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CURRENT TOPICS IN PLANT RESEARCH

Satellite Ecology (SATECO)—linking ecology, remote sensing and micrometeorology, from plot to regional scale, for the study of ecosystem structure and function

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Abstract There is a growing requirement for ecosystem science to help inform a deeper understanding of the effects of global climate change and land use change on terrestrial ecosystem structure and function, from small area (plot) to landscape, regional and global scales. To meet these requirements, ecologists have investigated plant growth and carbon cycling processes at plot scale, using biometric methods to measure plant carbon accumulation, and gas exchange (chamber) methods to measure soil respiration. Also at the plot scale, micrometeorologists have attempted to measure canopy- or ecosystem-scale CO_2 flux by the eddy covariance technique, which reveals diurnal, seasonal and annual cycles. Mathematical models play an important role in integrating ecological and micrometeorological processes into ecosystem scales, which are further useful in interpreting time-accumulated information derived from biometric methods by comparing with CO_2 flux measurements. For a spatial scaling of such plot-level understanding, remote sensing via satellite is used to measure land use/vegetation type distribution and temporal changes in ecosystem structures such as leaf area index. However, to better utilise such data, there is still a need for investigations that consider the structure and function of ecosystems and their processes, especially in mountainous areas characterized by complex terrain and a mosaic distribution of vegetation. For this purpose, we have established a new interdisciplinary approach named 'Satellite Ecology', which aims to link ecology, remote sensing and micrometeorology to facilitate the study of ecosystem function, at the plot, landscape, and regional scale.

Keywords Carbon cycle · CO_2 flux · Ecosystem · Ecophysiology · Remote sensing · Satellite ecology

Abbreviations

EVI	Enhanced vegetation index
GPP	Gross primary production
LAI	Leaf area index
LSM	Land surface model
MODIS	Moderate resolution imaging spectroradiometer
NDVI	Normalized difference vegetation index
NEE	Net ecosystem exchange
NEP	Net ecosystem production
NPP	Net primary production
PAI	Plant area index
PAR	Photosynthetic active radiation
RE	Ecosystem respiration
RA	Autotrophic respiration
RH	Heterotrophic respiration
RR	Root respiration
V_{cmax}	Maximum velocity of carboxylation

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Introduction

Carbon cycling studies and ecosystem ecology

Terrestrial ecosystems play a crucial role as a sink (absorber) of atmospheric CO_2. Current and future changes

in sink activity and the possibility of stimulating global warming due to climate and land use change and fossil fuel emissions are issues requiring urgent investigation (Cox et al. 2000; Davidson and Janssens 2006; IPCC 2007). In this context, it is quite important to understand the consequences of environmental fluctuation and ecosystem physiology since these are the fundamental aspects that determine ecosystem function with respect to global climate controls and their future changes (Canadell et al. 2000; Cramer et al. 2001; Sitch et al. 2003).

Among the factors responsible for CO_2 exchange between ecosystems and the atmosphere (Fig. 1), photosynthetic productivity (CO_2 uptake) of an ecosystem—namely gross primary production (GPP)—and respiratory CO_2 release—namely ecosystem respiration (RE)—are the most important (Valentini et al. 2000). GPP depends principally on the photosynthetic capacity of the ecosystem, i.e., the integration of single-leaf photosynthesis of the species constructing the canopy and leaf area index (LAI), and the spatial structure of the canopy. RE depends on the biomass of plants and heterotrophic organisms. However, since GPP (photosynthesis) and RE (respiration) are physiological processes, they are influenced greatly by meteorological conditions at various time-scales as well as resource availability, which is heterogeneous in space (Chapin et al. 2002; Muraoka et al. 2008). Understanding these traits responsible for the ecosystem carbon gain provides us with deeper insights into the mechanisms in ecosystem function and its future changes (Ehleringer and Field 1993; Mooney and Chapin 1994; Cox et al. 2000).

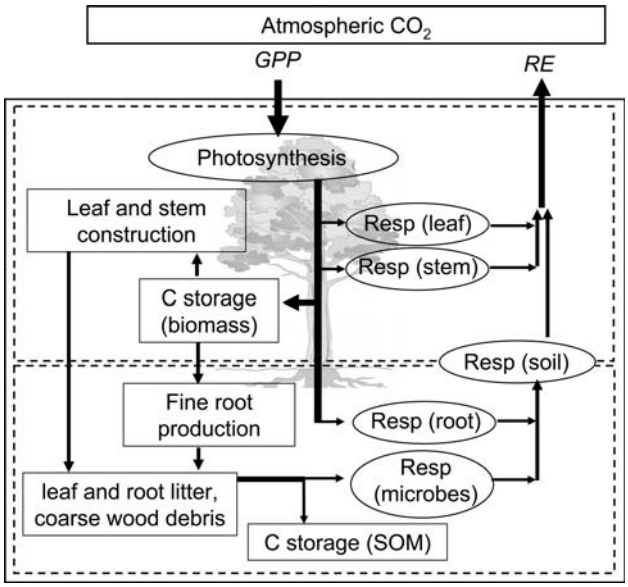

Fig. 1 Compartment model of carbon cycle in a forest ecosystem. CO_2 exchange between the atmosphere and the terrestrial ecosystems are determined by the balance between gross primary production (*GPP*) and respiration (*RE*, *Resp*). In the ecosystem part, parameters of the carbon pool are indicated by *rectangles*, and the carbon flows are indicated by *ovals*. *SOM* Soil organic matter

An ecosystem is the system produced by the interaction of organisms (plants, soil microbes, animals) and their environments (radiation, wind, temperature, water, mineral resources), and ecosystem biogeochemical processes (material and energy cycles) will have feedback effects on the dynamics of the structure and function of that ecosystem (Tansley 1935; Odum 1969; Canadell et al. 2000; Chapin et al. 2002). Approximately half of the organic components of terrestrial ecosystems (vegetation), including organisms and soil organic matter (SOM), consist of carbon. The flow of carbon also depends on the energy flow in the ecosystem, which is fundamental to the life of its organisms. Therefore, ecosystem structure and function, and the associated dynamics, can be evaluated in terms of pools and flows of carbon, which have further contributed to the progress of ecosystem ecology. In this context, if we focus on carbon, structure means the canopy, leaves, branches, stems, roots and soil microbes that construct the ecosystem, and function means photosynthesis, respiration and the resulting carbon budget and sequestration. Thus, understanding ecosystem structure and function, with respect to its interaction with the environment, requires a sense of plant and microbial ecophysiology. Plant science, including ecophysiology, ecology and vegetation sciences, have a great role to play in ecosystem science, and they are extended to Earth science via the link with biogeochemistry and climatology (Ehleringer and Field 1993; Buchmann 2002; Chapin et al. 2002).

Studies on ecosystem carbon cycling have focused mainly on the carbon budget of the target ecosystem (or plot), i.e., whether the system is a source or sink of carbon with respect to the atmosphere. This is because source/sink strength is a fundamental issue in global climate change research. However, since any research method used in determining carbon budget (biometry, eddy covariance or models) includes uncertainty derived from the technical limitations with respect to the processes of carbon cycling, research results still have uncertainties. For example, we can measure the biomass increment, foliage biomass, and daily-to-annual CO_2 flux of a certain forest to calculate the carbon budget (Ohtsuka et al. 2005; Saigusa et al. 2005), but turnover of fine roots, respiration in daytime, rhizodeposition and CO_2 recycling (photosynthetic fixation of CO_2 respired in the ecosystem) are topics to be challenged if accurate estimates are to be obtained (cf. Sternberg 1989; Buchmann 2000). It is also important to note that carbon budget should include flows other than CO_2 exchange in the soil–vegetation–atmosphere transport (SVAT) continuum, i.e., other trace gasses like CH_4, biogenic volatile organic compounds (VOC), and discharge to streams as dissolved organic carbon (DOC) and dissolved inorganic

carbon (DIC) (Shibata et al. 2005), in order to evaluate the net ecosystem carbon balance (sensu Chapin et al. 2006). Taking into account these uncertainties, and the issues to be considered in estimating an ecosystem's carbon budget and cycle, ecosystem ecology (including micrometeorological aspects) is required to measure the processes involved in the system, and their fluctuation, and to suggest resulting functions with its mechanistic response to, or constraint by, the climate and vegetation structure itself.

Such understanding promises better prediction of climate change effects on ecosystems and feedback effects of ecosystems to climate (Cox et al. 2000), and will also contribute to providing impetus for future questions in plant science. The viewpoints of plant science (in a broad sense) provide us with the means of measuring and evaluating the dynamics of carbon metabolism of ecosystems. This theme involves two major objectives; (1) to measure and evaluate the distribution of ecosystems and the temporal dynamics of internal carbon cycling in individual systems, and (2) to reveal the temporal and spatial dynamics of biotic and abiotic factors controlling carbon cycling in individual ecosystems, as well as their diversity. These two aspects are tightly linked each other, since the mechanisms of ecosystem stability or succession is highly dependent on the interaction of structure, function and material cycling within that system (Odum 1969; Schlesinger 1997; Chapin et al. 2002).

Although the processes involved are complicated, the dynamics of material cycle in an ecosystem are, in principle, similar to that in an individual plant—the theory of 'matter production and reproduction' by Monsi (1960). In individual plants, photosynthetic production is allocated to every organ, and in turn to growth and reproduction. In an ecosystem, by contrast, photosynthetic production is allocated not only to plant growth and reproduction, but also to heterotrophic organisms. Although the investment of photosynthetic production to heterotrophic organisms turns out to be respired CO_2, plants can acquire nutrients for further physiological activity. These cycles have been introduced into mathematical models to calculate the CO_2 flux in an ecosystem (see, e.g., Oikawa 1985; Ito and Oikawa 2000; Waring and Running 2007). Such models have now been recognized by Earth science modeling communities with the aid of ecologists, and introduced to models describing atmospheric (climatic) controls on land surface processes, i.e., ecosystems that involve vegetation and biogeochemical dynamics (Cramer et al. 2001). In this context, ecologists and plant scientists are required to reveal more detailed and mechanistic information on the ecological and physiological processes in material cycles.

There is a growing requirement for ecosystem science to help inform our deeper understanding of the effects of global climate change and land use change on terrestrial ecosystems, from the small area (plot) scale to the landscape, regional and global scale. To meet these requirements, ecologists have focused on plant growth and carbon cycling processes at the plot scale by using biometric methods to measure plant carbon accumulation (Curtis et al. 2002; Ohtsuka et al. 2005), and gas exchange (chamber) methods to measure soil respiration (Luo and Zhou 2006). Also at the plot scale, micrometeorologists have attempted to measure canopy- or ecosystem-scale CO_2 flux by the eddy covariance technique, which reveals diurnal, seasonal and annual cycles (Baldocchi et al. 2001). Mathematical models play an important role in integrating ecological and micrometeorological processes into ecosystem scales, or in evaluating the physical interaction at the boundary of the atmosphere and land surfaces (ecosystems), which are further useful in interpreting the time-accumulated information derived from biometric methods by comparing with CO_2 flux measurements (Wilson et al. 2001; Curtis et al. 2002; Ito et al. 2006). For spatial scaling of such plot-level understanding, remote sensing via satellite is useful in measuring land use/vegetation type distribution and temporal changes in ecosystem structure such as leaf area index, and GPP from the plot to global scales (Field et al. 1995; Running et al. 1999, 2004).

These various methods play an important role in measuring ecosystem function, but inconsistency among the outputs from these methods at the spatial scale of interest can be encountered, due partly to methodological and/or observational uncertainties (cf. Plummer 2000; Ustin et al. 2004). Since the observational or calculated results of ecosystem functions such as carbon budget are critical in environmental policy and decision making with respect to climate and land use changes (IGBP 2001; IPCC 2007), we need further efforts to provide consistent results that can be considered robust from the various viewpoints of ecology, meteorology and biogeochemistry. Inconsistencies can be derived from the different temporal and spatial resolutions of the methods (scale-gap), the parameters that can be measured by each method, the structure of the models, and the algorithms used in the analysis of remote sensing data.

To achieve a consistent and accurate approach, interdisciplinary understanding must be shared among scientists and research communities. This should be fundamental in studying spatial scaling since drivers of ecosystem functions may change depending on the scale of interest, i.e., individual plot scale ecosystems, landscapes (including forests), grasslands and agricultural fields, and the regional-to-continental scale. Since ecosystems involve organisms, physical environments and their interactions, a deeper understanding and monitoring of ecosystem function requires full collaboration between ecologists, meteorologists, biogeochemists and remote sensing scientists. The research issues include the structural and functional

consequences of biogeochemical cycles and vegetation processes, ecophysiological and physical understanding of spectral reflectance data obtained by remote sensing, and the spatial and temporal scaling analyses of ecosystem structure and function, considering relationships across scales.

To achieve this goal, we have established a new interdisciplinary approach named 'SATECO', which aims to link ecology, remote sensing and micrometeorology for studying ecosystem function at plot to landscape and regional scales. This is an intensive research/education program, '21st Century Centers of Excellence (COE)', supported by the Ministry of Education, Culture, Sports, Science and Technology in Japan. Our program seeks to link disciplines, not only by integrating data as in general ecosystem study projects, but also by achieving interdisciplinary and integrated understanding of studying ecosystems (Fig. 2). The program is based on a long-term, multidisciplinary study in the 'Takayama super-site' located in a cool-temperate deciduous broadleaf forest in mountainous landscape in central Japan, one of the most intensive and long-term study sites (Yamamoto et al. 1999; Yamamoto and Koizumi 2005; Saigusa et al. 2005) in FLUXNET, an international network of CO_2 flux measurements of terrestrial ecosystems [Baldocchi et al. 2001, (http://www.fluxnet.ornl.gov/fluxnet/index.cfm) (and its sub-networks; AsiaFlux (http://www.asiaflux.net/) and JapanFlux (http://www.japanflux.org/)], which was recently linked to JaLTER [Japan Long-Term Ecological Research network (http://www.jalter.org/)] under ILTER [International LTER (http://www.ilternet.edu)]. Based on the findings and trials in this study site, we are seeking to extend our research to the carbon metabolism and hydrological aspects at the landscape scale in a forested catchment in a mountainous region (Fig. 3).

In the following sections we will introduce the multidisciplinary efforts currently being made to understand the dynamics and mechanisms of carbon cycling and budget in the Takayama site—a deciduous broadleaf forest ecosystem located in a mountainous landscape in central Japan—and then discuss how we extend our viewpoint to the landscape scale by linking satellite remote sensing, ecosystem ecology and micrometeorology in the new interdisciplinary approach of SATECO. We attempted to write this review from the viewpoint of the contribution that plant science and ecology can make to other branches of ecosystem studies.

Multidisciplinary approach in Takayama

Net primary production (NPP) and net ecosystem production (NEP) are the most important and fundamental parameters in evaluating ecosystem function in any carbon cycling study. NEP is the balance between GPP and RE, which are the exchange terms of CO_2 between atmosphere and ecosystems (Fig. 1), and NPP is defined as the balance between GPP and plant respiration (RA; autotrophic respiration). These functions can be evaluated by ecological process (biometric) methods, eddy covariance techniques, gas exchange measurements using chamber systems, and ecophysiological modeling. Each method has its own strengths and weakness, and its own temporal and spatial resolution, which are linked tightly with each of the ecological processes (see also Canadell et al. 2000 for technical comparisons). Therefore it is highly important to combine these methods in order to better understand the consequences of biotic and abiotic processes and ecosystem-scale phenomena, although 'scale-gap' problems can sometimes be encountered. The authors and colleagues have been expending effort to install these techniques, each of which is traditionally tightly linked with disciplines such as ecology, plant science, micrometeorology and remote sensing, into a collaborative research site in a cool-temperate deciduous broadleaf forest at about 1,420 m above sea level, in mountainous landscape near Takayama city, Gifu Prefecture, central Japan (Fig. 3). We refer to this location as the 'Takayama site', which now has a role not only in coupling ecological and meteorological research, but also in an intensive examination of remote sensing data for its accurate use in spatial scaling. The forest canopy is dominated by *Quercus crispula* Blume, *Betula ermanii* Cham. and *Betula platyphylla* Sukatchev var. *japonica* Hara, the sub-canopy is dominated by *Acer rufinerve* Sieb. et Zucc., *Acer distyllum* Sieb. et Zucc., and the understory is dominated by the evergreen dwarf bamboo *Sasa senanensis* Fr. et Sav. The annual mean air temperature and yearly precipitation from 1980 to 2002 were 7.2°C and 2,275 mm, respectively.

Ecological processes and biometric analysis

Ecological research has attempted to quantify NPP by measuring increments of living plant biomass based on biometric analysis, leaf litter fall as a measure of leaf biomass, and soil respiration (Ohtsuka et al. 2005, 2007). In this method, much effort is needed to accurately measure soil respiration and to separate it into root respiration (RR) and heterotrophic soil microbial respiration (RH) (Lee et al. 2003; Mo et al. 2005). Intensive study of temporal and spatial distribution of soil respiration is highly important for carbon cycling research with respect to global warming (Valentini et al. 2000; Davidson and Janssens 2006). Due to the measurement accuracy of the biomass of trees, the ecological process method can reveal only the annual budget of carbon. However, the strength of this

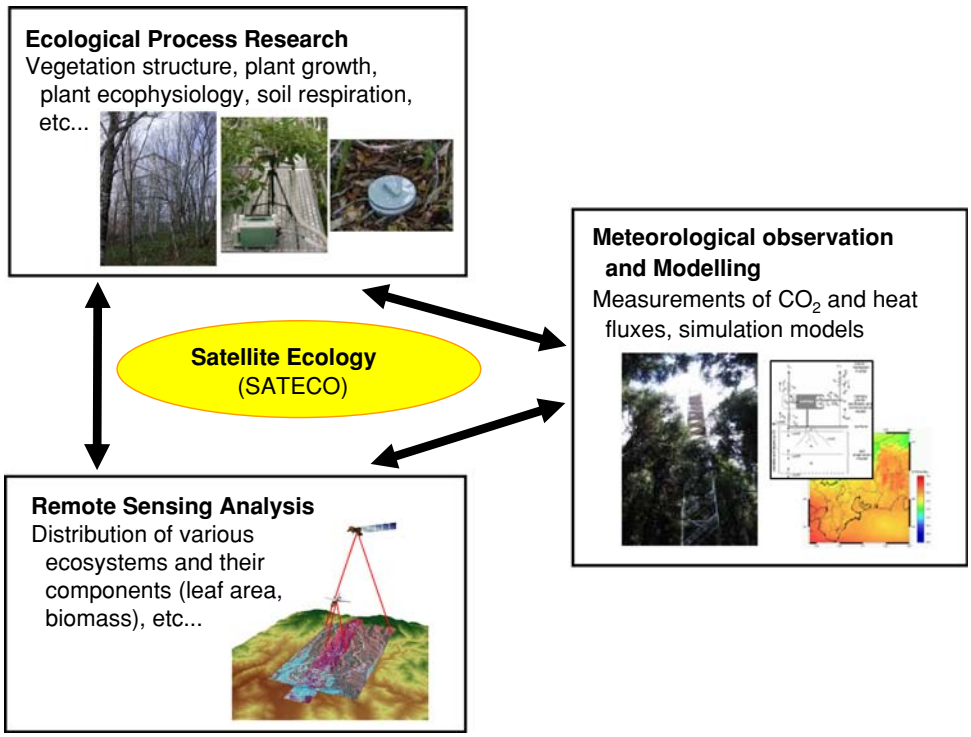

Fig. 2 Concept of linking disciplines in Satellite Ecology (SATECO)

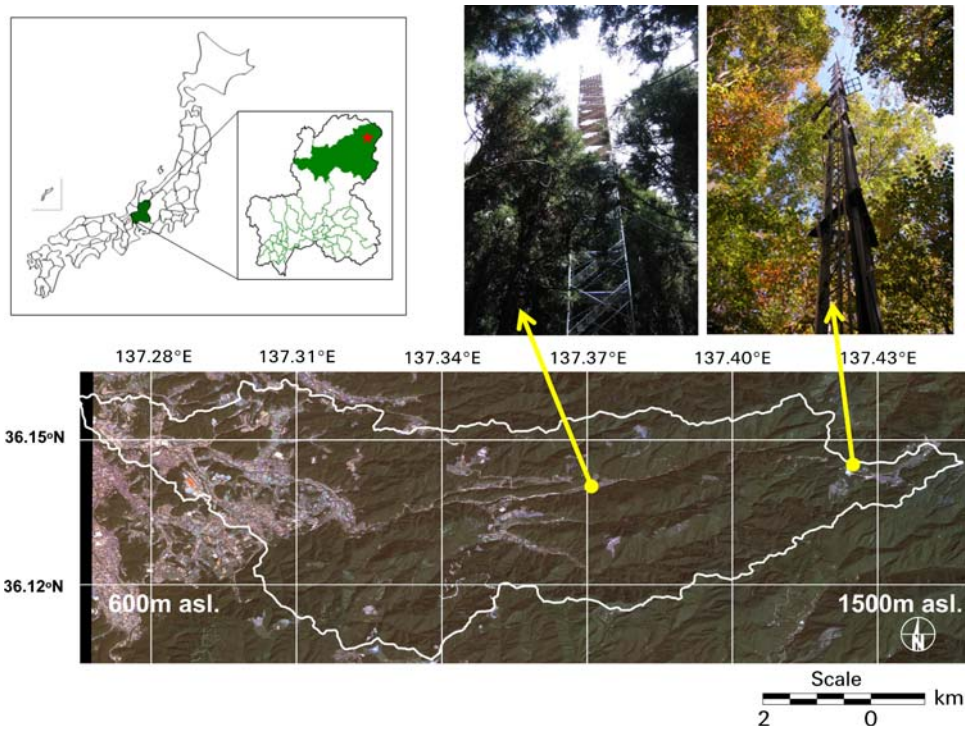

Fig. 3 Satellite image (*lower panel*) of Daihachiga-gawa River basin in Takayama city, Gifu, Japan (*upper left*). Studies are conducted in several sites in the area including two tower flux sites (registered to AsiaFlux and JaLTER), one of which is in a deciduous broadleaf forest and the other in an evergreen coniferous forest

method is that it can clarify where, and how much, carbon is pooled in the ecosystem. Careful, long-term measurements of the pool and flow of carbon, and an estimate of soil CO_2 efflux considering the spatial and temporal variations, reveal the ecological processes responsible for carbon cycling in the system (Ohtsuka et al. 2007).

In addition, ecological measurements of the processes provide us with important parameters for modeling. For

example, LAI is one of the most important parameters used to calculate canopy photosynthesis. Usually, LAI is estimated by optical techniques such as LAI-2000 (Li-Cor, Lincoln, NE), hemispherical photography (Jonckheere et al. 2004), or from measured transmittance of photosynthetic active radiation (PAR) through the canopy. But since these indirect optical methods measure plant area index (PAI), which comprises both leaf and stem area, in the Takayama site we attempted to measure the 'true' LAI by combining litter collection and monitoring leaf phenology. This study revealed that the 'true' LAI is much larger than the optical LAI (Nasahara et al. 2008), because the optical LAI is susceptible to the effects of leaf angle and clumping, which lead to underestimation of LAI. This finding further affects ecosystem simulation models. In addition, separation of leaf litter into several dominant tree species enables us to evaluate the contribution of each tree species to the whole forest carbon budget.

Eddy covariance flux measurements

Continuous measurements of CO_2 and heat fluxes using the eddy covariance technique with a tower system installed in the forest reveal the half-hourly to yearly cycle of ecosystem function (Yamamoto et al. 1999; Saigusa et al. 2002, 2005, 2008). In Takayama site, the system was installed in the winter of 1993 and measurements have been continued until the present. The data are analyzed together with micrometeorological factors such as incoming radiation, wind, CO_2 concentration, temperature and humidity, and therefore the physiological response of the ecosystems can be quantified. Comparisons of data from various observation sites reveal the consequence of vegetation characteristics and CO_2 flux (Owen et al. 2007; Saigusa et al. 2008). Basically the system measures [net ecosystem exchange (NEE), NEE = −NEP] as a net exchange rate of CO_2 between the atmosphere and ecosystems. Night time NEE is considered as RE and, by assuming the same temperature response of nighttime RE and daytime RE, GPP is calculated by summing daytime NEP and RE, which was estimated from daytime temperature. From an ecophysiological viewpoint, detailed consideration of how to deal with the daytime dark (mitochondrial) respiration in leaves, which might be reduced in the light (Brooks and Farquhar 1985), and growth respiration, which might be stimulated by photosynthesis (Cannell and Thornley 2000), will be needed.

Combining the biometric analyses of the biomass increment with the tower flux measurements of the carbon pool enabled us to reveal the pool and flux, from an hourly to a yearly timescale, and also helped identify missing parameters that each of methods may miss for technical reasons. Although some uncertainties remain in the results due to research methodology and physiological processes that underpin ecological phenomena like the respiration issue referred to above, combination of these methods reveals some interesting phenomena, for example, (1) annual NEP fluctuated greatly in the last decade with values ranging from about 60 to 330 g C m^{-2} $year^{-1}$, (2) GPP or NPP is largely responsible for that yearly fluctuation, and (3) regional scale climate conditions are responsible for the fluctuation of GPP (Saigusa et al. 2008).

Ecophysiolgical observation and modeling

Variation in canopy scale photosynthesis or respiration is critical in determining and understanding the yearly fluctuation in the ecosystem-scale carbon budget as it relates to temporal variation in climatic conditions (Ehleringer and Field 1993; Baldocchi and Meyers 1998; Ito et al. 2006). For example, canopy-scale photosynthesis depends on the single-leaf level photosynthetic property and leaf area distribution in the canopy (Caldwell et al. 1986), and response to (or constraint by) microclimate conditions of these factors can be modeled by combining photosynthesis (Farquhar et al. 1980) and stomatal conductance (Ball et al. 1987) models. Considering plant ecology, one should also consider the possibility that leaf photosynthetic capacity and canopy leaf area could be affected by climatic conditions during leaf expansion (Niinemets et al. 2004), or possibly even by photosynthetic production or climatic conditions during the previous year in which the leaf primordium was formed (Kimura et al. 1998).

At the Takayama site, the authors have attempted to find a connection between the single-leaf level photosynthetic property of the canopy tree species and the canopy-scale GPP. Since the canopy consists of tree species at different successional status (*Quercus* is classified as mid-late successional and *Betula* species are pioneer species), and differences in ecophysiological responses between different successional status could affect canopy-scale CO_2 exchange and water use (Leuzinger and Korner 2007), we need to reveal how single-leaf or branch level photosynthesis differs between species. A three-dimensional model to simulate the consequences of leaf photosynthesis and shoot architecture (Y-plant; Pearcy et al. 2005) revealed that steep leaf angle in *Betula* contributes to avoiding severe stomatal closure and photoinhibition, and hence to realizing higher photosynthetic activity as compared to *Quercus* (Fig. 4; Muraoka and Koizumi 2005, 2006).

At the canopy scale, combining seasonal changes in leaf photosynthetic properties, LAI and other ecological processes using a model is one way to interpret the seasonal and yearly variation in GPP (Wilson et al. 2001; Kramer et al. 2002; Ito et al. 2006). Our study calculating canopy GPP using NCAR-LSM (Bonan 1996) by incorporating in

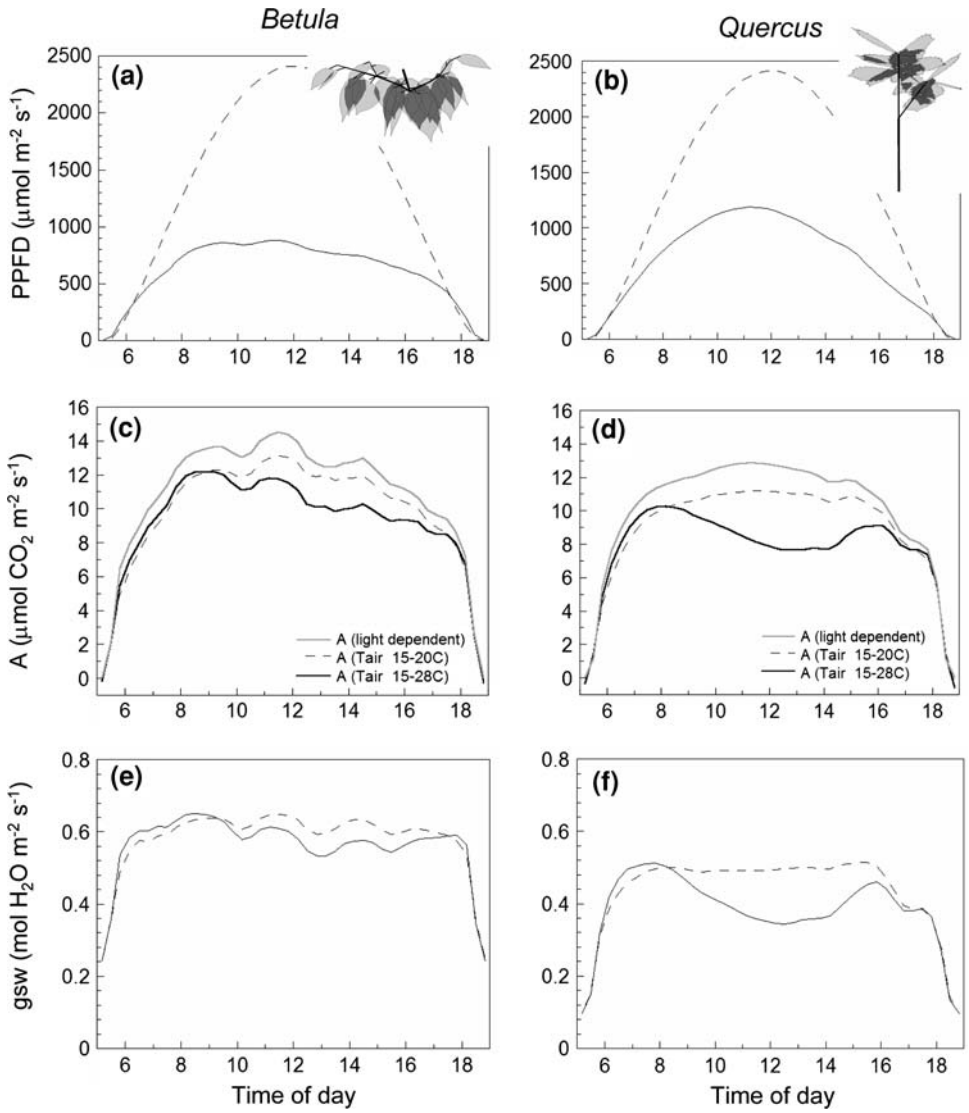

Fig. 4 Simulation results of light interception (**a**, **b**), photosynthesis (**c**, **d**) and stomatal conductance (**e**, **f**) for *Betula ermanii* (**a**, **c**, **e**) and *Quercus crispula* (**b**, **d**, **f**) using a three-dimensional plant structure–function model. Top figures show the shoot-level light interception assuming horizontal (*dashed line*) and actual (*solid line*) leaf angles. Photosynthetic rate (*A*) and stomatal conductance (*gsw*) are calculated assuming actual leaf angles with two temperature regimes; these photosynthetic rates were also compared with a simple light response model. Adapted from Muraoka and Koizumi (2006). *PPFD* Photosynthetic photon flux density

situ measurements of leaf photosynthetic capacity (measured with portable gas exchange equipment) and LAI (estimated by PAR transmittance) throughout the seasons for several years suggested a dynamic diurnal to daily and seasonal changes in GPP and also variations in annual cycle (Fig. 5). This calculation also revealed that yearly GPP varies by almost 10%, and that if we ignore seasonal changes in leaf photosynthetic capacity and use the summer maximum value in the model, GPP can be overestimated by 10–20% depending on the year.

Ecophysiological understanding and accurate estimation of soil and ecosystem respiration and its temporal and spatial variability is also a critical theme in current ecosystem carbon cycling research (Kang et al. 2003; Curtis et al. 2005; Ito et al. 2007). Usually, soil CO_2 efflux is measured by chamber systems, and in situ soil temperature and water content are measured simultaneously since these environmental factors are largely responsible for respiratory activity of organisms (roots and soil microbes) as well as CO_2 gas diffusion in the soil (Luo and Zhou 2006). The relationship between soil environmental factors and respiration rate is then curve-fitted to obtain mathematical equations for temporal or spatial scaling in the study area (Lee et al. 2003; Mo et al. 2005). These studies revealed the remarkable contribution of soil respiration to RE. On the other hand, there are some new findings that soil respiration is also dependent on canopy photosynthetic activity in timescales ranging from days to seasons (Ekblad and Hogberg 2001; Tang et al. 2005; Davidson et al. 2006). In addition, recent gas exchange studies have revealed that stem respiration also has daily and seasonal fluctuations (see, e.g., Damesin et al. 2002). These phenomena might be explained by the fact that respirations in stems, roots and soil organisms depends on the supply of resources (photosynthetic production matter), and root physiological activity may also be linked with foliage phenology (cf.

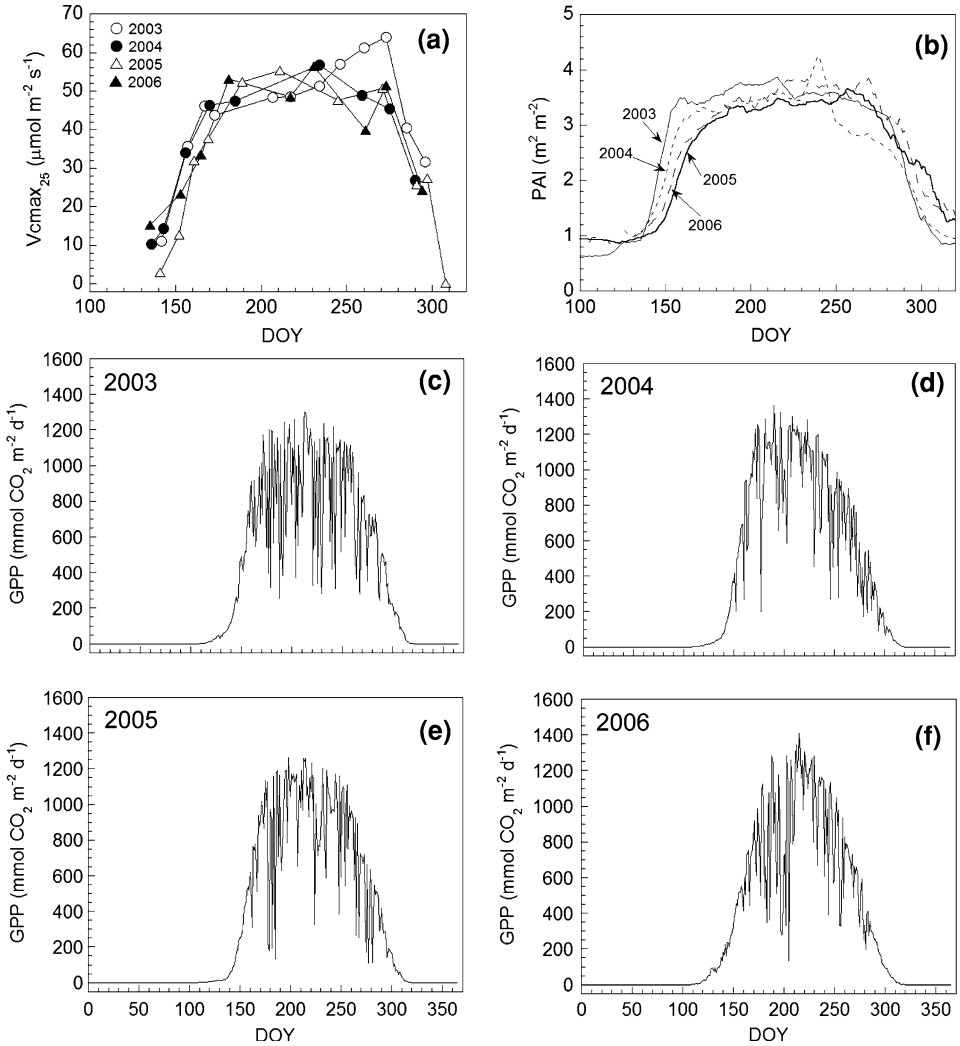

Fig. 5 Effects of seasonal and interannual variation in leaf V_{cmax} at a reference temperature of 25°C (**a**) and plant area index (PAI) (**b**) on canopy gross primary production (GPP) over 4 years (**c–f**). Values of V_{cmax} (**a**) are the mean of values from *B. ermanii* and *Q. crispula*, whose photosynthetic characteristics were predetermined by three to five sample leaves, respectively (see Muraoka and Koizumi 2005, 2006 for details). *DOY* day of year. Unpublished data by H. Muraoka

Noda et al. 2007). More efforts are needed to find the physiological and ecological links between photosynthetic and respiratory activities as well as to identify the steps limiting respiratory rate at the ecosystem scale for a better understanding that will further contribute to model improvement.

Spatial and temporal scalings by remote sensing and modeling

Currently, we need further mechanistic understanding and prediction of carbon metabolism on a broader spatial scale, with careful consideration of relationships across scales (Swanson et al. 1988; Cernusca et al. 1999; Tenhunen et al. 2001). Satellite remote sensing has contributed to measuring the spatial distribution of vegetation types or landuse types from the landscape to the global scale (Field et al. 1995; Running et al. 2004). In carbon cycling studies, remote sensing also plays a role in monitoring LAI and biomass, which are the major determinants of ecosystem photosynthetic productivity in mathematical models (see, e.g., Sasai et al. 2005). Accurate maps of ecosystem structure such as vegetation types, percentage coverage, stand age and density are highly required, not only to improve models and estimates of carbon budget, but also to gain insights into environmental management policies that consider ecosystem function.

For the past three decades, we have had several Earth observation systems in operation, e.g. Terra/Aqua MODIS (moderate resolution imaging spectroradiometer), QuickBird, Terra ASTER (advanced spaceborne thermal emission and reflection radiometer), IKONOS, SPOT VEGETATION, ALOS AVNIR2 (advanced visible and near infrared radiometer type 2) and so on. Although these sensors have different spatial, temporal and spectral resolutions that their observations, effective combination of the data enables us to measure ecosystem structural parameters which are partly validated in several vegetation types (Liang 2004). Remote sensing is no doubt useful in

monitoring ecosystems which scientists cannot themselves visit, and may provide us with valuable data on the distribution and density of vegetation and canopy phenology that will be essential in evaluating ecosystem function with underlying ecological processes (Turner et al. 2004). This is particularly critical in Japan, since most of the vegetation (especially forests) is distributed in mountainous regions. It is also true that forest research in respect to climate change impacts, as well as ecological research, dominates much of natural science in Japan, since forests dominate about 70% of the Japanese land area and thus play a critical role as a carbon pool (Fang et al. 2005).

In using satellite remote sensing to monitor ecosystem distribution, spatial resolution is the critical issue to be considered. Plot-scale research in carbon cycling is highly constrained in space, i.e., ecological process studies can cover an area as large as 10^4 m^2 for individual plots, and a footprint of eddy covariance data may cover from 100 m to several kilometers in distance (Schmid 2002; Baldocchi 2003; Kim et al. 2006a, b). On the other hand, the spatial resolution of satellite remote sensing ranges from about 2 m^2/pixel to 1 km^2/pixel depending on the sensors, and spatial resolution is in trade-off with temporal resolution (daily to monthly or longer). For example, MODIS provides daily data (including cloud contaminated) but its spatial resolution is $1/16 \cong 1$ km^2 depending on the products, while QuickBird, ALOS, ASTER provide relatively high spatial resolution ($\cong 15 \times 15$ m) but the temporal frequency of data acquisition is very low and irregular (depends on cloud coverage and other requests). The increasing overlap of the spatial resolution of different methods would enable us to monitor ecosystems along geometrical gradients, and at time intervals ranging from days to years, from various aspects of scientific interest.

Among the satellite sensors, MODIS provides daily observation data of land surface reflectance and thus it is potentially possible to estimate the daily changes in LAI (MOD15) and hence GPP (MOD17), but clouds often hide the land surface so the LAI or GPP is calculated as 8-day composite data and distributed upon request (http://daac.ornl.gov/MODIS/modis.html). The perpetual question in remote sensing studies is 'how well can remote sensing data and indices such as Normalized Difference Vegetation Index (NDVI) or Enhanced Vegetation Index (EVI) be converted to physiological, functional and structural variables or model parameters?' It is also quite important to reduce the 'scale-gap' between the techniques. Numerous studies have been published to test the accuracy of vegetation indices as the indicator of foliage density (LAI) and its phenology (Tucker et al. 2001) or GPP and related parameters (Xiao et al. 2004; Nakaji et al. 2008) in various terrestrial ecosystems. Especially intensive studies have been conducted in FLUXNET sites to validate such indices and MOD17 with the aid of eddy covariance data (Turner et al. 2003, 2005; Heinsch et al. 2006; Sims et al. 2008).

From an ecologist's viewpoint, it is strongly expected that remote sensing techniques to measure the photosynthetic capacity of canopies be used at the plot to landscape scale. Principally, spectral reflectance at a canopy scale reflects the anatomical, biochemical (pigments) and physiological features of single leaves and leaf angle, and their geometrical distribution in the canopy (Gamon and Qiu 1999; Peñuelas and Filella 1998; Verhoef 1984). Therefore, remote sensing data and vegetation indices at the canopy or landscape scale must reflect these characteristics, but intensive tests are still required in order to apply these techniques to monitor vegetation with high accuracy from the viewpoint of plant science.

A new interdisciplinary approach: 'Satellite Ecology'

If we could deepen our understanding of the relationship between remote sensing data (spectral reflectance signals) and ecosystem processes, then we could apply these techniques to ecological research in both vegetation science and ecosystem function estimates. So far, the regional-scale carbon budget has been estimated by mathematical models using vegetation and landuse type maps derived from inventory data or remote sensing. 'Representative' ecophysiological parameters are given to each type of ecosystem, and the outputs are finally summed up to yield regional estimates (e.g., Bonan 1996; Ito and Oikawa 2002; Sasai et al. 2005, 2007). However, if we can measure the key parameters of ecosystem function, such as V_{cmax} (maximum velocity of carboxylation), which is highly correlated with chlorophyll or nitrogen content at the leaf level (e.g., Hikosaka 2004), and vegetation structure in terms of functional types, canopy LAI and stand density, the final estimate of ecosystem- and regional-scale function would involve ecophysiological dynamics in space and time, which should be linked with topography and microclimate. This aspect has considerable importance for the study of ecosystem physiology, which is directly associated with ecosystem dynamics.

To achieve this step, tight linkage among disciplines such as ecosystem ecology, micrometeorology, hydrology and remote sensing is urgently required (Sellers et al. 1997; Cernusca et al. 1998; Tenhunen et al. 2001). This new interdisciplinary community, which is shifting from a multidisciplinary approach at the Takayama site, will need to (1) find reasons why some remote sensing data are not appropriate for monitoring mountainous landscapes that involve mosaics of different vegetation and land use, (2) investigate how to bring out the full potential of remote sensing data to measure the ecological processes responsible for carbon cycling and hydrology, and (3) construct a

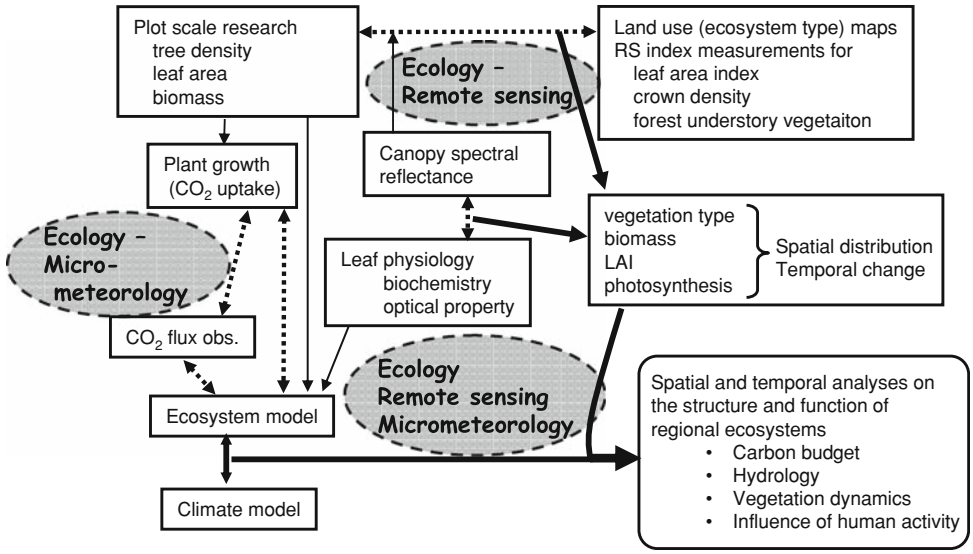

Fig. 6 Linking strategy of plot-scale research and remote sensing observation for constructing a landscape model in SATECO. *Solid lines* Research flow or connections, *broken lines* data validation

research system that can estimate landscape-scale ecological phenomena at high temporal and spatial resolution coupled with climatic variables. These efforts would be the corner-stone of a new discipline, 'SATECO', which will provides us with a multi-scale and multi-aspect understanding of ecosystem structure and function, and their dynamics.

Research focus in SATECO

For the research of SATECO, we set up a forested catchment study area in the basin of the Daihachiga-gawa River, which includes the Takayama site (Fig. 3). This area of about 60 km^2 has various topographical aspects. The altitudinal gradient encompasses about 900 m (600–1,500 m a.s.l.), and contains deciduous broadleaf forest, deciduous coniferous forest, evergreen coniferous forest, paddy fields, and small urban areas. We then set up some study plots within this area for intensive study of ecological process (biomass sampling, plant ecophysiology, soil respiration and soil microbial assay), remote sensing (by portable equipment at ground level for single-leaves and canopy, as well as airborne and satellite observations), and tower flux measurements (one in a deciduous broadleaf forest as mentioned above, and another new one in an evergreen coniferous forest). By careful investigation and validation at the plot scale with the aid of mathematical modeling of micrometeorology and ecosystem CO_2 and heat fluxes, we then investigated the landscape scale (Fig. 6), regional scale, and finally the Asian scale, considering the structural and functional relationships across each scale (Fig. 7). These intermediate scales on which we intensively focus in SATECO represent a kind of 'missing scale' in current global assessment of carbon dynamics in relation to climate change.

Linking plant ecophysiology and remote sensing

Ecophysiological characteristics in the canopy are the most fundamental aspects underlying carbon cycling processes, as they determine photosynthesis, respiration and energy budget. In addition, the canopy is the most 'obvious' aspect of ecosystems from the viewpoint of satellite sensors. As mentioned above, to improve or achieve an accurate method of spectral observation and conversion of data into the ecophysiological information that we want to measure, investigations at both the single-leaf and canopy levels are needed. Since spectral reflectance at the canopy scale is the product of single-leaf optical properties (reflecting pigment and water content, anatomy and physiology) and the geometrical distribution of leaves in the canopy (angle, orientation, number, area and spatial arrangement of leaves), we have been conducting simultaneous measurements of these characteristics throughout the growing season in a deciduous broadleaf forest site. These observational data are then integrated into a model that describes PAR and spectral (350–1,100 nm) distribution and photosynthetic parameters at the canopy scale. These estimated values are then used to convert satellite remote sensing data into canopy photosynthetic parameters (Nishida and Muraoka 2006).

We are investigating vegetation indices like NDVI and EVI, which have been used intensively to monitor vegetation distribution and photosynthetic productivity from the plot- to the global-scale with respect to climate change (Tucker et al. 2001), but their accuracy is still questionable. Our preliminary analysis of the Takayama site showed a large inconsistency between ground observations (vegetation phenology or flux-based GPP) and MODIS observations. These errors are expected to be derived from the scale-gap between the ground and satellite observations, and also from the reduced quality in satellite data due to

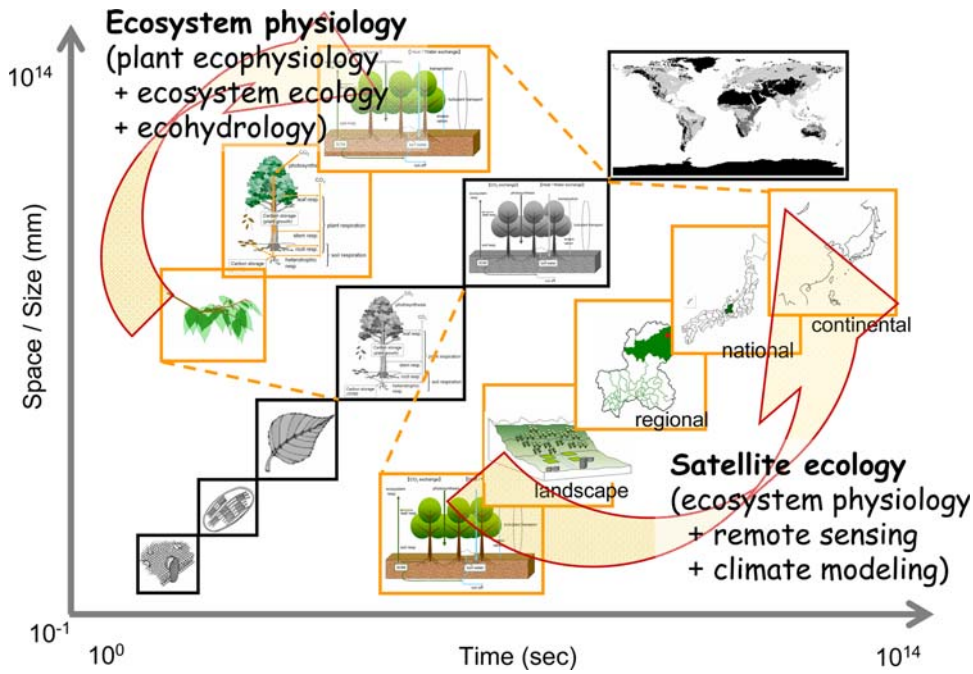

Fig. 7 Spatial and temporal scales of ecosystem processes and their relationships. Ecosystem physiology covers the single-leaf to canopy-, stand- and landscape-scale mechanistic understanding, and satellite ecology covers the canopy-, stand-, landscape- to regional-scale evaluation. Step-by-step research across each scale would be necessary for accurate understanding of ecosystem structure and function

cloud contamination or aerosols that are associated with complex terrain and the Asian monsoon climate.

To overcome the latter problem and enable us to validate the vegetation indices directly with ground observations, an observation system consisting of an automated digital camera with a fish-eye lens (ADFC) and hemispherical spectral radiometer (HSSR) was installed. The HSSR rotates upward and downward at 10-min intervals so that we can correlate the diurnal change in spectral reflectance with the digital image of the canopy (Fig. 8). The ADFC takes sky images every 2 min so that we can monitor the distribution of clouds over the research field to check the possibility of cloud contamination in the satellite data. This system is located at several study sites to monitor the phenology of forests, grassland and paddy fields in Japan, and is called the 'Phenological Eyes Network (PEN)' (http://www.pheno-eye.org/) (Nishida 2007). At the Takayama site, we set up PEN systems at the top of canopy towers in the deciduous broadleaf forest site and at the evergreen coniferous forest site. In addition, efforts have been made to improve the algorithm used to analyze hemispherical photographs to estimate the forest canopy LAI, which enables us to utilize the digital images taken automatically (Mikami et al. 2006).

Continuous measurements of NDVI and EVI at the forest sites enable us to investigate relationships with flux-based GPP as well as canopy leaf phenology directly. We have been testing the accuracy of EVI as an indicator of GPP from daily to yearly cycles (S. Nagai et al., in review), and NDVI as an indicator of canopy greenness with its yearly fluctuation. By combining this data with the digital images of the canopy surface, our colleagues are developing a new index to monitor canopy leaf phenology (Motohka et al. 2008).

Linking canopy, understory and soil processes in forest ecosystems

An important topic in our research program is how to obtain information on the spatial variability of soil ecological processes. Since satellite remote sensing cannot directly observe the soil layer, which is covered by vegetation, some connection between aboveground characteristics and soil processes needs to be found. As mentioned above, soil respiratory activity or potential should be linked with aboveground (foliage) ecophysiology. Therefore, we may be able to estimate the parameters of soil processes from the remotely sensed canopy information, which is also under intensive investigation. We already have data indicating that yearly soil respiration is correlated with yearly NPP throughout the forest types or ages we study (see also Baldochi 2008). In addition, the composition and biomass of soil microorganisms might be related to vegetation types. These two lines of investigation could provide us with knowledge to evaluate soil ecological processes by remote sensing.

Temperate deciduous forests in mountainous area in Japan are characterized by a high coverage of understory of evergreen dwarf bamboo. At the Takayama site, the contribution of *S. senanensis* to the whole forest carbon budget is remarkable (Ito et al. 2005; Sakai and Akiyama 2005). Since the understory is also the most difficult layer to observe directly by remote sensing, Maki et al. (2008) investigated how to predict the potential distribution of dwarf bamboo by combining ground observations, remote

sensing and digital elevation models. Dwarf bamboo tends to inhabit the understory of deciduous forests, and was observed to be distributed in relatively bright aspects. By combining this information, Maki and co-workers were able to construct a potential distribution map; validation of this map by an in situ vegetation survey found an accuracy of about 86%.

High spatial and temporal resolution model for CO_2 and heat fluxes

To integrate the knowledge and data we obtain in these studies, we are constructing a plot- to landscape-scale model that predicts CO_2, heat and water fluxes. The model, namely SATECO model, is based on the meso-scale climate model MM5 (Dudhia 1993), which calculates the input variables for the land surface model (LSM) (Bonan 1996) to calculate the fluxes determined by climate variables, ecosystem-dependent parameters such as V_{cmax}, soil respiration, LAI, stem area index (SAI), canopy height, etc. In keeping with the concept of SATECO, we seek to achieve a high spatial and temporal resolution model, i.e., a spatial resolution of 100 × 100 m, and in hourly time-steps. This spatial resolution would provide the necessary scale to validate the outputs with plot-scale observations of ecological processes and tower flux; if a coarser resolution were adopted, much information related to topographical

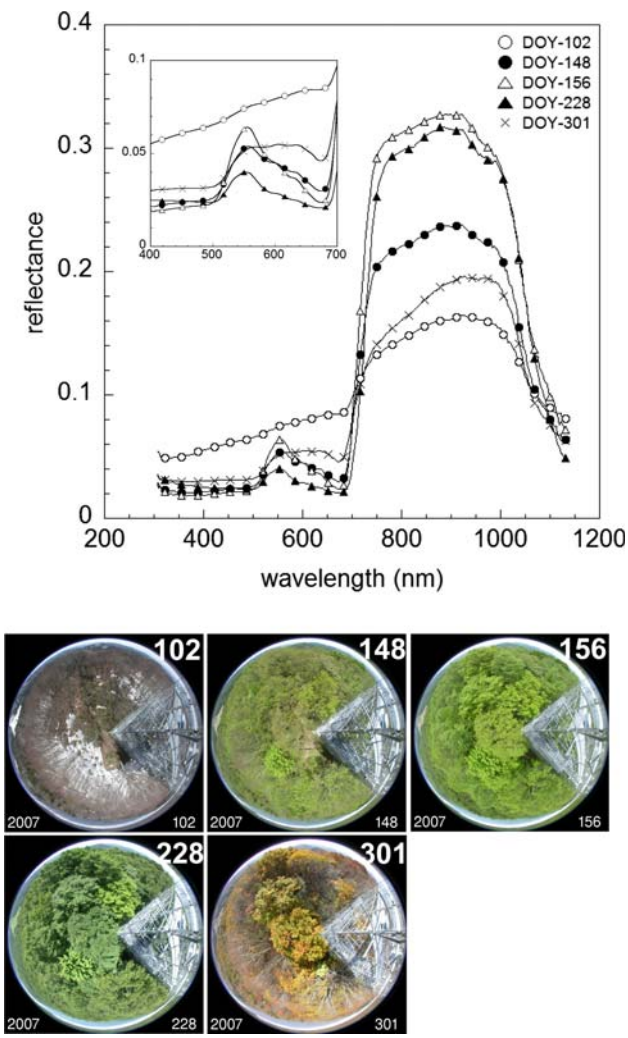

Fig. 8 Spectral profiles (*upper panels*) of canopy reflectance and photographs of those canopies (*lower panels*), measured by the Phenological Eyes Network (PEN) system at the Takayama site. Seasonal changes in canopy structure are reflected in the spectral reflectance data, which are then used to calculate the normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI). *DOY* day of year

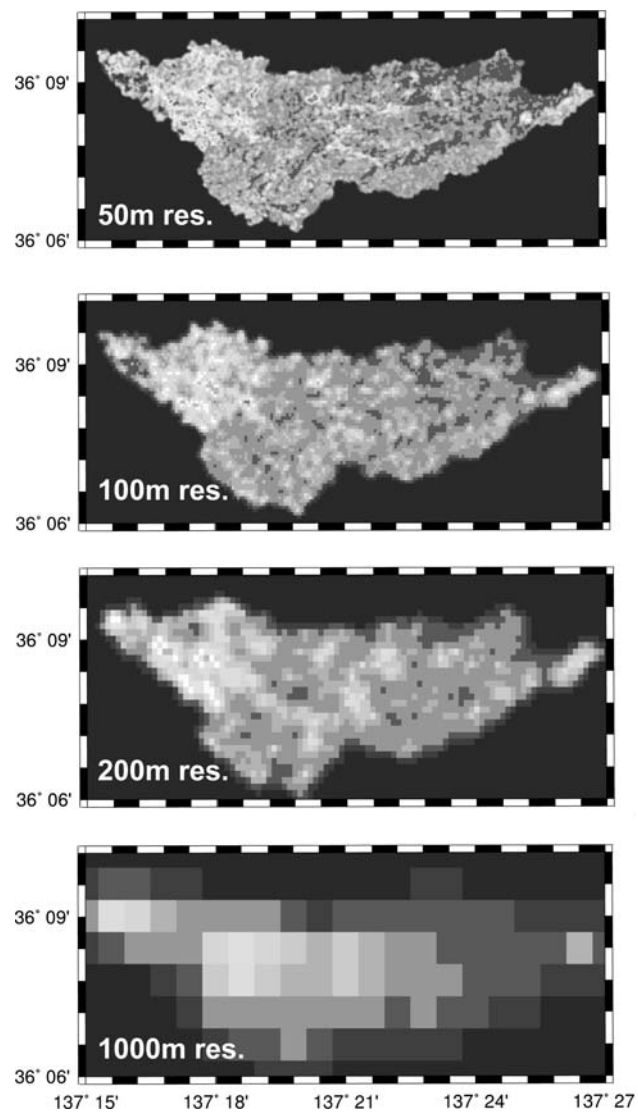

Fig. 9 Images of the Daihachiga-gawa River basin study area to show the influence of spatial resolution in evaluating the plot- to landscape-scale information at different resolutions. The images show the vegetation/land use distribution, as originally assessed by high resolution remote sensing (2–10 m mesh)

effects, which includes mosaic distribution of vegetation and land use types, may be missed (Fig. 9). The default spatial resolution of MM5 is 1 × 1 km; the outputs are then divided into 100 × 100 m resolution by considering the topographical features. The LAI over the study area is estimated by NDVI obtained from MODIS 250 m resolution data, which is converted into LAI values by referring to high spatial resolution vegetation/land use maps (2–10 m mesh) constructed by a combination of QuickBird, ALOS and CASI-III (airborne) (Wahid and Akiyama 2007). The ecosystem process-based model LSM was tested with the aid of in situ ecophysiological measurements and tower flux data.

Figure 10 summarizes the current results of the model analysis. The vegetation map shows the mosaic distribution of various ecosystems and land use along the complex terrain in the mountainous landscape. Comparison of the map of yearly GPP from MOD17 and our SATECO model reveals that the high spatial resolution in our model is absolutely required to estimate the distributions of ecosystem function, which would be more remarkable when we look at the data in shorter time-steps (hourly to daily,

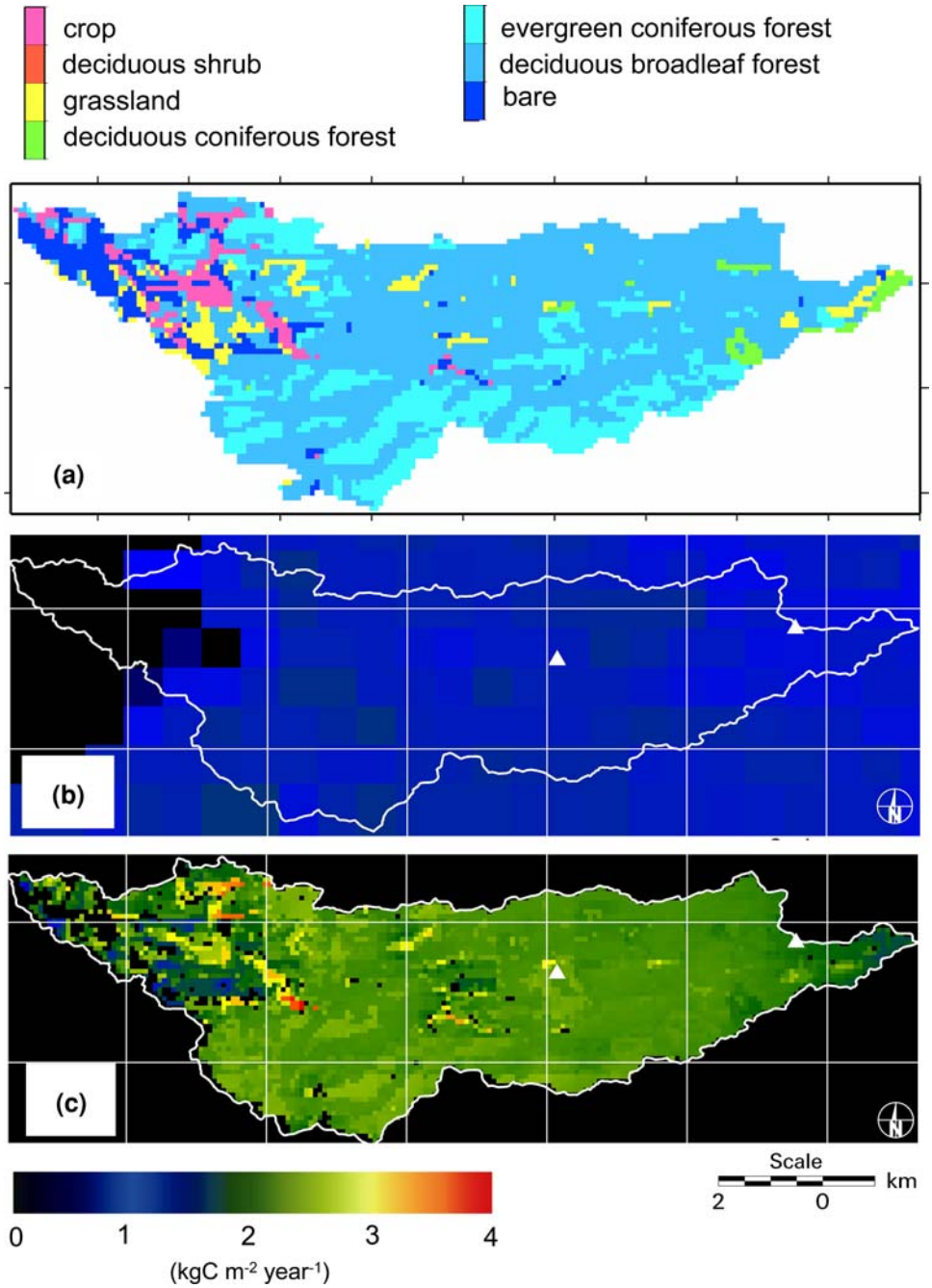

Fig. 10 Vegetation map at 100 m resolution (**a**), and yearly GPP of the area by MOD17 (**b**) and by SATECO model (**c**). Note that MOD17 has spatial resolution of about 1 km^2 whereas the SATECO model has a 100-m mesh

seasonal), and also that there is a larger difference in values of GPP between the models. The approximately doubled GPP in the SATECO model as compared to MOD17 is partly caused by an overestimation of incident radiation in the MM5 climate model, while GPP according to MOD17 is still lower than if we calculate GPP using the microclimate data observed at the flux tower in the study site. Such inconsistency between the models and tower flux data is likely due to the structure of the canopy model (calculation of light penetration in LSM), uncertain topographic and physiological influences on estimating ecosystem respiration in the flux data, as well as other ecological processes that have not yet been considered in the analysis. Currently we are working to improve the models as well as to find the missing processes to be incorporated in analyzing the model and flux data. An important challenge is also to incorporate vegetation dynamics and its effects on carbon dynamics (Sitch et al. 2003; Watanabe et al. 2004; Sato et al. 2007).

Future perspectives

Our SATECO activity has just started but, as mentioned above, its interdisciplinary character is derived largely from the multidisciplinary approach and long-term research at the Takayama site. Long-term research in an intensive field site (super-site) would enable us to observe trends of ecosystem behavior, including the effects of climate as well as internal biotic processes, and to understand the interaction of biotic and abiotic processes that defines the ecosystem as the 'system'. These research efforts should be linked with observation networks such as JapanFlux and JaLTER, and other international communities, to extend the vision of SATECO as a leading program of research and education, and also to contribute to environmental science and decision-making in environmental management.

So far, satellite remote sensing has provided us with numerous images of the Earth's surface in which we can observe the current situation of ecosystems and identify the issues to be investigated in this climate-changing world. However, for further progress in ecosystem science at the landscape- to global-scale, one must recognize, and some might have already recognized, that the viewpoints of ecology and plant science are essential because we are trying to observe and analyze vegetation processes. There is now promising progress towards the use of satellite remote sensing techniques to measure ecosystem processes and dynamics, which are greatly influenced by microclimate and human impacts as well as global climate change (Fig. 11). It would also be possible for us to define a hotspot of studies combining biodiversity (Gould 2000; Walther et al. 2002), interaction of carbon metabolism and hydrology in ecosystems (Tenhunen and Kabat 1999; Kim et al. 2006a, b) at the landscape scale that are tightly linked with human well being (IGBP 2001)—i.e., a new theme extending the scope of our current investigations.

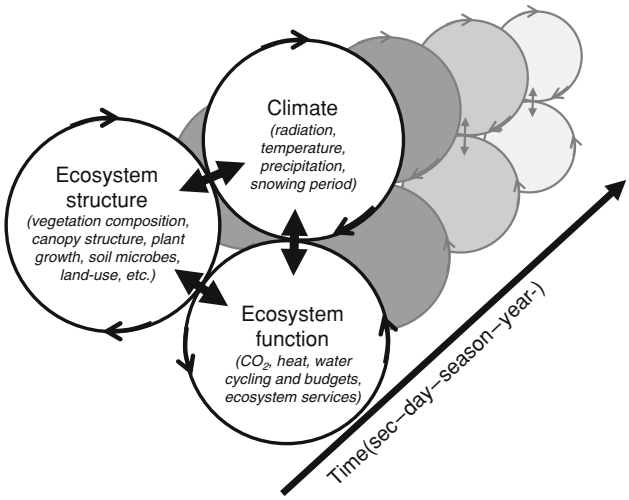

Fig. 11 Representation of the interactive dynamics of climate, ecosystem structure and function that SATECO and future ecosystem science should aim to explore. Climate, ecosystem structure and function interact with each other; any component can affect any other process (*arrows*). These relationships have often been investigated by assuming a steady-state in current ecosystem carbon dynamic research, but each interaction produces further interactions in continuing time-steps in various temporal scales (*gray circles*), revealing the dynamic inter-relationships among climate, ecosystem structure and function

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