})

$WP_{X=f,s,r}$ plant biomass [subscript X indicates foliage, stem, and root] (g DW m^{-2})

$WS_{X=L,MS}$ soil organic carbon [subscript X indicates litter and mineral soil] (g DW m^{-2})

$\Delta WP_{X=f,s,r}$ hourly change of plant biomass (g DW m^{-2} h^{-1})

WV wind velocity (m s^{-1})