Chapter 1

Phenology of Photosynthesis in a Deciduous Broadleaf Forest: Implications for the Carbon Cycle in a Changing Environment

Hiroyuki Muraoka

Abstract Photosynthetic carbon assimilation in plant leaves supports biomass accumulation and developmental growth and contributes to the regulation of atmospheric CO_2 concentration via the carbon cycle. Photosynthesis and its environmental responses have been the central theme of plant physiological ecology and ecosystem ecology, as photosynthesis is involved in a broad range of natural systems from cells to the biosphere. In particular, the environmental responses of tree leaves and forest ecosystems and their seasonal and interannual changes under ongoing climate change are central research interests in ecology and Earth system science. This chapter reviews the studies of leaf and canopy photosynthesis conducted in a cool-temperate deciduous broadleaf forest site in Japan. Long-term observations and open-field warming experiments were conducted to assess leaf phenology in canopy trees, leaf photosynthesis, and the light environment of understory shrubs, and the application of optical remote sensing on forest canopy photosynthetic productivity helped to clarify single-leaf level ecophysiology and forest ecosystem function. The advancement of integrated ecosystem science coupled with climate monitoring should help us to respond to the urgent need for key data regarding biodiversity and ecosystem conservation and management across landscapes from local to regional scales.

Keywords Climate change · Deciduous broadleaf trees · Ecosystem master site · Phenology · Photosynthesis

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H. Muraoka (✉)
River Basin Research Center, Gifu University, Gifu, Japan

Division of Biodiversity, National Institute for Environmental Studies, Tsukuba, Japan
e-mail: muraoka@green.gifu-u.ac.jp

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1.1 Introduction

The photosynthetic carbon assimilation that occurs in leaves supports plant developmental growth and biomass accumulation as well as the regulation of CO_2 concentration in the atmosphere via the carbon cycle (Chapin et al. 2012). Because photosynthesis affects natural systems from cells to the biosphere, photosynthesis and its environmental responses have been the central theme of plant physiological ecology and ecosystem ecology (Evans et al. 1988; Hikosaka et al. 2016). Photosynthesis is largely influenced by abiotic environmental conditions such as solar radiation, temperature, air humidity, soil water availability, and atmospheric CO_2 concentration, all of which vary spatially and temporally. In temperate regions where there are marked seasonal changes in meteorological conditions, the seasonal change of biological behavior in the natural environment, so-called phenology, has been studied with regard to leaf demography, photosynthesis, and shoot growth for various plants in grasslands (Monsi and Saeki 2005; Oikawa et al. 2006) and forests (Augspurger and Bartlett 2003; Kikuzawa and Lechowicz 2011; Wilson et al. 2000).

Recently, the phenology of vegetation has become a focus of Earth system science because its sensitivity to short- to long-term climate change in many organisms and its involvement in ecosystem functions through diverse biological and biogeochemical interactions have feedback effects on the climatic system (Piao et al. 2019; Richardson et al. 2013). Figure 1.1 illustrates the scheme of CO_2 exchange between the atmosphere and a forest ecosystem and the carbon cycle within an ecosystem. The CO_2 exchange can be roughly determined as the balance of photosynthetic absorption (gross primary production, GPP) and respiratory release of CO_2 by the ecosystem (ecosystem respiration, R_e). GPP is the total amount of carbon assimilated in single leaves across the entire forest canopy, and R_e is total amount of CO_2 respired from leaves, stem, root, and soil microorganisms. These CO_2 flux components change throughout the seasons in deciduous forests (e.g., Baldocchi et al. 2005; Richardson et al. 2007; Saigusa et al. 2005). Although numerous studies have investigated CO_2 exchange in response to environmental change across seasons and years, there are still knowledge gaps regarding the mechanistic and quantitative connections between single-leaf level ecophysiology, phenology, and the CO_2 flux of entire ecosystems in a changing environment across seasons and years (e.g., Piao et al. 2019; Rogers et al. 2017).

Long-term field studies have been conducted at various research sites around the world (cf. Mirtl et al. 2018). Such long-term research is needed to capture temporal changes and extreme events, thus improving our knowledge of ecosystem responses to environmental changes at decadal scales as well as the underlying mechanisms. These data also have been used to develop simulation models (e.g., Ichii et al. 2010; Ito et al. 2007) and to validate satellite remote sensing data (e.g., Turner et al. 2006; Xiao 2004), which allows findings to be scaled temporally from the past to the future and over spatially from local landscapes to regional to global for the evaluation of ecosystem function under climate change.

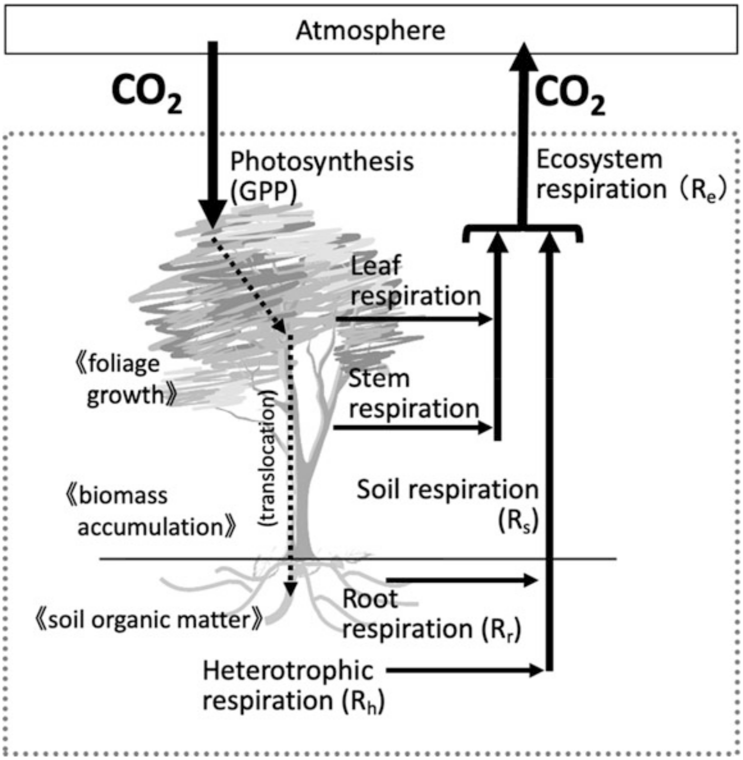

Fig. 1.1 Scheme of the carbon cycle in a forest ecosystem. CO_2 exchange between the atmosphere and the ecosystem is determined by photosynthesis (GPP) and respiration (R_e). The carbon fixed by photosynthesis is allocated for plant respiration (in leaves, stems, and roots) and growth, such as foliage growth and biomass accumulation. Plant litter (dead leaves, stems, and roots) is input to soil and consumed by heterotrophic organisms that release CO_2 by respiration (R_h)

A series of long-term studies on carbon dynamics was initiated in 1993 at a cool-temperate deciduous broadleaf forest in a mountainous region of central Japan by combining atmospheric science, ecology, soil biogeochemistry, simulation modeling, and remote sensing (Muraoka et al. 2015; Yamamoto and Koizumi 2005). The research site, called "Takayama site", has been a platform of these long-term ecosystem research and atmospheric observation contributing to ecosystem and Earth system sciences. In this chapter, I review the studies focused on the phenology of photosynthesis at the Takayama site and discuss the critical role of long-term and multidisciplinary studies conducted at an intensive research station, namely 'master site', for understanding and evaluating forest ecosystem function under climate change. Our research group initiated collaborative observation of phenology of the forest canopy in 2003 for a deeper understanding of the ecophysiological mechanisms of seasonal dynamics of CO_2 flux and short- to long-term changes in spectral signals obtained by satellite remote sensing (Fig. 1.2).

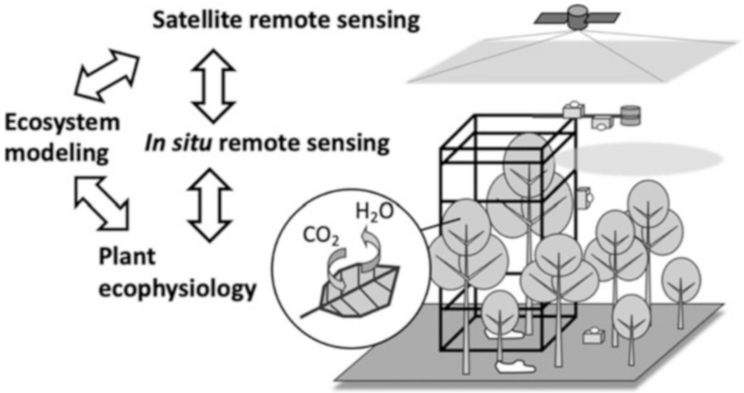

Fig. 1.2 Illustration of a long-term and multidisciplinary observation system for a forest ecosystem. Plant ecophysiological studies and in situ observations of tree and forest canopy enable a mechanistic understanding of the ecosystem function and scaling via model simulation. In addition, in situ optical remote sensing improves satellite remote sensing of ecosystem structure and function

1.2 Study Site and Plant Species

The Takayama site is located in a cool-temperate deciduous broadleaf forest (about 1420 m a.s.l.) at the Takayama Field Station (36°08.549′N, 137°25.340′E, 1342 m a.s.l.), River Basin Research Center, Gifu University, on complex terrain in a mountainous landscape in central Japan. Mean annual temperature and mean annual precipitation from 1996 to 2017 at the field station office (about 500 m south of the studied forest) was 7.2 °C and 2176.5 mm, respectively. The forest understory is covered with snow from December to April, and the maximum snow depth in the middle of winter reaches 1.5–1.8 m. The forest canopy of the study site has a height of approximately 18–20 m and is dominated by *Quercus crispula* Blume, *Betula ermanii* Cham., and *Betula platyphylla* Sukatchev var. *japonica* Hara. The subcanopy layer is represented by *Acer rufinerve* Sieb. et Zucc. and *Acer distylum* Sieb. et Zucc. and the understory layer by *Hydrangea paniculata* Sieb. and *Viburnum furcatum* Blume ex Maxim. The understory is dominated by the evergreen bamboo grass *Sasa senanensis* (Fr. et Sav.) Rehder and saplings of tree species.

At the Takayama site, the CO_2 flux between the atmosphere and forest ecosystem has been continuously observed since 1993 (Murayama et al. 2010; Saigusa et al. 2005; Yamamoto et al. 1999). Tree biomass and net primary production (Ohtsuka et al. 2009), soil respiration (R_s) and its components (root respiration, R_r; heterotrophic respiration, R_h; Mo et al. 2005), and leaf and canopy phenology (Muraoka and Koizumi 2005; Nasahara and Nagai 2015; Noda et al. 2015) have been measured, and in situ and satellite remote sensing (Muraoka et al. 2013; Nakashima et al. 2021; Noda et al. 2021; Shin et al. 2021) and modeling of the ecosystem carbon budget (e.g., Ito et al. 2007; Kuribayashi et al. 2017; Muraoka et al. 2010) have been intensively conducted. In addition, an open-field warming experiment on soil carbon

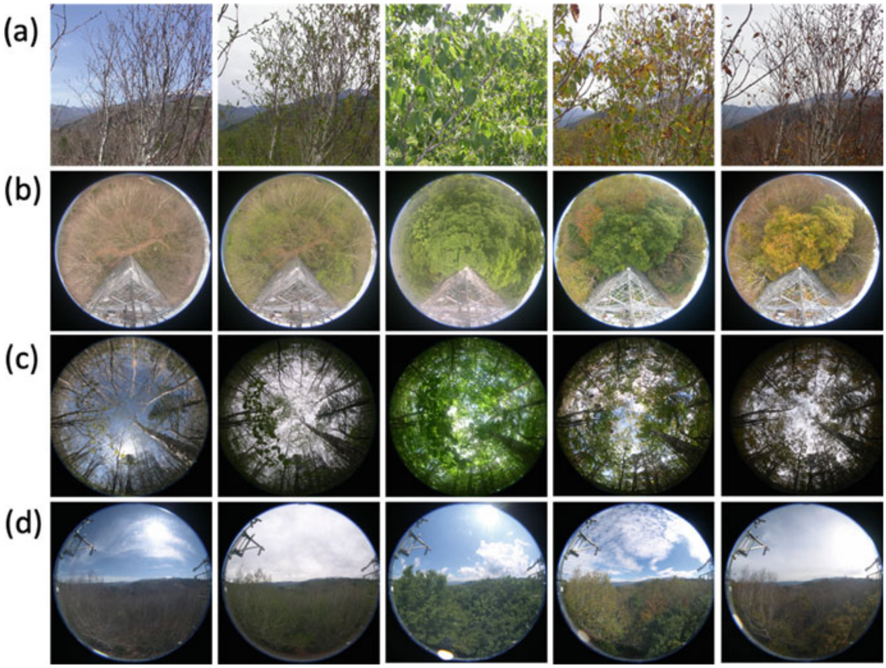

Fig. 1.3 Leaf phenology of (**a**) a branch of *Betula ermanii*, (**b**) forest canopy (view from above the forest), (**c**) forest canopy (view from understory), and (**d**) landscape, taken in 2021 on day of year 130, 140, 200, 289 and 300 (from left to right) at the Takayama site

dynamics was conducted (Chung et al. 2013; Noh et al. 2016, 2017). These long-term observations reveal remarkable seasonal changes in carbon flux and ecological processes at the site. These long-term and multidisciplinary studies in this research site are contributing to AsiaFlux (http://www.asiaflux.net/), Japan Long-Term Ecological Research Network (JaLTER, http://www.jalter.org/), International LTER Network (ILTER, https://www.ilter.network/), and Asia-Pacific Biodiversity Observation Network (APBON; Takeuchi et al. 2021, http://www.esabii.biodic.go.jp/ap-bon/index.html); for overviews of the multiple studies at this research site, see Muraoka (2015) and Muraoka et al. (2015).

In 2003, an automated system consisting of digital cameras and spectroradiometers was installed to observe individual tree branches and the forest canopy (Nasahara and Nagai 2015). Images from the digital cameras, taken hourly, provide visible and optical information about the forest canopy and tree crowns of respective species (Nagai et al. 2011). The spectroradiometers provide hyperspectral information of the incoming solar radiation and reflected radiation from the foliage, which can be used to calculate spectral vegetation indices (Motohka et al. 2010; Muraoka et al. 2013). These in situ remote sensing observations are conducted at several research sites in Japan and AsiaFlux sites, which together comprise the Phenological Eyes Network (PEN) (Nasahara and Nagai 2015). Figure 1.3 shows representative images taken by the automated digital camera system installed at the Takayama site. The collection of visible images of tree foliage (branch), the canopy, and the landscape will help to improve the interpretation of satellite remote sensing signals at broad spatial scales from a local forest ecosystem to a mountainous landscape. By using the data collected in the deciduous broadleaf forest, for example, Inoue et al. (2014) clarified that the timing of leaf expansion is rather similar among the tree species and dependent on air temperature, whereas that of leaf fall is variable. The combined observations of tree foliage photographs and leaf traits will allow us to identify the relationships between color (i.e., spectral) information and the leaf ecophysiological characteristics (pigments, morphology, and photosynthetic capacity) of plants and improve optical remote sensing of forest canopies.

1.3 Phenology of Leaf and Canopy Photosynthesis

1.3.1 Seasonal Change of Leaf Ecophysiological Traits in a Deciduous Broadleaf Forest

The deciduous broadleaf forest at the Takayama site is characterized by multiple plant species including tall canopy trees, subcanopy trees, and understory trees and an evergreen bamboo grass in the understory. The forest floor is covered by snow from December through early April. The leaves of bamboo grass reappear after snowmelt in April, and then the leaves of understory trees emerge in early May. In mid- to late May the leaves of subcanopy and canopy trees emerge. In summer the entire forest canopy is filled by green leaves of various plant species, and in autumn the leaves change to yellow or red and then fall in October (Fig. 1.3). The various patterns of leaf emergence between the canopy layers or between species have been described in many deciduous broadleaf forests in many places in the world, and those differences are hypothesized to be related to successional status of species differing in leaf flushing types (Koike 1990), ontogenic differences within a species (Augspurger and Bartlett 2003; Seiwa 1999; Vitasse 2013), and as an adaptive response to the seasonality of light availability in the forest understory (Augspurger et al. 2005; Seiwa 1998).

The seasonal change of leaf traits of canopy trees (*Q. crispula* and *B. ermanii*), understory trees (*H. paniculata* and *V. furcatum*), and evergreen bamboo grass (*S. senanensis*) was assessed based on measurements of maximum photosynthetic rate (A_{max}, index of photosynthetic capacity in a single leaf), dark respiration rate (R), index of chlorophyll concentration (SPAD), and leaf mass per area (LMA) as the morphological characteristic. In 2005, A_{max} and R were measured in intact leaves on the trees and bamboo grass by using a portable photosynthesis measuring systems (LI-6400, Li-Cor, Inc., Lincoln, NE, USA), and SPAD was measured in the same leaves by using a SPAD meter (SPAD-502, Minolta, Tokyo, Japan). The LMA of the same leaves was calculated as the ratio of leaf dry weight (leaves were oven-dried

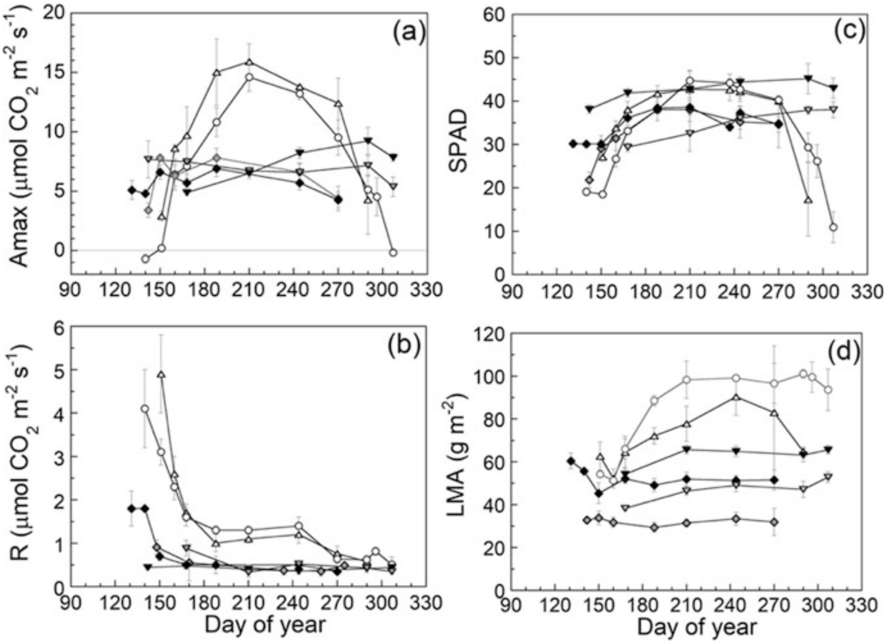

Fig. 1.4 Phenology of leaf ecophysiological characteristics in deciduous broadleaf trees at the Takayama site in 2005. (**a**) Leaf photosynthetic capacity (A_{max}), (**b**) dark respiration (R), (**c**) index of chlorophyll content (SPAD), and (**d**) leaf mass per area (LMA). Symbols and error bars indicate mean ± SD for three to five sample leaves. *Betula ermanii* (open triangle), *Quercus crispula* (open circle), *Hydrangea paniculata* (gray diamond), *Viburnum furcatum* (solid diamond), *Sasa senanensis* (overwintered leaf, solid reverse triangle; current-year leaf, gray reverse triangle). The current-year leaves of *S. senanensis* emerge in early summer and develop their photosynthetic capacity in summer and autumn. Data for *B. ermanii* and *Q. crispula* were included in Noda et al. (2015), and those for other plants are unpublished data by H. Muraoka

at 70 °C for 24 h) to leaf area in the laboratory. Canopy-top leaves were accessed via an 18-m-tall scaffold tower (for more details of measurement protocols, see Muraoka and Koizumi 2005; Noda et al. 2015).

The data show drastic changes in those leaf traits (Fig. 1.4). Leaves of understory trees and bamboo grass have relatively high A_{max} from the beginning of the snow-free season (i.e., growing season), corresponding with high SPAD and LMA. The leaf traits of these species were almost constant throughout the seasons until leaf fall in autumn. In contrast, A_{max} of canopy trees was remarkably low at the leaf emerging phase (~DOY 150) and increased rapidly until their maximum level in early summer (~DOY 200). In autumn, A_{max} and SPAD of canopy trees decreases and then leaf fall occurred. The seasonal development of A_{max} was associated with SPAD and LMA, whereas the decrease of A_{max} was associated only with SPAD. In this study we also found a drastic change of R, characterized by remarkably high values at the leaf emerging phase, a sharp decline along with physiological and morphological development, and stable values from early summer through the leaf senescence phase. The high R value during the leaf emerging phase reflects high growth respiration due to the leaf construction cost, and the values in summer through autumn reflect mostly maintenance respiration.

The seasonal patterns of leaf development and fall are also reflected in the seasonal change of the leaf area index (LAI) in this forest, which was estimated by intensive measurement of leaf area and number, as well as a litter-trap survey (Nasahara et al. 2008). The data presented in Fig. 1.4 give us basic information about the ecological linkage between leaf characteristics and the contributions of photosynthesis from different species to that of the entire forest (GPP) and hence the CO_2 exchange with the atmosphere.

1.3.2 Interannual Changes in Canopy Leaf Photosynthesis and GPP

Multiple-year measurement of CO_2 flux in the deciduous broadleaf forest ecosystem at the Takayama site revealed remarkable seasonal change, characterized by negative net ecosystem production (NEP) in winter, a transition to positive NEP in spring after snowmelt, high values in summer, a decline in autumn, and then a transition to negative NEP in early winter (Saigusa et al. 2005). The seasonal change of NEP could occur via two major mechanisms: climatic control and ecological control. Because NEP is roughly the balance between GPP and R_e, climatic factors such as solar radiation, air temperature, air humidity, soil temperature, and soil water availability influence photosynthetic activity in leaves (i.e., the CO_2 absorption process) and respiratory activities of plants (leaf, stem, root) and soil microorganisms (the CO_2 release processes). Long-term CO_2 flux measurements at many terrestrial ecosystems demonstrate these temporal and interactive changes (e.g., Hirata et al. 2007; Owen et al. 2007; Saigusa et al. 2008). For a deeper understanding of the biological mechanisms underlying these ecosystem responses, we should consider the seasonal change of leaf photosynthetic capacity (e.g., A_{max}) as shown in Fig. 1.4.

To examine the extent to which the seasonal change of leaf-level photosynthetic capacity influences the GPP of the forest ecosystem, Ito et al. (2006) incorporated the leaf characteristics measured at the Takayama site into an ecosystem carbon cycle simulation model. Their simulations indicated that the leaf phenology is the main driver of the seasonal change and annual amount of GPP and hence NEP. If the leaf photosynthetic capacity were assumed to be constant throughout the season, then GPP would be overestimated by 8% and NEP by 38% (Ito et al. 2006). Likewise, Wilson et al. (2001) demonstrated that the phenology of leaf photosynthesis explained the seasonal change of CO_2 flux measured by the eddy covariance method in a North American deciduous broadleaf forest. A new finding by Ito et al. (2006) was that the phenology of dark respiration is also quantitatively responsible for the seasonal change of R_e in the deciduous forest. Thus, leaf photosynthetic capacity varies throughout the seasons, especially for canopy trees, and is largely responsible for the seasonal change of GPP, since these species account for a major fraction of LAI of the entire forest canopy at the Takayama site.

Next, researchers aimed to identify the mechanism driving the interannual change of GPP in this forest, which was observed by the eddy covariance method. Saigusa et al. (2005) reported that the plant area index (similar to LAI) of the forest and the seasonal timing of development varied among years, indicating that phenological timing of the forest canopy leaves differ among years. In addition, Ohtsuka et al. (2009) investigated interannual changes in the annual NEP, net primary production (NPP) of woody biomass and tree foliage, R_s, and R_e at the Takayama site. They noted interannual variation in NPP of woody biomass, but NPP of foliage was rather stable. Thus, although the amount of foliage is relatively stable among years, the annual amount of photosynthetic carbon gain is variable. These findings led to important questions about the consequence of leaf photosynthetic activity, phenology, and ecosystem carbon sequestration in a changing environment over seasons and years.

To address these questions, we have been conducting periodic measurements of leaf photosynthetic capacity and corresponding traits in dominant canopy tree species at the Takayama site since 2003 (Muraoka and Koizumi 2005; Noda et al. 2015). Muraoka et al. (2010) estimated the impacts of phenology of leaf photosynthesis and canopy LAI as well as their interannual variation (i.e., early or late leaf growth in spring, early or late leaf senescence in autumn). They used 5 years of data on leaf photosynthetic characteristics, LAI, and micrometeorological factors in a process-based carbon cycle model and demonstrated drastic seasonality of GPP and its interannual changes (Fig. 1.5). These findings indicated that (1) spring temperature could affect GPP through leaf phenology, (2) incoming radiation determined GPP in summer in this forest located in the Asian monsoon region, and (3) annual GPP would be overestimated by 15% if leaf phenology were ignored. The results also suggested that interannual variation in the phenology of canopy LAI would influence photosynthetic productivity of evergreen bamboo grass through changes in the understory light environment. These findings provide important insights into the consequence of tree leaf ecophysiological response to a changing environment and photosynthetic activity at the forest canopy level, highlighting the need to consider the phenology of leaf-level photosynthesis in simulation models to better predict the ecosystem carbon cycle.

The seasonality of photosynthetic carbon fixation would affect not only CO_2 flux components but also biomass accumulation (i.e., plant growth) in the forest. In a recent study at the Takayama site, Shen et al. (2020) found that tree ring growth of *Fagus crenata* Blume, *Q. crispula*, and *B. ermanii* has a seasonal pattern, and it is correlated with the seasonality of meteorological conditions in the previous year and current year, particularly air temperature and water availability in summer and autumn. These environmental factors influence photosynthetic activity, consumption of photosynthetic products, and growth.

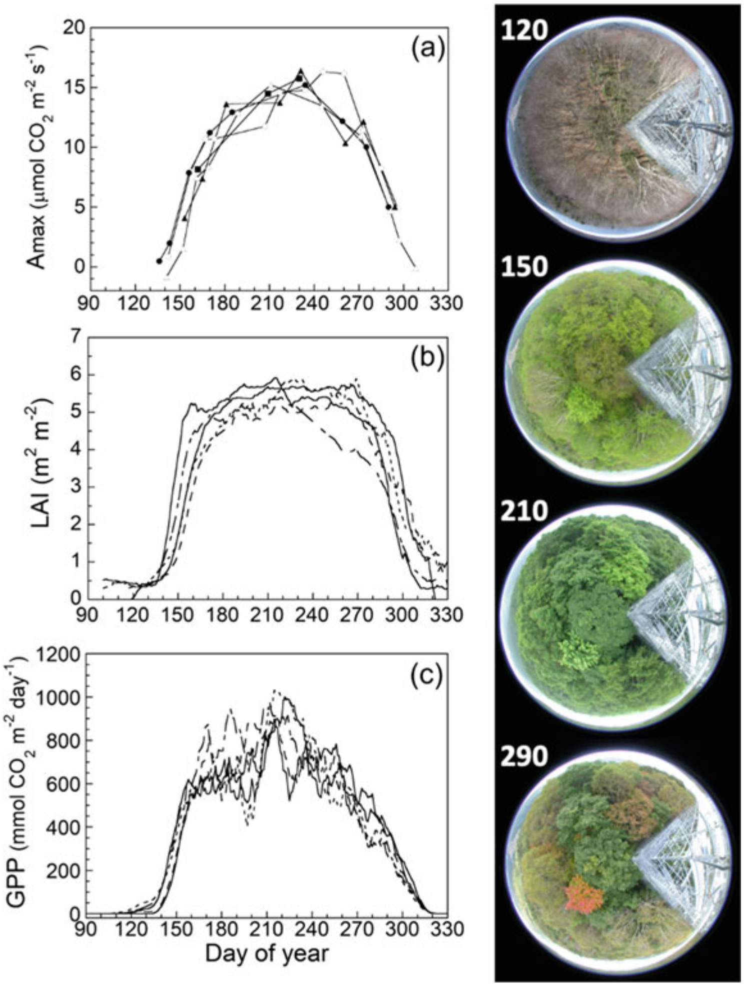

Fig. 1.5 Seasonal changes in (**a**) leaf photosynthetic capacity (A_{max}), (**b**) canopy leaf area index (LAI) and (**c**) estimated GPP of canopy at the Takayama site. A_{max} is the average of values for *Betula ermanii* and *Quercus crispula*. Different lines indicate different study years (2003–2007), and symbols indicate mean ± SD for three to five sample leaves. Canopy images in spring (DOY 120), early summer (DOY 150), late summer (DOY 210), and autumn (DOY 290) are also shown. Graphs (**b**) and (**c**) are redrawn from Muraoka et al. (2010)

1.3.3 Combining Long-Term Observations and an Open-Field Experiment on Leaf Phenology

Long-term ecological research (LTER) enables us to identify important aspects of ecosystems, such as the patterns of changes, their biotic and abiotic drivers, and the impacts of short-term and long-term climatic change on ecosystem structure and function (e.g., Kim et al. 2018; Mirtl et al. 2018). Intensive data gathered from the single-leaf to forest ecosystem scale at the Takayama site can provide insights into the biological response of tree leaves to changing environments over seasons and years, as well as the consequence for single-leaf and ecosystem-scale CO_2 flux (Muraoka and Koizumi 2009; Tang et al. 2016).

Long-term monitoring of trees has revealed changes in the timing of leaf unfolding and flowering with changing temperatures in Japan (Doi and Katano 2008; Matsumoto et al. 2003), Europe (Menzel et al. 2006; Vitasse et al. 2009), and North America (Gunderson et al. 2012), and analyses suggest that these phenological changes are correlated with warming. The accumulated data on leaf phenology is useful for developing an empirical model to predict the timing of leaf emergence, leaf development and senescence, and leaf fall (Hänninen et al. 2019; Richardson et al. 2006). By integrating leaf data obtained from 2003 to 2010, Noda et al. (2015) investigated the relationships in *Q. crispula* and *B. ermanii* between an abiotic driver (temperature) and various leaf ecophysiological traits, including photosynthetic capacity (A_{max}), R, maximum velocity of carboxylation (V_{cmax}), chlorophyll and nitrogen content, and LMA. They demonstrated that the leaf phenological pattern could be consistently predicted by temperature. Seasonal growth—leaf physiological and morphological development—could be predicted by the cumulative temperature from early spring to early summer (growing degree days, GDD), and physiological senescence could be predicted by cumulative (decreasing) temperature from late summer to autumn (chilling degree days, CDD). The findings of this study are generally consistent with the outcomes from studying automated digital camera images of forest canopy, namely that GDD and CDD can be used as indicators of leaf onset and leaf fall timing (Inoue et al. 2014; Nagai et al. 2013). In addition to air temperature, leaf physiological and morphological development in deciduous broadleaf trees is dependent on environmental factors such as local light availability (Niinemets 2004).

This finding under interannual variation in meteorological conditions would further support us to apply empirical models to simulate the seasonal change of leaf photosynthetic capacity and foliage growth to predict forest canopy photosynthesis. By applying the leaf phenological patterns, Kuribayashi et al. (2017) investigated the impacts of increasing atmospheric CO_2 concentration and global warming (increase of 2.38–2.49 °C) on leaf phenology, GPP, R_e, and NEP of a cool-temperate deciduous broadleaf forest at the Takayama site. They demonstrated that GPP and NEP would be increased by 25.2% and 35.4%, respectively, due to rising temperature, which led to earlier leaf expansion and delayed leaf fall by about 10 days and higher photosynthetic activity in early summer and autumn, as well as to the CO_2 fertilization effect on photosynthesis in summer. Improving the leaf phenology model, however, will require integrated analysis that also considers physiological mechanisms, because leaf expansion is not only driven by temperature but also by photoperiod (Way and Montgomery 2015), and perhaps other environmental factors such as radiation and water availability (cf. Cleland et al. 2007; Polgar and Primack 2011; Tang et al. 2016).

The impacts of global warming on leaf phenology also have been investigated in open-field warming experiments (Chung et al. 2013; Richardson et al. 2018; Rustad et al. 2001). By installing an open-top chamber, heating cable, or heating lamp, the air temperature around a branch or the temperature of the branch itself can be raised to the desired experimental temperature conditions, while other environmental factors, particularly solar radiation, remain similar among the different temperature treatments (Nakamura et al. 2010, 2016; Yamaguchi et al. 2016). For example, open-field warming experiments on canopy-top leaves of adult *B. ermanii* trees in northern Japan showed that leaf flush advanced by 6.5 days under +1.18 to 1.35 °C conditions (Nakamura et al. 2016).

At the Takayama site, we conducted a warming experiment from 2011 to 2017 by installing open-top chambers on branches of *Q. crispula* and *B. ermanii* at the top of their crowns (ca. 14–16 m above ground). Each open-top chamber (1.15 m × 1.7 m × 1.75 m high) is made of transparent acrylic board and vinyl sheeting and surrounds the branch for about 1 m of its length. The daytime air temperature in the open-top chambers was higher than in the control treatment by 1.4–1.6 °C. On average, this warming treatment advanced leaf expansion by 1.6 days in *Q. crispula* and by 2.2 days in *B. ermanii*, while the leaf expansion in the ambient treatment changed by 14–16 days in response to a 5 °C temperature anomaly in spring (H. Muraoka et al., submitted). A rise in temperature not only influences leaf phenology but also photosynthetic capacity and its temperature-dependence (e.g., Yamaguchi et al. 2016). Figure 1.6 shows the relationship between A_{max} and leaf temperature in warmed and control leaves of *Q. crispula* (H. Muraoka, unpublished data). In early June, a few weeks after leaf emergence, A_{max} was higher in warmed leaves than in control leaves, reflecting the earlier leaf expansion in the former. A_{max} was also approximately 10% higher in warmed leaves in summer, which is consistent with the findings that warmed leaves had higher chlorophyll content (estimated by SPAD) and nitrogen concentration (H. Muraoka, unpublished data). The higher A_{max} in October indicates delayed senescence in warmed leaves. In a cool-temperate deciduous broadleaf forest, Hikosaka et al. (2007) and Yamaguchi et al. (2016) also showed that the temperature-dependence of photosynthesis changes in response to the temperature condition which changed across the growing season as well as being altered by open-top chambers.

To what extent do these changes in photosynthetic capacity and temperature-dependence influence photosynthetic productivity at the forest canopy level (i.e., GPP) in cool-temperate deciduous broadleaf forest? To answer this question, we must consider the impacts of current meteorological anomalies to explain the interannual changes of GPP over the past 30 years, as well as the impacts of future climate change. Although drought or extreme heat rarely impacts the forest at the Takayama site, as occurs in other terrestrial ecosystems in the world (e.g., Reichstein et al. 2013), we should consider how climate change stress affects photosynthesis through altered leaf phenology as extreme climate events are likely to occur under ongoing climate change.

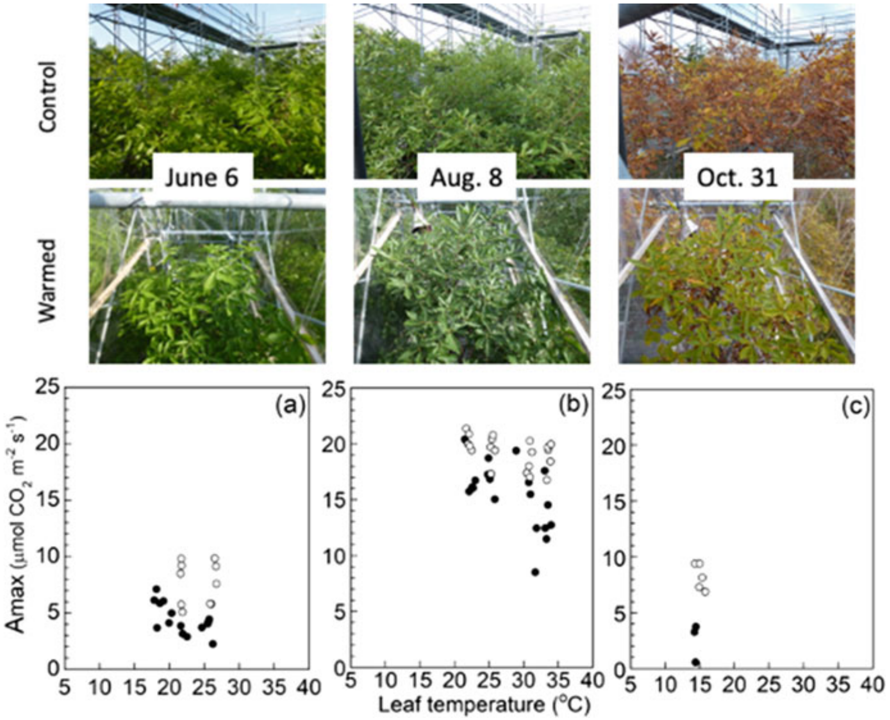

Fig. 1.6 Relationship between leaf temperature and leaf photosynthetic capacity (A_{max}) of *Quercus crispula* in control (solid circle) and warmed (open circle) treatments in the open-field warming experiment at the Takayama site. Photographs show branches of respective treatments on the measurement dates. On October 31, many leaves in the warmed treatment remain green, whereas those in the control treatment have already turned yellow

1.3.4 Leaf Photosynthesis and Phenology in Forest Understory Trees

The cool-temperate deciduous broadleaf forest at the study site has rich woody species diversity in the understory. *Hydrangea paniculata* and *V. furcatum* inhabit the understory and grow up to approximately 3 m. Forest understory plants generally experience limited light availability, which is the energy source for leaf photosynthesis (Montgomery and Chazdon 2001; Muraoka et al. 1997; Pearcy et al. 2005). In such a light-limited environment on the forest floor, Muraoka et al. (2003) reported that saplings of canopy and subcanopy trees and understory trees maximize their light interception by geometrical arrangement of leaf display in their given micro-habitats. Mature *H. paniculata* and *V. furcatum* arrange their leaf display along the branches to minimize the overlap between the leaves and maximize the efficiency of light interception in the understory (Muraoka and Koizumi 2005). In a forest understory where leaf photosynthesis is generally limited by low light availability, phenology and acclimation of leaf photosynthesis to light heterogeneity are also keys to understanding how the plants survive in such an environment (Augspurger et al. 2005; Montgomery and Chazdon 2001; Muraoka et al. 2002; Pearcy and Sims 1994). As shown in Fig. 1.4, A_{max} values of *H. paniculata* and *V. furcatum* are high even in the very early phase of their phenology, suggesting that these species are adapted to utilize the high light only available before leaf expansion of canopy trees.

To understand the relationships among canopy leaf phenology, light penetration to the forest understory, and leaf photosynthetic productivity of the understory trees, we conducted a 2-year study at the Takayama site. Figure 1.7 illustrates the light intensity (photosynthetically active photon flux density: PPFD) measured above the canopy-top and in forest understory, relative PPFD (ratio of understory to canopy-top PPFD), leaf photosynthetic capacity, and estimated daily photosynthesis of *H. paniculata* and *V. furcatum* (C. Ohashi and H. Muraoka, unpublished data). In this study, we selected two places in the forest understory, one where the canopy-top layer is dense and another where the canopy-top has a gap due to branch or tree fall. Light intensity is high throughout the seasons, but the daily integrated PPFD is influenced by solar angle and weather. With leaf expansion of the canopy trees, light penetration to the understory expressed as relative PPFD decreased from about 0.6 to 0.05 and remained low in the summer. In autumn, the relative PPFD increased with leaf fall of the canopy trees. Thus, understory plants are shaded for most of the growing season. A_{max} of understory leaves was high in the early growing season, and then decreased toward summer and autumn. Moreover, A_{max} was higher in leaves at the gap site than at the closed-canopy site in both species.

Based on measured PPFD and leaf photosynthetic characteristic, we then estimated daily photosynthesis (A_{day}), which reflects the seasonal change of A_{max}, penetration of light through the canopy-top layer, and the different light availability in the gap and closed-canopy sites (Fig. 1.7). The estimated A_{day} suggests that (1) photosynthetic productivity tends to be higher early in the growing season (which is obvious in the second year), (2) *H. paniculata* has higher A_{max} and hence higher A_{day} than *V. furcatum* throughout the seasons, and (3) higher A_{max} and light availability in the gap led to higher A_{day} in both species. We estimated that about 84% of photosynthetic production in *H. paniculata* is achieved after canopy closure, whereas in *V. furcatum* up to 39% of photosynthetic production is achieved before canopy closure. This study demonstrated the different strategy of the two shrub species to utilize the light resources in the understory. The high A_{max} of *H. paniculata* in the early and mid-growing season led to a high photosynthetic rate by utilizing sunflecks penetrating through gaps in the canopy. The higher A_{max} at the gap site, which can be considered as a light acclimation response to the heterogeneous light environment in the understory, also contributed to higher A_{day}. In *V. furcatum*, the relatively rapid leaf development early in the growing season enables the species to utilize the high light available before canopy closure, and this seems to be a strategy to avoid canopy shade (cf. Augspurger et al. 2005).

Our study of the light environment within a forest implies the possible influence of global warming on photosynthetic productivity in understory plants via the changes in leaf phenology of the canopy trees. Another question is how the timing

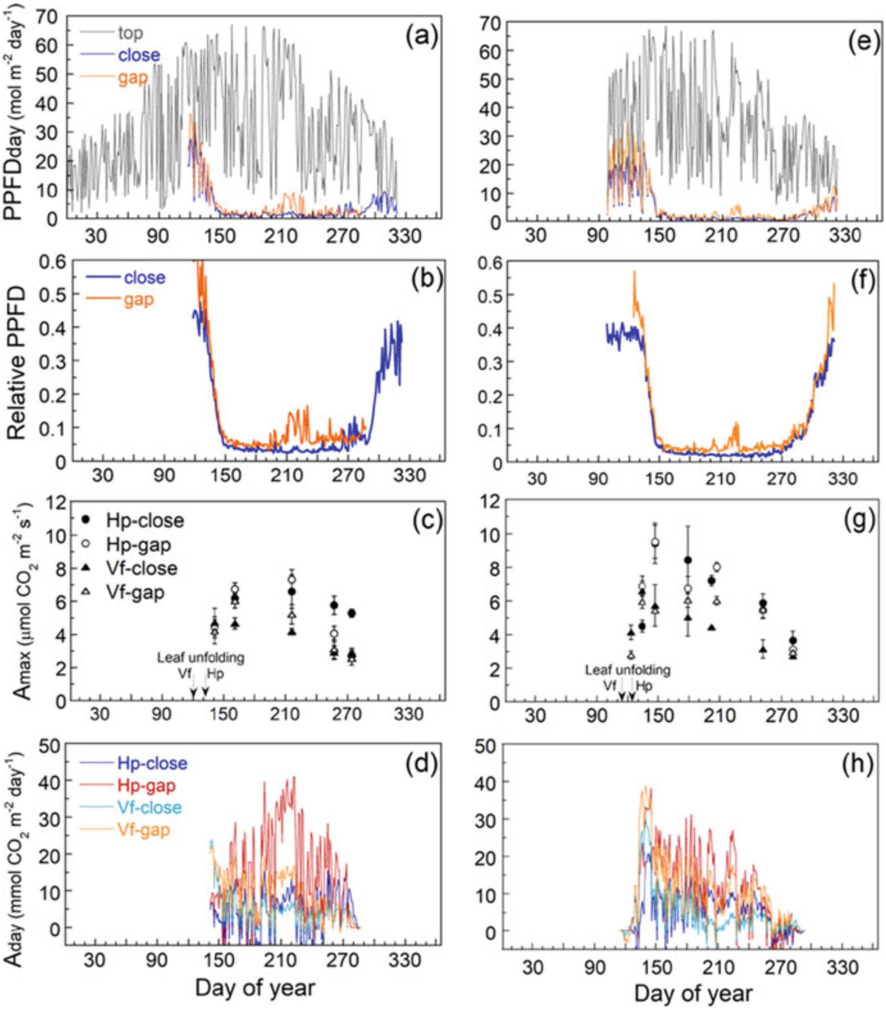

Fig. 1.7 Seasonal changes in (**a**, **e**) light intensity above the forest canopy and in the understory (PPFD), (**b**, **f**) relative PPFD in the understory, (**c**, **g**) leaf photosynthetic capacity (A_{max}), and (**d**, **h**) daily leaf photosynthesis (A_{day}) of *Hydrangea paniculata* and *Viburnum furcatum*, respectively. Measurements of PPFD and A_{max} were made in closed-canopy and gap sites in the forest understory. Symbols in (**c**) and (**g**) indicate mean ± SD for three sample leaves. (C. Ohashi and H. Muraoka, unpublished data)

of snowmelt on the forest floor interactively impacts leaf phenology and photosynthesis in the understory.

1.4 Combining In Situ Surveys and Satellite Remote Sensing for Phenology Observations

Satellite remote sensing of terrestrial ecosystems enables us to monitor the spatial and temporal dynamics in a changing environment (Running et al. 2004). With the advancement in spatial and temporal resolution as well as spectral characteristics, satellite remote sensing of the physiological characteristics of the vegetation canopy has provided invaluable information on biodiversity and ecosystem structure and function (e.g., Anderson 2018; Ustin et al. 2009; Vihervaara et al. 2017). The phenology of terrestrial vegetation serves as an indicator of the impacts of climate change on plant ecophysiological characteristics at the landscape, regional, and global scale (Piao et al. 2019; Richardson et al. 2013; Tang et al. 2016). To improve remote sensing observation techniques for its use in ecosystem studies, however, we must conduct intensive in situ studies to connect optical signals with the ecophysiological characteristics on the ground (Noda et al. 2021; Ustin et al. 2009). At the Takayama site, we have developed an observation system to link ecological and optical forest canopy information with the satellite remote sensing signals to advance the use of satellites in ecological research, known as the “Satellite Ecology” concept (Muraoka and Koizumi 2009). The importance of ground-truthing data in validating satellite observations is discussed by Nagai et al. (2020).

Satellite remote sensing of seasonal changes and the geographic distribution of canopy structure and photosynthetic productivity of terrestrial vegetation has been achieved through use of optical sensors onboard Earth observation satellites such as Landsat, Terra and Aqua with Moderate resolution Imaging Spectroradiometer (MODIS), Advanced Land Observing Satellite (ALOS), Global Change Observation Mission-Climate (GCOM-C), and Sentinel-2. The satellites’ optical sensors measure the reflected spectrum for visible bands such as blue, green, and red, as well as an infrared band. Then these signals are used to calculate vegetation indices such as the Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), or Green-Red Vegetation Index (GRVI) which provide estimates of the greenness of the land surface as a proxy of canopy leaf area and photosynthetic productivity (Motohka et al. 2010; Muraoka et al. 2013; Nagai et al. 2010; Turner et al. 2006; Xiao 2004). While these vegetation indices have been used to estimate the canopy structure (e.g., LAI) or to detect the timing of leaf onset (greening) and offset (leaf fall) in the last 20–30 years (e.g., Piao et al. 2015; Running et al. 2004), detailed examination and verification of the optical information in relation to canopy structure and photosynthetic productivity (GPP) are essential for accurate estimation from space (Muraoka and Koizumi 2009; Noda et al. 2021).

To assess the applicability of vegetation indices for estimating photosynthetic productivity at spatial scales ranging from landscape to national in Japan, where forests are distributed mainly in mountainous areas, we investigated the relationship between vegetation indices and GPP estimated at the Takayama site (Muraoka et al. 2013). Vegetation indices were calculated from hyperspectral data obtained by a spectroradiometer mounted on the scaffold tower (Fig. 1.2); this spectroradiometer is part of the PEN observation system. Measuring the spectral reflectance just above the canopy enables us to obtain data without any atmospheric noise, such as clouds and aerosols, which are problems with optical satellite remote sensing (Nagai et al. 2020). The vegetation indices were compared with GPP of the forest canopy predicted by an ecosystem model incorporating the observed leaf-level photosynthesis, canopy LAI, and micrometeorological conditions (for a discussion of the model, see Sect. 1.3.2). Among NDVI, EVI and GRVI, EVI showed the clearest relationship with GPP, for both its daily integrated value and maximum value within a day, throughout the seasons and years (Fig. 1.8). Here it should be noted that the relationship between EVI and GPP was not simply a linear function but showed hysteresis between the lines for spring—summer and summer—autumn, suggesting that optical properties of single leaves and hence canopies need to be considered carefully (see also Noda et al. 2021). Then the obtained relationship was used to convert the EVI value to daily maximum rate of GPP, an indicator of photosynthetic capacity of forest ecosystems, over the central region of the main island of Japan (Fig. 1.8).

The above study focused on the photosynthetic *capacity*, which is close to the potential (maximum) level of photosynthesis in an ecosystem. However, the Greenhouse gases Observing SATellite (GOSAT, launched in 2009) provides a signal of chlorophyll fluorescence emitted from the vegetation surface (e.g., Frankenberg et al. 2011), called sun-induced fluorescence (SIF). SIF has been assessed for its utility for estimating the photosynthetic *activity*, which should be close to the actual photosynthetic rate driven by physiological and meteorological factors (e.g., Yang et al. 2015). At the Takayama site, Nakashima et al. (2021) examined the accuracy and applicability of SIF to the estimation of GPP by combining in situ hyperspectral data of the canopy surface and CO_2 flux measurements. Because chlorophyll fluorescence indicates the physiological status of photosynthesis in leaves (Genty et al. 1989; Muraoka et al. 2000), SIF is expected to be an indicator of the environmental response as well as the impact of climate change stress on photosynthesis at the ecosystem scale. However, we still need to explore the ecophysiological mechanisms of SIF by considering underlying photosynthetic reactions at the single-leaf level as well as the canopy geometrical and optical structures to accurately utilize the SIF signals at broader scales ranging from canopy to landscape (cf. Hikosaka and Noda 2019). In addition, we need to develop a methodology to detect photosynthetic capacity or activity under cloudy conditions, which is crucial for observations in regions with a humid Asian monsoon climate.

1.5 Conclusion

In this chapter, I reviewed studies of leaf and canopy photosynthesis conducted in a cool-temperate deciduous broadleaf forest in Japan. The research findings from the Takayama site clearly describe the relationship between phenology and meteorological factors and phenologically influenced changes in carbon flux. Ecophysiological

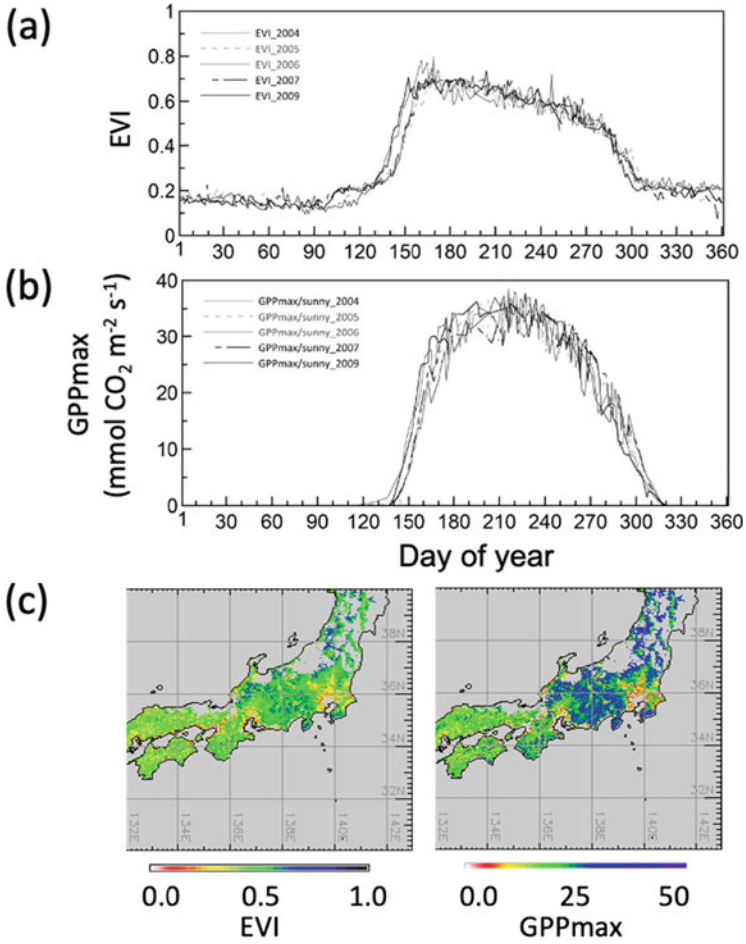

Fig. 1.8 Seasonal changes in the (**a**) Enhanced Vegetation Index (EVI) obtained by spectroradiometer and (**b**) daily maximum GPP under sunny conditions estimated by a model simulation at the Takayama site from 2004 to 2009. The relationship between daily maximum canopy photosynthetic rate, estimated by model simulation, and EVI obtained at the Takayama site was used to convert satellite-based EVI to GPP across central Japan (**c**). Graphs (**a**) and (**b**) were redrawn from the original data in the study by Muraoka et al. (2013)

studies focusing on photosynthesis and phenology highlight the temporal changes at daily, seasonal, and annual time scales, which deepens our understanding of the dynamic linkages of the processes to overall forest ecosystem function (Fig. 1.2). Long-term and multidisciplinary research reveals the time-dependent linkages among processes occurring in different ecosystem compartments; elaboration of these linkages is supported by advanced technology, such as measurement systems for physiology and biochemistry, sensors for in situ and satellite remote sensing, and CO_2 flux observation systems, as well as simulation models. These methodologies

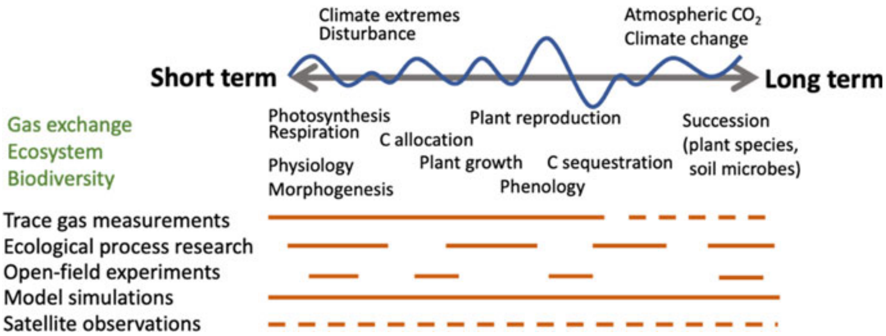

Fig. 1.9 Schematic of the relationships between research targets in gas exchange, ecosystem dynamics, and biodiversity as well as available technologies for in situ and satellite observations, experiments, and model simulations under environmental changes that occur over the short to long term. Research topics have unique temporal scales, resolution or continuity, and corresponding technologies, but combining the technologies (i.e., multidisciplinary studies) allows us to identify complicated mechanisms and consequences of ecosystem structure and functions over various spatial and temporal scales. The orange lines show image of temporal resolution or continuity of research: broken lines represent intermittent or periodical measurements, while a long line represents continuous measurements or estimation

have various spatial resolutions that can be applied to the scale of interest—from a single leaf to the landscape—and integration of the data obtained through these various methods provides an overall picture of ecosystems and their changes (Fig. 1.9; see also Muraoka and Koizumi 2009).

The challenges discussed in this chapter regarding a mechanistic understanding of the components involved in a given ecosystem can be overcome by conducting long-term observations and open-field experiments, coupled with observations of atmospheric dynamics at in situ research sites, that is, ‘master sites’ like the one at Takayama (Fig. 1.2). Developing an ecosystem research infrastructure—the integrated observation of ecosystem structure and function, followed by data analysis and sharing—is crucial for timely monitoring of the steady state and detecting the impacts of climate change (Chabbi and Loescher 2017). Networks of such research sites and scientists, such as JaLTER, JapanFlux, AsiaFlux, and APBON, will help us to integrate data and knowledge gathered from different scientific perspectives covering the broad geographic and climatic range found among various ecosystems. Comprehensive analysis of the system may allow us to identify key ecosystem variables, such as Essential Climate Variables (ECV; Global Climate Observing System 2016) and Essential Biodiversity Variables (EBV; Pereira et al. 2013), that are crucial to track and compare in future efforts to extend these principles to larger scales (cf. Haase et al. 2018). These essential variables should facilitate truly meaningful interpretation of satellite remote sensing data and the improvement of ecosystem models used to evaluate the potential consequences of climate change. The knowledge and observation designs generated from such comprehensive research are crucial for biodiversity and ecosystem conservation and management in landscapes from local to regional scales.

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